

Neuropsychological evidence for a strategic control of multiple routes in imitation

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Previous studies have suggested that imitators can reproduce known gestures shown by a model using a semantic, indirect route, and novel gestures using a sublexical, direct route. In the present study we aimed at testing the validity of such a dual-route model of action imitation. Patients with either left-brain damage (LBD) or right-brain damage (RBD) were tested on an action imitation task. Actions were either meaningful ($n=20$) or meaningless ($n=20$), and were presented in an intermingled list and, on a different day, in separate lists. We predicted that, in the mixed condition, patients would use a direct route to imitate meaningful and meaningless actions, as it allows the imitation of both action types. In the blocked condition, patients were expected to select the semantic route for meaningful actions and the direct route for meaningless actions. As hypothesized, none of the 32 patients showed dissociations between imitation of meaningful and meaningless actions in the mixed presentation. In contrast, eight patients showed a dissociation between imitation of meaningful actions and imitation of meaningless actions in the blocked presentation. Moreover, two of these patients showed a classical double dissociation between the imitation of the two action types. Results were interpreted in support of the validity of a dual-route model for explaining action imitation. We argue that the decrease in imitation of meaningful actions, relative to meaningless actions, is caused by a damage of the semantic route, and that the decline in imitation of meaningless actions, relative to meaningful actions, is produced by a breakdown of the direct route. The brain areas that were lesioned in all six LBD patients who showed a dissociation were in the superior temporal gyrus and the angular gyrus, whereas the two RBD subjects had common lesions of the pallidum and of the putamen. The brain structures affected in our patients with selective apraxia are consistent with those reported before in other neuropsychological reports. They are also in agreement with areas found activated in imaging studies in which the neural mechanisms underlying imitation were examined.

Keywords: ideomotor apraxia; inferior parietal cortex; angular gyrus; mirror neurons; hippocampus

Abbreviations: BA = Brodmann area; LBD = left-brain damage; PET = positron emission tomography; RBD = right-brain damage

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Introduction

The human predisposition to imitate actions performed by others has long been noted in studies of normal and pathological behaviour. Early work with newborns suggested that humans are likely to be endowed with such ability from birth (Metzoff and Moore, 1997). Even adults show a strong mimic tendency (Brass *et al.*, 2001) that may, however, be pathologically reduced in brain-damaged patients. This is one of the deficits that characterize ideomotor apraxia, a syndrome commonly observed in right-handed individuals following brain damage to the left hemisphere (Basso *et al.*, 1980; De Renzi *et al.*, 1980;

Kertesz and Ferro, 1984; De Renzi and Faglioni, 1999, for a review), although right-handed apraxic patients whose lesions spare the left hemisphere have also been reported (Von Monakow, 1914, case 11; Brun, 1921, case 7; Morlaas, 1928, cases 9, 10, 11; De Renzi *et al.*, 1980; De Renzi, 1989). Moreover, De Renzi *et al.* (1980) found that 20% (16/80) of the patients with a right hemisphere lesion performed pathologically on an action imitation task.

Besides the reduced ability to imitate the gestures shown by the experimenter, patients with ideomotor apraxia may show an impaired ability to perform skilled limb

movements on verbal command (Merians *et al.*, 1997). However, as patients with ideomotor apraxia often suffer from co-occurring aphasia, in order to circumvent poor comprehension imitation is preferred (Alexander *et al.*, 1992; De Renzi and Faglioni, 1999). Dissociations in performance between imitation and pantomiming to verbal command have also been observed in some occasions. Ochipa *et al.* (1994), for instance, described a left-brain damaged (LBD) patient with ideomotor apraxia whose imitation performance was more impaired than his performance when pantomiming in response to verbal command. The selective deficit on imitation—labelled ‘visuo-imitative apraxia’ (Mehler, 1987, who tested only meaningless actions; Merians *et al.*, 1997)—was later replicated in a LBD patient, SS, but in this case performance on verbal command was as good as that of control subjects (Merians *et al.*, 1997). Instead, the term ‘conduction apraxia’ (Ochipa *et al.*, 1994) was used to describe patients who had, in addition to an imitation deficit, also abnormal pantomiming to verbal command.

Rothi *et al.* (1991) brought about the first cognitive model of praxis analogous to models of language production (e.g. Patterson and Shevell, 1987) with which they aimed at explaining the processing steps involved in different motor tasks (e.g. action imitation and pantomiming on command) and the possible breakdowns that can occur at input, output or at any other point of the processing routes. What is relevant for the purpose of the present study is that Rothi *et al.*'s (1991) model postulates the existence of different neural mechanisms for imitating either meaningful or meaningless actions: the meaningless actions can be imitated only using a direct (or sublexical) route (which, however, can be used for imitation of meaningful actions too), while the lexical–semantic route can be selected to reproduce meaningful actions only. The direct route connects the visual analysis to the innervatory patterns, and the semantic route comprises different processing stages, including the action input lexicon, the semantic system and the action output lexicon, before accessing the innervatory patterns (the latter stage is in common with the direct route). Rothi *et al.*'s (1991) original model has been subsequently simplified of some components (e.g. innervatory patterns), but also enriched of a putative memory subsystem, holding temporarily the meaningful or meaningless action to be imitated, before being performed (Cubelli *et al.*, 2000; Rumiati and Tessari, 2002), while an explicit role was assigned to an internal representation of the body (Goldenberg and Hagmann, 1997; Buxbaum, 2001). Figure 1 depicts the dual-route model for imitation simplified by Rumiati and Tessari (2002; Tessari, and Rumiati, 2004).

So far, however, there have been only a few reports directly testing the predictions derived from Rothi *et al.*'s model with regard to action imitation. Goldenberg and Hagmann (1997) documented a damage of the direct

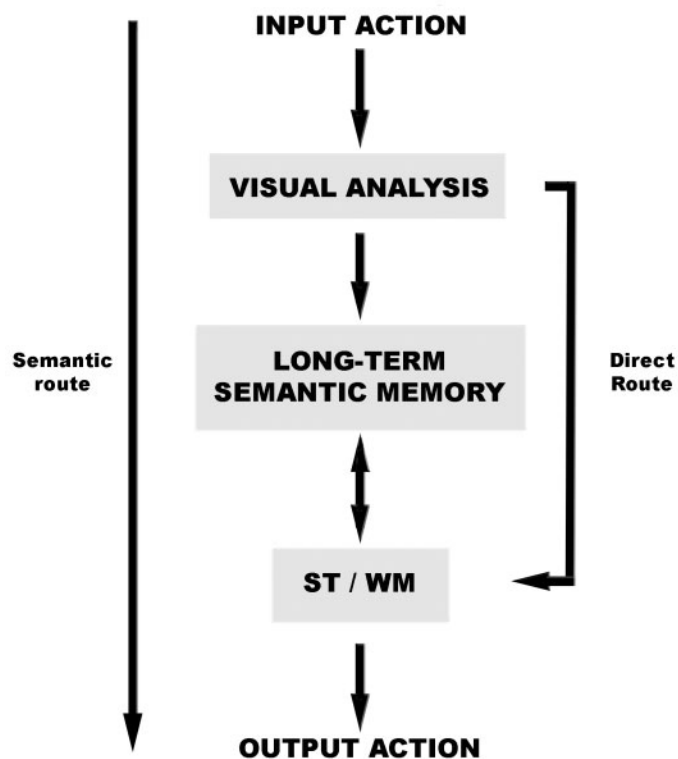


Fig. 1 A modified version of Rumiati and Tessari's (2002) two-route model for explaining imitation of actions is presented here. Following visual analysis, known, meaningful actions automatically activate the selection of the semantic long-term memory route. The direct route is selected to imitate novel, meaningless actions, but it is also used to reproduce both meaningful and meaningless actions when these are presented intermingled. ST/WM = short-term/working memory.

route in that two patients (LK and EN) were worse at imitating meaningless than meaningful actions. In addition to a faulty direct route, the two patients had a damaged body representation, for they also failed to reproduce similar meaningless postures on a manikin. Likewise, Peigneux *et al.* (2000) described a right-handed patient with a left occipito-parietal lesion who showed bilateral visuo-imitative apraxia. The patient's imitation of meaningful gestures was better than that on meaningless gestures and of their reproduction on a manikin compared with their matched meaningful gestures. The possible interaction between action imitation and a supramodal representation of the body has been acknowledged also by other authors (Buxbaum *et al.*, 2000; Buxbaum, 2001; Schwoebel *et al.*, 2002).

In a brief report, Bartolo *et al.* (2001) reported two patients, BS and EE, who imitated meaningless gestures worse than controls, but only for the former the imitation of meaningless gestures differed significantly from that of meaningful actions. They also described a third patient, MF, who was able to reproduce meaningless actions but performed poorly on all tests requiring a known gesture to

be reproduced. As those described by Goldenberg and Hagmann (1997), patient BS (and maybe EE) supposedly had a damaged direct route, whereas patient MF was said to have a deficit of the semantic route. However, since the input lexicon and semantic system were intact in MF—as she was still able to discriminate and comprehend meaningful actions—the authors proposed that the functional breakdown laid in the output lexicon or in accessing it. One can argue that the patient could have selected the spared direct route to reproduce meaningful actions, however, the sense of familiarity of the meaningful actions automatically triggered the semantic route.

As to the anatomical underpinnings of imitation deficits, of the two LBD patients described by Goldenberg and Hagmann (1997), LK had a lesion of the supracalcarine portions of Brodmann areas 17 and 18, and one affecting the posterior portion of the inferior temporal gyrus (BA 37) and the angular gyrus (BA 39), while EN had a smaller lesion restricted to the inferior part of the angular gyrus. The authors argued that, since apraxia was severe in EN, the inferior portion of the angular gyrus (BA 39) must be responsible for apraxia in both patients. As to the patients in Bartolo *et al.* (2001), they all had a left ischaemic stroke resulting in temporo-parietal, internal capsule and thalamus, and fronto-temporo-parietal lesions in BS, EE and MF, respectively.

In contrast to these single-case reports, no differences in imitation of meaningless and meaningful actions were found, for instance, in two large group studies (De Renzi *et al.*, 1980; Toraldo *et al.*, 2001). The single case and the group studies above differed in one aspect: the patients showing the selective deficit in imitation of either meaningless (Goldenberg and Hagmann, 1997; Bartolo *et al.*, 2001) or meaningful (Bartolo *et al.*, 2001) actions were tested with separate lists of the two types of action; in contrast, those patients who did not show any selective deficit (De Renzi *et al.*, 1980; Cubelli *et al.*, 2000; Toraldo *et al.*, 2001) were asked to imitate actions that were presented intermingled (i.e. the test devised by De Renzi *et al.*, 1980). Thus, as also argued by Cubelli *et al.* (2000) who failed to find dissociations in imitation of meaningful and meaningless actions, the way in which meaningful and meaningless stimuli are administered to patients may account for presence/absence of the dissociation in an action imitation task, similarly to that observed in studies on naming words and non-words (e.g. Monsell *et al.*, 1992; Tabossi and Laghi, 1992).

This issue was recently addressed by Tessari and Rumiati (2004), who have demonstrated that when healthy individuals with reduced cognitive resources due to time pressure are forced to imitate, they may adopt different strategies. When meaningful and meaningless actions were presented in separate blocks, subjects selected the route according to the nature of the most frequent stimulus: the semantic route for reproducing meaningful actions and the direct

route for the meaningless actions. When, however, the two kinds of gesture were presented intermingled, subjects selected the direct route to reproduce both types of actions, because it avoids the pay costs for switching between the two routes. Performing the task under time pressure reduced the cognitive resources available to the healthy participants and this scarcity might be comparable with that experienced by patients after brain-damage. Following up this analogy then, Tessari and Rumiati's (2004) findings with healthy controls would explain why brain-damaged patients, asked to imitate mixed meaningful and meaningless actions, did not show any dissociation (De Renzi *et al.*, 1980; Toraldo *et al.*, 2001): they selected the direct route to perform both meaningful and meaningless actions, being the most parsimonious strategy, that leads to comparable imitation of the two action types.

A number of imaging studies have investigated the neural mechanisms sustaining imitation (e.g. Grafton *et al.*, 1996; Rizzolatti *et al.*, 1996b; Iacoboni *et al.*, 1999; Decety *et al.*, 2002; Koski *et al.*, 2002; Buccino *et al.*, 2004), but only a few did test the hypothesis that differential activations would reflect the processing route selected to reproduce the action (Peigneux *et al.*, 2004; Rumiati *et al.*, 2005). Using positron emission tomography (PET), Peigneux *et al.* (2004) scanned subjects carrying out different tasks, including pantomime to command, imitation of novel and familiar gestures, and a functional-semantic association task. The results from this study largely support the multiple-route model put forth by Rothi *et al.* (1991), with the exception of the input and output action lexicons for the separation of which Peigneux *et al.* (2004) found no evidence, and thus proposed a unique system that codes for familiar gestures. Interestingly, Peigneux *et al.* (2004) found that when subjects imitated familiar (either symbolic or non symbolic) gestures, activations were observed in the left angular and middle frontal gyri, and the right supramarginal gyrus and inferior parietal lobule. In contrast, when subjects imitated novel gestures, activations in the inferior and superior parietal lobes were reported bilaterally. In another PET study, Rumiati *et al.* (2005) documented 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 imitation of meaningless actions. In contrast, imitation of novel, meaningless actions, relative to pantomimes, led to an increased neural activity in the parieto-occipital junction, and the occipitotemporal junction in the right hemisphere, in the superior temporal gyrus in the left hemisphere, and in the superior parietal cortex bilaterally. Taken together, these imaging findings support the view that these putative routes for imitation have regions in common as well as others specifically dedicated to imitation of either meaningful or meaningless actions.

In the present study, the validity of a multiple route model of action imitation, as well as their cerebral correlates, were tested by having a group of unselected

unilateral brain damaged patients ($n=32$) and a group of healthy, age-matched individuals ($n=20$) to imitate meaningful and meaningless actions from either separate or intermingled lists. At the group level, three predictions were made: (i) controls were expected to perform better than patients; (ii) right-brain damage (RBD) better than LBD patients; and (iii) patients, irrespective of the lesion side, were expected to perform better in the blocked than in the mixed condition. At the single-patient level, we predicted no dissociation in imitation of meaningful and meaningless actions in the mixed condition, but possible simple and double dissociations in the blocked condition. Observing a double dissociation between the imitation of meaningful and meaningless actions will support the argument that the two processing routes for imitation can indeed be functionally separable, as suggested by previous observations (Goldenberg and Hagmann, 1997; Bartolo *et al.*, 2001).

Material and methods

Participants

All participants gave informed consent according to the Declaration of Helsinki. The study was approved by the Ethics Committee of the Scuola Internazionale Superiore di Studi Avanzati.

Patients

A group of 32 patients (mean age = 67.19 years, SD = 10.31; mean education = 10 years, SD = 5.00) took part in the study. They were recruited in the rehabilitation and neurological unit of the Ospedali Riuniti in Trieste. To be included in the study, patients had to meet the following criteria: to have a single focal unilateral left- or right-hemispheric lesion, as determined by clinical information and CT or MRI scans; to be not older than 80 years; to have at least 5 years of education, and to be right-handed on the Edinburgh Inventory (Oldfield, 1971). Thirty patients suffered from a vascular lesion, two patients from a tumour. None of the patients included in the study had a history of alcohol or other substance abuse, and all were physically able to complete the experiment. The demographic variables are summarized in Table 1. All patients have on average been tested 8.03 weeks after the illness onset (SD = 5.87), except for case 13, tested 2 years after onset, and cases 14 and 27, tested 1 year after onset.

A neuropsychological evaluation was carried out on all patients in order to assess general intelligence, language functions, executive functions, memory and visuo spatial and attentional abilities (Table 2). Table 3 shows the patients' individual performance on all imitation conditions whereas Table 4 reports patients' performance on imitation of the pantomimes of object use (the meaningful actions), on their recognition, and on the use of the objects. In the action recognition task, patients were asked to name the pantomimes made by the experimenter. If patients had naming difficulties (due to aphasia), we asked them to point to the line drawing of an action that featured the one pantomimed by the examiner. The line drawing depicting the target action was presented together with two distractors, one featuring an action that required similar movements as the target, and one an action semantically related to the target. The three line drawings were presented simultaneously to the patients on white cards.

Table 1 Demographic variables

	N	Education		♂	♀	Age	
		Mean	SD			Mean	SD
LBD	22	9.82	5.13	12	10	69.69	9.91
RBD	10	9.50	3.37	5	5	62.60	10.30
Controls	20	10.84	3.30	12	8	65.00	13.98

The demographic variables of all participants (patients and healthy controls) who took part in the study.

Patients' performance was scored as correct or incorrect. In the object use task, patients were asked to actually use one object after the other, using the hand ipsilateral to the lesion. After each trial, the examiner removed the object and presented the next one. Patients' performance was video-recorded and later scored as correct or incorrect.

Controls

Twenty healthy adults (mean age = 65 years, SD = 13.98; mean education = 10.84 years, SD = 3.30) served as controls for the experimental tests.

Stimuli

They consisted of 20 pantomimes of object use (meaningful actions) and 20 novel actions (meaningless actions) selected from a larger pool of stimuli by three independent raters who visually assessed whether they were recognizable or not; they also controlled whether a meaningful action and its corresponding meaningless action were overall similar in complexity (for a full verbal description of the stimuli involved, see Tessari and Rumiati, 2004). Similar to the meaningful actions, the meaningless counterparts were composed of a distal (hand) and a proximal (arm). The actions were performed by one of us (A.T.) using the right hand and arm and patients were required to imitate them with the ipsilesional limb. Different from a study carried out with healthy subjects, in which the action stimuli were performed by the model using the left hand and shown on the TV screen (Tessari and Rumiati, 2004), here we opted for the right hand because the actions were presented directly to the patients by the examiner who was right handed.

Design and procedure

Both meaningful and meaningless actions were presented on two different days: on the first day the two types of actions were presented intermingled, and on the second day (1 or 2 days later), they were presented in separate blocks. We always administered the mixed condition first because patients who performed the blocked condition first, would have probably kept activated the two routes according to the stimulus type even in the mixed condition, when the direct route is likely to be selected because it allows to imitate both meaningful and meaningless actions.

The mixed presentation began with two consecutive meaningless actions in order to favour the selection of the direct route from the beginning; once having selected a strategy, patients are unlikely to switch to a different one because, due to the brain damage, they have reduced cognitive resources. This condition is comparable to the test used in the group studies where no

Table 2 Neuropsychological assessment

Cases	Language		Intelligence	Visual processing		Neglect	STM			LTM		Executive functions						
	Naming		Raven	VOSPI	VOSP	Barrage	Visual	Auditory–verbal	Spatial	Face recognition	Rey's word		Weigl	TMT ^b	FAS	WCST		
	AAT	TS screening	Token								IR	DR				Categories-perseverations		
1																		
2	83		32.5	24	20	17	Ok	5					21		10	240 "		
3	90		35.5	30	20	17	Ok	11.5					23		9	70 "		
4	90		32.5	28	20	19	Ok	10.5					21		8	490 " ^b		
5	90		33	28	20	19	Ok	10			5		24		10	150 "		
6	90		33.5	23	20	19	Ok	10					22		11	150 "		
7	87		21 ^a	t.i. ^a	19	17	X		5				24		8			
8	90		n.a.	35	20	19	Ok	12					20		15	153 "		
9		30	n.a.	35	20	17	Ok		5				24	31	10	15 98 "		
10		30	n.a.	17 ^a	20	11 ^a	X		5					19	2	9	28	
11	55		31.5	33	19	14	Ok	10					18		5 ^c	t.i. ^b		
12		22	25		20	16	Ok		4					15	1	6 ^c	t.i. ^b	
13	63		30	26	20	18	Ok		3									
14	23		33	30	20	19	Ok		4								6–0%	
15	84		30	20	19	13	Ok	4	2				22		4	t.i. ^b		
16	87		31	26	20	17	Ok	10					25		8	92 "		
17	88		28.5	27	19	17	Ok	7					23		7	t.i.		
18	88		30.5	27	17	15	Ok	8					22		11			
19	86		n.a.		19	15	Ok		4					15	1	5		
20	90		n.a.	33	20	18			5			4	20		9			
21		30	n.a.	35	20	16	Ok		5					20	4	9	259 " ^b 23	
22	57 ^d		n.a.		19	15	Ok		6					33	2	13	t.i. ^b	
23	25		25	23	20	16	Ok	11									5–25%	
24	90		34	32	20	16	Ok	13	6				24		15	110 "		
25		20	n.a.	19 ^a	20	17	X	12	4				25		5	t.i. ^a		
26	52		32	36	20	15	Ok		6						10	97 "		
27	15		25		20	16	Ok						21		6			
28		27	n.a.	20	20	15		9	5				4	24	22	4	10	360 " ^b 20
29	86		33	35	19	17	Ok		4					31	7	6	308 " 29	
30		6	n.a.	26	20	15	Ok								3	8	t.i. ^b	
31	76		n.a.	22	18	16	Ok							30	5	8	291 " ^b	
32	60		30	30	18	17							12		9			

Standardized neuropsychological tests were used to assess general intelligence (Raven Progressive Matrices PM47, Raven *et al.*, 1986), language functions (Comprehension: Token test, Spinnler and Tognoni, 1987; Production: AAT, naming test, Luzzatti *et al.*, 1996; naming from the Short Neuropsychological Screening, Lunardelli, Tessari, Sverzut, Zadini, Rumiati, in preparation), executive functions (Weigl's tests, Spinnler and Tognoni, 1987; Wisconsin Card Sorting Test, WCST, Berg, 1948; Trail Making Test (TMT), form B, Reitan, 1958; FAS, Novelli *et al.*, 1986), memory (short-term memory (STM): visual span, WAIS, Italian version, Cimino, 1981; auditory–verbal span, Spinnler and Tognoni, 1987; visuo–spatial span, Corsi test, De Renzi and Nichelli, 1975; Spinnler and Tognoni, 1987; long-term memory, LTM: face recognition, Warrington, 1984; Rey's 15 Words Test, Rey, 1958) and visuo–spatial and attentional abilities (VOSP, tests 1 and 2, James and Warrington, 1991; barrage test, Albert, 1973). t.i.: test interrupted because the patient was not able to perform the task. n.a.: test not administered. ^aDeficit due to neglect. ^bThe patient's ability to switch was normal, but he had spatial attention problems. ^cThe patient's performance was influenced by many errors due to perseverations. ^dPatient with acromatopsia who performed normally on sections 1 and 3 but not on the colour-naming task. Pathological scores are reported in bold.

Table 3 Individual performance on imitation tasks

Cases	Apraxia (De Renzi)	Mixed					Blocked				
		MF	z	ML	z	P	MF	z	ML	z	P
LBD											
11	67	11	-2.19	14	-2.19	ns	15	-5.24	14	-3.88	ns
12	49	11	-3.19	10	-3.69	ns	11	-7.24	12	-3.88	ns
13	46	5	-6.19	6	-5.69	ns	10	-8.24	5	-8.61	<0.05
14	43	4	-6.69	5	-6.19	ns	9	-9.24	4	-9.28	<0.05
15	65	17	-0.19	15	-1.19	ns	14	-4.24	14	-2.53	ns
16	58	8	-4.69	8	-4.69	ns	10	-8.24	13	-3.2	ns
17	64	13	-2.19	14	-1.69	ns	16	-2.24	12	-3.88	ns
18	63	16	-0.69	16	-0.69	ns	18	-0.24	18	0.18	ns
19	59	10	-3.69	9	-4.19	ns	17	-1.24	10	-5.23	<0.05
20	45	5	-6.19	8	-4.69	ns	7	-11.24	5	-8.61	ns
21	62	11	-3.19	12	-2.69	ns	15	-3.24	17	-0.5	ns
22	64	18	0.32	18	0.32	ns	17	-1.24	20	1.53	ns
23	35	4	-6.69	7	-5.19	ns	8	-10.24	3	-9.96	<0.05
24	68	14	-1.69	15	-1.19	ns	20	1.76	18	0.18	ns
25	70	13	-2.19	14	-1.69	ns	18	-0.24	19	0.85	ns
26	65	7	-5.19	11	-3.19	ns	14	-4.24	18	0.18	ns
27	30	1	-8.19	4	-6.69	ns	2	-16.24	2	-10.64	ns
28	69	17	-0.19	16	-0.69	ns	17	-1.24	18	0.18	ns
29	63	13	-2.19	12	-2.69	ns	12	-6.24	13	-3.2	ns
30	38	5	-6.19	8	-4.69	ns	2	-16.24	7	-7.26	<0.05
31	62	9	-4.19	13	-2.19	ns	10	-8.24	17	-1.18	<0.05
32	33	1	-8.19	3	-7.19	ns	3	-15.24	1	-11.31	ns
RBD											
1	68	17	-0.68	17	-0.19	ns	16	-2.24	16	-1.18	ns
2	63	14	-1.69	13	-2.19	ns	18	-0.24	13	-3.2	<0.05
3	67	13	-3.19	13	-3.19	ns	13	-7.24	12	-2.53	ns
4	57	11	-0.19	11	-0.19	ns	11	-2.24	14	-1.18	ns
5	62	17	-3.19	17	-1.69	ns	16	-3.24	16	-2.53	ns
6	69	16	-0.69	16	-0.69	ns	18	-0.24	13	-3.2	<0.05
7*	48	9	-4.19	9	-4.19	ns	16	-2.24	12	-3.88	ns
8	64	11	-3.19	11	-3.19	ns	17	-1.24	17	-0.5	ns
9	69	17	-0.19	15	-1.19	ns	17	-1.24	18	0.18	ns
10*	64	15	-1.19	15	-1.19	ns	15	-3.24	13	-3.2	ns

Single patients' scores on the imitation tasks are reported. The *P* value refers to a Fisher exact probability test in which imitation performance on meaningful (MF) and meaningless (ML) actions either in the mixed or blocked condition was compared. Significant comparisons are reported in bold. Strong dissociations (see Shallice, 1988) are reported in bold and classical dissociation in bold italic. The asterisk indicates patients with neglect. Object use is expressed in percentage of correct responses. The z-scores were calculated with respect to controls. Case numbers in bold represents patients resulting apraxic to the imitation test here used.

differences in imitation of the two action types were found (De Renzi *et al.*, 1980; Toraldo *et al.*, 2001).

On the second day, participants were presented first with a block of meaningful actions, and then with a block of meaningless actions. In either mixed or blocked condition, participants were asked to imitate each action immediately after the experimenter performed it. Participants' performance was video-recorded and later scored independently by two raters blind to the experimental conditions. The raters provided an accuracy score and an error classification. As to the accuracy score, a correct action was scored 1, whereas an action containing any of the mistakes indicated below was scored 0. The maximum score that a patient could obtain for both conditions was 80 (20 meaningless and 20 meaningful actions in the mixed condition plus 20 meaningless and 20 meaningful actions in the blocked condition). The error classification aimed at providing a qualitative analysis of the

imitative responses and was based on criteria used in previous studies (e.g. Tessari and Rumiati, 2004):

- (i) Spatial error of the hand: the overall movement of the limb is correct, but the hand posture is wrong;
- (ii) Spatial error of the arm: the movement is recognizable but is performed with the arm forming in the wrong angle with the body;
- (iii) Orientation error: the movement is recognizable but is performed with the arm moving in the wrong direction;
- (iv) Semantic errors are further divided into three subcategories:
 - (a) Prototypicalization: participants reproduce the prototypical version of the meaningful action instead of the one presented.

Table 4 Tasks based on sensorimotor representations

Case	Damaged hemisphere	MF action imitation (blocked)	Action recognition	Object use
11	LBD	75	95	100
12	LBD	55	100	100
13	LBD	50	95	100
14	LBD	45	95	100
15	LBD	70	100	57
16	LBD	50	85	100
17	LBD	80	100	75
18	LBD	90	100	100
19	LBD	85	95	100
20	LBD	35	70	100
21	LBD	75	100	100
22	LBD	85	100	100
23	LBD	40	20	100
24	LBD	100	100	79
25	LBD	90	95	100
26	LBD	70	100	100
27	LBD	10	100	70
28	LBD	85	100	70
29	LBD	60	100	100
30	LBD	10	90	100
31	LBD	50	100	95
32	LBD	15	100	100
1	RBD	80	100	100
2	RBD	90	100	100
3	RBD	65	100	100
4	RBD	55	100	100
5	RBD	80	100	100
6	RBD	90	100	100
7	RBD	80	95	100
8	RBD	85	100	100
9	RBD	85	100	100
10	RBD	75	95	100

Patients' performance on imitation of meaningful actions, on their recognition, and on object use expressed in percentage.

- (b) Body Part as a Tool (BPAT): participants perform a movement using the arm–hand–finger as if it were the tool. It has been proposed that BPAT responses correspond to a failure to inhibit the activation of gesture representation that is fairly automatic due to its strong symbolic content (Raymer *et al.*, 1997); an alternative explanation is that these errors may be caused by a failure to update the body representation to include the tool (Daprati and Sirigu, 2006).
- (c) Visual-semantic: an action visually similar and semantically related to the target action is produced.
- (v) Visual: an action visually similar to the target-action is produced. Visual errors are divided further into three subcategories:
 - (a) Perseveration: it involves the repetition of an action, or part of an action, that has previously been presented (note that it was not possible to distinguish between motor and visual perseveration).
 - (b) Lexicalization: a meaningful action, visually similar to the meaningless target action but not included in the list, is produced;

(c) Substitution: a visually similar meaningful action, not included in the list, is produced instead of the meaningful action that was presented.

- (vi) Omission: the imitation of the target action is omitted.
- (vii) Unrecognizable gesture: the response involves a movement that the raters failed to recognize.

Lesion analyses

An experienced neuroradiologist, who was not informed about the hypotheses of the study, identified the areas which resulted lesioned on the CT-scans of all patients but one (case 14, for whom we had a MR-scan), onto the normalized MNI template (www.bic.mni.mcgill.ca/cgi/icbm_view) using MRICro (<http://www.mricro.com>; Rorden and Brett, 2000). Subsequently, the location of the lesions has been identified both using the Automated Anatomical Labelling map (Tzourio-Mazoyer *et al.*, 2002) provided by the software and with reference to the atlas of Duvernoy (1991). Table 5 reports the anatomical structures and the Brodmann areas damaged in each of the patients showing the dissociation in imitation of meaningful and meaningless actions in the blocked condition.

A three-step analysis was carried out on the lesion data. In the first step, we considered all the LBD patients who showed a dissociation between imitation of meaningful and meaningless actions, independently of the type of action selectively affected. Using MRICro, we overlaid the lesions from each patient, to identify the cerebral regions damaged in all of them (Fig. 4A).

Secondly, patients who had a selective impairment of either meaningful (following LBD) or meaningless (following either LBD or RBD) were examined separately. For each of the three groups, overlay lesion plots revealed which cerebral regions were damaged in all the patients within a group (Fig. 4B–D).

Finally, we identified regions relevant for a selective disturbance in imitation of either meaningful or meaningless movements. This was done by means of a lesion-subtraction analysis, using MRICro as described in Rorden and Karnath (2004; see also Karnath *et al.*, 2004 and Goldenberg and Karnath, 2006) (Fig. 5). This method permits to overcome the difficulties intrinsic in simply overlaying lesions of patients who show a given disorder: the site of the lesions, indeed, may reflect vulnerability of certain regions to injury (e.g. due to their vasculature or susceptibility to sheer and impact) rather than their direct contribution to the development of that disorder. Therefore, simply overlapping lesions of patients who show a specific deficit often highlights regions involved in the function as well as regions that are simply more susceptible to damage. One possible solution consists in directly comparing lesions of patients showing the impairment of interest with those of patients showing lesions in the same hemisphere and with comparable relevant neurological and neuropsychological variables but without such an impairment. The basic assumption underlying this approach is that the relative incidence of damage to regions unrelated to the disorder of interest should be equally represented in both patient groups and will not be highlighted in subtraction plots. Therefore, the resulting subtraction image should show regions that are both most frequently damaged in one group of patients, as well as being typically spared in the other one. As subtractions were made between groups of different sizes, we used relative percentages rather than absolute values. Automatic three-dimensional rendering of the lesion data were performed using MRICro.

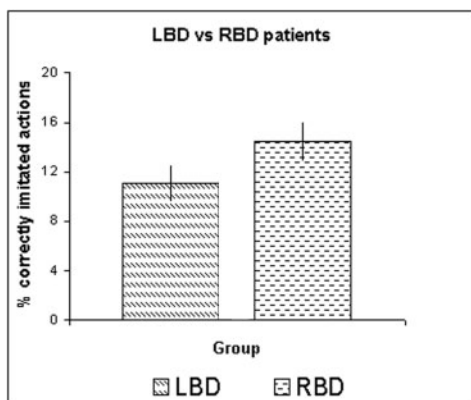


Fig. 2 Means of correctly imitated actions by unilateral left (on the left side) and right (on the right side) brain-damaged patients. Error bars represent the standard error.

Behavioural results

Correct responses on the imitation tasks were examined first at the group level, and subsequently at the single-case level. As there was no significant difference between the accuracy scores of the two raters (all $P > 0.05$), in the Results section we report the analyses carried out on the mean scores.

Group analyses: imitation

Overall controls performed better than patients (independent samples t -test, $t(49) = -22.18$, $P < 0.001$; controls' mean = 71.05, SD = 4.59, and patients' mean = 48.87, SD = 17.96) on the critical imitation task.

Patients' correct responses were inserted in an ANOVA with one between-subjects factor—Hemisphere (LBD versus RBD)—and two within-subject factors—Presentation (mixed actions versus blocked actions) and Stimulus Type (meaningful actions versus meaningless actions). Overall, RBD patients (mean = 14.45, SD = 5.09) performed better than the LBD patients (mean = 11.08, SD = 7.05), $F(1, 30) = 4.24$, $P < 0.05$. Results are plotted in Fig. 2. The Presentation factor [$F(1, 30) = 9.81$, $P < 0.005$, Fig. 3], but not the Stimulus Type factor ($P > 0.05$), was found significant: the imitation performance was overall better in the blocked (mean = 13.48, SD = 4.98) than in the mixed condition (mean = 12.05, SD = 4.46). The Presentation \times Stimulus Type interaction only showed a trend to significance [$F(1, 30) = 3.51$, $P = 0.07$].

Further overall analyses

Overall, the mixed presentation in our test turned out to be more sensitive in identifying the apraxic deficit than the clinical test devised by De Renzi *et al.* (1980) (Wilcoxon, $z = -3.61$, $P < 0.001$). The finding that our test is more difficult can be explained with the fact that in our study we presented the stimuli only once, compared with the three presentations allowed by De Renzi *et al.* (1980).

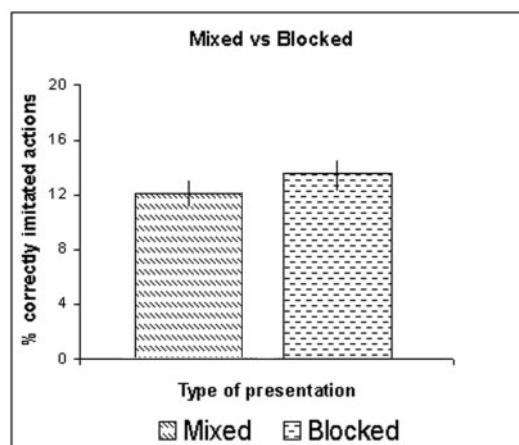


Fig. 3 Means of correctly imitated actions in both mixed (on the left side) and blocked (on the right side) presentation. Error bars represent the standard error.

Pearson correlations were performed on patients' performance on the imitation, object use and action recognition tasks (patients' performance is reported in percentage in Table 4). Results showed that there was a weak correlation between action recognition and action imitation ($r = 0.32$, $P = 0.07$, two-tailed), whereas none of the other correlations were found significant (action recognition and object use: $r = -0.13$, $P = 0.46$, two-tailed; action imitation and object use: $r = -0.05$, $P = 0.80$, two-tailed).

Single case analysis

Possible dissociations may have gone unobserved in the group analysis because of the well-known averaging artefact (Shallice, 1988). The result from a test of the homogeneity of variance performed for the Presentation and Stimulus Type factors seems to support this view. In fact, a greater variability was found across subjects for the imitation of meaningful actions in the blocked condition (skewness = -1.028). We therefore compared the imitation performance on meaningful and meaningless actions within the mixed and the blocked conditions for each patient. The results of all comparisons are reported in Table 3. Eight patients showed a significant difference between the imitation of meaningful and meaningless actions in the blocked presentation (all $P < 0.05$), but none showed any difference in the mixed condition. Of the eight patients, six imitated meaningful better than meaningless actions and two showed the reverse pattern (Table 3).

Cases 2, 6 and 19 showed a classical dissociation in imitation of meaningful and meaningless actions: when compared with control subjects, they performed poorly on meaningless (all $z < -1.65$) but not on meaningful actions (Shallice, 1988; Deloche and Willmes, 2000). Cases 13, 14 and 23 showed a strong dissociation (Shallice, 1988) between their ability to imitate meaningful and meaningless

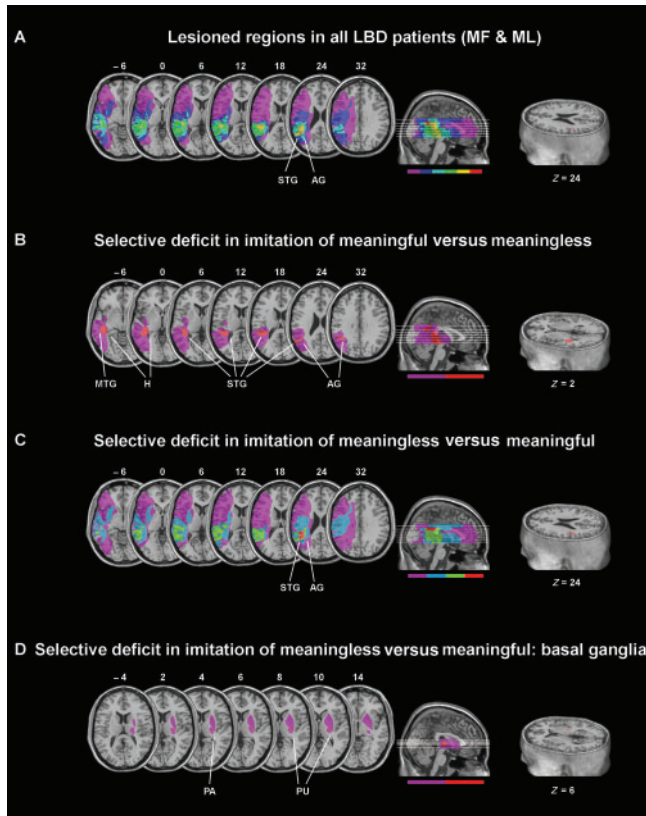


Fig. 4 (A) The overlay of the lesions of all the LBD patients who showed a dissociation in imitation, irrespective of the type of action which was more impaired, is depicted. (B) Two LBD patients who imitated meaningless (ML) better than meaningful (MF) actions (cases 30 and 31). (C) Four LBD patients who imitated meaningful better than meaningless actions (cases 13, 14, 19, 23). (D) Two RBD patients who imitated meaningful better than meaningless actions (cases 2 and 6). In each figure, the number of overlapping lesions is illustrated by different colours coding increasing frequencies from a violet ($n = 1$) to red (indicating the maximum number of subjects in each group) colour. Coordinates of the transverse sections are given. The height of the individual slices is also shown, on the medial view of the MNI template. In the rightmost part of each image the regions lesioned in all subjects of each group are superimposed onto a 3D rendering of the MNI template, which has been sectioned to show deep lesions. H = hippocampus, MTG = middle temporal gyrus, AG = angular gyrus, PA = Pallidum, PU = putamen.

actions, as their overall performance was lower than that of the control subjects for both action types (all $z < -1.65$). Cases 30 and 31 showed the reverse dissociation (i.e. they reproduced meaningless better than meaningful actions) but whereas case 30 showed a strong dissociation, in that she imitated both meaningful and meaningless actions worse than control subjects (both $z < -1.65$), case 31 showed a classical dissociation, as only meaningful actions were imitated less accurately than controls ($z < -1.65$).

From a theoretical perspective, classical dissociations suggest that there may be two mechanisms (the direct and the semantic routes) supporting the imitation of

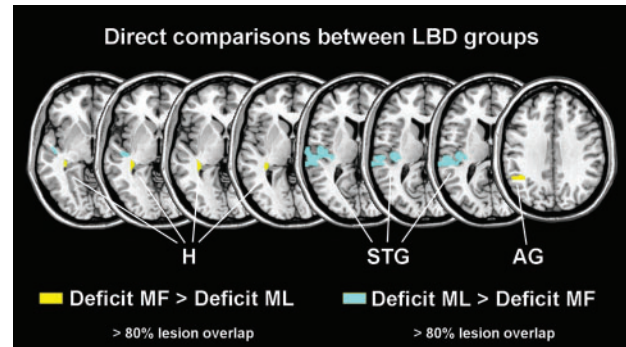


Fig. 5 Plot of the subtracted superimposed lesions of the group of patients with a selective deficit for imitation of meaningful versus meaningless and vice versa. The regions damaged more frequently in the group of patients with a selective deficit for imitation of meaningful actions after subtraction of the group with a selective deficit for imitation of meaningless actions are shown in yellow colour. The regions damaged more frequently in the group of patients with a selective deficit for imitation of meaningless actions after subtraction of the group with a selective deficit for imitation of meaningful actions are shown in light blue colour. Only those regions in which the difference of percentage of overlapping lesions for a specific group of subjects (after subtraction from the other group) are above 80% (difference 81–100%) are shown. Coordinates of the transverse sections are given. H = hippocampus, STG = superior temporal gyrus, AG = angular gyrus.

meaningless and meaningful actions, respectively. To strengthen this statement, however, one would need to demonstrate that the two mechanisms double dissociate in at least two different patients. Indeed, a classical double dissociation emerged when comparing cases 19 and 31: case 19 imitated meaningful actions better than case 31, and case 31 imitated meaningless actions better than case 19 (Table 6 reports all the comparisons between patients). Instead, those patients who showed strong dissociations (cases 13, 14, 23 and 30) may suffer from multiple damage to both imitation mechanisms (direct and semantic).

Error analysis

Table 7 summarizes the different types of errors made in either condition by the eight patients who show a selective deficit in imitation of either meaningful or meaningless actions. All patients made more errors in the mixed condition, irrespective of the action type, and in the blocked condition of meaningless actions with the exception of cases 30 and 31. These two patients, who supposedly have a damaged semantic route, made more errors in the block of meaningful actions than in any other condition in which the direct route was more likely to be used, as well as more semantic errors when imitating meaningful actions in the blocked than in the mixed presentation. This is in accordance with the accuracy results in the blocked presentation in which imitation was better, suggesting that, in both cases, the semantic route was selected. In contrast, the remaining cases, who had a damaged putative direct route, made overall more errors in the mixed conditions, and in the block of meaningless actions.

Table 5 Lesional correlates of stimulus-specific apraxia

	Cerebral regions affected by the lesion	Brodmann areas involved in the lesion
Case 2	<i>Right:</i> basal ganglia (putamen, pallidum)	
Case 6	<i>Right:</i> basal ganglia (caudal putamen, pallidum, caudate)	
Case 13	<i>Left:</i> insula; supramarginal gyrus; angular gyrus; superior, middle, and inferior temporal gyri.	22; 37; 39; 40; 41; 42
Case 14	<i>Left:</i> precentral gyrus; superior, middle and inferior frontal gyri; insula; cingulum; cuneus; postcentral gyrus; superior and inferior parietal lobules; supramarginal gyrus; angular gyrus; precuneus; basal ganglia; superior, middle and inferior temporal gyri	1; 2; 3; 4; 6; 7; 8; 9; 11; 18; 19; 20; 21; 22; 23; 24; 32; 37; 38; 39; 40; 41; 42; 43; 44; 45; 46; 47
Case 19	<i>Left:</i> precentral gyrus; superior and middle frontal gyri; supplementary motor area; cingulum; postcentral gyrus; superior and inferior parietal lobules; supramarginal gyrus; superior temporal gyrus	19; 20; 21; 22; 30; 36; 37; 38; 40; 41; 42
Case 23	<i>Left:</i> parahippocampal gyrus; fusiform gyrus; basal ganglia; superior, middle and inferior temporal gyri; angular gyrus; cerebellum.	2; 3; 4; 5; 6; 7; 8; 9; 18; 23; 32; 39; 40; 41; 43; 44
Case 30	<i>Left:</i> superior and inferior parietal lobules; angular gyrus; superior, middle and inferior temporal gyri; middle and inferior occipital gyri; hippocampus	19; 20; 21; 22; 37; 39; 40; 41; 42
Case 31	<i>Left:</i> insula; supramarginal gyrus; superior and middle temporal gyri; angular gyrus; parahippocampal gyrus; hippocampus	21; 22; 37; 39; 40; 41; 42

Cerebral regions that are damaged in each of the eight patients showing a significant dissociation between imitation performance on meaningful and meaningless actions.

Table 6 Comparisons among patients showing dissociations

		MF		ML	
		<i>P</i>		<i>P</i>	
Case 30 versus	Case 2	<0.001	Case 30 < Case 2	<0.05	Case 30 < Case 2
	Case 6	<0.001	Case 30 < Case 6	=0.05	Case 30 < Case 6
	Case 13	<0.05	Case 30 < Case 13	ns	Case 30 = Case 13
	Case 14	<0.05	Case 30 < Case 14	ns	Case 30 = Case 14
	Case 19	<0.001	Case 30 < Case 19	ns	Case 30 = Case 19
	Case 23	ns	Case 30 = Case 23	ns	Case 30 = Case 23
Case 31 versus	Case 2	<0.05	Case 31 < Case 2	ns	Case 31 = Case 2
	Case 6	<0.05	Case 31 < Case 6	ns	Case 31 = Case 6
	Case 13	ns	Case 31 = Case 13	=0.05	Case 31 > Case 13
	Case 14	ns	Case 31 = Case 14	<0.005	Case 31 > Case 14
	Case 19	<0.05	Case 31 < Case 19	<0.05	Case 31 > Case 19
	Case 23	ns	Case 31 = Case 23	<0.01	Case 31 > Case 23

The performance of cases 30 and 31 compared with that of cases 2, 6, 13, 14, 19 and 23 on the Wilcoxon statistics.

Lesion results

We first identified the cerebral structures which were lesioned in both LDB patients groups independently of whether they had a deficit in imitation of meaningful or of meaningless actions as compared with healthy controls. These were centred in proximity of the temporoparietal junction, at the border between the medial and posterior portion of the superior temporal gyrus and the ventral-most portion of the angular gyrus (Fig. 4A).

Subsequently, we examined the structures whose damage was associated with a selective impairment in the imitation of either meaningful or meaningless actions. Using the

ROI-intersection facility provided with MRICro, we highlighted those regions that were damaged in all patients within a group. Figure 4B–D shows conventional lesion density plots for each of the three groups of patients. The number of overlapping lesions are colour-coded with increasing frequencies from violet ($n=1$) to red (maximum number of subjects in a given group). The two LDB patients with a selective deficit for imitation of meaningful, compared with meaningless, actions, had lesions which maximally overlapped in the medial portion of the middle temporal lobe, the lateral and dorsal-most portion of the hippocampus and the dorsal portion of the angular gyrus

Table 7 Error analysis

	Case 2		Case 6		Case 13		Case 14		Case 19		Case 23		Case 30		Case 31																			
	Mixed		Blocked		Mixed		Blocked		Mixed		Blocked		Mixed		Blocked																			
	MF	ML	MF	ML	MF	ML	MF	ML	MF	ML	MF	ML	MF	ML	MF	ML																		
Spatial-hand	15.0	15.0	5.9	11.8	5.9	11.8	7.4	22.2	10.7	8.9	5.4	11.8	23.5	2.94	23.53	3.77	3.77	5.66	13.21	12.28	12.28	12.28	17.54	21.88	18.75	6.25	12.50							
Spatial-arm	5.0	5.0	5.9	5.9	11.8	3.7	5.6	7.7	3.6	10.4	2.9	2.9	2.94	2.94	2.94	2.94	2.94	3.6	3.6	7.02	7.02	1.75	3.51	8.38	6.25	6.25	6.25							
Arm-orientation	5.0	5.0	5.9	5.9	5.6	3.7	3.7	1.2	5.4	2.1	3.6	8.8	5.9	5.9	5.9	5.9	3.8	5.7	5.7	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00							
Semantic	5.0	5.0	5.9	5.9	1.9	3.7	3.7	3.6	3.6	1.8	1.8	2.9	2.94	2.94	2.94	2.94	3.77	3.77	5.26	3.51	3.51	5.26	3.1	3.1	9.4	9.4	9.4							
Semantic	5.0	5.0	5.9	5.9	3.7	3.7	3.7	1.8	1.8	1.8	1.8	5.9	2.94	2.94	2.94	2.94	3.77	5.66	7.02	3.51	3.51	7.02	3.1	3.1	9.38	9.38	9.38							
BPAT	5.0	5.0	5.9	5.9	3.7	3.7	3.7	1.8	1.8	1.8	1.8	5.9	2.94	2.94	2.94	2.94	3.77	5.66	7.02	3.51	3.51	7.02	3.1	3.1	9.38	9.38	9.38							
Visuosemantic	5.0	5.0	5.9	5.9	3.7	3.7	3.7	1.8	1.8	1.8	1.8	5.9	2.94	2.94	2.94	2.94	3.77	5.66	7.02	3.51	3.51	7.02	3.1	3.1	9.38	9.38	9.38							
Visual	5.0	5.0	5.9	5.9	3.7	3.7	3.7	1.8	1.8	1.8	1.8	5.9	2.94	2.94	2.94	2.94	3.77	5.66	7.02	3.51	3.51	7.02	3.1	3.1	9.38	9.38	9.38							
Omission	5.0	5.0	5.9	5.9	3.7	3.7	3.7	1.8	1.8	1.8	1.8	5.9	2.94	2.94	2.94	2.94	3.77	5.66	7.02	3.51	3.51	7.02	3.1	3.1	9.38	9.38	9.38							
Unclassifiable	5.0	5.0	5.9	5.9	3.7	3.7	3.7	1.8	1.8	1.8	1.8	5.9	2.94	2.94	2.94	2.94	3.77	5.66	7.02	3.51	3.51	7.02	3.1	3.1	9.38	9.38	9.38							
Visual	5.0	5.0	5.9	5.9	3.7	3.7	3.7	1.8	1.8	1.8	1.8	5.9	2.94	2.94	2.94	2.94	3.77	5.66	7.02	3.51	3.51	7.02	3.1	3.1	9.38	9.38	9.38							
Perseverations	5.0	5.0	5.9	5.9	3.7	3.7	3.7	1.8	1.8	1.8	1.8	5.9	2.94	2.94	2.94	2.94	3.77	5.66	7.02	3.51	3.51	7.02	3.1	3.1	9.38	9.38	9.38							
Lexicalization	5.0	5.0	5.9	5.9	3.7	3.7	3.7	1.8	1.8	1.8	1.8	5.9	2.94	2.94	2.94	2.94	3.77	5.66	7.02	3.51	3.51	7.02	3.1	3.1	9.38	9.38	9.38							
Substitutions	5.0	5.0	5.9	5.9	3.7	3.7	3.7	1.8	1.8	1.8	1.8	5.9	2.94	2.94	2.94	2.94	3.77	5.66	7.02	3.51	3.51	7.02	3.1	3.1	9.38	9.38	9.38							
Total amount	30.00	30.00	10.00	10.00	30.00	30.00	23.53	23.53	11.76	41.18	27.78	24.07	18.52	29.63	28.57	21.43	19.64	30.36	29.41	32.35	8.82	29.41	26.42	20.75	22.64	30.19	26.32	19.30	31.58	22.81	34.38	21.88	31.25	12.50
of errors																																		

Error types out of the total number of errors for all the conditions (i.e. mixed and blocked presentation together) are reported in percentages showing a dissociation in imitation of meaningful (MF) and meaningless (ML) actions. Empty cells mean that patients did not make any error.

(Fig. 4B; cases 30 and 31). In the four LBD patients with a selective deficit for imitation of meaningless, compared to meaningful, actions, the maximum overlap of lesions was centred in a region located at the border between the superior temporal gyrus and the ventral portion of the angular gyrus (Fig. 4C; cases 13, 14, 19 and 23). Finally, in those two patients in whom a specific deficit for imitation of meaningless actions was associated with a subcortical right hemispheric damage, lesions maximally overlapped in a region comprising the caudal portions of the pallidum (pars lateralis), the putamen and the posterior limb of the internal capsule (Fig. 4D, cases 2 and 6).

Finally, lesion subtraction analysis (see Rorden and Karnath, 2004 and the Material and methods section) was used to identify the cerebral structures that were more frequently damaged in patients with a selective deficit for imitation of meaningful or meaningless gestures. In the resulting subtraction image (Fig. 5), yellow colour indicates regions that were commonly damaged in patients with reduced imitation of meaningful, but spared in patients with reduced imitation of meaningless, pantomimes. Light blue colour, instead, indicates regions that were damaged in the patients with reduced imitation of meaningless, but spared in patients with reduced imitation of meaningful, pantomimes. The results of this analysis fit the general pattern highlighted by the lesion density plots for each single group. Indeed, an impairment at imitating meaningful pantomimes was more often associated with lesions centred in the lateral and dorsal portion of the hippocampus, extending to the bordering white matter, and the dorsal angular gyrus. The opposite deficit, instead, was specifically associated with lesions involving the superior temporal gyrus.

General discussion

Comments on group- and single-case results

The aims of the present study were to test the validity of a dual-route model of action imitation by studying apraxic patients, and to investigate its cerebral correlates by analysing their brain lesions. At a group level, patients performed the imitation task worse than controls and, irrespective of the lesion side, they showed a better performance in the blocked than in the mixed condition, even though the latter was administered first. However, altogether LBD patients' accuracy was worse than that of RBD patients. The differences observed in action imitation between LBD and RBD patients are consistent with those of many studies supporting the specialization of the left hemisphere in higher motor control (e.g. Liepmann, 1920; Basso *et al.*, 1980; De Renzi *et al.*, 1980; Rapcsak *et al.*, 1993). The right hemisphere too seems to play a role, in particular, in the imitation of finger configurations, while the left hemisphere sustains the imitation of hand–arm as well as finger movements (Goldenberg, 1996, 1999). More recently, Goldenberg and Karnath (2006) reported that imitation of finger postures entails anterior regions in the

left hemisphere, including the opercular portion of the inferior frontal gyrus, whereas imitation of hand postures is carried out by the left inferior parietal lobule and the left temporo-parieto-occipital junction.

The lack of significant correlations between action recognition, object use and action imitation of all patients suggest that these three abilities do not entirely share the same representations or computations. Our results are at variance, for instance, with those of Buxbaum *et al.* (2005), who found a strong correlation between imitation and action recognition in a group level analysis. They are, however, in keeping with studies that describe deficits affecting only one of these abilities at a time (De Renzi and Lucchelli, 1988; Rumiati *et al.*, 2001; Rosci *et al.*, 2003).

Relevant for the evaluation of the multiple-route model of imitation are the results derived from the single case analysis, in particular the simple dissociations (meaningful better than meaningless actions: cases 2, 6, 13, 14, 19 and 23; meaningless better than meaningful actions: cases 30 and 31) and a classical double dissociation (cases 19 and 31) between deficits and normal performance in the imitation of meaningless and meaningful actions observed in the blocked condition.

The effect of the type of list and the strategic selection of routes

The double dissociation (and to some extent the simple dissociations) reported here provide additional evidence that there might be two possible mechanisms, or routes, sustaining action imitation: a lexical–semantic route for recognizing and reproducing known, meaningful actions and a sublexical or direct route for translating the visual input (the seen action) into a motor output (the imitated action). Either route can be selectively damaged by a brain lesion, giving rise to different deficit patterns.

Our results obtained in the blocked conditions are consistent with previous reports of patients who imitated meaningful better than meaningless actions in comparable experimental conditions (Goldenberg and Hagmann, 1997; Bartolo *et al.*, 2001) and one who showed the opposite dissociation (Bartolo *et al.*, 2001). Instead, our results in the mixed condition are in keeping with those from group studies in which no dissociation was found in imitation when meaningful and meaningless actions were presented intermingled (De Renzi *et al.*, 1980; Cubelli *et al.*, 2000; Toraldo *et al.*, 2001).

Our study provides direct evidence that the condition in which the imitation is prompted (either using a blocked or a mixed condition) triggers the selection of the route for accomplishing the task (for a similar view, see also Cubelli *et al.*, 2006). Namely, when meaningful and meaningless actions were presented in separate lists, patients were inclined to use the lexical–semantic or the direct route, respectively. In contrast, if they were requested to imitate meaningful and meaningless actions in the mixed list, they

selected the route that allowed them to perform more actions without wasting resources in switching routes. This is only apparently an instance of a reduced cognitive flexibility of the type often observed in patients with dysexecutive syndrome and lesions of the prefrontal cortex. Only a few of the apraxic patients in our study had lesions in these regions and only a couple of them showed a perseverative behaviour on a clinical test (Weigl test). We would like to propose that the cognitive inertia in changing the route once triggered by the context seems an inevitable adaptation to the strategy that is most suitable for the task at hand (e.g. the direct route in the mixed condition). It is worth noting that the manner in which meaningful and meaningless gestures are presented affected also the performance of healthy subjects performing an imitation task under particular circumstances (Tessari and Rumiati, 2004). Similar to brain damaged patients, healthy individuals who performed a task with severe time constraints have a cognitive system characterized by reduced processing capacities. Thus, in the mixed condition healthy individuals too strategically selected the direct mechanism to save resources by avoiding switching costs (Tessari and Rumiati, 2004).

That reduced cognitive resources can affect action imitation has also been suggested by Bekkering *et al.* (2005) to account for the defective imitation performance of meaningless actions of LBD and RBD patients, as well as healthy controls. These authors found that the LBD apraxic patients often omitted the subgoals at the bottom of the hierarchy such as, for instance, the particular effector used to perform the task (middle finger versus index finger) and reproduce preferably those at higher positions (i.e. the objects or the locations). They interpreted the decline of the patients' imitative performance as due to a shortage of resources which favour the goals that are more important at the expense of those which are less so.

The direct and the semantic routes

The functional breakdown in patients who imitated meaningless actions worse than meaningful actions is to be located along the direct route (cases 2, 6, 13, 14, 19 and 23). Of them, those patients who performed meaningful actions worse than controls (strong dissociations) may also have a deficit of the semantic route (cases 13, 14 and 23). In contrast, the selective deficit of cases 30 and 31 in imitating meaningful actions can only be accounted for by a breakdown at some processing step along the semantic route. As these two patients were able to recognize the gestures they had trouble to reproduce, it is likely that the damage in these patients occurs after having accessed the semantic system. In addition, since case 31 imitated meaningless actions normally ($z = -1.18$), based on the model sketched in Fig. 1 we argue that the breakdown in this patient may lie after the semantic memory, in accessing the ST-WM system. Similar to

what has been proposed for patient MF discussed by Bartolo *et al.* (2001), case 31 could have reproduced meaningful actions using the direct, sublexical route; however, as meaningful actions seem familiar to her, the processing along the semantic route is triggered even though does not work efficiently. Moreover, once the patient has selected the semantic route, given the limited processing resources due to the lesion, she does not switch to the direct route even though it is intact. As for case 30, although her performance was better with meaningless than with meaningful actions, her imitation performance on meaningless action was not normal ($z = -7.26$). Thus, we may have to hypothesize that case 30 had a damage of the semantic route and one of the direct route (to date her performance was poor also in the mixed condition, in which the direct route is more likely to be selected) (see also Halsband *et al.*, 2001).

Neural bases of the multiple route model of imitation

By and large, neuropsychological and neuroimaging studies (Iacoboni *et al.*, 1999, 2001; Decety *et al.*, 2002; Koski *et al.*, 2002; Tanaka and Inui, 2002; Grèzes *et al.*, 2003; Buccino *et al.*, 2004; Muhlau *et al.*, 2005; Rumiati *et al.*, 2005) have explored the issue of the cerebral correlates of action imitation independently of the stimulus type. According to the existing literature, imitation seems to be sustained by a network of brain regions including: the inferior frontal gyrus, the dorsal and ventral premotor cortex, the inferior and superior parietal cortex and the posterior superior temporal cortex (see Brass and Heyes, 2005, for a recent review). These areas, activated also during action observation, have been interpreted (Iacoboni *et al.*, 1999) as the human homologue of the mirror neuron system described in monkey brain (di Pellegrino *et al.*, 1992; Gallese *et al.*, 1996). However, little is known about the specific correlates of imitation of different types of actions except for the results reported by Rumiati *et al.* (2005) and Peigneux *et al.* (2004) in which subjects actually imitated meaningful and meaningless actions (but see Grezès *et al.*, 1999, for a study in which activations changed depending on the level of familiarization with perceived meaningless actions).

In our study, the intersection analysis within each group (see Fig. 4) revealed that those LBD patients who imitated meaningful better than meaningless actions had lesions overlapping in the superior temporal lobe and the ventral portion of the angular gyrus, whereas the lesions of RBD patients showing the same behavioural pattern overlapped in the basal ganglia. Moreover, the lesion subtraction analysis has confirmed that the involvement of the superior temporal cortex leads more frequently to a selective deficit in imitating meaningless, compared with meaningful, actions (Fig. 5).

These three brain structures (superior temporal lobe, angular gyrus and basal ganglia) have already been reported to be associated with imitation of meaningless actions. For instance, the two patients in Goldenberg and Hagmann (1997) with selective apraxia for meaningless actions had lesions encroaching upon the left angular gyrus. The lesion of the patient documented by Bartolo *et al.* (2001) with the same type of apraxia is said to affect the left temporo-parietal cortex, but no further information is provided. Besides the angular gyrus, Rumiati *et al.* (2005) identified other regions that seem to be recruited when healthy subjects imitated meaningless actions: right parieto-occipital junction and occipitotemporal junction, the left superior temporal lobe and the superior parietal cortex bilaterally. In particular, the superior temporal cortex has been often indicated as an area, both in humans and in monkey, that provides relatively higher-level visual descriptions of observed actions, independent of changes in illumination, colour, distance and identity of the person that performs the action (Perrett *et al.*, 1989).

At first glance the involvement of basal ganglia in imitation of actions may seem surprising, however it has been documented before in both neuropsychology and neuroimaging. Ideomotor apraxia, for instance, has been observed in patients with Parkinson's disease, progressive supranuclear palsy and corticobasal degeneration (see Leiguarda, 2001; Zadikoff and Lang, 2005, for a review), diseases all affecting the normal functioning of basal ganglia. In particular, Salter *et al.* (2004) reported that patients with corticobasal degeneration were impaired at imitating transitive and intransitive non-representational gestures relative to intransitive representational gestures. This study, however, does not tell us whether the basal ganglia in the right hemisphere play a specific role in imitation, as our results seem to suggest. A recent study by Kessler *et al.* (2006) clarifies this issue. By using whole-head magnetoencephalography (MEG), these authors observed that in addition to the left ventrolateral premotor, bilateral temporal and parietal areas, the right basal ganglia were also involved in imitation of biological movements. Kessler *et al.* (2006) suggested that the basal ganglia participate in an early stage of the processing of biological movements, possibly by selecting suitable motor programmes that match the stimulus. The basal ganglia have been found to be involved also in the selection of kinematic parameters (i.e. amplitude and velocity), in the direction of arm movements, as well as in several mechanisms of response selection, such as inhibition of inappropriate responses dedicated to behaviourally relevant stimuli, and learning associations between stimuli, responses and reinforcement (Rushworth *et al.*, 1998; Lawrence *et al.*, 1999). All these putative roles of the basal ganglia are potentially necessary for imitation of meaningless actions which put a greater demand on the conversion mechanism that translates the visual input into a motor output.

In contrast, lesion subtraction analysis revealed that the two patients showing the reverse dissociation (i.e. better imitation of meaningless 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. The same portion of the angular gyrus has been found active during imitation of meaningful actions in two PET studies by Rumiati *et al.* (2005) and Peigneux *et al.* (2004). In addition, its involvement is in keeping with the findings observed by Haaland *et al.* (2000), who investigated the neural correlates of ideomotor apraxia in patients with anterior, posterior and anterior plus posterior lesions (showing a greater impairment when imitating meaningful transitive, than meaningless, gestures). They observed the damage in patients with anterior and posterior lesions to maximally overlap in a left hemispheric network, comprising the middle frontal gyrus and the inferior parietal cortex (BA 40; see Haaland *et al.*, 2000, Fig. 3C). Of particular interest, with respect to our findings, are the results concerning the patients with posterior lesions, who are comparable with the patients in our study who show a selective deficit for meaningful gestures. In these patients, the damage was located in a region (BA 39, 40; see Haaland *et al.*, 2000, Fig. 3B) approximately corresponding to the one which, in our subtraction analysis, was specifically associated with the selective deficit in imitating meaningful gestures.

The involvement of the hippocampus in the imitation of meaningful gestures is consistent with the well-known role of this structure in the retrieval of previously acquired memories. Rumiati *et al.* (2005) reported the parahippocampal gyrus being more strongly activated during imitation of meaningful, compared with meaningless, gestures. In their study, the activated region was located in a more anterior and ventral position with respect to the portion lesioned in patients with a selective deficit for meaningful actions. However, the importance of the presently reported hippocampal region in the retrieval of learned motor abilities has also been shown by Vogt *et al.* (2005). These authors investigated the effect of motor expertise on imitation learning, using a task in which participants (professional guitarists versus naïve subjects) were required to imitate as closely as possible visually presented guitar-chords (previously trained versus untrained). Interestingly, they observed the dorsal-most portion of the hippocampus (approximately at the same location as the region described here) to be activated by both chord-types in professional guitarists, but only by previously trained chords in naïve subjects. The imaging results reported by both Rumiati *et al.* (2005) and Vogt *et al.* (2005), together with the present patients study, indicate a critical role of the hippocampal structures in the retrieval of learned gestures.

In conclusion, we propose that ideomotor apraxia, characterized as a failure to imitate actions and traditionally

linked with lesions of the left inferior parietal cortex (Buxbaum *et al.*, 2005), should be revisited as a multifaceted deficit associated with a complex network of brain areas. In particular, imitation recruits common as well as dedicated areas that are specific to the type of stimulus to be initiated.

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