

# Neuropsychological perspectives on the mechanisms of imitation

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Cognitive neuroscientists have contributed to the understanding of imitation according to their expertise. Neuropsychologists first established over a century ago that lesions to the left hemisphere of right-handed individuals lead to a dramatic reduction of their ability to imitate gestures. In contrast, after frontal lobe damage, patients may experience severe difficulties in inhibiting their imitative tendency. These findings suggested that our tendency to imitate is mostly sustained by the left hemisphere and that we normally manage successfully to keep it under control. Neuropsychologists went on investigating other aspects of gesture imitation. These include the existence of putative mechanisms involved in imitating different types of gestures (e.g. meaningful and meaningless or transitive and intransitive), the strategic control over these mechanisms and whether there are differences in imitation depending on the action goal or the body part used. Based on neuropsychological findings, some cognitive models of gesture imitation have been forwarded, the most influential of which will be reviewed here. In particular, reference will be made to the dual route model and to accounts that associate the imitative deficit to putative degraded body representations.

**Keywords:** ideomotor apraxia; parietal cortex; body representation; intransitive gesture; dual route

## 1. A COMPARATIVE APPROACH TO THE STUDY OF IMITATION

Imitation has been investigated by scholars with different kinds of expertise (see the review by Rumiati & Tessari 2007). Developmental psychologists and ethologists focused on establishing when, in the life of an individual or in the evolution of our species, the imitative tendency emerges and how it then develops. The discoveries of Meltzoff & Moore (1977, 1983, 1989) that newborns are able to imitate simple facial and hand gestures even within their first hour of life have modified the view, generally accepted until then, that humans gradually learnt to imitate over the first years of life. Human imitation is not observed after two to three months old until it is resumed again in eight to twelve-month-olds. Neonatal imitation of facial gestures is not an evolutionary acquisition of humans alone. Infants of chimpanzees imitate from the first week of life until they are about two to three months old (Myowa 1996; Bard & Russell 1999; Myowa-Yamakoshi *et al.* 2004), while infant macaques (Ferrari *et al.* 2006) imitate only in the first days of life. Social psychologists have reported many instances in which imitation occurs automatically and unconsciously, and have highlighted its role in constituting a foundation for social communication and for fostering a sense of 'affiliation' among humans (Dijksterhuis &

Bargh 2001; van Baaren *et al.* 2009). Experimental psychologists have established that indeed adults show a strong imitative tendency that is normally inhibited. Specifically, recent experiments suggest that simply observing a finger movement evokes a strong tendency to execute that action (Brass *et al.* 2000, 2001; see also Massen & Prinz 2009). However, since evoked imitations are not always adaptive in everyday situations, they are usually inhibited.

## 2. WHEN IMITATION GOES WRONG

After frontal lobe damage, the tendency to imitate observed behaviour may get out of control. Luria (1966) called this pathological condition *echopraxia*. He reported that when patients were instructed to respond to one movement with a different one, e.g. 'when I show you my fist you must show me your index finger, when I show you my index finger you must show me your fist', they tended to imitate the observed action while ignoring the verbal command. Years later, Lhermitte *et al.* (1986) described a similar syndrome that they called *imitation behaviour*. They tested 125 patients for the presence of imitation behaviour by showing them gestures without providing preliminary instructions. Ninety per cent of the patients with frontal lesions, particularly those with lesions of the medio-basal cortex, showed overt imitative response tendencies, even when they were told to stop imitating. Using the same procedure as the French neuropsychologists, De Renzi *et al.* (1996) tested for imitative behaviour in 78 patients with hemispheric focal lesions divided, on the basis of their computerized tomographic data, into a frontal ( $n = 52$ ) and a

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non-frontal group ( $n = 26$ ). At odds with the claim of Lhermitte *et al.* (1986), they found that imitation behaviour was present, but at a much lower incidence (39% of the frontal patients) and was mainly associated with medial and lateral lesions. The different incidence between their study and that of Lhermitte *et al.* (1986) might be due to differences in the criteria used for patient selection. Recently, Brass *et al.* (2003) assessed in 32 patients (half with frontal lesions and half without) whether inhibition of imitative responses and of overlearned responses share the same inhibitory processes by directly comparing the imitation–inhibition task (as used in Brass *et al.* 2000) and the Stroop task<sup>1</sup> (Stroop 1935). They found that some patients with an impaired performance on the Stroop task were not impaired in the imitation–inhibition task and *vice versa*, and that performance on each task correlated differently with performance on other frontal tasks. Inhibition of imitative response tendencies and that of overlearned response tendencies were also found to be associated with discrete brain regions, as shown in an imaging study performed by the same group (Brass *et al.* 2005). Whereas inhibition of overlearned responses requires a fronto-parietal network involved in interference control and task management, the inhibition of imitative responses involves the anterior fronto-medial cortex and the right temporal–parietal junction that are required to distinguish between self-generated and externally triggered motor representations. The only overlapping area they found was in the right inferior frontal gyrus, probably related to the generation of the stop signal.

There are other ways in which imitation might go wrong. About a century ago, neuropsychologists documented how the imitative tendency might become dramatically impoverished in individuals who suffer from a condition termed *ideomotor apraxia* (IMA). In the following sections, we will describe different manifestations of this condition produced by brain damage and its association or dissociation with other abilities; we will also review the most prominent explanations of IMA and we will suggest the brain regions associated with this deficit.

### 3. WHERE DOES IMITATION STAND RELATIVE TO OTHER COGNITIVE FUNCTIONS?

An early conceptualization of apraxic deficits (Liepmann 1900, 1920) distinguishes between IMA—characterized as a deficit in imitating action and/or performing them on verbal command—and ideational apraxia (IA)—defined as a selective deficit in using objects and tools. IA is not simply a more severe form of IMA as some sceptics argued (Sittig 1931; Zangwill 1960), as demonstrated by reports of patients with impaired imitation but normal object and tool use and *vice versa* (e.g. De Renzi & Lucchelli 1988; Rosci *et al.* 2003). Recently, Goldenberg (2009) proposed that, in the case of imitation, the system needs to understand the spatial relationships between body parts, while in tool/object use, it needs to understand the spatial relationships between the hand and the tool or between tools and objects. It is not clear whether this analogy between imitation and tool

and object use requires the existence of a unique mechanism in the parietal cortex that is responsible for extracting spatial relationships in *both* tasks. If this were the case, then a prediction should be made that a lesion affecting the ability to extract spatial relationships should give rise to *both* IA and IMA. However, evidence that IA and IMA may occur independently is already available.

The imitative deficit is not the only symptom of IMA. Patients with IMA can also be impaired at pantomiming the use of an object on verbal command (e.g. ‘show how you would use a hammer’, Merians *et al.* 1997; Halsband *et al.* 2001; Buxbaum *et al.* 2005). On the other hand, impaired imitation of gestures, but spared ability to pantomime them following a verbal instruction, has also been reported (Goldenberg & Hagmann 1997; Peigneux *et al.* 2000). The imitative deficit (and/or deficits in pantomiming to command) is often, although not always, associated with aphasia: double dissociations between the imitative deficit and aphasia (comprehension and production deficits) have been documented repeatedly (e.g. De Renzi *et al.* 1980; Papagno *et al.* 1993).

A deficit at imitating gestures may also be observed in association with a deficit in recognizing or understanding them. The correlations observed between pantomime recognition and pantomime imitation ( $r = 0.80$ ,  $p < 0.0001$  and  $r = 0.52$ ,  $p < 0.001$  for hand and arm postures, respectively) led Buxbaum *et al.* (2005) to propose that the same representations ground production and perception of object-directed (i.e. transitive) hand actions. An association of deficits in imitation and recognition of gestures has been observed at a group level by Negri *et al.* (2007;  $r = 0.59$ ,  $p = 0.001$ ), while Tessari *et al.* (2007) found only a trend ( $r = 0.32$ ,  $p = 0.07$ ). At variance with the group-level pattern, in the study by Negri *et al.* (2007), patient P.T. was found to be impaired at imitating meaningful (object-associated and intransitive actions) as well as meaningless gestures, but he was able to recognize object-associated pantomimes. In that of Tessari *et al.* (2007), cases 30 and 31 imitated meaningful, object-related pantomimes (10 and 50%, respectively) significantly better than meaningless gestures, but could nevertheless correctly identify them (90 and 100%, respectively). Bartolo *et al.* (2001) described a patient, M.F., who performed poorly on all tests of production of meaningful gestures, including imitation, but was flawless in meaningless gesture imitation; interestingly, her discrimination and comprehension of meaningful actions were spared. These dissociating patterns indicate that gesture imitation can be impaired despite normal performance in gesture perception and that the ability to imitate gestures might not be necessary for recognizing them.

### 4. CONCEPTUAL CHARACTERIZATION OF IMITATION DEFICITS IN MODELS OF APRAXIA

Liepmann (1900) was the first who proposed, based on empirical observations, a theory of gesture production, still generally accepted nowadays, that distinguished between the formulation of the idea of a movement (or movement formula) and its implementation into

the corresponding innervations. Whereas a deficit of formulation of the idea of a movement would give rise to IA, a deficit of its execution would lead to IMA. Liepmann's original schema has subsequently been revisited by other scholars, Poeck (1982), De Renzi (1985) and Roy & Square (1985) among others, all of whom maintained the essential dichotomy between the two levels of movement production.

However, to account for the dissociations in performance of different tasks involving gestures at input or output, Rothi *et al.* (1991) proposed a cognitive neuropsychological model of limb praxis inspired by models of language production. The main features of the model are depicted in figure 1.

The model distinguishes a visual modality and a verbal modality, each of which contains inputs (a visual gesture or an object, and a verbal command) and outputs (a gesture or a name) as well as intermediate processing stages. A visual gesture can be imitated using a semantic or a non-semantic route. In addition to the visual analysis, the semantic route encompasses the input praxicon that allows the recognition of a familiar gesture, the semantic or conceptual system, that stores its content, and the output praxicon that permits to produce it (in Negri *et al.* (2007), praxicons are referred to as axemes). The non-semantic route is necessary for imitating novel gestures, in the same way that the sublexical mechanism of language production models is necessary for reading novel, regular words and non-words. The model accounts also for how we pantomime the use of a visually presented object or to a verbal command (figure 1). This model has been subsequently modified by others (e.g. Goldenberg & Hagmann 1997; Cubelli *et al.* 2000; Buxbaum 2001; Tessari *et al.* 2007). The main modifications made on the original model are the following: the substitution of the innervatory patterns with a temporary memory system for gestures (Cubelli *et al.* 2000, gestural buffer; Tessari *et al.* 2007, short-term/working memory) and the introduction of intrinsic and extrinsic egocentric forms of spatio-motor coding computed by the dorsal stream (Buxbaum 2001). These procedures are used for processing all gestures but are particularly critical in the absence of environmental or memorial constraints such as, for instance, in pantomiming the use of objects or in producing meaningless movements.

Various neuropsychological studies have been carried out in order to test predictions derived from this model. As far as imitation is concerned, neuropsychological (Goldenberg & Hagmann 1997; Peigneux *et al.* 2000; Bartolo *et al.* 2001; Tessari *et al.* 2007) and neuroimaging (Peigneux *et al.* 2004; Rumiati *et al.* 2005) studies have demonstrated that the two routes or mechanisms have a psychological reality and dedicated neural correlates. Specifically, patients with lesions of the parietal cortex (and of the angular gyrus in particular) were described to be impaired in the imitation of meaningless gestures, but still able to imitate meaningful gestures (Mehler 1987; Goldenberg & Hagmann 1997; Peigneux *et al.* 2000; Tessari *et al.* 2007). Using positron emission tomography (PET), Peigneux *et al.* (2004) observed activations in the left angular and middle frontal gyri, and in the right supramarginal

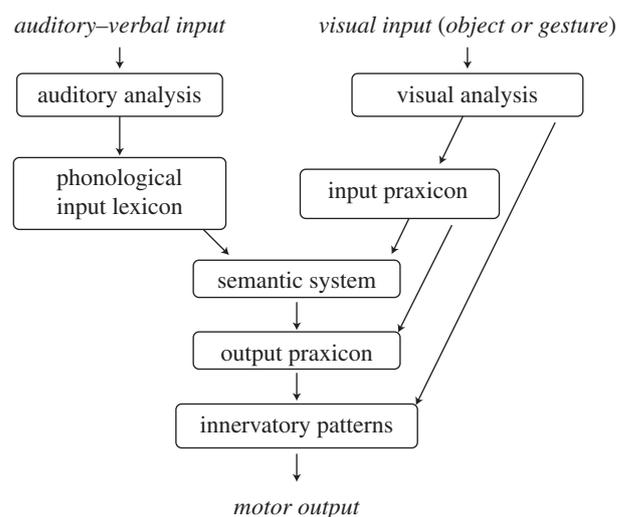


Figure 1. A simplified version of the model of praxis proposed by Rothi *et al.* (1991). According to this model, imitation of familiar gestures relies on the semantic, indirect route that encompasses the input praxicon, the semantic system, the output praxicon and the innervatory patterns; imitation of new gestures relies on the non-semantic, direct route that, from visual analysis, leads directly to the innervatory patterns.

gyrus and inferior parietal lobule when subjects imitated familiar gestures and in the inferior and superior parietal lobes bilaterally when subjects imitated novel gestures. Peigneux *et al.* (2004) failed, however, to find imaging evidence in favour of the independence of input and output praxicons: evidence that was provided behaviourally in a neuropsychological study by Negri *et al.* (2007). In another PET study, some of us (Rumiati *et al.* 2005) found increased activations in the inferior temporal, the angular and the parahippocampal gyri of the left hemisphere when subjects imitated pantomimes of object use, relative to the imitation of meaningless gestures. Imitation of meaningless gestures, relative to pantomimes, led to an increased neural activity in the parieto-occipital and the occipito-temporal junctions in the right hemisphere, in the superior temporal gyrus in the left hemisphere and in the superior parietal cortex bilaterally. Thus, in addition to regions that are generally engaged in imitation, there are other regions that are associated only with imitation of either meaningful or meaningless gestures.

## 5. THE DUAL ROUTE MODEL AND OTHER ACCOUNTS OF IMITATION

Different theories have been put forward to explain imitation. The active intermodal matching model (Meltzoff & Moore 1977, 1997) holds that imitation is a matching-to-target process, based on the proprioceptive feedback loop that allows infants to evaluate motor performance against the perceived target. This is possible because infants code movements within an innate supramodal system that unifies observation and execution of motor acts. The associative-sequence learning model (Heyes 2001) assumes that the imitative capacity is a product of general processes of associative learning. The ideomotor theory claims

that observing somebody else executing an action activates an internal motor representation in the observer, as observed and internal actions share a similar content or code. According to these accounts, imitation is accomplished by a unique mechanism. However, for Bekkering *et al.* (2000) and Wohlschläger *et al.* (2003), imitation is an interpretative process that is influenced by goals. According to directed theory of imitation (GOADI), the perceived gesture undergoes a decomposition–recomposition process that is dependent on a goal hierarchy and on available resources.

Based on a series of studies conducted in our laboratory (Rumiati & Tessari 2002, 2007; Tessari & Rumiati 2004; Tessari *et al.* 2006, 2007), we tested the dual route hypothesis, according to which imitation is *not* accomplished by a unique operation but by two different mechanisms. In agreement with previous conceptualizations illustrated earlier (Rothi *et al.* 1991; Goldenberg & Hagmann 1997; Cubelli *et al.* 2000; Buxbaum 2001), we proposed that humans can imitate familiar gestures using the *semantic* or *indirect* route and unfamiliar gestures using the *non-semantic* or *direct* route.

This is what happens in normal circumstances. However, a reduction in cognitive resources, caused either by experimental manipulations with healthy participants (Tessari & Rumiati 2004) or by brain damage (Tessari *et al.* 2007), seems to influence which route to select for imitating gestures. The studies with healthy participants revealed that speeded imitation was significantly more accurate for meaningful than for meaningless gestures when they were presented in separate lists, suggesting that two different routes were used. In contrast, when the two types of gestures were presented intermingled, the advantage of meaningful over meaningless imitation disappeared, suggesting that participants selected the direct route for imitating both stimulus types (Tessari & Rumiati 2004; see also Cubelli *et al.* 2006). The lack of difference in the imitation of meaningful and meaningless gestures could not be accounted for by meaningless gestures impoverishing overall performance; in fact, the same pattern was observed when meaningless (experiment 1) or both meaningless and meaningful actions (experiment 2) were presented for longer times (Rumiati & Tessari 2007). In all these studies, the meaningful gestures employed were pantomimes of object use (e.g. hammering), while the meaningless ones were gestures obtained by modifying the relationship between the hand–arm and the trunk of the meaningful version.

The analysis of the errors made by subjects also provided information about the mechanism selected during imitation (Tessari & Rumiati 2004). Subjects made more semantic errors when imitating meaningful gestures in the blocked than in mixed conditions and in a condition in which there was a preponderance of meaningful gestures, indicating that the semantic mechanism was selected more often in the former than in the latter condition. Lexicalization errors (i.e. a meaningful gesture that is visually similar to the meaningless target one but that is not included in the list) were made when subjects imitated meaningless gestures, and were more

numerous in the blocked than in the mixed condition when the non-semantic strategy subserved imitation of both meaningless and meaningful gestures. Overall similar behavioural patterns were observed in 32 unilateral brain-damaged patients (Tessari *et al.* 2007). When meaningful and meaningless gestures were presented intermingled, patients' ability to imitate either action types did not differ (see De Renzi *et al.* 1980; Cubelli *et al.* 2000; Toraldo *et al.* 2001, for similar findings). However, when patients' ability to imitate was evaluated using separate lists, six patients had a selective imitation deficit for meaningless actions (see Goldenberg & Hagmann 1997; Peigneux *et al.* 2000; Bartolo *et al.* 2001, for similar results), and two had a selective imitation deficit for meaningful actions (see Bartolo *et al.* 2001 for similar results). This study suggests that patients performing the imitation task in the mixed condition selected the non-semantic route because it allows the reproduction of all gestures and avoids high costs of switching between routes. The selective deficits observed in the blocked imitation condition suggest that individual imitative mechanisms were damaged. Thus, route selection does not seem to depend exclusively on the type of action to be imitated (meaningful and meaningless), but also on other factors such as external (list) and internal (resources) conditions.

Press & Heyes (2008) proposed the 'stimulus selection hypothesis' as an alternative interpretation of the findings of Tessari & Rumiati (2004). Using an automated reaction time, as well as accuracy, measure, Press & Heyes (2008) first replicated Tessari & Rumiati's (2004) findings and then examined the imitation of meaningful and meaningless 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. They found that, for both gesture types, performance was worse immediately after meaningless than after meaningful trials. In contrast to Tessari & Rumiati (2004), they also found that, even at the beginning of the experiment, responding to meaningful gestures was no better than responding to meaningless ones. Consistently with their hypothesis, Press & Heyes (2008) argued that the properties of the action stimulus play a substantial role in determining the selection of the route and that effects of block composition on imitation need not be generated through strategic switching between routes.

## 6. IMITATION OF INTRANSITIVE GESTURES

The studies on route selection reviewed so far were concerned with how we imitate transitive, object-related gestures (e.g. hammering); however, whether the dual route account holds true also for intransitive gestures (e.g. waving goodbye) still needs to be demonstrated. Experimental psychology studies with healthy adults showed that both transitive and intransitive gestures are subject to automatic imitation as demonstrated by Brass *et al.* (2000, 2001) and by Press *et al.* (2008), respectively. Neuropsychological group studies typically showed that apraxic patients have more difficulties in producing transitive than intransitive gestures on verbal command (Foundas *et al.* 1999), by imitation (Haaland *et al.* 2000;

Buxbaum *et al.* 2005, 2007) or in both modalities (Roy *et al.* 1991). Two left-brain-damaged patients have also been described with a complete preservation of the ability to perform intransitive gestures paired with a severe deficit at pantomiming transitive gestures (Rapcsak *et al.* 1993; Dumont *et al.* 1999). These reports seem to imply that there are independent mechanisms for processing transitive and intransitive gestures (e.g. Buxbaum 2001). As a clear complementary dissociation has not yet been reported (Cubelli *et al.* 2000), it is premature to conclude that transitive and intransitive actions are processed by different mechanisms. Recently, we have reported that healthy adults, engaged in a speeded imitation task, performed meaningful intransitive gestures significantly better than meaningful transitive gestures, suggesting that, compared with the intransitive ones, transitive gestures pose greater processing demands on the mind–brain, presumably because of the involvement of objects (Carmo & Rumiati 2009).

While, in general, the production of transitive gestures seems to be affected more by left hemisphere lesions (Bartolo *et al.* 2001; Tessari *et al.* 2007), the ability to generate intransitive gestures can be equally disrupted by damage to either cerebral hemisphere (Buxbaum *et al.* 2007). But, there are also studies suggesting that defective performance with both transitive and intransitive gestures is more likely to follow left than right hemisphere damage (Hanna-Pladdy *et al.* 2001).

A recent imaging study showed that planning either tool use pantomimes or intransitive gestures was associated with asymmetrical increases in the same regions of left parietal (the intraparietal sulcus, the supramarginal gyrus and the caudal superior parietal lobule) and dorsal premotor cortices (Króliczak & Frey *in press*). Interestingly, these effects were greater for tool use pantomimes, but only when performed with the right hand. Króliczak & Frey concluded that transitive and intransitive actions are represented in a common, left-lateralized praxis network, irrespective of the hand used.

Here we report original data from an experiment in which we aimed at verifying whether the dual route hypothesis, already tested for transitive gestures (Rumiati & Tessari 2002, 2007; Tessari & Rumiati 2004; Tessari *et al.* 2006), holds true for intransitive gestures. From the imaging results just mentioned (Króliczak & Frey *in press*), it seems plausible that one would obtain a common pattern across the two action types. In the present experiment, we allowed subjects only 600 ms for imitation—150 ms less than the time subjects were allowed in Tessari & Rumiati (2004)—because intransitive gestures are easier than transitive gestures (Carmo & Rumiati 2009).

A successful replication of the original findings would demonstrate that the action meaning and the strategic control effects are not specific to object-related pantomimes, rather they represent a more general way in which the human mind–brain operates when it has to cope with a shortage of resources.

#### (a) *Extreme speeded imitation of intransitive gesture experiment*

Thirty-nine right-handed (on the Edinburgh Inventory, mean = 81.75, s.d. = 23.93) subjects (mean age of

23.1, s.d. = 3.3) participated in this experiment. Subjects were randomly assigned to one of the two conditions (condition is a between-subject factor): 19 subjects (eight males) performed the task in the blocked condition and 20 (six males) performed the task in the mixed condition. In the blocked condition, meaningful and meaningless gestures were presented separately, whereas in the mixed condition, they were presented intermingled. Each condition comprised four sub-blocks; in the mixed condition, each sub-block contained 36 gestures (18 meaningful and 18 meaningless) presented in a random order that varied from sub-block to sub-block. In the blocked condition, two sub-blocks contained 36 meaningful gestures each and two contained 36 meaningless gestures each. Each subject performed a total of 144 trials. In the blocked condition, the order of type of stimulus (meaningful or meaningless) was counterbalanced across subjects. Each trial started with the video display of a gesture that lasted for 1500 ms, followed by a 350 ms blank screen, at the end of which a sound of 250 ms went off, warning the subject that the following trial was about to start. Subjects were asked to reproduce each gesture (performed by the actor using his left hand) with their right limb, immediately after its presentation and before the next trial started, and they were asked to press a button with their right hand at the onset of the video. They were asked to release the button as soon as the video had ended and to imitate immediately the seen gesture as accurately as possible. Their performance was recorded and subsequently scored by two independent raters. Subjects were not informed about the composition of the lists or the purpose of the study, and they all gave their informed consent for taking part in the study, which was approved by SISSA Ethics Committee.

The analyses reported herewith are based on scores averaged across the two raters (level of agreement between them on a Cohen's kappa = 0.50, s.e. = 0.01). A repeated-measures ANOVA was performed on correct responses as a dependent variable, with Meaning (meaningful, MF; meaningless, ML) as a within-subject factor and Condition (blocked, mixed) as a between-subject factor. The main effects of Meaning ( $F_{1,38} = 19.45$ ,  $p < 0.001$ ) and Condition ( $F_{1,38} = 4.69$ ,  $p < 0.05$ ), as well as the Meaning  $\times$  Condition interaction ( $F_{1,38} = 4.65$ ,  $p < 0.05$ ), were significant. Two paired-wise *t*-tests revealed that in the blocked condition, MF (mean = 86.15, s.e. = 1.99) were performed significantly better than ML gestures (mean = 77.85, s.e. = 2.08), ( $t(17) = 3.93$ ,  $p = 0.001$ ); in the mixed condition, there was no difference in accuracy between MF (mean = 77.88, s.e. = 1.95) and ML (mean = 75.03, s.e. = 2.03) gestures. Two independent one-way ANOVAs showed that MF gestures were performed significantly better in the blocked (mean = 86.15, s.e. = 1.99) than in the mixed condition (mean = 77.88, s.e. = 1.95) ( $F_{1,37} = 8.78$ ,  $p < 0.01$ ). Conversely, no difference in performance was found for ML gestures ( $F_{1,37} = 0.934$ ,  $p > 0.01$ ) (with Bonferroni correction). Results are plotted in figure 2.

#### (b) *Further analyses: learning effects*

In order to verify whether subjects' performance changed during the experiment, average slopes across the

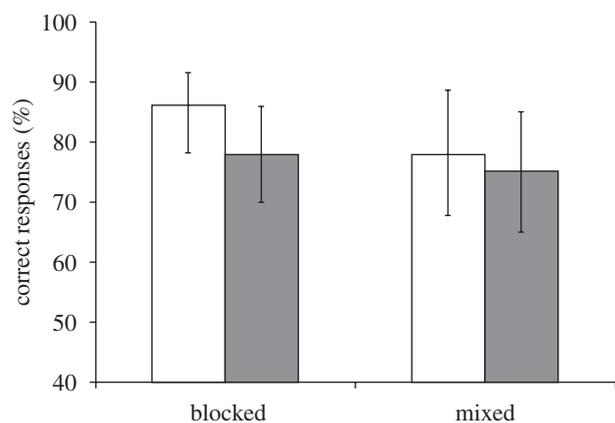


Figure 2. Percentages of correctly imitated meaningful (MF) and meaningless (ML) gestures plotted depending on whether they were performed in a blocked or mixed condition. The bars represent the standard deviation from the mean. Open column, MF; filled column, ML.

four sub-blocks were calculated for MF and ML gestures in each condition (mixed and blocked), and each compared with a non-increasing function. Results are plotted in figure 3. In the mixed condition, a significant increase in accuracy was observed for both MF and ML gestures ( $t(19) = 4.05$ ,  $p < 0.001$ , and  $t(19) = 3.55$ ,  $p < 0.01$ , respectively), whereas in the blocked condition, a significant increase in accuracy was observed only for ML gestures ( $t(18) = 2.3$ ,  $p < 0.05$ ; MF actions:  $t(18) = 1.24$ ,  $p > 0.1$ ).

In the mixed condition, at the beginning of the experiment (i.e. the first sub-block), there was no difference in the imitation of MF and ML gestures ( $t(19) = 1.732$ ,  $p > 0.05$ ). At the beginning of the experiment, the ability to imitate ML actions did not change as a function of the experimental condition ( $F_{1,37} = 2.106$ ,  $p > 0.05$ ), whereas the ability to imitate MF gestures in the blocked condition was significantly higher than in the mixed list ( $F_{1,37} = 15.629$ ,  $p < 0.001$ ).

## 7. DISCUSSION

In this experiment, we replicated the effects previously found using transitive gestures (e.g. Tessari & Rumiati 2004). Consistent with the dual route hypothesis, in the blocked condition, subjects were more accurate at imitating intransitive gestures with meaning than those without meaning, while in the mixed condition, no differences were observed. Likewise, in the mixed condition, to save resources that would otherwise be eroded by switching between non-semantic and semantic mechanisms, normal subjects selected only one mechanism for reproducing both types of gestures.

When the non-semantic route was presumably selected, such as, for instance, when subjects imitated ML gestures in the ML blocked condition and both MF and ML gestures in the mixed condition, a significant increase in accuracy was systematically observed. In contrast, when the semantic mechanism was presumably selected, such as, for instance, in the MF blocked condition, we failed to observe an increase across sub-blocks. We suggest that the non-semantic

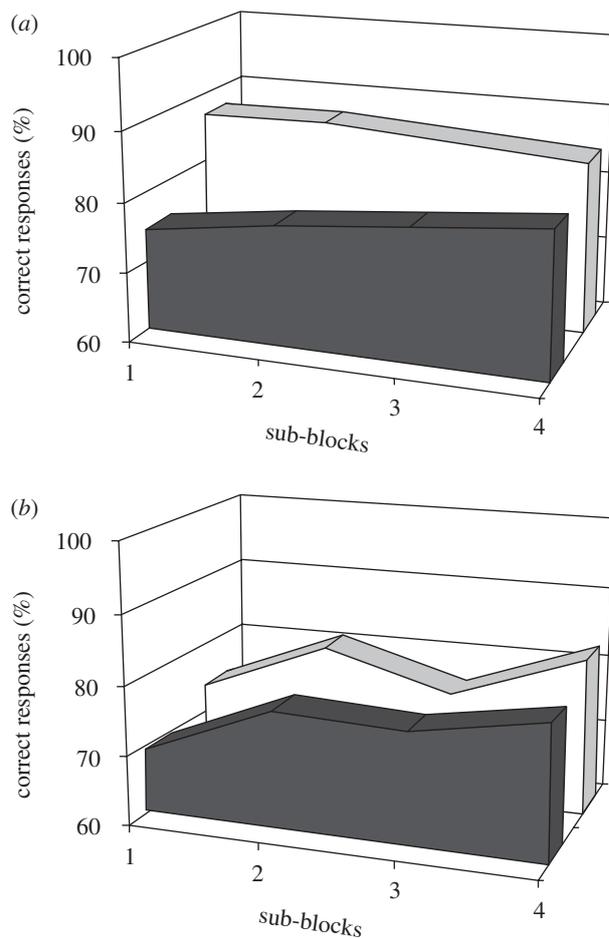


Figure 3. (a) Percentages of correctly imitated gestures, performed in the blocked condition, plotted as a function of meaning (meaningful (MF, open) and meaningless (ML, filled)) and of sub-blocks. (b) Percentages of correctly imitated gestures, performed in the mixed condition, plotted as a function of meaning (meaningful (MF, open) and meaningless (ML, filled)) and of sub-blocks.

route can be effectively used for learning through imitation, whereas the semantic route has very poor learning properties.

### (a) *Lateralization and body-part specific disturbances of imitation*

Disorders of imitation can be classified depending on the body parts that are affected, of which the most frequently assessed are the upper limbs and the mouth, although sometimes lower limbs are included in the assessment. Studying patients' deficits in imitating gestures made using different body parts contributes to the understanding of whether imitation is mediated by an internal body representation and, eventually, on the nature of such representation.

It is worth remembering that unlike most motor symptoms caused by brain damage, apraxia follows unilateral lesions and yet it affects both sides of the body, clearly indicating a cognitive, rather than a peripheral, origin of this deficit (see Goldenberg (2009) for a similar argument). Usually, in right-handed individuals, the inability to imitate limb movements is observed following damage to the left hemisphere (Basso *et al.* 1980), although a deficit might also

occur after right brain damage (RBD) (e.g. De Renzi *et al.* 1980), especially when imitating finger configurations (Goldenberg & Strauss 2002; Della Sala *et al.* 2006) or movement sequences (Canavan *et al.* 1989). A reduced ability to imitate is more common or severe after lesions of the left parietal cortex (Kolb & Milner 1981; De Renzi *et al.* 1983; Basso *et al.* 1985; Alexander *et al.* 1992; Haaland *et al.* 2000; Halsband *et al.* 2001; Weiss *et al.* 2001; Buxbaum *et al.* 2005; Tessari *et al.* 2007), although it can result also from frontal or subcortical lesions (e.g. Leiguarda 2001; Peigneux *et al.* 2001; Salter *et al.* 2004).

In contrast, fewer cases of patients presenting with IMA also encompassing leg actions have been reported in the past (Liepmann 1905, the Imperial Counsellor; Sittig 1931, cases F.S. & A.H.; Geschwind & Kaplan 1962). In a group study that aimed at verifying possible differences in imitation depending on the effector used, Lehmkuhl *et al.* (1983) found that aphasic left brain damage (LBD) patients were equally impaired at imitating arm/hand movements and leg/foot movements, while patients with RBD showed no impairment at all. Likewise, in a recent group study, Ambrosioni *et al.* (2006) found that of the 17 LBD patients found with arm apraxia, six also showed severe leg apraxia.

According to Goldenberg *et al.* the two cerebral hemispheres might have different competencies for imitation performed by different effectors. In particular, imitation of meaningless actions was found to be more prone to errors in LBD patients when gestures involved hands and in RBD patients when they involved finger postures (Goldenberg 1996, 1999; Goldenberg & Strauss 2002). Moreover, in Goldenberg & Strauss (2002), LBD affected imitation of hand and foot gestures more than imitation of finger gestures, whereas RBD had the strongest effect on finger gestures and affected foot more than hand gestures. Like Lehmkuhl *et al.* (1983), Goldenberg & Strauss (2002) found that hand and foot gestures are equally affected in patients with LBD but, unlike them, they found a substantial impairment of foot gestures also in patients with RBD. Goldenberg's view is that body part coding of meaningless gestures depends on left hemisphere function and that additional right hemisphere contributions are afforded when demands on perceptual discrimination rise.

Haaland *et al.* (2000) analysed the lesions of patients with and without an imitation deficit for meaningless gestures and found that compared with those without apraxia, apraxic patients were more likely to have lesions in posterior parietal areas (Brodmann areas 7, 39 and 40) and in frontal areas (Brodmann areas 4, 6, 8, 9 and 46). The error pattern differed depending on the lesion site: while errors involving hand position were made only by patients with parietal lesions, errors concerning the configuration of fingers were made by all patients with frontal lesions and by 60 per cent of the parietal patients.

These results fit with a dissociating pattern observed in LBD patients by Goldenberg & Karnath (2006), who found that some could imitate hand but not finger postures, whereas others could imitate finger but not hand postures. The impaired imitation of finger postures was associated with a lesion

involving the inferior frontal gyrus and adjacent insular cortex, extending subcortically into the putamen and caudate nucleus, whereas impaired imitation of hand postures was associated with a more posterior lesion, involving the middle temporal gyri, middle occipital gyri and the inferior parietal lobule. These anatomical findings cannot easily be explained in terms of somatotopic organization of sensory and motor representations of the human body, as the lesions responsible for disturbed imitation of finger and hand postures did not correspond to upper limb representations in known somatotopic motor maps.

### (b) *Dual route hypothesis and body representations*

Some neuropsychological studies directly investigated the interactions between body representations and imitation of gestures. However, although the interest in how the knowledge about the body is represented in the brain dates back to almost a century, there is still no agreement on the number of body representations that there are in the brain, on the kind of information they code or on how we should call them (see the review by Corradi-Dell'Acqua & Rumiati (2007)). Besides the sensorimotor maps (Penfield & Jasper 1954), recently, the existence of at least other three body representations has been hypothesized based on pattern dissociations (Sirigu *et al.* 1991; Schwoebel & Coslett 2005): the *body semantics*, *body schema* and *body structural description*. The *body semantics* (or *body image*, Coslett 1998) is a conscious representation that stores lexical-semantic information about the body (Schwoebel & Coslett 2005). The *body schema* is an online, dynamic map of the current positions of body parts relative to one another, built on multiple sensory and motor inputs, which interacts with motor systems to generate actions (Head & Holmes 1911; Heilman *et al.* 1986; Parsons 1994). The *body structural description*, derived primarily from visual input, codes the spatial arrangement of effectors and the relationships between them and when damaged yields to *autotopagnosia* proper. This term refers to the patients' inability to localize, within the whole body structure, body parts on verbal command, independently of whether the body is theirs or someone else's, including a manikin (Pick 1908; De Renzi & Scotti 1970; Odgen 1985; Semenza 1988; Buxbaum & Coslett 2001). Using functional magnetic resonance imaging (fMRI), Corradi-Dell'Acqua *et al.* (2009) found that *body schema* and *body structural description* system are associated with differential neural substrates, thus suggesting that these are independent representations.

The putative representations just described have been identified by testing how patients do on tasks hypothesized to tap each of them; in some cases, however, the tasks employed do not seem to be appropriate because, in addition to tapping the desired body representation, they also rely on other mechanisms and/or structures. This is the case, for example, of the *body schema* as characterized in the study of Schwoebel & Coslett (2005). They described 13 patients with a damaged *body schema* who performed abnormally either on the imagined or real finger movements (e.g. Sirigu *et al.*

1996) or on the handedness task (Parsons 1987), but accurately on all other body representation measures. The tasks used to tap a putative *dynamic body representation* involve also the ability to rotate mentally body parts (as well other non-bodily stimuli, if subjects are instructed to imagine rotating them with their hand). However, it is possible that the representation involved here is the structural description and that this is functionally separable from the mental transformations upon them. Ochipa *et al.* (1994) and Sirigu *et al.* (1996) reported two patients with a motor imagery impairment, associated with IMA, but with an intact body representation, offering one side of a dissociation.

Another problem is that there is no agreement on which of the putative body representations need to be damaged in order to cause imitation impairments. Goldenberg (1995) and Goldenberg & Hagmann (1997), for instance, proposed that the imitation deficit is caused by damage to a non-semantic route *and* to the body structural description. This proposal is based on the finding that LBD apraxic patients scored worse than LBD patients without apraxia or RBD patients, on an imitation task as well as on a task in which it was required to reproduce the same postures on a life-sized manikin (Goldenberg 1995). In addition, RBD patients' performance on tasks tapping visuospatial abilities (i.e. block design and manipulation of beads) was inferior to that of both LBD groups. Goldenberg concluded that patients' reduced ability to reproduce gestures on their own body as well as on a manikin was caused by a unique functional disturbance of a common body structural description and that the double dissociation between imitation of meaningless gestures and performance on block design suggested that the former did not rely on general visuospatial abilities. The association of deficits in reproducing postures on the human and on the manikin body was observed again in two single cases (L.K. and E.N., Goldenberg & Hagmann 1997). Interestingly, the lesions of the two patients overlap in the inferior portion of the angular gyrus in the left hemisphere.

Results from an fMRI study seem to fit Goldenberg's neuropsychological findings (Chaminade *et al.* 2005). Chaminade *et al.* (2005) had participants watch a human model performing bodily gestures and then to execute either an identical or a different action, with the same or different limbs. They found that imitation of simple body gestures requires both a visuospatial description of the observed model, sustained by visual perception areas in the right occipito-temporal and superior parietal cortices, and a visuospatial description of one's own body, supported by the left inferior parietal lobule.

The view that imitation is dependent on a body mapping has been challenged in a study by Bekkering *et al.* (2005). They found that IMA patients, compared with RBD patients and controls, were particularly impaired at imitating hand gestures and combined finger and hand gestures, but not at imitating finger gestures. However, on a closer inspection, finger selection turned out not to be preserved in these patients. Bekkering *et al.* (2005) interpreted their results in terms of imitation being mediated by goals, with the distal aspects of imitation such as reaching for the

correct object being more important than the means used to achieve the goal of a modelled action.

Other neuropsychologists (Buxbaum *et al.* 2000; Schwoebel *et al.* 2004; Schwoebel & Coslett 2005) proposed that the defective imitation is caused by a damage to the body schema and not to the body structural description as in Goldenberg's view. Buxbaum *et al.* (2000) described a patient, B.G., with progressive IMA, who was profoundly impaired in gesturing in imitation, to command and to the sight of the object, but performed nearly normally with tool in hand. Critically, her performance was severely impaired on the imitation of meaningless gestures and on tasks requiring spatial and mental sensorimotor transformations of body parts. The authors proposed that B.G.'s pattern of deficits was attributable to damage to a unitary set of the procedures or representations coding the dynamic positions of the body parts of self and others. According to the model about the body information described earlier, B.G.'s deficits are caused by damage to the body schema. To accommodate these findings, Buxbaum *et al.* (2000) modified the two-route model proposed by Rothi *et al.* (1991) by implementing a common set of procedures or representations coding the dynamic positions of the body parts of self and others, i.e. the body schema. To account for B.G.'s behavioural deficits without modifying Rothi *et al.*'s account, Buxbaum *et al.* mention that they should hypothesize a deficit involving the semantic route (input and output praxicons), the non-semantic route or the innervatory patterns, common to both routes.

Schwoebel *et al.* (2004) came to similar conclusions on the basis of a study in which they tested the ability of a group of LBD patients to imitate meaningful and meaningless gestures, as well as their integrity of all putative body representations. They found that the correlation between performance on action imitation and specific body representation tasks differed, depending on whether the action was a meaningful or a meaningless one. Specifically, the ability to imitate meaningful gestures correlated with the performance on tasks tapping the body schema and the body image. However, imitative performance with meaningless gestures correlated with the performance on the task tapping the body schema only.

## 8. CONCLUSIONS

Neurologically damaged patients offer a model for studying the mechanisms underlying imitation in humans. For over a century, the observations on patients suffering from IMA have allowed neuroscientists to establish some fundamental facts about imitation. More recently, imitation and its deficits have been discussed in relation to putative body representations. However, there is no agreement to date as to which representation of the body should give rise to a defective imitation when damaged. In addition to contacting a body representation, the tasks employed in the studies to tap the supposed dynamic body schema also require the involvement of motor imagery. Thus it is not evident whether the defective imitation is to be attributed to a damaged body

representation or to a defective ability to imagine mentally the transformations of body parts. Recent imaging work has demonstrated that the body structural representation and mental transformation upon them can be disentangled. Moreover, the characterization of the body representation that codes our own body parts as well the body parts of others has been recently challenged, suggesting that these two types of representations should be maintained distinct in the brain. Although there are obvious reasons why the motor system and the body should interact, the nature of the body representation that is engaged in the imitation of gestures awaits clarification. Finally, it is not yet clear whether *damage* of an internal body representation, be it the body schema or the body structural representation, is *necessary* to give rise to a defective imitation.

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## ENDNOTE

<sup>1</sup>The classical Stroop task requires a highly overlearned response such as reading to be inhibited in favour of an unusual response—naming the colour of a word. The interference occurs because the irrelevant stimulus dimension (i.e. the meaning of the word) is processed more automatically and faster than the relevant stimulus dimension (i.e. the colour of the word).

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