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Exploring the functional and anatomical bases of mirror-image and anatomical imitation: The role of the frontal lobes

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Abstract

Humans are the most imitative species on earth, but how imitation is accomplished and which areas of the brain are directly involved in different kinds of imitation is still under debate. One view is that imitation entails representing observed behaviours as a set of hierarchically organised goals, which subsequently drive the construction of an action pattern [Bekkering, H., Wohlschläger, A., & Gattis, M. (2000). Imitation of gestures in children is goal-directed. *The Quarterly Journal of Experimental Psychology*, *53*, 153–164; Wohlschläger, A., Gattis, M., & Bekkering, H. (2003). Action generation and action perception in imitation: An instance of the ideomotor principle. *Philosophical Transactions of the Royal Society of London*, *358*, 501–515]. On this view, when working memory resources are limited, only the goals at the top-end of the hierarchy will be accurately reproduced. In the present study, neurologically intact participants and patients with frontal and non-frontal lesions were asked to make imitative responses that were either mirror-image (e.g., the observer's right side corresponding to the model's left side) or anatomically (e.g., the observer's right side corresponding to the model's right side) matching. Experiment 1 confirmed that individuals with brain damage, though globally impaired compared with neurologically intact controls, nevertheless followed the same goal hierarchy. However, there was a selective deficit in performing anatomical imitation for the frontal group. Experiment 2 demonstrated that the problem for frontal patients stemmed from an impaired ability to remember and reproduce incompatible stimulus-response mappings, which is fundamental for the selection of the appropriate frame of reference during anatomical imitation.

Keywords: Imitation; Frontal cortex; Action understanding; Goal; Intention; Spatial compatibility

1. Introduction

A fundamental issue in research on imitation is to give an account of how a model's actions are parsed, represented and reproduced by the imitator. One theoretical perspective suggests that the imitator aims to match their own movements as closely as possible to those of the model by representing both actions within a single representational framework of organ relations (the "active intermodal matching" (AIM) model, e.g., Meltzoff & Moore, 1994, 1997). A second approach places more emphasis on the imitator's ability to perceive the goals of the model. According to the goal-directed theory of imitation (GOADI, e.g., Bekkering, Wohlschläger, & Gattis, 2000; Wohlschläger, Gattis, & Bekkering, 2003) the imitator first deconstructs the observed action into a hierarchy of abstract goals (not body movements), then uses this representation as a basis for reconstructing the action. Distinctive predictions about how imitation might be disrupted by brain damage follow from these two perspectives. In the current study we suggest that the pattern of disruption to imitation following frontal brain injury can help constrain functional and neural models of imitation.

Most evidence on the anatomical organisation of imitation comes from studies using functional brain imaging to measure brain activity correlated with imitation. Such studies provide support for the notion that the posterior part of the inferior frontal cortex plays a key role in processes such as action understanding and intention coding, which may be components of imitation (Iacoboni, 2005; Iacoboni et al., 1999, 2005; Nishitani & Hari, 2000, 2002). In particular, it has been shown that the presence of explicit action goals in the behaviour to be imitated increases the activity in this area, compared with when the action is not directed towards an object (Koski et al., 2002).

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This finding suggests that imitation is sensitive to the observer's representation of the goals of the action. Moreover, it has been suggested that the preference shown by children (Bekkering et al., 2000; Gleissner, Meltzoff, & Bekkering, 2000; Schofield, 1976; Wapner & Cirillo, 1968) as well as adults (Avikainen, Wohlschläger, Liuhanen, Hänninen, & Hari, 2003; Ishikura & Inomata, 1995) for mirror-image imitation (e.g., the imitator's right side corresponds to the model's left side) over anatomical imitation (e.g., the imitator's right side corresponds to the model's right side) arises because mirror-image actions are most strongly triggered through the mirror neuron system located in this same frontal area (Koski, Iacoboni, Dubeau, Woods, & Mazziotta, 2003).

These imaging studies correlate frontal lobe activity with imitation, but they do not demonstrate the necessary role of frontal cortex in imitative performance. To provide evidence on the causal role of neural structures, an interventionist approach is needed, using either lesion studies or trans-cranial magnetic stimulation (TMS) to alter activity in the critical brain region. Heiser, Iacoboni, Maeda, Marcus, and Mazziotta (2003), used repetitive TMS (rTMS) to stimulate the posterior part of Broca's area and found a significant impairment in the imitation of random sequences of finger key presses. Other evidence for a necessary role of frontal cortex in imitation comes from neuropsychological work indicating that, following frontal lobe damage, there may be a strong tendency for spontaneous imitation of other people's gestures, even if there is an explicit instruction not to imitate ("imitation behaviour", e.g., De Renzi, Cavalleri, & Facchini, 1996; Luria, 1966; Lhermitte, Pillon, & Serdaru, 1986). Further neuropsychological data on imitation comes from a study by Bekkering, Brass, Woschina, and Jacobs (2005). Patients with left-sided lesions suffering from ideomotor apraxia were overall more impaired than patients with right-sided lesions and healthy controls in the imitation of multi-component actions. Importantly, their performance in copying one of the components of the action, namely finger movements, varied as a function of the relevance of the goal within the context of the task. These results strongly suggest that imitative performance depends upon the importance attributed by the observer to each goal composing a particular movement, and offer support to the goal-directed view of imitation.

However, existing neuropsychological studies do not give very clear indications on the role of frontal brain areas in sustaining imitation. Studies of spontaneous imitation behaviour following frontal brain lesions have provided rather inconsistent findings. For example, while Lhermitte et al. (1986) found that imitation behaviour was associated with damage to low medial regions of the frontal lobe, De Renzi et al. (1996) observed that the same pathology was more often associated with upper medial as well as lateral lesions. Similarly, in the Bekkering et al. (2005) study it is unclear whether frontal lobe damage was responsible for patients' imitative difficulties because lesion sites were not reported and ideomotor apraxia can be associated with both frontal and parietal lesions (e.g., see Pilgrim & Humphreys, 1991). Moreover, Bekkering et al. (2005) did not assess whether the ideomotor apraxic group, in the different tasks, maintained the same goal hierarchy as the patient (right hemisphere) and normal control groups. Thus, although this study is informative about how the perceived importance of a goal influences the accuracy with which it is imitated, it is unclear whether patients in this study were in fact representing the multi-component actions according to the same hierarchy as the comparison groups.

Given the lack of a systematic investigation of imitation in patients with frontal brain damage, our criterion for inclusion of a patient in our frontal group was the presence of a lesion anywhere in the frontal lobes. Our aim was to use an experimental approach to provide constraints on theories of the functional and anatomical bases of imitation, while recognising that we would not be able to identify the function of specific regions within the frontal lobes. To this end we tested the ability of frontal patients to imitate hierarchically-organised actions in a mirror-image or anatomical fashion. Their performance was compared with that of both age-matched controls and patients with non-frontal lesions (our patient control group).

Different predictions follow from the AIM and the GOADI accounts. According to AIM (Meltzoff & Moore, 1994, 1997), imitation depends upon a supramodal system, which represents the actions of self and other as non-decomposed motor units. It follows that there should be a general deficit in imitation in frontal lobe patients, but this should hold across all components of the goal hierarchy. Also, because AIM holds that imitation consists in the imitator parsing the model's movements in terms of the anatomy used to produce them (then reproducing the same movement with their own corresponding anatomy), anatomical imitation should be the easier or more natural mode of imitation compared with mirror-image imitation.

Alternative predictions are made by the GOADI account (Bekkering et al., 2000; Wohlschläger et al., 2003). This holds that imitation is dependent on a hierarchical representation of action, based on its component goals, maintained in working memory. When working memory resources are exceeded a version of the original act containing only the more important goal(s) will be reproduced (Wohlschläger et al., 2003). First, it is possible that a frontal lesion might cause impairment in the ability to represent the goals and intentions of the actor. Second, impairment of the ability to process sequences of high-order actions might lead to a qualitatively different pattern of imitation to normal and patient control groups, with frontal patients in particular having difficulty in maintaining a goal hierarchy in their imitation. Third, frontal patients might be able to construct an action hierarchy, but lack the ability to keep the inferred goals and their hierarchical representation in working memory. In this case, frontal patients may organise their imitation into the same goal hierarchy as patients with non-frontal lesions and healthy subjects, but make more errors than the two comparison groups. Furthermore, anatomical imitation should be more difficult than mirror-image imitation, because it might pose higher working memory demands on the imitator (Bekkering et al., 2000). These predictions were examined in Experiment 1, which compared the performance of frontal patients and control groups on mirror-image and anatomical imitation of multi-component actions.

2. Experiment 1

In Experiment 1, healthy individuals and patients with brain lesions of either non-frontal areas or frontal cortex had to make anatomical or mirror-image imitations of hierarchically-organised actions. We used a modified version of the task reported by Avikainen et al. (2003). Participants were asked to imitate the actions of the experimenter while she used one of two possible grips (goal grip) to put one of two identical pens (goal pen) into one of two identical cups (goal cup). We conducted a preliminary pilot study, in order to verify what is the normal hierarchy of goals for this task.

2.1. Pilot study

A sample of 14 normal adults (3 females, 11 males; mean age 61.5 years, range 50–76 years) was tested. Half of the participants were asked to imitate on-line at the same time as the experimenter's modelled action (the on-line group; as in Avikainen et al., 2003). The other participants were asked to wait until the experimenter put her pen back into the initial position before starting their own action (the off-line group). Although off-line imitation requires the participant to remember the action, we anticipated that off-line imitation would be more suitable for working with brain-damaged participants, because it avoids interference between the action being observed and the action that the participant is trying to execute. Both groups had to perform a block of 80 mirror-image trials and a block of 80 anatomical trials. Performance was videotaped and scored according to whether participants carried out the actions following the same procedure as the experimenter (with variations in speed being allowed). An ANOVA with group (off-line, on-line) as a between-subjects factor and imitation (mirror-image, anatomical) and goal (cup, pen, grip) as within-subjects factors revealed significant main effects of imitation ($F(1, 12) = 11.3$, $p = .006$) and goal ($F(2, 24) = 3.8$, $p = .037$). There was no effect of whether the task was performed on-line or off-line ($F(1, 12) = 1.9$, $p = .194$). On average, people found mirror-image imitation easier than anatomical imitation (93.7% correct responses for mirror-image imitation, 88.3% for anatomical imitation). A LSD post hoc comparison showed that reproduction of the correct grip was significantly lower than both the cup and the pen, suggesting that the normal hierarchy of goals for this task is cup, pen, grip (95.0% correct responses for the cup, 92.1% for the pen, 85.9% for the grip).

2.2. Method

2.2.1. Participants

Nine patients with frontal lobe damage (two females, seven males; mean age 60.2 years, range 32–74 years), seven patients with posterior lesion (two females, five males; mean age 61.6 years, range 48–83 years) and seven healthy controls (two females, five males; mean age = 60.4 years, range 50–71 years) took part in this experiment. Details of the lesion for each patient can be found in Table 1. All the participants gave their informed consent prior to the inclusion in this study, which has been performed in accordance with the ethical standards of the 1964 Declaration of Helsinki.

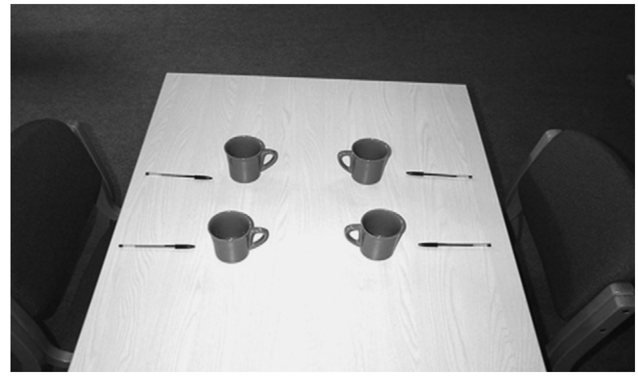


Fig. 1. Apparatus of Experiment 1 and Experiment 2.

2.2.2. Apparatus

The experimenter and the participant sat one in front of the other on opposite sides of a table. They both had two identical cups and two identical pens in front of them (Fig. 1). The participant was asked to imitate the experimenter while she used one of two possible grips (goal: grip) to put one of the two pens (goal: pen) into the cup localized on her left- or right-side (goal: cup). The experimenter's and the participant's movements were recorded by a digital video camera positioned one meter away from them.

2.2.3. Procedure

Given some patients' inability to use one hand (due to hemiplegia), all participants were asked to use their ipsilesional hand throughout the task. Participants had to perform, in two different sessions, mirror-image imitation and anatomical imitation. Each of the eight different movements resulting from the combination of the three goals was repeated ten times in each of the two sessions, for a total of 160 trials. All the movement sequences were performed in a random order and balanced across condition (mirror-image, anatomical) and goal (cup, pen, grip). Half of the participants in each group had to perform mirror-image imitation in the first session and anatomical imitation in the following session, while for the other half the presentation order was reversed. At the beginning of each session, the participants were instructed about which kind of imitation they were going to perform, and they were asked to wait until the experimenter put her pen back into the initial position before starting their own action. Participants were not told the three goals of the action, so that they had to infer the goals and their hierarchy by themselves. To establish that the participant understood the instructions to imitate in a mirror-image or anatomical fashion, a warm-up task was administered, where participants had to imitate ipsilateral and contralateral hand movements directed near or to the ears. There were four possible movements: hand near the left ear, hand near the right ear, hand to the left ear, hand to the right ear. All the movements – if necessary – were repeated until all of them were performed correctly.

2.3. Results

2.3.1. Correct responses

The data were scored on the basis of whether participants followed the patterns of action made by the experimenter. First of all, a one-way ANOVA was used to test if the three groups differed in the overall number of correct imitations. There was a significant effect ($F(2, 20) = 13.8$, $p < .001$), and a LSD post hoc comparison revealed that the control group performed significantly better than the frontal ($p < .001$) and the parietal ($p = .004$) groups.

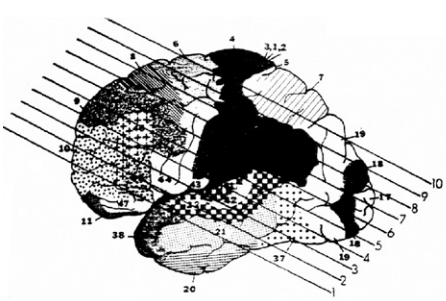
Subsequently, for each group, the number of correct responses in reproducing every action was entered into a repeated-measures ANOVA with imitation (mirror-image, anatomical) and goal (cup, pen, grip) as factors; LSD post hoc comparisons were used to explore the significant effects (see

Table 1
Details of the patients who took part in Experiment 1 and Experiment 2

Patient	Sex	Age	Main lesion site (frontal group)	Lesion reconstruction from MRI scan
DS	M	68	Left inferior, middle and superior frontal gyri	
GA	M	50	Bilateral medial and anterior temporal lobes, extending into the left medial frontal region	
JeB	F	69	Right inferior frontal gyrus, postcentral gyrus, angular and supramarginal gyri	
JoB[a]	F	60	Left thalamus and ischemic change related to anterior horns of lateral ventricles	
MP	M	57	Right inferior frontal gyrus, postcentral gyrus, angular and supramarginal gyri, superior temporal gyrus	
PH	M	32	Left medial and superior temporal, left inferior and middle frontal gyri	
PW	M	73	Right inferior and middle frontal gyri, right superior temporal gyrus	
RW[a]	M	74	Bilateral frontal lesion, with extended left medial frontal damage	
SP[b]	M	51	Left medial frontal lesion, bilateral medial and anterior temporal lobes	
WBA	M	59	Right inferior and middle frontal gyri, right superior temporal gyrus	

Table 1 (*Continued*)

Patient	Sex	Age	Main lesion site (posterior group)	Lesion reconstruction from MRI scan
CN	M	48	Bilateral medial temporal lobes (more pronounced on left)	
DB	M	69	Left inferior parietal (angular gyrus), superior and middle temporal gyri	
DM	F	52	Left medial and inferior occipito-temporal region	
MH	M	52	Left angular and supramarginal gyri, lentiform nucleus	
PF	F	56	Left inferior parietal (angular and supramarginal gyri) and superior temporal gyri	
RH	M	71	Left inferior parietal (angular and supramarginal gyri) and superior temporal gyri	
TP	M	83	L occipito-temporo-parietal region	



Lesions have been drawn onto standard slices from Gado, Hanaway, and Frank (1979). The bottom figure shows the 10 slices used. Only slices 3–8 are depicted here. The left of each slide represents the left hemisphere.

[a] Patients who took part in Experiment 1 only.

[b] Patients who took part in Experiment 2 only.

Table 2
Significant effects of the analyses of variance on the number of correct responses for every goal (cup, pen, grip) and on the number of errors for every typology (opposite, symmetrical, asymmetrical) (Experiment 1)

Analysis	Group	Factors	Effect	*F*-value	d.f.	*p*
Correct responses						
1	Frontal	Imitation × goal	Imitation	20.4	1, 8	.002
			Imitation × goal	10.1	2, 16	.001
2		Goal [mirror-image imitation]		7.6	2, 16	.005
			Cup > grip			*.010*
			Pen > grip			*.052*[**]
3		Imitation [cup goal]		4.2	8	.003
4		Imitation [pen goal]		4.2	8	.003
Errors						
1	Frontal	Imitation × error	Imitation	24.5	1, 8	.001
			Error	8.1	2, 16	.004
			Imitation × error	6.7	2, 16	.008
2		Error [anatomical imitation]		8.9	2, 16	.003
			Opp > symm			*.006*
			Opp > asymm			*.048*
			Asymm > symm			*.037*

Post hoc comparisons are presented in italic. Correct responses: all other $F < 2.8$, all $p > .146$. Errors: all other $F < 2.7$, all $p > .108$.
[**] Marginally significant effect.

Table 2). For the frontal group there was a significant main effect of imitation, with mirror-image imitation generally easier than anatomical imitation (82.4% correct versus 56.7% correct). However, there was also a significant imitation × goal interaction (Fig. 2). First, the effects of goal were examined for the two types of imitation. In the mirror-image imitation condition a repeated-measures ANOVA with goal (cup, pen, grip) as factor revealed a significant effect, with the grip (69.9% correct responses) being imitated less accurately than the cup (91.7% correct responses) and the pen (85.6% correct responses). All goals were imitated with above-chance accuracy. In the anatomical imitation condition a similar ANOVA revealed no significant effects. This time, only the grip was above chance (binomial test, $p = .018$), while the cup and the pen were imitated at chance level (binomial test, $p = .434$ for the cup, $p = .911$ for the pen). Then, *t*-tests were used to examine the effects of imitation for each goal. The ability to imitate the cup and the pen was significantly worse in the anatomical condition compared to the mirror-image condition (91.7% versus 55.4% correct responses for the cup; 85.6% versus 50.7% for the pen), whereas there was no difference for the grip (69.9% versus 64.0% correct responses). In sum, frontal patients were not only more impaired for anatomical imitation than for mirror-image imitation, but the pattern of impairment across goals was different in mirror-image and anatomical imitation.

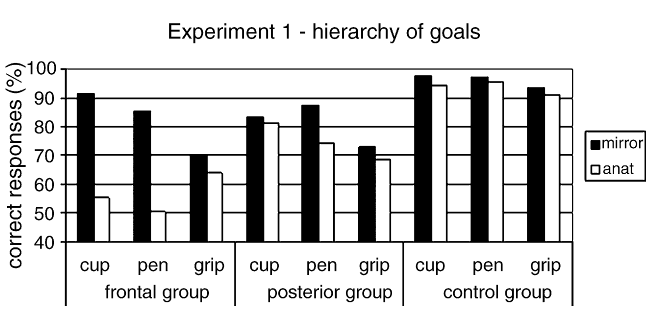


Fig. 2. Experiment 1. Percentage of correct responses made by each group (frontal patients, posterior patients, healthy controls) for every goal (cup, pen, grip) in the mirror-image imitation condition and in the anatomical imitation condition.

Similar analyses did not reveal any significant difference within the posterior group nor within the control group. For both groups, all scores were above chance.

2.3.2. Errors

Errors were divided into three categories: "opposite" errors were those where the actions with both the pen and the cup were wrong in the same trial, and therefore the action would be correct in the other type of imitation; "symmetrical" errors were those where an observed oblique movement (e.g., the left pen put in the right cup) was repeated as a straight one (e.g., the right pen put in the right cup); "asymmetrical" errors were those where an observed straight movement was repeated as an oblique one.

Different predictions can be made for the error pattern of the frontal group. According to the AIM account (Meltzoff & Moore, 1994, 1997), the three kinds of error should be equally common, both in the mirror-image condition and in the anatomical condition, given that the frontal patients may simply show a general decline in imitative ability. In contrast, GOADI (Bekkering et al., 2000; Wohlschläger et al., 2003) predicts that the symmetrical errors will be more frequent in both conditions, on the basis of the developmental literature showing that children tend to ignore secondary goals (e.g., the pen) in order to reach for the most important goal (e.g., the cup) in the more direct possible way (Bekkering et al., 2000; Gleissner et al., 2000).

These categories of error do not take into account the goal grip, so we considered the average number of errors made for each category both when the grip was imitated correctly and when it was imitated wrongly. The results when the grip was correct and when it was incorrect showed a very similar trend and were combined in the analyses, because the number of errors when the grip was incorrect was too small to allow for the inclusion of grip as a factor.

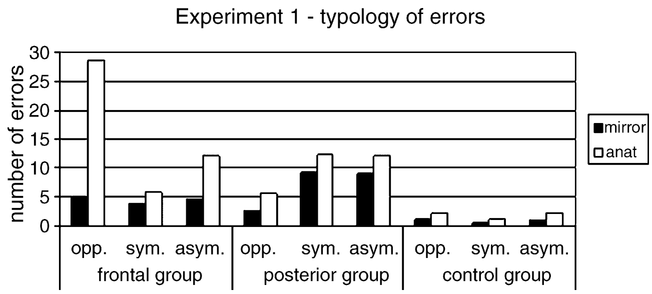


Fig. 3. Experiment 1. Average number of opposite, symmetrical and asymmetrical errors made by each group (frontal patients, posterior patients, healthy controls) in the mirror-image imitation condition and in the anatomical imitation condition.

For each group, a repeated-measures ANOVA with imitation (mirror-image, anatomical) and type of error (opposite, symmetrical, asymmetrical) as factors was performed; LSD post hoc comparisons were used to explore the significant effects (see Table 2).

For the frontal group there was a significant main effect of imitation and of error and a significant imitation × error interaction (Fig. 3). In the mirror-image imitation condition a repeated-measures ANOVA with type of error (opposite, symmetrical, asymmetrical) as factor did not reveal a significant effect. The three kinds of error were equally common. In the anatomical imitation condition a similar ANOVA revealed a significant effect of type of error, with the opposite errors (28.7 errors) being more frequent than the symmetrical (5.9 errors) and the asymmetrical errors (12.0 errors).

Similar analyses did not reveal any significant difference within the posterior group nor within the control group.

2.3.3. *Test for ideomotor apraxia*

One potential complication with interpreting our findings is that five out of the seven patients in the non-frontal group presented damage to the left parietal lobe, which might produce ideomotor apraxia, a disorder of skilled movement often characterized by a deficit in the imitation of actions (Liepmann, 1900). Therefore, we compared the scores obtained by our two groups of patients (frontal, posterior) in the 24-items test ideated by De Renzi, Motti, and Nichelli (1980) to assess the presence of ideomotor apraxia. Two of the patients in the frontal group (JoB and RW, both with left-sided lesion) and two of the patients in the posterior group (CN and DM, the only two posterior patients without parietal involvement) were not available for testing. If anything, this should have made more likely the detection of a deficit in the posterior group compared with the frontal group, because ideomotor apraxia is usually caused by left-sided frontal and (especially) parietal lesions. However results showed that there was no difference between the two groups in their ability to imitate gestures ($t(10) = .7$, $p = .508$).

2.4. *Discussion*

The key finding from Experiment 1 was the discrepancy shown by frontal patients in mirror-image versus anatomical imitation. In the mirror-image condition frontal patients were able to infer the normative hierarchy of goals, and to remember and reproduce each goal of the action at above-chance levels (though less accurately than healthy controls). In contrast, in the anatomical condition frontal patients performed at chance levels for the two highest goals in the action hierarchy, yet above-chance for the lowest goal. This pattern cannot be explained by the AIM model of imitation (e.g., Meltzoff & Moore, 1994, 1997), on the basis of which anatomical imitation should have been easier than mirror-image imitation. Nor can it be explained by the GOADI theory (e.g., Bekkering et al., 2000; Wohlschläger et al., 2003), where frontal lesions might have impaired patients' ability to infer the action hierarchy, or where impaired working memory might have led to a disproportionate number of errors on the lowest goal in the hierarchy.

In Experiment 2 we examined two alternative sources of difficulty on the imitation tasks. First, it has been suggested that mirror-image imitation is the spontaneously activated response when actions have to be re-produced (Avikainen et al., 2003; Bekkering et al., 2000; Gleissner et al., 2000; Ishikura & Inomata, 1995; Schofield, 1976; Wapner & Cirillo, 1968). If this is the case, then difficulty inhibiting the mirror-image response set might be an important explanation for errors in anatomical imitation. Importantly though, only for the cup and the pen would failure to inhibit the mirror-image action result in an incorrect response. The fact that the most frequent type of error made by frontal patients was the opposite error is consistent with this possibility because it could be due to performance of a mirror-image movement in response to an anatomical instruction.

However, another potential source of difficulty in the imitation tasks was the need to process incompatible stimulus-response mappings. In order to identify correctly the goals of the action during imitation, participants need to map their own frame of reference onto the experimenter's. In the case of mirror-image movements, the frame for the actor's own movements corresponds to the frame for the experimenter's movements. In contrast, for anatomical imitation, the frame for the experimenter's movements must be left–right transformed to map to the frame for the actions of the participant. A wide body of research has focused on stimulus-response compatibility (SRC) effects, whereby responses tend to be faster and less error-prone when stimulus and response locations are the same (with respect to their respective reference frames) compared to when they differ, regardless of whether stimulus location is relevant or irrelevant to the task (e.g., Fitts & Seeger, 1953; Heyes & Ray, 2004; Kornblum, Hasbroucq, & Osman, 1990). It follows that anatomical imitation, where responses differ in the observer's and the experimenter's reference frames, is the more difficult task. According to this account mirror-image imitation is not a prepotent response. Instead, mirror-image actions are simply easier to represent and to remember than anatomical imitations because they are based on a spatially compatible stimulus-response mapping. In our task, for anatomical imitation, the correct responses for cup and pen were spatially incompatible with the stimulus within a framework based on the actor's body, whereas the grip action was spatially compatible. This might have led to the disproportionate number of opposite errors observed in Experiment 1.

Experiment 2 was an attempt to distinguish between these accounts.

3. Experiment 2

In Experiment 2 we attempted to increase the inhibition demands of our task by asking participants to perform mirror-image and anatomical imitation in the same session, switching from one to the other in the middle of the session. It has been demonstrated that responses after a task switch are substantially slower and usually more error prone, and that this effect is due to both task-set reconfiguration processes (switch cost) and to the carry-over of the previous task-set activation (residual cost) (for a review see Monsell, 2003). Therefore, if the inhibition account of the results of Experiment 1 is correct, in this new task we would expect frontal patients to be very sensitive both to the switch cost and to the residual cost, so that their performance in the anatomical trials should be worse when they are preceded than when they are followed by mirror-image trials. Crucially, because the cup and the pen were already at chance level in the anatomical condition of Experiment 1, we expect them now to fall below chance after the switch, while the grip should be at chance or above. In contrast, given that mirror-image imitation is the natural and prepotent response, mirror-image trials should be imitated with the same accuracy before and after the switch.

Different predictions on the behaviour of the frontal group follow from the spatial compatibility account. Because of the extra load induced by the switch, we might observe a drop in the average level of performance compared to the results of Experiment 1. This should apply to all the after-switch trials, in the mirror-image as well as in the anatomical condition. However, there is no reason to expect performance to fall below chance in any of the goals, since there is not a particular tendency to make a prepotent mirror-image action—it is simply that spatially incompatible anatomical actions are difficult to represent. In this difficult condition, random selection of the appropriate reference frame would generate chance-level performance.

3.1. Method

3.1.1. Participants

Individuals with frontal and posterior lesions took part in this study; their details can be found in Table 1. There were eight patients in the frontal group (one female, seven males; mean age 57.4 years, range 32–73 years), and seven patients in the posterior group (two females, five males; mean age 61.6 years, range 48–83 years).

3.1.2. Apparatus

The apparatus was the same as in Experiment 1 (Fig. 1) and, as before, the participant was asked to imitate the experimenter while she used one of two possible grips to put one of two pens into a cup localized on her left- or right-side.

3.1.3. Procedure

Participants had to alternately perform, in the same session, two blocks of mirror-image imitation trials and two blocks of anatomical imitation trials. Half of the participants in each group started with mirror-image imitation (sequence: 20 mirror-image trials–20 anatomical trials–break–20 mirror-image trials–20 anatomical trials), while for the other participants the order was reversed (sequence: 20 anatomical trials–20 mirror-image trials–break–20 anatomical trials–20 mirror-image trials). In a second session, participants completed the task again following the sequence they did not perform in the first session. Each of the eight different movements resulting from the combination of the three goals was repeated ten times during the two sessions, for a total of 160 trials. All the movement sequences were performed in a random order and balanced across time (before the switch, after the switch) condition (mirror-image, anatomical) and goal (cup, pen, grip). At the beginning of each session, participants were instructed about which sequence they would have to follow, but they were not told which were the three goals of the action. The same mirror-image and anatomical imitation warm-up tasks used in Experiment 1 were administered.

3.2. Results

3.2.1. Correct responses

The number of correct responses in reproducing every goal was measured. First of all, a t-test was used to test if the two patient groups differed in the overall number of correct imitations. As in Experiment 1, there was no significant effect ($t(13) = .5$, $p = .592$).

Subsequently, for each group, a repeated-measures ANOVA with time (before the switch, after the switch), imitation (mirror-image, anatomical) and goal (cup, pen, grip) as factors was performed; LSD post hoc comparisons were used to explore the significant effects (see Table 3). For the frontal group there was a significant main effect of imitation and significant imitation × goal and time × goal interactions (Fig. 4). Mirror-image imitation was overall easier than anatomical imitation (77.6% correct responses for mirror-image imitation, 55.8% for anatomical imitation), but performance was different in the two imitation conditions and in the two times depending on the goal. First, the effect of goal was analysed separately for the two different types of imitation. In the mirror-image imitation condition a repeated-measures ANOVA with goal (cup, pen, grip) as factor revealed a significant effect, with the grip (65.0% correct responses) being imitated less accurately than the cup (85.5% correct responses) and the pen (82.3% correct responses). In the anatomical imitation condition a similar ANOVA did not reveal a significant effect. Performance was similar before and after the switch, and for all three goals; both before and after the switch, scores in the cup and the pen did not differ from chance. This replicates the findings from Experiment 1. Then, the effect of goal was analysed separately for the two different times. A repeated-measures ANOVA with goal (cup, pen, grip) as factor did not reveal a significant effect before or after the switch.

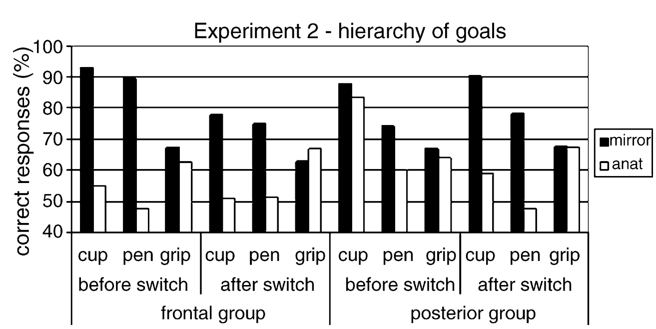


Fig. 4. Experiment 2. Percentage of correct responses made by each group (frontal, posterior) before and after the switch for every goal (cup, pen, grip) in the mirror-image imitation condition and in the anatomical imitation condition.

Table 3
Significant effects of the analyses of variance on the number of correct responses for every goal (cup, pen, grip) and on the number of errors for every typology (opposite, symmetrical, asymmetrical) (Experiment 2)

Analysis	Group	Factors	Effect	*F*-value	d.f.	*p*
Correct responses						
1	Frontal	Time × imitation × goal	Imitation	8.7	1, 7	.021
			Imitation × goal	5.6	2, 14	.016
			Time × goal	3.8	2, 14	.048
2		Goal [mirror-image imitation]		6.3	2, 14	.011
			Cup > grip			*.028*
			Pen > grip			*.056***
3	Posterior	Time × imitation × goal	Imitation	8.6	1, 6	.026
Errors						
1	Frontal	Time × imitation × error	Imitation	15.8	1, 7	.005
			Error	11.1	2, 14	.001
			Imitation × time	7.8	1, 7	.027
			Imitation × error	5.4	2, 14	.018
2		Time × error [mirror-image imitation]	Time	10.0	1, 7	.016
			Error	7.6	2, 14	.006
			Opp > symm			*.015*
			Opp > asymm			*.043*
3		Time × error [anatomical imitation]	Error	8.5	2, 14	.004
			Opp > symm			*.016*
			Opp > asymm			*.028*
4	Posterior	Time × imitation × error	Imitation	9.1	1, 6	.024

Post hoc comparisons are presented in italic. Correct responses: all other $F < 3.2$, all $p > .077$. Errors: all other $F < 3.1$, all $p > .081$.
** Marginally significant effect.

For the posterior group, a repeated-measures ANOVA with time (before the switch, after the switch), imitation (mirror-image, anatomical), and goal (cup, pen, grip) as factors showed only a significant main effect of imitation, with mirror-image imitation being easier than anatomical imitation (77.5% correct responses for mirror-image imitation, 63.6% for anatomical imitation). In both mirror-image and anatomical imitation performance did not change after the switch, and this held for each of the three goals.

3.2.2. Errors

Errors were again divided into three categories: “opposite”, “symmetrical” and “asymmetrical”. If the inhibition account is correct, we would expect the opposite error to be the most frequent type of error in the anatomical imitation and for the frontal group only. In contrast, if the spatial compatibility account is correct, we would expect the frontal patients to show an increase in the frequency of the opposite error type in both the mirror-image and the anatomical imitation conditions after the switch, reflecting uncertainty about which reference frame to maintain.

As in Experiment 1, the average number of errors made for each category when the grip was correct and when it was incorrect showed a very similar trend and were combined in the analyses. For each group, a repeated-measures ANOVA with time (before the switch, after the switch), imitation (mirror-image, anatomical) and type of error (opposite, symmetrical, asymmetrical) as factors was performed; LSD post hoc comparisons were used to explore the significant effects (see Table 3).

For the frontal group there was a significant main effect of imitation and of error. There were also significant imitation × time and imitation × error interactions (Fig. 5). In the mirror-image imitation condition a repeated-measures ANOVA with time (before the switch, after the switch) and error (opposite, symmetrical, asymmetrical) as factors revealed a significant effect of time and of error. In the anatomical imitation condition there was only a significant effect of error. In both mirror-image and anatomical imitation conditions the opposite error was the most common mistake. However, only in mirror-image imitation were more errors made after the switch than before the switch (1.5 errors before the switch, 4.1 after the switch), while there was no effect of time on anatomical imitation (7.9 errors before the switch, 7.5 after the switch).

For the posterior group there was an overall imitation effect, with more errors for the anatomical than for the mirror-image imitation. Posterior patients did not make more mistakes after the switch than before the switch, and this held for all types of error (8.9 opposite, 2.8 symmetrical, 4.4 asymmetrical errors before the switch; 3.9 opposite, 3.8 symmetrical, 7.2 asymmetrical errors after the switch).

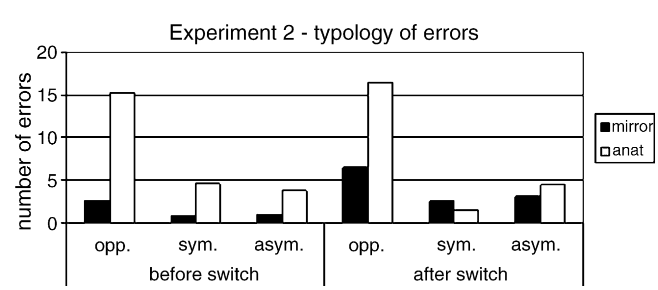


Fig. 5. Experiment 2. Average number of opposite, symmetrical and asymmetrical errors made by the group of frontal patients before and after the switch in the mirror-image imitation condition and in the anatomical imitation condition.

3.3. Discussion

Experiment 2 focused on the difference between mirror-image and anatomical imitation under conditions where patients had to switch from one form of imitation to another. Of most interest is the performance of the frontal group. If such patients had difficulty in inhibiting a prepotent mirror-image response, then increasing the inhibition load – by introducing a switch – should have made it harder for the frontal group to inhibit the mirror-image than the anatomical response. Performance should have been worse in the anatomical condition after the switch compared with before the switch, while there should have been little or no effect in the mirror-image imitation. Contrary to this prediction, in the error analyses, we found that the frontal group made significantly more opposite errors after the switch compared with before the switch in the mirror-image condition only; there was no difference in the number of pre- or post-switch errors for anatomical imitation. Moreover, if mirror-image imitation is the prepotent response that must be inhibited to perform anatomical imitation, then the baseline for cup and pen in anatomical imitation should be zero, not chance. Yet the frontal group's performance was not driven below chance levels even in the condition that should have had the highest inhibitory demands (when they performed anatomical imitation immediately after mirror-image imitation). Thus, the data offer no support for the inhibition account.

Instead, our findings are more consistent with the spatial compatibility account. Performance was overall better in the mirror-image than in the anatomical imitation, which we suggest is because the mirror-image frame of reference is easier to represent than the anatomical one. In addition, in the error analyses, the number of opposite errors in the mirror-image imitation condition increased after the switch. The reverse pattern was not observed in the anatomical condition probably because performance was already at chance level before the switch. (Recall that, according to the spatial compatibility account, there is no reason to believe that it would drop below chance, if the confusion induced by the changes of stimulus-response mapping made frontal patients more likely to select the spatial reference frame unsystematically.) Finally, it was found that the opposite error was reliably the most frequent type of error both in the mirror-image and in the anatomical imitation, suggesting that both conditions were affected by the switch manipulation. Importantly, this result also shows that, despite chance performance in the anatomical imitation, participants were not guessing for each goal, but were simply mistaken about which stimulus-response mapping would be appropriate.

4. General discussion

There were three main results of interest. First, we found that both patients with frontal lobe damage and (control) patients with posterior damage maintained a hierarchy of actions when required to carry out mirror-image imitations. Thus, there was no evidence for a problem in hierarchical programming of action in either patient group. Second, the frontal patients had a selective deficit when anatomical imitations were required. Third, we found no evidence that this deficit with anatomical imitation was due to a problem in inhibiting a prepotent mirror-image action, since the patients did not fall below chance even when they had to switch from making mirror-image imitations to anatomical imitations: had mirror-image actions dominated, then anatomical imitations should have fallen below chance. In contrast, the deficit in anatomical imitation is more consistent with the frontal patients having problems maintaining a reference frame for actions when components of the action stimulus are spatially incompatible with components of the action response.

The results of Experiment 1, where a hierarchy of actions was demonstrated for all groups suggest that imitation is not simply based upon a process of direct physical reproduction of the movements performed by the model, as proposed, for example, by the AIM model (Meltzoff & Moore, 1994, 1997). Instead, this pattern is consistent with the proposal that imitation is based on the identification of action goals and on their organisation into hierarchical structures (Bekkering et al., 2000; Wohlschläger et al., 2003). One limitation of our study is that the lesion localizations of the patients included in the frontal group were quite diverse. As a consequence, it might well be that neuropsychological studies focusing on patients with lesions confined to specific frontal sub-regions might find impaired imitative performance related to difficulties in understanding intentions (Brunet, Sarfati, Fardy-Bayle, & Decety, 2000; Iacoboni et al., 2005), in parsing, storing and executing the sequential and hierarchical organisation of events (Sirigu et al., 1995, 1996; Zalla, Plassiart, Pillon, & Sirigu, 2001; Zalla, Pradat-Diehl, & Sirigu, 2003), or in working memory (Allain, Etcharry-Bouyx, & Le Gall, 2001; Chao & Knight, 1998; McDowell, Whyte, & D'Esposito, 1997). Nevertheless, the assumption of the GOADI model that a general decrease in processing capacity would lead a participant to produce a version of the original action which includes only the top-end goals of the hierarchy, certainly contributes to explain the overall pattern of worse performance in the patient groups compared to the control group in Experiment 1. Another potential contribution to the general pattern of worse performance in the two patient groups is that both frontal and posterior (parietal) areas may contain mirror neurons, which discharge both when the participant performs an action and when he observes a similar action being made by the experimenter (Decety et al., 1997; Gallese, Fogassi, Fadiga, & Rizzolatti, 2002; Grafton, Arbib, Fadiga, & Rizzolatti, 1996; Rizzolatti et al., 1996). Future neuropsychological investigation of patients selected on the basis of damage to frontal or parietal areas known to contain mirror neurons would allow a proper evaluation of the potential contribution of these neural populations to imitation. However, neither the GOADI model nor the possibility of damage to mirror neurons seem likely explanations for the more detailed pattern of findings in the current study, in particular the discrepancy between frontal patients' relatively spared performance with mirror-image imitation and their relatively impaired performance with anatomical imitation.

The results of Experiment 2 suggested that the frontal group's distinctive impairment with anatomical imitation was best explained by difficulty in selecting the appropriate spatial frame of reference for the imitated action, rather than difficulty inhibiting a prepotent mirror-image response. A number of studies have indeed shown that the frontal lobes (in particular dorsal cortical structures) are involved in processing incompatible stimulus-response mappings (Ridderinkhof, Ullsperger, Crone, & Nieuwenhuis, 2004; Wang, Ulbert, Schomer, Marinkovic, & Halgren, 2005). It would be important for future work to examine sub-groups of frontal patients, to identify whether the same frontal structures are critical for processing incompatible stimulus-response mappings in imitation tasks. Importantly, this finding does not contradict the contention that actions are imitated on the basis of their perceived goals (Bekkering et al., 2000; Wohlschläger et al., 2003). Nor does it rule out an important role for inhibitory control in imitative behaviour, or a role for frontal structures in serving this control function (Aron, Robbins, & Poldrack, 2004; Lhermitte et al., 1986; Luria, 1966; Milner, 1963; Rogers et al., 1998). However, our findings do add to a range of data highlighting the importance of stimulus-response compatibility in the explanation of some aspects of imitation.

Previous studies have suggested that imitation is affected by the same processes which mediate responses to stimuli on the basis of arbitrary stimulus-response mappings (Brass, Bekkering, Wohlschläger, & Prinz, 2000; Brass, Zysset, & von Cramon, 2001; Brass, Derrfuss, von Cramon, & von Cramon, 2003; Heyes & Ray, 2004; Stürmer, Aschersleben, & Prinz, 2000). However, in none of these studies were participants explicitly asked to imitate a naturalistic action performed by a real human being. Instead, participants were instructed to execute certain movements in response to the presentation of video sequences of the animated hand of a real human model (Brass et al., 2000, 2001, 2003; Stürmer et al., 2000), or to imitate the movements of a computer graphic representation of a human being (Heyes & Ray, 2004). Our study used a natural human action as the model for imitation, and so provides valuable converging evidence on the role of stimulus-response compatibility in imitation and on the necessary role of frontal brain structures in resolving incompatibility between the action stimulus and the imitative response.

Finally, differences in stimulus-response compatibility may also help explain the well-known finding that mirror-image imitation is more “natural” or “spontaneous” than anatomical imitation for pre-school as well as school-aged children (Bekkering et al., 2000; Gleissner et al., 2000; Schofield, 1976; Wapner & Cirillo, 1968). Casey, Thomas, Davidson, Kunz, and Franzen (2002) showed that school-aged children performed significantly worse than adults on a stimulus-response compatibility task, and that the prefrontal brain activation observed in adults during the execution of the task was more refined and focal than in children. It seems possible, then, that maturation of the frontal lobes is a constraint on children’s developing ability to represent incompatible stimulus-responses mappings, and that this in turn leads to a bias towards mirror-image imitation.

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