Neural basis of pantomiming the use of visually presented objects

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Neuropsychological studies of patients suffering from apraxia strongly imply a left hemisphere basis for skilful object use, the neural mechanisms of which, however, remain to be elucidated. We therefore carried out a PET study in 14 healthy human volunteers with the aim to isolate the neural mechanisms underlying the sensorimotor transformation of object-triggers into skilled actions. We employed a factorial design with two factors (RESPONSE: naming, pantomiming; and TRIGGER: actions, objects) and four conditions (IA: imitating the observed pantomime; IO: pantomiming the use of the object shown; NA: naming the observed pantomime; NO: naming the object shown). The design thus mainly aims at investigating the interaction [i.e. (IO–IA)–(NO–NA)] which allows the assessment of increased neural activity specific to the sensorimotor transformation of object-triggers into skilled actions. The results (P < 0.05, corrected) showed that producing a wide range of skilled actions triggered by objects (controlled for perceptual, motor, semantic, and lexical effects) activated left inferior parietal cortex. The data provide an explanation for why patients with lesions including left parietal cortex suffer from ideomotor and ideational apraxia. One group of authors has adhered to Liepmann’s original suggestion that one should distinguish between ideomotor and ideational apraxia. Patients with ideational apraxia suffer from a deficit of performing object-related skilled actions (De Renzi and Lucchelli, 1988; De Renzi et al., 1968; Lehmkuhl and Poeck, 1981).

Acquiring skills in object use involves a variety of aspects. In many cases such as driving a car, it requires the development of a complex hierarchy of control structures, (which incidentally may also be present in apes, see Byrne, 2002). In others, such as those involved in many sports, exquisite timing in response to external triggers must be attained (see, e.g., McLeod, 1987). In yet others such as those needed in carpentry, it requires knowledge of naïve physics (Goldenberg and Hagmann, 1998). One key ability common to all these skilful actions is, however, to acquire a set of routines each corresponding to specific learned components of a skill. In a more theoretical language, these routines could correspond to specific sets of parameter settings within a general system for the control of action, such as that suggested by Wolpert and Ghahramani (2000). A second key ability is to be able to elicit each of these components by a specific perceptual trigger (or triggers). When, for instance, a patient is presented with an object, and asked to use it (or to pantomime its use), he or she must have learned both the appropriate movement and its eliciting condition. For the second of these key abilities, it is well established that even low-level (visual) object characteristics may help to elicit an action appropriate to an object—Gibson’s (1979) concept of affordance. In humans, the existence of such object-triggered affordances is supported by both experimental (Rumiati and Humphreys, 1998; Tucker and Ellis, 1998) and neuropsychological (Humphreys and Riddoch, 2002; Riddoch and Humphreys, 1998) evidence. Object-specific triggering cannot, however, just depend upon the low-level visual characteristics of objects; just consider the actions elicited by an electric plug, an electric iron, and so on.

The conceptual framework of Norman and Shallice (1980) extends the affordance concept by postulating the existence of an object trigger system which activates specific action schemata. A basic biased competition mechanism—called contention schedul-
ing and implemented in Cooper and Shallice (2000)—then allows routine actions to be produced without conflict by activating relevant and inhibiting irrelevant schemata at appropriate times set by environmental triggers. Thus, a neuropsychological deficit observed in patients with left hemisphere lesions who show ideational apraxia (defined as a selective deficit in performing highly practiced actions involving objects; De Renzi and Lucchelli, 1988; Liepmann 1905; Rumiati et al., 2001) can be interpreted as damage to or a disconnection between components of this system.

The complexity of the set of processes involved in the production of skilled actions is very difficult to analyze by standard lesion methods as complex skillful actions depend upon and modulate the already complex set of processes required in more basic visuomotor operations. In addition, neuropsychological attempts to analyze the neural basis of skillful object use have proved difficult because patients tend to have rather large lesions and additional deficits, for example, impaired imitation of actions, action or object agnosia, or aphasia. This neuropsychological dilemma (see Marshall and Fink, 1995) provides a special opportunity to use functional imaging to elucidate the organization of these subsystems which when damaged give rise to the relevant neuropsychological disorders. So far, however, functional imaging of object use has been limited to a highly restricted set of very simple actions such as grasping (Grafton et al., 1996a), also using various forms of grip (Grezes et al., 2003), the manipulation of meaningless objects (Binkofski et al., 1999; Grekes et al., 2002), learning of one specific set of movements (Jenkins et al., 1994; Stephan et al., 1995), or has used the analogy of “mental simulation” of the actions (Decety et al., 1994; Grafton et al., 1996b; Stephan et al., 1995).

In this paper, we primarily aim at investigating whether there is evidence for specific mechanisms underlying the triggering of actions by objects. This is strongly suggested by neuropsychological evidence of utilization behavior following medial prefrontal lesions (Lhermitte, 1983; Shallice et al., 1989). However, the locus of lesions which give rise to such effects—medial prefrontal cortex (see De Renzi and Barbieri, 1992)—corresponds to the impairment of parts of a Supervisory System which inhibits any such behavior rather than of the trigger system itself. It is therefore not relevant for localizing the trigger system. Based on animal neurophysiological data (Rizzolatti et al., 1997; Sakata et al., 1995; Taira et al., 1990), functional imaging studies (Binkofski et al., 1999; Grafton et al., 1996a; Grekes et al., 2002) and, to some extent, neuropsychological studies of patients suffering from ideational apraxia (De Renzi and Lucchelli, 1988; Rumiati et al., 2001), a more plausible hypothesis for the locus of the trigger system for action schemata, could be left inferior parietal cortex.

A major technical problem when employing functional magnetic resonance imaging to study the neural mechanisms underlying skillful actions is the production of movement artifacts as a result of performing the task. This has led some investigators to use tasks in which subjects are required to imagine performing the action (Decety et al., 1994; Grafton et al., 1996b). In contrast, PET is less sensitive to movement artifacts and thus allows the assessment of proper skillful actions in the scanner. We accordingly performed a study in which normal volunteers produced 90 different skillful object-related pantomimes while lying in a PET scanner. We used pantomiming of object and tool use (rather than actual object and tool use) as this task predicts well and correlates with performance on actual object and tool use in apraxia (De Renzi and Lucchelli, 1988; Goldenberg and Hagmann, 1998), but avoids practical problems such as object placement in the subjects’ hands which causes difficulties in the scanning environment (e.g. timing, the necessity to have another person in the scanning room, etc.). In addition, it has been established in neuroimaging studies that the mere viewing of objects affords actions that can be performed with them (Grèzes and Decety, 2002). To isolate the neural mechanisms specific to object-triggered action schemata and their selection, we employed a factorial design with two factors (RESPONSE: naming, pantomiming; and TRIGGER: pantomimes, objects) and four conditions (IA: imitating the observed pantomime; IO: pantomiming the use of the object shown; NA: naming the observed pantomime; NO: naming the object shown). This contrast between object-triggering of an action and imitation is somewhat analogous to the procedure used for different forms of grip by Grezes et al. (2003). The design controls for the perceptual, semantic, lexical, and sensorimotor aspects of both object- and action-related processing. The experimental design specifically focuses on the selection of the action i.e. (IO—IA)−(NO−NA) which allows the assessment of increased neural activity specific to the selection of action schemata triggered by objects.

Materials and methods

Subjects

Fourteen healthy right-handed males volunteers (mean age 26.14 ± 6.05 years) with no history of neurological or psychiatric illness gave informed consent. Handedness was assessed by the Edinburgh Inventory test (Oldfield, 1971). The study was approved by the ethics committee of the University Hospital of the RWTH—Aachen, Germany.

Experimental design and stimuli

A factorial design with the factors TRIGGER (objects and actions) and RESPONSE (pantomiming and naming) was employed. This results in four conditions: (i) IA, imitating the action observed; (ii) IO, pantomiming the use of the object shown; (iii) NA, naming the pantomime observed; and (iv) NO, naming the object shown. In the ‘action performance’ conditions, subjects were asked either to imitate the pantomime shown (IA) or to pantomime an action specific to the object shown (IO) with their right hand or arm. Like language, high-level motor control is a left-hemisphere cognitive ability so that when a lesion occurs in the left hemisphere, an apraxic deficit of both upper limbs is often observed in right-hand patients (De Renzi et al., 1968, 1982; Heilman, 1997; Liepmann, 1905). This implies that to study the neural basis of pantomiming and object use, it should be sufficient to test one hand. In the ‘naming’ conditions, subjects were asked to name either the pantomime (NA) or the object (NO) shown. Videotapes were used for displaying the triggers (pantomimes, objects) on a Video Display Unit (VDU) installed straight ahead of the subjects within reaching distance (eye-to-monitor distance 0.7 m; horizontal visual angle: 27°; visual vertical angle: 21°). The triggers (i.e. objects and pantomimes) were displayed with a visual angle of 18° in the vertical and horizontal plane. Object stimuli included manipulable items such as iron, toothpaste and jug, and tools such as screwdriver, bottle opener and paint roller. The pantomimes used as stimuli were movements that we would perform had we such objects and tools in hand. For each rCBF measurement, subjects first viewed a white screen for 15 s,
followed by the stimulus sequence which lasted 90 s. Each trigger was presented for 2.5 s followed by an inter-stimulus-interval (ISI) of 0.5 s. Thus, 30 stimuli were shown during each rCBF measurement. A black fixation cross was superimposed on the screen throughout the experiment to prevent differences in eye movements across the different conditions. Videotape recordings were performed online throughout the experimental sessions to monitor subjects’ responses and thus allow for off-line performance analyses. For analysis of differential eye movements across conditions, eye movements were recorded during the rCBF measurements using an infrared device (iView-system SMI, Teltow, Germany).

**PET hardware and procedures**

Measurements of regional cerebral blood flow (rCBF) were taken using an ECAT HR+PET-scanner (CTI-Siemens) and 15O-butanol using standard technology and procedures previously described in detail (see, e.g., Weiss et al., 2000, 2003). Subjects laid comfortably in the PET scanner. An intravenous cannula was placed in their left cubital vein for injection of the radioactive tracer. Twelve PET scans with three repeats per condition were carried out for each subject thus resulting in a total of 168 observations (12 rCBF scans per subject, 14 subjects). The order of rCBF measurements was counterbalanced within and across subjects.

**Imaging processing and statistical analysis**

Following standard image preprocessing (including image realignment, image normalization into standard stereotactic space, and smoothing), statistical analyses were performed using SPM99, (http://www.fil.ion.ucl.ac.uk/spm). For each pixel, across all subjects and all scans, the mean relative rCBF values were calculated separately for each of the main effects. Comparisons of the means were made using the $t$ statistic and thereafter transformed into normally distributed $Z$ statistics. The resulting set of $Z$ values constituted a statistical parametric map (SPM$_{(Z)}$ map). For the contrasts of interest, the significance of these statistical parametric maps was assessed by comparing the expected and observed distribution of the $t$ statistic under the null hypothesis of no differential activation effect on rCBF. Only activations that were significant at $P < 0.05$ (corrected for multiple comparisons across the entire brain volume) or better are reported.

### Table 1

<table>
<thead>
<tr>
<th>Region</th>
<th>Side</th>
<th>$X$</th>
<th>$Y$</th>
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<tbody>
<tr>
<td>Pantomiming &gt; naming</td>
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<td></td>
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<tr>
<td>(IA + IO &gt; NA + NO)</td>
<td></td>
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<tr>
<td>Motor cortex</td>
<td>L</td>
<td>–30</td>
<td>–22</td>
<td>66</td>
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<tr>
<td>Supplementary motor area</td>
<td>L</td>
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<td>–14</td>
<td>54</td>
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<tr>
<td>Cerebellum</td>
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<td>–50</td>
<td>–24</td>
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<tr>
<td>Inferior parietal cortex (BA 40)</td>
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<td>–30</td>
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<tr>
<td>Frontal operculum</td>
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<td>48</td>
<td>2</td>
<td>8</td>
<td>5.7</td>
</tr>
<tr>
<td></td>
<td>L</td>
<td>–44</td>
<td>–2</td>
<td>4</td>
<td>9.6</td>
</tr>
<tr>
<td>Dorsolateral prefrontal cortex</td>
<td>L</td>
<td>–34</td>
<td>34</td>
<td>30</td>
<td>7.6</td>
</tr>
<tr>
<td>Lateral ventral premotor cortex</td>
<td>R</td>
<td>56</td>
<td>8</td>
<td>20</td>
<td>5.0</td>
</tr>
<tr>
<td></td>
<td>L</td>
<td>–54</td>
<td>6</td>
<td>30</td>
<td>6.2</td>
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<tr>
<td>Temporo-occipital junction (V5)</td>
<td>R</td>
<td>48</td>
<td>–58</td>
<td>14</td>
<td>5.0</td>
</tr>
<tr>
<td></td>
<td>L</td>
<td>–56</td>
<td>–68</td>
<td>2</td>
<td>5.4</td>
</tr>
<tr>
<td>Putamen</td>
<td>L</td>
<td>–26</td>
<td>–4</td>
<td>6</td>
<td>5.0</td>
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The data were analyzed for the main factors TRIGGER (i.e. objects > pantomimes: IO + NO > IA + NA; pantomimes > objects IA + NA > IO + NO) and RESPONSE (i.e. naming > pantomining: NA + NO > IA + IO; pantomining > naming: IA + IO > NA + NO). Finally, as the experimental design aimed specifically at investigating the neural basis of the object-trigger system, we assessed the interaction terms [i.e. (IO–IA)–(NO–NA); (IA–IO)–(NA–NO)] which controls for the perceptual, motor, semantic, and language aspects of both object- and action-related processing. For all statistical comparisons of interest, the stereotactic coordinates of the pixels of local maximum significant changes in relative rCBF within areas of significant relative rCBF change associated with the specific conditions were determined. The anatomical localization of these local maxima was assessed by reference to a standard stereotactic atlas (Talairach and Tournoux, 1988). Additional validation of this method of localization was obtained after superimposition of the SPM$_{(Z)}$ maps on the group mean MRI image calculated after each individual’s MRI had been stereotactically transformed into the same standard stereotactic space.

**Results**

**PET**

Tables 1–4 show the local maxima of the areas of increased neural activity, as assessed by PET rCBF measurements, associated with the main effects. Analysis of the factor RESPONSE
revealed the expected differential neural activations associated with pantomiming (relative to naming, Table 1) and with naming (relative to pantomiming, Table 2), respectively. Analysis of the factor TRIGGER revealed differential neural activations associated with object processing (relative to observing actions, Table 3) and with observing pantomimes (relative to object processing, Table 4), respectively. These activations replicate previous studies concerned with naming (Perani et al., 1999), motor task performance (Fink et al., 1997; Stephan et al., 1995), and object and action recognition (Chao et al., 1999; Decety et al., 1997; Martin et al., 1995).

More importantly, with regard to the purpose of the study, selecting and producing a wide range of skilled actions triggered by objects (controlled for perceptual, motor, semantic, and lexical effects) specifically activated, as hypothesized, left inferior parietal cortex (dIPL, vIPL) as indicated by the interaction term (IO–IA)–(NO–NA) (Fig. 1). Additional areas of activation showing a significant interaction were observed in left dorsolateral prefrontal cortex (DLPFC), the left anterior cingulate cortex (ACC), and the left ventrolateral prefrontal cortex (VLPFC). Analysis of the corresponding rCBF plots shows clearly different patterns of neural responses for these areas (i.e. differential interaction patterns) which allow one to attribute the areas activated to differential cognitive processes (Fig. 1). Within left inferior parietal cortex, there is a more anterior and inferior region (labeled as vIPL) activated by both pantomiming conditions (IO and IA) to similar degrees (percentage signal change in condition IA 2.25 ± 0.75% versus condition IO 2.78 ± 1.46%; P = 0.6). This activation pattern suggests that this area is involved in object-related action performance irrespective of whether a pantomime was performed to an object or whether a pantomime was imitated. By contrast, the more dorsal and posterior

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</thead>
<tbody>
<tr>
<td>Temporo-occipital junction (V5)</td>
<td>R</td>
<td>54</td>
<td>−62</td>
<td>6</td>
<td>18.3</td>
</tr>
<tr>
<td></td>
<td>L</td>
<td>−46</td>
<td>−68</td>
<td>8</td>
<td>15.2</td>
</tr>
<tr>
<td>Primary visual cortex</td>
<td>R</td>
<td>6</td>
<td>−92</td>
<td>8</td>
<td>17.5</td>
</tr>
<tr>
<td></td>
<td>L</td>
<td>−4</td>
<td>−94</td>
<td>10</td>
<td>15.3</td>
</tr>
<tr>
<td>Lateral dorsal premotor cortex</td>
<td>R</td>
<td>44</td>
<td>−2</td>
<td>48</td>
<td>7.1</td>
</tr>
<tr>
<td></td>
<td>L</td>
<td>−50</td>
<td>−2</td>
<td>52</td>
<td>6.6</td>
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Table 4
Local maxima of the areas of increased neural activity associated with the main effect of ACTIONS

Fig. 1. Selecting and producing a wide range of skilled actions triggered by objects (controlling for perceptual, motor, semantic, and lexical processing) as assessed by the interaction term (IO–IA)–(NO–NA) activated the dorsal inferior parietal cortex [−52, −44, 46] (t = 5.19), the ventral inferior parietal cortex [−58, −32, 30] (t = 5.30), the ventrolateral prefrontal cortex [−48, 44, 6] (t = 6.46), the anterior cingulate cortex [−4, 30, 34] (t = 5.55), and the dorsal lateral prefrontal cortex [−48, 8, 44] (t = 5.46), all in the left hemisphere. The plots of the percentage of rCBF-signal change associated with the activated areas are displayed clockwise starting from the up right position.
activation in left inferior parietal cortex (labeled as dIPL), an area that has not previously been selectively activated, is specific to pantomiming condition when objects triggered the action. This rCBF response pattern suggests that this area is the locus of the trigger system (percentage signal change in condition IA 0.47 ± 0.48% versus condition IO 2.20 ± 0.95%; P < 0.001).

There were three activations sites in the anterior part of the left hemisphere (Fig. 1). The VLPFC was most active in the two tasks with different inputs and different outputs, namely, the pantomime of object use (IO) and the naming of pantomimes (NA). In contrast, the left dorsolateral frontal cortex and the anterior cingulate cortex (ACC) were more active when subjects named pantomimes (NA). Since the DLPFC and the premotor cortex have a common (lateral) border, we assessed whether the dorsolateral frontal activation was located indeed within the DLPFC or within the premotor cortex (i.e. Brodmann area 6). For this purpose, we determined the position of the local maximum, that is, the coordinates of the maximally activated voxel within this activation \((-48, +8, +44), \text{blue crosshairs}\), with respect to a cytoarchitectonically defined probability map of the premotor cortex (i.e. Brodmann area 6; Geyer et al., 2001). Fig. 2 clearly shows that the local maximum lies anterior to Brodmann area 6. Furthermore, the rCBF plot (see Fig. 2) shows specific activation of the maximally activated voxel within this activation of the interaction term in the condition NA (naming pantomime), which strongly implies that the observed area of activation is prefrontal [as a premotor activation would be expected to show up in both conditions requiring motor responses (imitation of pantomime, IA, and pantomimicing of object use, IO)].

The analysis of the second interaction term, that is, from the imitation perspective \((\text{IA–IO})–(\text{NA–NO})\), led to no significant activation.

**Behavioral data**

Pantomime and naming performances were scored by three independent judges. Since there were no differences among judges’ scores, two different ANOVAs for repeated measures with Task (IA, IO or NA, NO) and Repeat (1, 2, 3) as factors were applied to the averaged action and naming scores, respectively. Fig. 3 plots the subjects’ mean scores for the performance in the four tasks averaged across the three repeats. As for actions, both the main
effects of Task \( F(1)=16.73, P<0.001 \) and Repeat \( F(2)=8.042, P<0.002 \) were significant but not the interaction. The results suggest that subjects found it more difficult to imitate pantomimes (mean accuracy in performing the IA condition 25.24 ± 3.06, 84%, for \( n=30 \)) than to pantomime the use of objects (mean accuracy in performing the IO condition, 26.82 ± 2.11, 89%), and that their performance improved across repeats. In particular, there was a significant difference between subjects’ performance in repeats 1 and 2, and 1 and 3 when they imitated pantomimes, and only between repeats 1 and 3 when they pantomimed the use of objects (all \( P<0.05 \)). With regard to naming, the only significant result was the main effect of Task \( F(1)=16.73, P<0.001 \) indicating that naming pantomimes (mean accuracy in performing the NA condition 14.95 ± 3.31, 50%) was more effortful than naming objects (mean accuracy in performing the NO condition 24.24 ± 3.10, 81%).

**Eye movements**

As far as eye movement data are concerned, the analysis showed no significant differential eye movements across the conditions: subjects were able to maintain fixation throughout all conditions.

**Discussion**

The main purpose of this study was to establish the neural basis of pantomimizing object and tool use in the normal human brain. We employed a pantomimizing task as it predicts well actual object and tool use (De Renzi and Lucchelli, 1988; Goldenberg et al., 1996a) but it is easier to implement in a PET scanning environment. Our data extend previous imaging and neuropsychological data by allowing a specification of the areas sustaining the production of object-related pantomimes. The analysis of the rCBF data associated specifically with each condition allows us to assign differential contributions of the areas activated to specific cognitive aspects of task performance. The key result is the identification of a region in the more dorsal part of inferior parietal cortex which is specifically activated when objects trigger pantomimes. We argue that this area is the part of inferior parietal cortex which is specifically activated to specific cognitive aspects of task performance. This region when lesioned—or disconnected from more anterior areas—may lead to the selective deficit shown by apraxic patients who experience impaired everyday use of objects: ideational apraxia (De Renzi and Lucchelli, 1988; Goldenberg and Hagmann, 1998) but it is easier to implement in a PET scanning environment. Our data extend previous imaging and neuropsychological data by allowing a specification of the areas sustaining the production of object-related pantomimes. The analysis of the rCBF data associated specifically with each condition allows us to assign differential contributions of the areas activated to specific cognitive aspects of task performance.

The rCBF results suggest that the evolutionary development of our repertoire of skilled actions has led to the colonization of cortical regions adjacent to those which are concerned with the elicitation of grasp movements. This is an analogous relation to that suggested for temporal cortex on the relation between movement and action recognition by Martin and Chao (2001). Recent neurophysiological and neuroanatomical studies have clarified that the parietal lobe in monkey consists of a multiplicity of areas with specific connections to the premotor cortex. Together, these areas mediate distinct sensorimotor transformations related to the control of hand, arm, eye, or head movements (for a review, see Rizzolatti et al., 2002; Rizzolatti and Luppino, 2001) and in particular, eye–hand coordination during reaching (Marconi et al., 2001).

If we turn to the more anterior activation sites, an interaction was shown in the left DLPFC and the left ACC. Interestingly, the rCBF plots of these activation sites seem to parallel the task difficulty of the respective conditions as assessed by the error rates. Why, however, should naming pantomimes be particularly difficult? Allport and Wiley (2000) have shown that when different tasks involve the same stimuli within a single session, task sets inappropriate at a particular time need to be inhibited. One possibility is that the activation observed in the DLPFC is just anterior of the sites of grip elicitation by objects observed by Grézes et al. (2003). The activation observed may thus be related to the need to suppress an inappropriate but dominant response, that although they retain little linguistic and semantic knowledge (Buxbaum et al., 1997; Lauro-Grotto et al., 1997).
is, imitating the action observed rather than naming it to correspond adequately to the task instructions (Fink et al., 1999).

As far as the VLPFC was concerned, the area was most active when subjects pantomimed the object use (IO) and named actions (NA). If one examines the naming task, then there is a large swathe of VLPFC activation where action naming is significantly more activated \((t = 9.2)\) than object naming. More dorsally, there is a region which for the two object presentation tasks is significantly more activated \((t = 6.5)\) when an action has to be produced rather than named. The significant interaction may thus just correspond to the overlap between two graded regions as that occurring in processing of spatial and object information in prefrontal cortex (Courtney et al., 1998). An alternative possibility is that these two tasks are the ones that differentially require action semantics (Lauro-Grotto et al., 1997).

In summary, our findings suggest that there is a close link between seen objects and tools and the information associated with their use. In right-handed individuals, the key brain structure for an object system that triggers actions is in the dorsal inferior parietal cortex of the left hemisphere, as this was the most activated area when subjects pantomimed the use of objects and tools. The findings reported here are in good accordance with neuropsychological data of apraxic patients and provide an explanation for why left parietal damage may result in impaired tool use (and impaired pantomiming of tool use) despite intact semantic and linguistic functions.

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