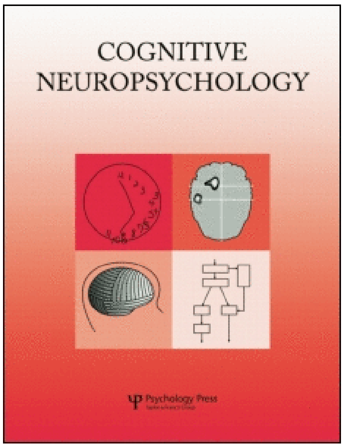


Cognitive Neuropsychology
Publication details, including instructions for authors and subscription information:
http://www.informaworld.com/smpp/title~content=t713659042

The effect of action goal hierarchy on the coding of object orientation in imitation tasks: Evidence from patients with parietal lobe damage

Claudia Chiavarino [ab]; Ian A. Apperly [a]; Glyn W. Humphreys [a]
[a] Behavioural Brain Sciences Centre, University of Birmingham, Birmingham, UK [b] Center for Cognitive Science, University of Turin, Turin, Italy

First Published on: 21 February 2008

To cite this Article Chiavarino, Claudia, Apperly, Ian A. and Humphreys, Glyn W.(2008)'The effect of action goal hierarchy on the coding of object orientation in imitation tasks: Evidence from patients with parietal lobe damage',Cognitive Neuropsychology,25:7,1011 — 1026

To link to this Article: DOI: 10.1080/02643290701862274

URL: http://dx.doi.org/10.1080/02643290701862274

COGNITIVE NEUROPSYCHOLOGY, 2008, 25 (7–8), 1011–1026

Psychology Press
Taylor & Francis Group

The effect of action goal hierarchy on the coding of object orientation in imitation tasks: Evidence from patients with parietal lobe damage

Claudia Chiavarino
Behavioural Brain Sciences Centre, University of Birmingham, Birmingham, UK, and Center for Cognitive Science, University of Turin, Turin, Italy

Ian A. Apperly and Glyn W. Humphreys
Behavioural Brain Sciences Centre, University of Birmingham, Birmingham, UK

In order to explore parietal patients' difficulties in the processing of orientation information, we asked parietal patients ($N = 8$) and healthy and brain-damaged controls to imitate multicomponent actions where object orientation was one component. In Experiment 1 orientation was not the most relevant aspect of the action to be imitated, and the parietal group showed significant difficulties in processing object orientation. However, in Experiment 2, where orientation was placed at the top end of the goal hierarchy, the parietal group were able to process stimulus orientation sufficiently to place it within the goal hierarchy of the action and to reproduce it accurately. We conclude that patients with parietal lesions might be able to include object orientation in a goal hierarchy, but if their processing of orientation information is impaired they might be disproportionately prone to errors when object orientation is lower in the goal hierarchy and so not prioritized for processing resources.

Keywords: Imitation; Parietal cortex; Action understanding; Orientation; Goal.

The parietal lobes play a crucial role in a variety of cognitive processes, from the visual analysis of objects to the execution of skilled movements (for a review see Culham & Kanwisher, 2001). Some regions of the parietal lobe, in particular, are thought to be part of the view-dependent "dorsal stream" (Ungerleider & Mishkin, 1982), which plays a crucial role in mediating the visual control of objects for the guidance of action (Milner & Goodale, 1995). There is also evidence that the left parietal cortex is critically involved in action imitation (De Renzi, Faglioni, Lodesani, & Vecchi, 1983; Kolb & Milner, 1981; Liepmann, 1900). In the current studies we use an imitation paradigm as a novel means of investigating the nature of parietal patients' difficulties with processing the orientation of objects.

Neuropsychological studies have provided evidence in favour of the existence of two functionally and anatomically separate cortical systems for

Correspondence should be addressed to Claudia Chiavarino, Centre for Cognitive Science, Department of Psychology, University of Turin, Via Po 14, Turin, 10123, Italy (E-mail: claudia.chiavarino@unito.it).

This work was supported by grants from the Medical Research Council (MRC) and the Stroke Association (UK). We thank all our patients for their kind participation.

http://www.psypress.com/cogneuropsychology
DOI:10.1080/02643290701862274

processing information about objects. For example, patients with optic ataxia (Balint, 1909), following parietal damage, can be impaired in orienting their hand with respect to target objects and in adjusting their grip while reaching for them, while they may retain the ability to recognize and describe the identity, orientation, and location of these same objects (Jeannerod, 1986; Perenin & Vighetto, 1988). In contrast, damage to the ventral visual areas can cause visual form agnosia (Benson & Greenberg, 1969), a condition whereby patients are unable to name objects and to discriminate shapes and orientations, but are accurate when the task requires them to orient their hands in order to grasp an object (Milner, 1997; Milner et al., 1991). These contrasting profiles support the existence of a view-dependent "dorsal stream" involved in the spatial coding of objects for the guidance of action and a view-invariant "ventral stream" that is more involved in perceptual recognition (Milner & Goodale, 1995).

Consistent with the view that regions of parietal cortex are critically involved in processing object-directed actions, patients with parietal lesions often have an impaired ability to imitate actions, especially if the parietal damage is localized in the left hemisphere (De Renzi et al., 1983; Kolb & Milner, 1981; Liepmann, 1900). This impairment has been often studied in relation to meaningless intransitive actions (e.g., Goldenberg, 1995), but it is now recognized that it causes marked difficulties in the imitation of transitive (both meaningful and meaningless) actions as well (Buxbaum, Kyle, Grossman, & Coslett, 2007; Sunderland, 2007). Ideomotor apraxia is a disorder of skilled movement that is not caused by general weakness or by motor disorders, and it is manifested in spatial, temporal, and postural errors in response to the instruction to imitate gestures, pantomime tool use, or execute gestures in response to verbal commands (De Renzi, Faglioni, & Sorgato, 1982; Heilman & Rothi, 1993). Spatial errors include difficulties in orienting the hand to objects and in orienting objects in space (Rothi, Raymer, & Heilman, 1997). Recent views on ideomotor apraxia claim that this disorder affects the conceptual representation of the observed gestures (i.e., Goldenberg, 1995; Sunderland, 2007), rather than the motor programming process only (i.e., Rothi, Ochipa, & Heilman, 1991).

In addition to problems in using orientation information for action, there is also evidence indicating that parietal patients can have problems in using orientation information for perceptual judgements. For example, right parietal lesions can be associated with orientation agnosia (Cooper & Humphreys, 2000; Turnbull, Laws, & McCarthy, 1995), whereby deficits in the perception of orientation extend to visual recognition tasks with patients showing poor knowledge of the correct orientation of objects (Darling, Pizzimenti, & Rizzo, 2003; Harris, Harris, & Caine, 2001). In other cases, parietal patients can show deficits at localizing simple visual elements defined by orientation differences relative to their context (Riddoch et al., 2004).

However, there is also evidence to suggest a more complex relationship between neuroanatomy and the processing of object orientation in action. For instance, Goodale, Jakobson, and Keillor (1994) found that a patient with visual form agnosia following a ventral visual lesion was also impaired in precise adjustment of grip if she had to wait more than 2 seconds before reaching for an object. Hence there is evidence for a ventral contribution to orientation processing at least under some conditions. Consistent with this, the difficulties that many parietal patients have with visually guided action towards objects may be alleviated when there is a delay between target presentation and movement execution, presumably due to the contribution from ventral visual processes under these conditions (Himmelbach & Karnath, 2005; Milner, Paulignan, Dijkerman, Michel, & Jeannerod, 1999). Moreover, Jeannerod, Decety, and Michel (1994) found that, for a patient with parietal damage, grip formation during object prehension became more accurate when familiar objects were used. Again we may presume ventral mediation of this effect.

This variability in the deficits shown by parietal patients has been attributed to several factors: the size and exact location of the brain lesion within the parietal lobe (Goodale & Humphrey, 1998; Milner & Goodale, 1995), including the fact that the ventral and the dorsal streams functionally interact more closely in the visual control of movements than it was initially thought (Himmelbach & Karnath, 2005; Rossetti & Pisella, 2002); the presence of visual feedback (Haaland et al., 1999); or the necessity to use an object-centred perspective rather than a viewer-centred one when orientation judgements are made (Cooper & Humphreys, 2000). In the present study we kept these factors as constant as possible and used imitation tasks as a novel means of examining the way in which parietal patients process information about object orientation and the conditions under which such information is processed incorrectly. In particular, we assessed whether the coding of orientation information may be impaired following parietal damage particularly when orientation information was not strongly "weighted" for the task. The "weighting" of the information here was manipulated by varying the position of object orientation information in the goal structure of an imitation task.

Bekkering and colleagues (Bekkering, Wohlschläger, & Gattis, 2000; Wohlschläger, Gattis, & Bekkering, 2003) have argued that imitative actions can reflect the goals of the actor, with different components of the actions being organized according to a hierarchy of importance. According to this view, processing resources are allocated as a function of the position of the action in the goal hierarchy. Consequently, an action at the top of the hierarchy should be reproduced most accurately, with a progressive decrease in accuracy for actions lower down (Avikainen, Wohlschläger, Liuhanen, Hänninen, & Hari, 2003; Bekkering et al., 2000; Gleissner, Meltzoff, & Bekkering, 2000; Wohlschläger & Bekkering, 2002; Wohlschläger et al., 2003). This has been tested by asking patients with ideomotor apraxia to imitate finger movements, where it has been observed that the correct finger was selected for action when it was at the top of the goal hierarchy—that is, when participants were exclusively required to imitate finger configurations—but not when it occupied a lower position—that is, when, in addition to the finger used by the model, participants had to pay attention to which ear the movement was directed to and to whether the action ended at the ear or 10 cm from it. The same results were replicated when the action was directed towards an external object rather than towards a body part (Bekkering, Brass, Woschina, & Jacobs, 2005).

An increasing number of studies have used imitation paradigms in order to investigate the principles that guide humans in the organization of goals into hierarchies of importance. Their results suggest that children as much as adults are sensitive to the hierarchical structure of observed actions (Cuijpers, van Schie, Koppen, Erlhagen, & Bekkering, 2006; Whiten, Flynn, Brown, & Lee, 2006) and that objects and—a little less—their treatments (such as their orientation) are generally prioritized for processing resources compared to the choice of the effector (such as the fingers used to grasp them), or the movement path (such as the direction in which the objects move), or the movement end-state (such as the location where the objects end up; Wohlschläger et al., 2003). According to the GOADI (goal-directed imitation) theory proposed by Wohlschläger et al. (2003), this happens because of the ideomotor principle, following which during imitation it is the motor programme more strongly associated with the achievement of the action goal that is normally executed. It also appears that immediate and final action goals are underpinned by different brain circuits (Hamilton & Grafton, 2006; van Schie & Bekkering, 2007). It follows that, in a three-component task with object, object orientation, and final location of the object as goals (see Experiment 1), the predicted action hierarchy would be object > orientation > location. Similarly, in a three-component task with object orientation, object's direction of movement, and finger used to grasp the object as goals (see Experiment 2), the prediction is that object orientation should be placed at the top end of the goal hierarchy.

On the basis of this literature, we used an approach similar to that of Bekkering et al. (2005)

in order to examine the nature of parietal patients' difficulty processing object orientation. From the GOADI theory (Wohlschläger et al., 2003) it follows that, if preserving the orientation of an object is one of a task's main goals, the object orientation should be preserved during imitation. However, this may be less likely if object orientation falls lower down on a goal hierarchy and if patients have some difficulty in coding object orientation when orientation coding is assigned little attentional weight (cf. Duncan & Humphreys, 1989).

We manipulated the availability of resources for processing object orientation in two ways. First, we manipulated the characteristics of the three-component action that participants were required to imitate so that object orientation was an intermediate goal in the hierarchy in Experiment 1 and the main goal of the hierarchy in Experiment 2. Second, we added a fourth goal to the target action. In Experiment 1 the fourth goal came above object orientation in the action hierarchy, so would be expected to put pressure on the resources available for imitating object orientation. In Experiment 2 the imitation was altered so that object orientation would be represented at a higher level in the action hierarchy of typical imitators. Therefore, provided object orientation was correctly prioritized by parietal patients, the additional goal in Experiment 2 should not have a severe effect on imitation of object orientation. The performance of the parietal patients was contrasted with that of both normal control participants and a "control" group of patients with frontal and fronto-temporal lesions, who should not have difficulty in coding object orientation in imitation tasks.

EXPERIMENT 1

Method

Participants

A total of 8 patients with parietal lesions (6 with left, 2 with right parietal lesions; 2 females, 6 males; mean age 65.6 years, range 51–83 years), 6 patients with frontal and/or fronto-temporal lesions (2 with left, 2 with right, and 2 with bilateral lesions; all males; mean age 56.5 years, range 32–74 years), and 8 healthy controls (2 females, 6 males; mean age 66.0 years, range 49–77 years) took part in this study (see Appendix). 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. Prior to taking part in the study, basic judgements of line orientation were measured using the Birmingham Object Recognition Battery (BORB; Riddoch & Humphreys, 1993). No patient had a clinical deficit at the time of testing (see Appendix). The parietal and frontal groups did not differ in performance, $t(14) = -1.18$; $p = .258$. In addition to this, measures of general intellect (IQ equivalent on the National Adult Reading Test, NART; Nelson & Willison, 1991) and of executive function were taken (the Brixton text; Burgess & Shallice, 1997). The parietal and frontal groups did not differ on either the NART or the Brixton test (both $t < 1.0$).

Apparatus

The experimenter and the participant sat face to face at opposite sides of a table. They each had in front of them a pink and a yellow object (created by covering four identical oblong erasers with coloured paper) and an A4 sheet of paper looking like the example shown in Figure 1 (1a and 1b). In the three-goal condition, the participant was asked to imitate the experimenter while she put one of the two objects (goal object) onto one of the two crosses drawn on the sheet of paper (goal location) in one of the two possible orientations (goal orientation)—that is, following the horizontal or the vertical line of the cross. We carried out a pilot study on a sample of undergraduate students ($N = 15$), and we used error rates as a measure of goal importance (i.e., the lowest error rate corresponded to the highest position within the action goal hierarchy).

Results confirmed our predictions by indicating that the goal hierarchy for this action was object > orientation > location (all $p < .05$, Friedman and Wilcoxon tests). In the four-goal condition, a circle was added on the sheet of paper, and the

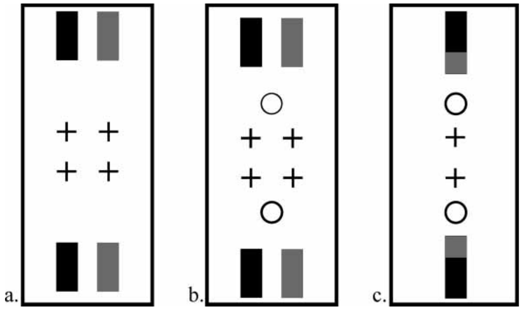


Figure 1. *Apparatus used in the mirror-image imitation tasks of Experiments 1 and 2. (a) In the three-goal condition of Experiment 1 participants imitated the experimenter while she positioned a pink or a yellow object on the horizontal or on the vertical line of the left- or the right-sided cross. (b) In the four-goal condition of Experiment 1 participants additionally had to tap the object on the circle the same number of times as the experimenter (one, two) before putting it on the cross. (c) In Experiment 2 the task required to grasp a highlighter using one of two possible finger configurations (thumb–index finger, thumb–middle finger), to tap its yellow or black end on the circle (in the three-goal condition there was always a single bounce; in the four-goal condition there could be one or two bounces) and to position it on the horizontal or on the vertical line of the cross.*

object was tapped once or twice on it before reaching the cross (goal movement). Pilot data indicated that the four-goal hierarchy was object > movement > orientation > location (all $p < .05$, Friedman and Wilcoxon tests). Introducing an additional goal added a cognitive load in the four-goal condition, which was hypothesized to make the goal hierarchy more evident, by affecting the low-end goal(s) more than the top-end goal(s). This goal was not included in the analyses. The experimenter's and the participant's movements were recorded by a digital video camera positioned 1 m away.

Procedure

Where possible, participants were asked to use their right hand to make mirror-image imitative responses (i.e., the experimenter's right side corresponding to the participant's left side) to the movements performed by the experimenter with her left hand. Two patients with left parietal damage and two with left frontal/fronto-temporal lesions were hemiplegic for their right upper limb and used their left arm for imitation. In these cases, the experimenter used her right hand to demonstrate the action. In face-to-face imitation, imitating the mirror-image hand is known to be easier than imitating the anatomically corresponding hand (Avikainen et al., 2003; Ishikura & Inomata, 1995). Each of the eight different movements resulting from the combination of the three target goals (object, orientation, location) was repeated 10 times, for a total of 80 trials. Each participant was given all the trials in the same random order during four sessions, according to the sequence A–B–B–A: 20 three-goal movements in the first session; 20 four-goal movements in the second session; 20 four-goal movements in the third session; 20 three-goal movements in the fourth session. In each session, participants were explicitly instructed about what the goals of the action were, and they were asked to wait until the experimenter put her object back into the initial position before starting their own action (no indications about speed of execution were given). In addition, they were given eight practice trials (one for each of the eight different movements resulting from the combination of the three target goals), which—if necessary—were repeated until all of them were performed correctly.

Performance evaluation

The number of correct responses in reproducing each of the three target goals was measured. For each goal, an error was counted every time the participant chose the other category (i.e., horizontal instead of vertical orientation). A second rater, blind to the purpose of the study, scored a sample of the data ($N = 3$). Interrater agreement was 99.7%. Data were analysed with the analysis of variance (ANOVA), and least significant difference (LSD) post hoc tests were used to investigate the significant effects. Table 1 reports the confidence intervals for each group mean.

Results and discussion

An ANOVA with condition (three-goal, four-goal) and goal (object, orientation, location) as within-subject factors and group (parietal,

Table 1. *Confidence intervals for each of the group means, Experiment 1*

		Goal					
		Object		*Orientation*		*Location*	
Condition	*Group*	*Lower bound*	*Upper bound*	*Lower bound*	*Upper bound*	*Lower bound*	*Upper bound*
3-goal	Parietal	39.7	40.0	34.9	38.4	38.0	40.3
	Frontal	39.8	40.2	37.6	41.7	38.4	41.0
	Control	39.8	40.2	37.4	40.9	37.4	39.6
4-goal	Parietal	39.2	40.1	28.4	34.1	32.6	37.2
	Frontal	38.8	39.9	35.9	42.4	32.8	38.2
	Control	39.5	40.5	36.5	42.2	36.4	41.1

frontal, control) as a between-subjects factor revealed a significant main effect of condition, goal, and group and significant Condition × Group, Goal × Group, Condition × Goal, and Condition × Goal × Group interactions. Overall, the parietal group was more impaired than both the frontal and the control groups, who did not differ from each other: main effect of group, $F(2, 19) = 5.6$, $p = .012$; parietal versus control, $p = .005$; parietal versus frontal, $p = .025$. Performance for each group was analysed separately (see Figure 2).

For the control group, there was only a significant main effect of goal, with the goal object being imitated significantly more accurately than the goal location: main effect of goal, $F(2, 14) = 3.8$, $p = .049$; object versus location, $p = .047$. The absence of any interaction between condition and goal indicated that the presence of the fourth goal (movement) made no difference to the hierarchy for the other goals, and from Figure 3 it appears that movement is higher in the goal hierarchy than is orientation or location.

For the parietal group, there was a significant main effect of condition and of goal, and a significant Condition × Goal interaction. The goal orientation was imitated significantly less accurately than the object and location goals: main

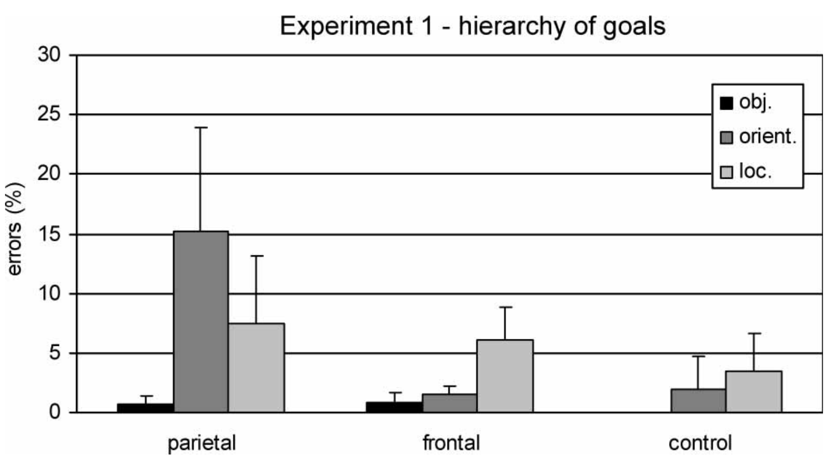


Figure 2. *Experiment 1: Percentage of errors made by each group of participants (parietal, frontal, control) for every target goal (object, orientation, location). Error bars represent standard deviations. The sum of the scores for the three-goal and four-goal conditions is shown (see Figure 3).*

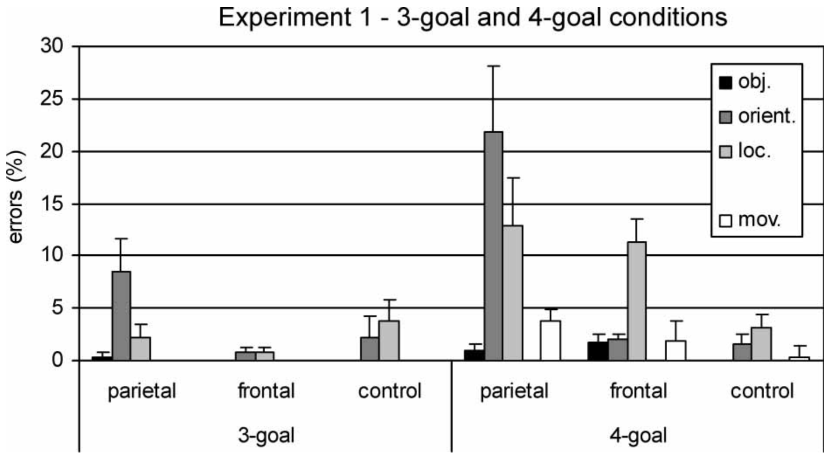


Figure 3. *Experiment 1. Percentage of errors made by each group of participants for every goal (object, orientation, location, movement) in the three-goal condition and in the four-goal condition. Error bars represent standard deviations.*

effect of goal, $F(2, 14) = 12.1$, $p = .001$; orientation versus object, $p = .007$; orientation versus location, $p = .015$. It is notable that orientation was imitated with lowest accuracy, despite the fact that this goal appeared in the middle of the hierarchy. As expected, the presence of an extra goal (in the four-goal condition) exacerbated the tendency for errors on goals lower in the hierarchy (orientation and location), but did not affect the error rate on the main goal (object).

For the frontal group, there was a significant main effect of condition and of goal and a significant Condition × Goal interaction. The goal location was reproduced significantly less accurately than the object and orientation goals: main effect of goal, $F(2, 10) = 9.7$, $p = .004$; location versus object, $p = .026$; location versus orientation, $p = .022$. Thus, unlike the parietal patients, the frontal patients had little difficulty imitating object orientation. This pattern was exacerbated in the four-goal condition, with significantly poorer performance only on object location.

Given that six of the patients in our parietal sample had left-side lesions we checked that the errors of the parietal group were not merely the result of ideomotor apraxia, which would cause them difficulties in the imitation of body postures (i.e., in reproducing the finger configuration necessary to "orient" the object in a particular way). Therefore, we administered to all our participants the 24-items test ideated by De Renzi, Motti, and Nichelli (1980) to assess the presence of ideomotor apraxia. We compared the scores obtained by our two groups of patients (frontal, parietal) with an independent samples t test. Results show that there was no difference between the two groups in their ability to imitate gestures, $t(12) = 1.5$, $p = .169$. A differential level of clinical apraxia was not responsible for the pattern of performance in the parietal patients. The data also remained the same when the one parietal patient who showed some deficit on orientation judgements when initially tested was removed.

These data suggest that the parietal patients of our sample were impaired in the imitation of orientation, and this was not due to a difficulty in effecting motor responses, a problem due to ideomotor apraxia, or to a problem in perceptual judgements of orientation when that was the main task (e.g., on the BORB test). The aim of Experiment 2 was to investigate whether these same patients can imitate orientation if the task is set up in such a way that orientation occupies the main goal of the action's goal hierarchy.

EXPERIMENT 2

Method

Participants

A total of 8 patients with parietal lesions (5 with left, 3 with right lesions; 1 female, 6 males; mean age 66.3 years, range 51–85 years), 5 patients with frontal and/or fronto-temporal lesions (1 with left, 2 with right, and 2 with bilateral lesions; all males; mean age 57.4 years, range 32–74 years), and 8 healthy controls (5 females, 3 males; mean age 56.5 years, range 52–61 years) took part in this study (see Appendix).

Apparatus

The experimenter and the participant sat face to face at opposite sides of a table. They each had in front of them a yellow pen with a black cap and an A4 sheet of paper looking like the example shown in Figure 1c. In the three-goal condition, the participant was asked to imitate the experimenter while she took the highlighter with her thumb and either her index finger or middle finger (goal finger) and, after bumping once its yellow or black end (goal direction) on the circle drawn on the sheet of paper, put it onto the cross following the horizontal or the vertical orientation (goal orientation). As in Experiment 1, orientation was the last goal of the action to be performed by the experimenter. We carried out a pilot study on a sample of undergraduate students ($N = 15$), and we used error rates as a measure of goal importance (i.e., the lowest error rate corresponded to the highest position within the action goal hierarchy). Results confirmed our predictions by indicating that the hierarchy for this action was orientation > direction > finger (all $p < .05$, Friedman and Wilcoxon tests). In the four-goal condition, the object had to bounce once or twice on the circle before reaching the cross (goal movement). Pilot data suggested that the hierarchy for this action was orientation > movement > direction > finger (all $p < .05$, Friedman and Wilcoxon tests). The experimenter's and the participant's movements were recorded by a digital video camera positioned 1 m away.

Procedure

Where possible, participants were asked to use their right hand to make mirror-image imitative responses to the movements performed by the experimenter (i.e., the experimenter's right side corresponding to the participant's left side). One patient with left parietal damage and two with left frontal/fronto-temporal lesions were hemiplegic for their right upper limb and used their left arm for imitation. Each of the eight different movements resulting from the combination of the three target goals (orientation, direction, finger) was repeated 10 times, for a total of 80 trials. Each participant was given all the trials in the same random order during two sessions, according to the sequence AB–BA: 20

Table 2. *Confidence intervals for each of the group means, Experiment 2*

		Goal					
		Orientation		*Direction*		*Finger*	
Condition	*Group*	*Lower bound*	*Upper bound*	*Lower bound*	*Upper bound*	*Lower bound*	*Upper bound*
3-goal	Parietal	33.0	38.0	35.4	39.1	22.7	31.1
	Frontal	30.9	37.1	34.6	39.4	23.5	34.1
	Control	33.0	38.0	35.4	39.1	22.7	31.1
4-goal	Parietal	36.7	39.3	30.7	38.3	22.0	32.1
	Frontal	32.9	36.3	30.4	40.0	19.6	32.4
	Control	36.7	39.3	30.7	38.3	22.0	32.1

three-goal movements followed by 20 four-goal movements in the first session; 20 four-goal movements followed by 20 three-goal movements in the second session. In each session, participants were explicitly instructed about what the goals of the action were, and they were asked to wait until the experimenter put her object back into the initial position before starting their own action (no indications about speed of execution were given). In addition, they were given eight practice trials (one for each of the eight different movements resulting from the combination of the three target goals), which—if necessary—were repeated until all of them were performed correctly.

Performance evaluation

The number of correct responses in reproducing each of the three target goals was measured. For each goal, an error was counted every time the participant chose the other category (i.e., horizontal instead of vertical orientation). A second rater, blind to the purpose of the study, scored a sample of the data ($N = 3$). Interrater agreement was 98.8%. Data were analysed with the ANOVA, and LSD post hoc tests were used to investigate the significant effects. Table 2 reports the confidence intervals for each group mean.

Results and discussion

An ANOVA with condition (three-goal, four-goal) and goal (orientation, direction, finger) as within-subjects factors and group (parietal, frontal, control) as a between-subjects factor revealed a significant main effect of goal and of group and significant Goal × Group and Condition × Goal interactions. Overall, the control group performed more accurately than both the frontal and the parietal groups, who did not differ from each other: main effect of group, $F(2, 18) = 8.0$, $p = .003$; parietal versus control, $p = .003$; frontal versus control, $p = .003$. Performance for the two patient groups was analysed separately (see Figure 4).

For the control group, there were no significant effects. Although not statistically reliable, the direction of the data was that, in this task, orientation was the main goal of the hierarchy, direction the middle goal, and finger the lowest goal. Figure 5 shows that, in the four-goal condition, the additional goal (movement) occupied the second highest position in the goal hierarchy. These results are consistent with the goal hierarchy observed in the pilot study.

For the parietal group, there was a significant main effect of goal, with the goal finger being imitated significantly less accurately than the

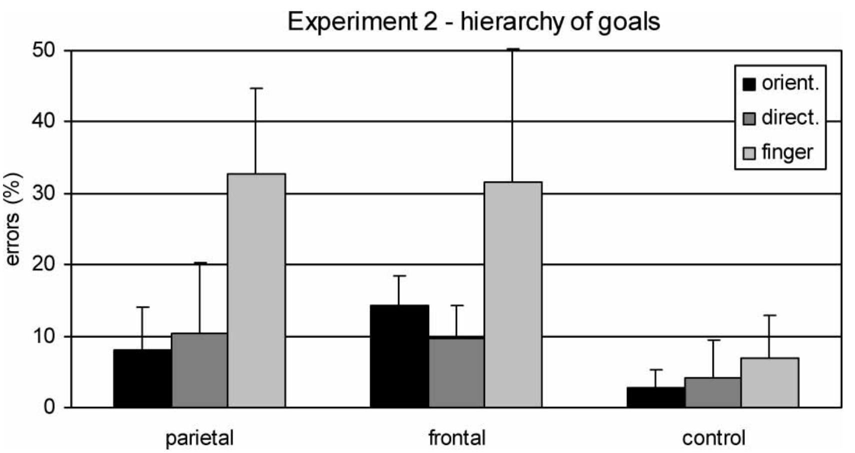


Figure 4. *Experiment 2. Percentage of errors made by each group of participants (parietal, frontal, control) for every target goal (orientation, direction, finger). Error bars represent standard deviations. The sum of the scores for the three-goal and four-goal conditions is shown (see Figure 5).*

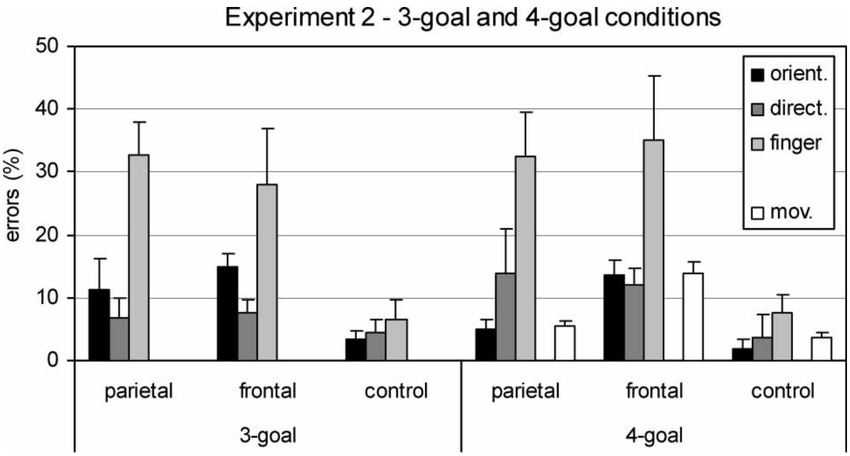


Figure 5. *Experiment 2. Percentage of errors made by each group of participants for every goal (orientation, direction, finger, movement) in the three-goal condition and in the four-goal condition. Error bars represent standard deviations.*

orientation and the direction goals, which tended to occupy higher positions in the hierarchy: main effect of goal, $F(2, 14) = 18.8$; finger versus orientation, $p < .001$; finger versus direction, $p = .004$.

For the frontal group, again, there were no significant effects.

Performance was worse and less consistent in Experiment 2 than in Experiment 1 for each of the groups. This might be because there was only one object and one location in Experiment 2 (as opposed to two objects and two locations in Experiment 1). This might have made the goals more easily confusable in Experiment 2. Furthermore, selection of the finger was relatively difficult for most patients irrespective of the location of their brain lesion, and it was consequently often ignored. Most importantly, however, these results clearly show that parietal patients were no more impaired than frontal patients at imitating orientation when orientation was the main goal of the action. Also, this successful imitation of orientation excludes the possibility that the impairment of the same patients in Experiment 1 was due to a difficulty in reproducing the finger configuration required to orient objects in the appropriate way, nor could the difficulty in Experiment 1 be attributed to a core impairment in coding object orientation per se. The parietal patients have difficulty in reproducing object orientation in imitative action only when orientation in represented at a low level in a goal hierarchy.

GENERAL DISCUSSION

We asked participants to imitate actions where object orientation was one of the action goals, and, in two experiments, we differentially manipulated the position of orientation coding in an action goal hierarchy. In Experiment 1 orientation was the intermediate goal in the hierarchy, and parietal patients were selectively impaired in reproducing it compared to healthy and brain-damaged control groups. Moreover, for the parietal group only, the number of correct responses for object orientation significantly worsened from the three-goal to the four-goal condition—that is, when an extra goal (higher than orientation in the goal hierarchy) was introduced in the action to be imitated. These results confirm that patients with parietal lesions are vulnerable to deficits in orientation processing (Darling et al., 2003; Harris et al., 2001; Jeannerod, 1986; Perenin & Vighetto, 1988; Turnbull et al., 1995), while further suggesting that such deficits in action can be determined by the position of orientation-dependent actions in a goal hierarchy. Indeed, Experiment 2 showed that, when object orientation was the main goal of the action's goal hierarchy, the parietal patients were able to reproduce orientation-dependent actions at the same level as were the brain-damaged control participants (if anything, frontal patients' performance was slightly worse). Thus the results cannot be accounted for by a deficit in low-level processes concerned with orientation perception (see also Appendix for confirmatory data). Also, our screening data (NART and Brixton) indicated that the groups did not differ in general intellectual or executive function, suggesting that the deficit for the parietal patients in Experiment 1 was linked to the representation of orientation in a goal hierarchy.

We propose that this difference in imitative performance between Experiments 1 and 2 was a consequence of our manipulation of the cognitive load placed on orientation in the two tasks, reflecting the different position that orientation held in the goal hierarchy across the studies: In Experiment 2 orientation occupied the top-end position of the hierarchy, while in Experiment 1 it occupied an intermediate position. When orientation was represented at a low level in an action hierarchy, we suggest that there is reduced attentional weight allocated to actions (cf. Duncan & Humphreys, 1989), and for patients with parietal lesions the reduction in attentional weight is particularly pronounced on reproducing object orientation. This was not due to a basic problem in orientation perception at the time of testing (see Appendix), but reflects the vulnerability to parietal damage for representations of object orientation for action, when there is reduced attention.

It should be noted that some of the tasks used previously to examine orientation processing in parietal patients involved perception only or action only. In contrast, the current task required visual perception while observing the experimenter, remembering the actions performed, and then imitation of those actions. Within the imitation paradigm, results similar to those reported here were observed by Bekkering and colleagues (Bekkering et al., 2005) in a group of ideomotor apraxic patients, who could imitate finger movements only when they constituted the main goal of the action. Because their study focused on ideomotor apraxia, patients were divided into groups according to the presence of a left- or right-sided lesion and of ideomotor apraxia. In contrast to this, our patients had specific parietal lesions, and they did not suffer from ideomotor apraxia. Also, in the Bekkering et al. (2005) study, the task in which finger selection was the main goal and the task where it was a secondary goal were not carefully matched for the number of action goals, and, in addition, the exact position of the target goal within the goal hierarchy of the action was not specified. Our study takes into account these variables and clearly shows that the parietal patients were able to process orientation sufficiently to place it within the goal hierarchy of an action and to reproduce it accurately when it was at the top-end of the goal hierarchy. Their difficulties in processing object orientation showed only when orientation was not the most relevant aspect of the action to be imitated. In such cases there is not an absolute deficit in basing actions on object orientation; rather the deficit is contingent on the location of orientation in the hierarchy of action. This in turn may reflect the allocation of attentional resources during imitation, with fewer resources being allocated to actions further down the goal hierarchy. Parietal patients' deficit in processing object orientation emerges when relatively few resources are allocated to this attribute of objects.

First published online 21 February 2008

REFERENCES

Avikainen, S., Wohlschläger, A., Liuhanen, S., Hänninen, R., & Hari, R. (2003). Impaired mirror-image imitation in Asperger and high-functioning autistic subjects. *Current Biology*, *13*, 339–341.

Balint, R. (1909). Seelenlähmung des "Schauens", optische Ataxie, räumliche Störung der Aufmerksamkeit [Psychic paralysis of gaze, optic ataxia, and spatial disorder of attention]. *Monatschrift für Psychiatrie und Neurologie*, *25*, 51–181.

Bekkering, H., Brass, M., Woschina, S., & Jacobs, A. M. (2005). Goal-directed imitation in patients with ideomotor apraxia. *Cognitive Neuropsychology*, *22*, 1–14.

Bekkering, H., Wohlschläger, A., & Gattis, M. (2000). Imitation of gestures in children is goal-directed. *The Quarterly Journal of Experimental Psychology*, *53*, 153–164.

Benson, D. F., & Greenberg, J. P. (1969). Visual form agnosia: A specific deficit in visual discrimination. *Archives of Neurology*, *20*, 82–89.

Burgess, P. W., & Shallice, T. (1997). *The Hayling and Brixton tests*. Bury St. Edmunds, UK: Thames Valley Test Co.

Buxbaum, L. J., Kyle, K., Grossman, M., & Coslett, H. B. (2007). Left inferior parietal representations for skilled hand–object interactions: Evidence from stroke and corticobasal degeneration. *Cortex*, *43*, 411–423.

Cooper, A. C. G., & Humphreys, G. W. (2000). Task-specific effects of orientation information: Neuropsychological evidence. *Neuropsychologia*, *38*, 1607–1615.

Cuijpers, R. H., van Schie, H. T., Koppen, M., Erlhagen, W., & Bekkering, H. (2006). Goals and means in action observation: A computational approach. *Neural Networks*, *19*, 311–322.

Culham, J. C., & Kanwisher, N. G. (2001). Neuroimaging of cognitive functions in human parietal cortex. *Current Opinion in Neurobiology*, *11*, 157–163.

Darling, W. G., Pizzimenti, M. A., & Rizzo, M. (2003). Unilateral posterior parietal lobe lesions affect representation of visual space. *Vision Research*, *43*, 1675–1688.

De Renzi, E., Faglioni, P., Lodesani, M., & Vecchi, A. (1983). Performance of left brain-damaged patients on imitation of single movements and motor sequences. Frontal and parietal-injured patients compared. *Cortex*, *19*, 333–343.

De Renzi, E., Faglioni, P., & Sorgato, P. (1982). Modality-specific and supramodal mechanisms of apraxia. *Brain*, *105*, 301–312.

De Renzi, E., Motti, F., & Nichelli, P. (1980). Imitating gestures: A quantitative approach to ideomotor apraxia. *Archives of Neurology*, *37*, 6–10.

Duncan, J., & Humphreys, G. W. (1989). Visual search and stimulus similarity. *Psychological Review*, *96*, 433–458.

Gado, M., Hanaway, J., & Frank, R. (1979). Functional anatomy of the cerebral cortex by computed tomography. *Journal of Computer Assisted Tomography*, *3*, 1–19.

Gleissner, B., Meltzoff, A. N., & Bekkering, H. (2000). Children's coding of human action: Cognitive factors influencing imitation in 3-year-olds. *Developmental Science*, *3*, 405–414.

Goldenberg, G. (1995). Imitating gestures and manipulating a manikin—the representation of the human body in ideomotor apraxia. *Neuropsychologia*, *33*, 63–72.

Goodale, M. A., & Humphrey, G. K. (1998). The objects of action and perception. *Cognition*, *67*, 181–207.

Goodale, M. A., Jakobson, L. S., & Keillor, J. M. (1994). Differences in the visual control of pantomimed and natural grasping movements. *Neuropsychologia*, *32*, 1159–1178.

Haaland, K. H., Harrington, D. L., & Knight, R. T. (1999). Spatial deficits in ideomotor limb apraxia: A kinematic analysis of aiming movements. *Brain*, *122*, 1169–1182.

Hamilton, A. F. de C., & Grafton, S. T. (2006). Goal representation in human anterior intraparietal sulcus. *The Journal of Neuroscience*, *26*, 1133–1137.

Harris, I. M., Harris, J. A., & Caine, D. (2001). Object orientation agnosia: A failure to find the axis? *Journal of Cognitive Neuroscience*, *13*, 800–812.

Heilman, K. M., & Rothi, L. J. G. (1993). Apraxia. In K. M. Heilman & E. Valenstein (Eds.), *Clinical neuropsychology* (pp. 141–164). New York: Oxford University Press.

Himmelbach, M., & Karnath, H.-M. (2005). Dorsal and ventral stream interaction: Contributions from optic ataxia. *Journal of Cognitive Neuroscience*, *17*, 632–640.

Ishikura, T., & Inomata, K. (1995). Effects of angle of model demonstration on learning of motor skill. *Perceptual and Motor Skills*, *80*, 651–658.

Jeannerod, M. (1986). The formation of finger grip during prehension: A cortically mediated visuomotor pattern. *Behavioural Brain Research*, *19*, 99–116.

Jeannerod, M., Decety, J., & Michel, F. (1994). Impairment of grasping movements following a bilateral posterior parietal lesion. *Neuropsychologia*, *32*, 369–380.

Kolb, B., & Milner, B. (1981). Performance of complex arm and facial movements after focal brain lesions. *Neuropsychologia*, *19*, 491–503.

Liepmann, H. (1900). Das Krankheitsbild der Apraxie (motorischen Asymbolie) [The syndrome of apraxia (motor asymbolia)]. *Monatschrift für Psychiatrie und Neurologie*, *8*, 15–44, 102–132, 188–197.

Milner, A. D. (1997). Vision without knowledge. *Philosophical Transactions of the Royal Society of London, Series B, Biological Sciences*, *352*, 1249–1256.

Milner, A. D., & Goodale, M. A. (1995). *The visual brain in action*. Oxford, UK: Oxford University Press.

Milner, A. D., Paulignan, Y., Dijkerman, H. C., Michel, F., & Jeannerod, M. (1999). A paradoxical improvement of misreaching in optic ataxia: New evidence for two separate neural systems for visual localization. *Proceedings of the Royal Society of London, Series B, Biological Sciences*, *266*, 2225–2229.

Milner, A. D., Perrett, D. I., Johnston, R. S., Benson, P. J., Jordan, T. R., Heeley, D. W., et al. (1991). Perception and action in visual form agnosia. *Brain*, *114*, 405–428.

Nelson, H. E., & Willison, J. R. (1991). *Restandardisation of the NART against the WAIS–R*. Windsor, UK: NFER Nelson.

Perenin, M. T., & Vighetto, A. (1988). Optic ataxia: A specific disruption in visuomotor mechanisms. I. Different aspects of the deficit in reaching for objects. *Brain*, *111*, 643–674.

Riddoch, M. J., & Humphreys, G. W. (1993). *The Birmingham Object Recognition Battery (BORB)*. Hove, UK: Lawrence Erlbaum Associates Ltd.

Riddoch, M. J., Humphreys, G. W., Jacobson, S., Pluck, G., Bateman, A., & Edwards, M. G. (2004). Impaired orientation discrimination and localization following parietal damage: On the interplay between dorsal and ventral processes in visual perception. *Cognitive Neuropsychology*, *21*, 597–624.

Rossetti, Y., & Pisella, L. (2002). Several "vision for action" systems: A guide to dissociating and integrating dorsal and ventral functions. In W. Prinz & B. Hommel (Eds.), *Attention and performance XIX* (pp. 62–119). Oxford, UK: Oxford University Press.

Rothi, L. J. G., Ochipa, C., & Heilman, K. M. (1991). A cognitive neuropsychological model of limb apraxia. *Cognitive Neuropsychology*, *8*, 443–458.

Rothi, L. J. G., Raymer, A. M., & Heilman, K. M. (1997). Limb praxis assessment. In L. J. G. Rothi & K. M. Heilman (Eds.), *Apraxia: The neuropsychology of action* (pp. 61–73). Hove, UK: Psychology Press.

Sunderland, A. (2007). Impaired imitation of meaningless gestures in ideomotor apraxia: A conceptual problem not a disorder of action control? A single case investigation. *Neuropsychologia*, *45*, 1621–1631.

Turnbull, O. H., Laws, K. R., & McCarthy, R. A. (1995). Object recognition without knowledge of object orientation. *Cortex*, *31*, 387–395.

Ungerleider, L. G., & Mishkin, M. (1982). Two cortical visual systems. In D. J. Ingle, M. A. Goodale, & R. J. W. Mansfield (Eds.), *Analysis of visual behaviour* (pp. 549–586). Cambridge, MA: MIT Press.

van Schie, H. T., & Bekkering, H. (2007). Neural mechanisms underlying immediate and final action goals in object use reflected by slow wave brain potentials. *Brain Research*, *1148*, 183–197.

Whiten, A., Flynn, E., Brown, K., & Lee, T. (2006). Imitation of hierarchical action structure by young children. *Developmental Science*, *9*, 574–582.

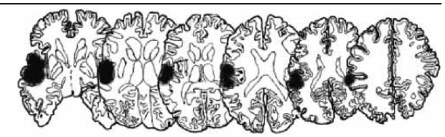
Wohlschläger, A., & Bekkering, H. (2002). Is human imitation based on a mirror-neurone system? Some behavioural evidence. *Experimental Brain Research*, *143*, 335–341.

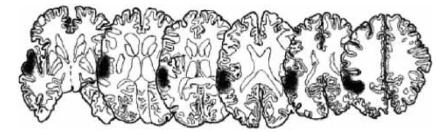
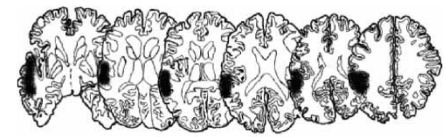
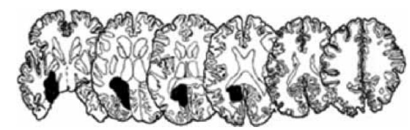
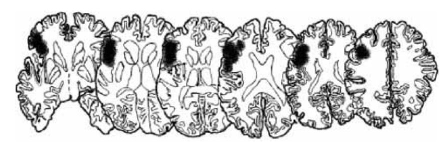
Wohlschläger, A., Gattis, M., & Bekkering, H. (2003). Action generation and action perception in imitation: An instance of the ideomotor principle. *Philosophical Transactions of the Royal Society of London, Series B, Biological Sciences*, *358*, 501–515.

APPENDIX

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

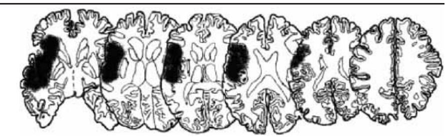
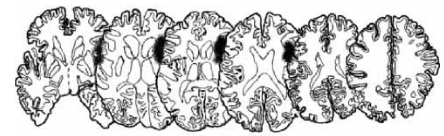
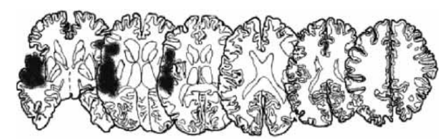
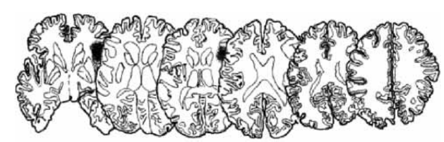
Lesions have been drawn onto standard slices from Gado, Hanaway, and Frank (1979). The bottom figure shows the 10 slices used. Only Slices 3 to 8 are depicted here. The left of each slide represents the left hemisphere. For the Birmingham Object Recognition Battery (BORB) test, the control mean = 24.8/30, SD = *2.6.*

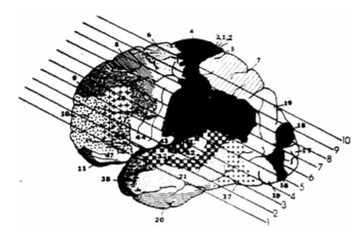
Group	*Patient*	*Sex*	*Age*[a]	*Handedness*	*Main lesion site (aetiology, years post lesion)*	*BORB orientation perception score*[d]	*Brixton Test*	*NART*	*Lesion reconstruction from MRI scan*
Parietal	D.B.	M	69	R	Left angular gyrus, left superior and middle temporal gyri (stroke, 7)	26	20	95	
	F.L.	M	68	R	Left intraparietal sulcus, bilateral occipital gyrus, lenticular nuclei (carbon monoxide poisoning, 8)	23	25	90	
	J.B.[b]	F	69	R	Right angular and supramarginal gyri, right inferior frontal and postcentral gyri (stroke, 4)	6	20	105	
	M.H.	M	51	R	Left angular and supramarginal gyri, lentiform nucleus (anoxia, 8)	23	34	104	
	M.P.	M	58	R	Right angular and supramarginal gyri, right superior temporal, inferior frontal and postcentral gyri (stroke, 8)	24	21	108	

	P.F.	F	56	R	Left angular and supramarginal gyri, left superior temporal gyrus (stroke, 6)	25	31	110	
	R.H.	M	71	L	Left angular and supramarginal gyri, left superior temporal gyrus (stroke, 6)	24	32	85	
	S.B.[c]	M	85	R	Left temporo-parietal region (stroke, 2)	25	Not tested	90	Scan not available
	T.P.[b]	M	83	R	Left medial occipital, posterior parietal and medial temporal regions (stroke, 5)	27	26	Not tested	
	W.W.[c]	M	72	R	Right posterior and inferior parietal cortex including the angular gyrus (stroke, 3)	28	12	110	
Frontal	D.S.	M	68	R	Left inferior, middle and superior frontal gyri (stroke, 6)	25	20	105	
	G.A.	M	50	R	Bilateral medial and anterior temporal lobes, extending into the left medial frontal region (herpes simplex encephalitis, 10)	25	20	103	

(*Continued overleaf*)

Appendix (Continued)

Group	*Patient*	*Sex*	*Age*[a]	*Handedness*	*Main lesion site (aetiology, years post lesion)*	*BORB orientation perception score*[d]	*Brixton Test*	*NART*	*Lesion reconstruction from MRI scan*
	P.H.	M	32	R	Left medial and superior temporal gyri, left inferior and middle frontal gyri (stroke, 4)	28	12	80	
	P.W.	M	73	R	Right inferior and middle frontal gyri, right superior temporal gyrus (stroke, 1)	26	30	92	
	S.P.[b]	M	51	R	Left medial frontal region, bilateral medial and anterior temporal lobes (herpes simplex encephalitis, 4)	27	20	110	
	W.B.A.	M	59	R	Right inferior and middle frontal gyri, right superior temporal gyrus (stroke, 2)	26	26	115	



Note: M = male. F = female. R = right. L = left.
[a] In years. [b] Patients J.B., T.P., and S.P. took part only in Experiment 1. [c] Patients S.B. and W.W. took part only in Experiment 2. [d] $N = 30$.