

The Role of Action Knowledge in the Comprehension of Artefacts— A PET Study

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Activation of the left ventral premotor cortex (PMv) has in previous imaging studies been associated with the processing of visually presented artefacts. It has been suggested that this activation reflects processing of action knowledge and that action knowledge contributes to the comprehension of artefacts. The purpose of the present study was to test whether activation of the left PMv is common for all tasks involving the comprehension of artefacts or whether it is task specific. This was done by comparing performance and regional cerebral blood flow (rCBF) associated with two categorization tasks and two naming tasks divided by category (natural objects vs artefacts). The left PMv (BA 6/44) was more activated by the categorization task for artefacts than by the categorization task for natural objects and the naming task for artefacts. However, the left PMv was not associated with the contrast between the naming task for artefacts and the naming task for natural objects nor with the processing of artefacts in general. If the PMv does mediate action knowledge, these results suggest that action knowledge does not contribute directly to the comprehension of artefacts but may support the categorization of artefacts. The significance of these findings is discussed in relation to category-specific recognition impairments for artefacts. © 2002 Elsevier Science

Key Words: action knowledge; categorization; category-specificity; object decision; object recognition; PET; semantics.

INTRODUCTION

A central question in cognitive neuroscience concerns how conceptual knowledge is organized in the brain. Evidence relevant to this issue comes from studies of patients with impaired comprehension of artefacts along with relatively spared comprehension of natural objects or vice versa (Forde and Humphreys, 1999). Recently, functional imaging studies have revealed that the processing of artefacts activate the left ventral premotor cortex (PMv) (Chao and Martin,

2000; Grabowski *et al.*, 1998; Grafton *et al.*, 1997; Gerlach *et al.*, 2000). Since this area is likely to be the human homologue of the monkey F5 area (Binkofski *et al.*, 1999; Rizzolatti and Arbib, 1998) which is involved in mediating goal-directed actions such as grasping, holding and manipulation of objects (Rizzolatti and Fadiga, 1998), and since patients with category-specific disorders for artefacts often have lesions likely to involve the PMv (Gainotti *et al.*, 1995), it has been suggested that comprehension of artefacts may rely directly on motor-based knowledge of object utilization (action knowledge¹) mediated by the left PMv (Chao and Martin, 2000) (which together with the left inferior parietal lobe and the left posterior middle temporal region may form a visuo-motor action network (Devlin *et al.*, 2001)). Although this hypothesis is plausible, it is difficult to assess from the imaging studies conducted until now because they often have not linked the activation of the left PMv to a specific level in visual object processing (e.g., structural, semantic, phonological). Thus, in a positron emission tomography (PET) study of Gerlach *et al.* (1999) no association was found between artefacts and the left PMv on object decision tasks where objects had to be matched to visual memory, suggesting that the association must arise at a higher level in visual object processing. We later confirmed this suggestion in a related study where we investigated category effects on a semantic level by contrasting the rCBF associated with categorization of either natural objects or artefacts with the rCBF associated with object decisions to the same categories

¹ The term action knowledge is not necessarily the term adopted in the studies referred to in this article, and when it is, it is often not defined. In the following we define action knowledge as knowledge comprising representations of complex actions that mediate object utilization. This knowledge is distinct from semantic knowledge (comprising information of, e.g., object functions and inter-object associations), and from the praxis production system (comprising structural knowledge contained in motor programs) (for a related definition, see Raymer and Ochipa (1997)). Although this definition will apply to the discussion of our results, it may not correspond to the definition intended in other studies.

(Gerlach *et al.*, 2000). In this study, activation of the PMv was found during the categorization of artefacts compared with both the categorization of natural objects and object decisions to artefacts.² Because categories are composed of objects that can be treated as equivalent in some respect, we speculated that the left PMv activation observed during categorization reflected that artefacts, as opposed to natural objects, are equivalent in that they are manipulable. Although this suggestion is compatible with psycholinguistic evidence suggesting that lexical categories may evolve from, and the act of categorization rely on, motor-based knowledge of action equivalency (Lakoff, 1987), it raises the question of whether action knowledge matters for the comprehension of artefacts or whether action knowledge only comes into play in specific contexts (in this case during categorization)? To examine this, we contrasted the two categorization tasks reported earlier (Gerlach *et al.*, 2000) with two naming tasks, involving either natural objects or artefacts. Thus, the present study involves the same subjects and the same categorization tasks as used in the earlier study (Gerlach *et al.*, 2000). The difference is that we now compare the categorization tasks with naming tasks instead of object decision tasks. If the comprehension of artefacts is always based on action knowledge mediated by the left PMv, we should expect to see activation of this area during both the categorization task for artefacts and the naming task for artefacts. Alternatively, if action knowledge is important only for the categorization of artefacts, we should not.

MATERIALS AND METHODS

Subjects. Fifteen right-handed healthy volunteers (7 female, 8 male) ranging in age from 22 to 30 years (mean age, 26 years) participated in this study. Informed written consent was obtained according to the Declaration of Helsinki II and the study was approved by the local ethics committee of Copenhagen (J.nr. (KF) 01-339/94).

PET scanning. PET scans were obtained with an eighteen-ring GE-Advance scanner (General Electric

² It is of interest that the left PMv in the study of Gerlach *et al.* (2000) was activated by a broad range of artefacts (see the Appendix) and not only tools, which have been the most commonly used artefactual stimuli in activation studies (e.g., Chao and Martin, 2000; Grabowski *et al.*, 1998; Grafton *et al.*, 1997; Martin *et al.*, 1996). Thus, if the left PMv does mediate action knowledge this finding suggests that action knowledge is probably important for the processing of other artefacts beside tools. Provided that action knowledge does play a role in category-specific disorders for artefacts this suggestion would also be compatible with reports of patients with this type of disorder because they are usually impaired in recognizing a broad range of artefacts and not only tools (e.g., Sacchett and Humphreys, 1992; Warrington and McCarthy, 1983; Warrington and McCarthy, 1987).

Medical Systems, Milwaukee, WI) operating in 3-D acquisition mode, producing 35 image slices with an interslice distance of 4.25 mm. The total axial field of view was 15.2 cm with an approximate in-plane resolution of 5 mm. The technical specifications have been described elsewhere (DeGrado *et al.*, 1994).

Each subject received 12 intravenous bolus injections of 200 MBq (5.7 mCi) of H₂¹⁵O with an interscan interval of 10–12 min. The isotope was administered in an antecubital intravenous catheter over 3–5 s followed immediately by 10 ml of physiological saline for flushing. Head movements were limited by head-holders constructed by thermally moulded foam.

Before the activation sessions a 10-min transmission scan was performed for attenuation correction. Images were reconstructed using a 4.0-mm Hanning filter transaxially and an 8.5-mm Ramp filter axially. The resulting distribution images of time integrated counts were used as indirect measurements of the regional neural activity (Fox and Mintun, 1989).

MRI scanning. For accurate anatomical localization of activated foci structural MRI scanning was performed on every subject with a 1.5 T Vision scanner (Siemens, Erlangen, Germany) using a 3-D magnetization prepared rapid acquisition gradient echo sequence (TR/TE/TI = 11/4/100 ms, flip angle 15°). The images were acquired in the sagittal plane with an in-plane resolution of 0.98 mm, and a slice thickness of 1.0 mm. The number of planes were 170 and the in-plane matrix dimensions were 256 × 256.

Image analysis. For all subjects the complete brain volume was sampled. Image analysis was performed using Statistical Parametric Mapping software (SPM-96, Wellcome Department of Cognitive Neurology, London, UK) (Frackowiak and Friston, 1994). All intra-subject images were aligned on a voxel-by-voxel basis using a 3-D automated six parameters rigid body transformation and the anatomical MRI scans were coregistered to the individual averages of the 12 aligned PET scans. The average PET scans and corresponding anatomical MRI scans were subsequently transformed into the standard stereotactic atlas of Talairach and Tournoux (1988) using the PET template defined by the Montreal Neurological Institute (Friston *et al.*, 1995a). The stereotactically normalized images consisted of 68 planes of 2 × 2 × 2-mm voxels. Before statistical analysis, images were filtered with a 16-mm isotropic gaussian filter to increase the signal-to-noise ratio and to accommodate residual variability in morphological and topographical anatomy that was not accounted for by the stereotactic normalization process (Friston, 1994). Differences in global activity were removed by proportional normalization of global brain counts to a value of 50.

Tests of the null hypothesis, which rejects regionally specific condition activation effects, were performed

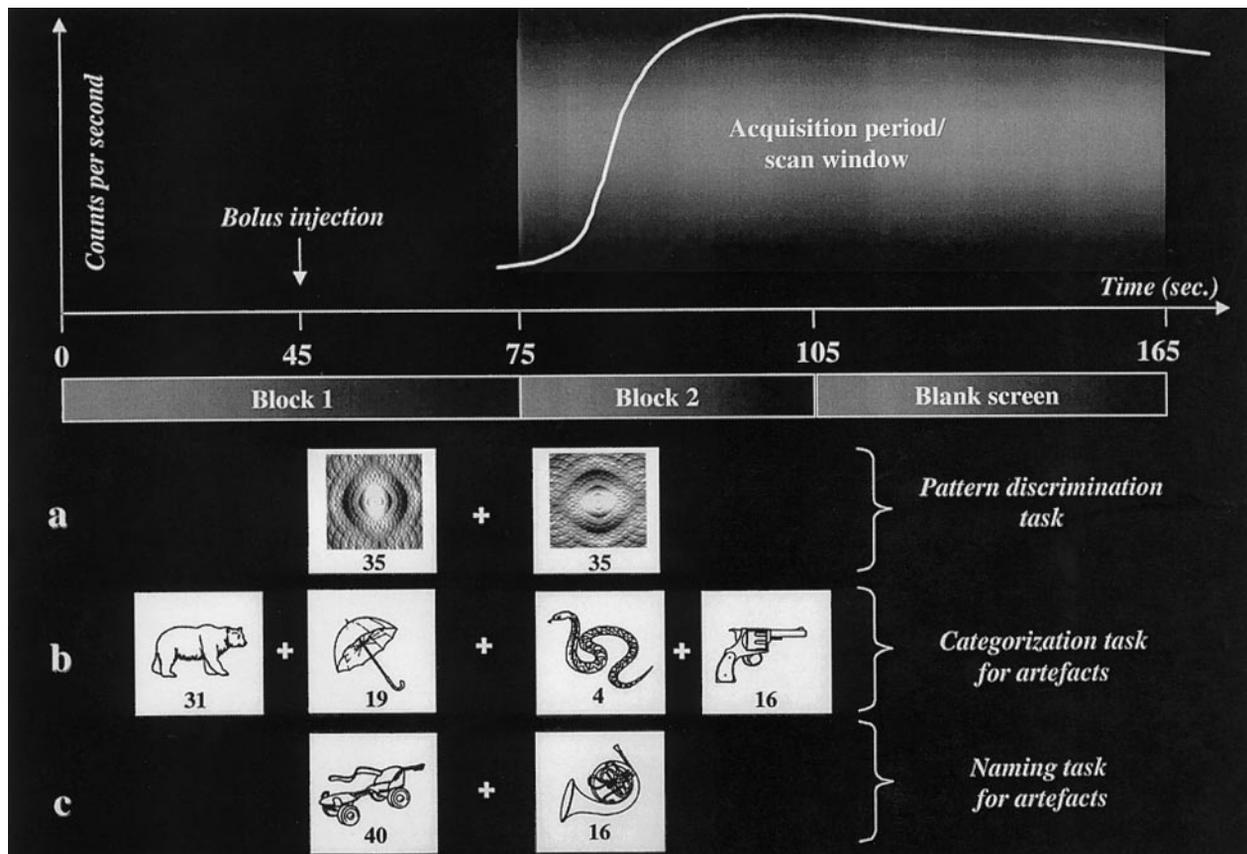


FIG. 1. Illustration of the relationship between PET data acquisition and the task design for the three tasks: (a) the pattern discrimination task, (b) the categorization task for artefacts, and (c) the naming task for artefacts. For the categorization tasks the first block of stimuli, comprising a total of 50 items, was displayed before bolus injection and before the bolus was estimated to reach the brain. The second block of stimuli, comprising a total of 20 items, was displayed in the actual uptake phase of the tracer and ended before washout was likely to begin. The same was true of the naming tasks except that in these tasks the first block of stimuli comprised a total of 40 items whereas the second block comprised a total of 16 items. The pattern discrimination task was arranged in a similar manner as the categorization tasks except for the fact that it was not blocked.

comparing conditions on a voxel-by-voxel basis. The resulting set of voxel values constituted a statistical parametric map of the t statistic, $SPM\{t\}$. A transformation of values from the $SPM\{t\}$ into the unit gaussian distribution using a probability integral transform allowed changes to be reported in Z scores ($SPM\{Z\}$). Significantly activated areas were determined based on the change in a single voxel at a threshold of $P < 0.05$ ($Z > 4.4$) after correction for multiple nonindependent comparisons. The voxel significance threshold was estimated according to Friston *et al.* (1991, 1995b) using the theory of Gaussian fields. The resulting foci were then characterised in terms of peak Z scores above this level.

Cognitive tasks. The experiment originally consisted of 12 different tasks, although only a subset will be reported here. This subset includes: (i) a pattern discrimination task, (ii) two categorization tasks, and (iii) two naming tasks. The order of tasks was randomized across participants.

In the pattern discrimination task the subjects saw

two different patterns (Fig. 1a). The subjects were instructed to press the “vertical”-key (index finger) on a serial response box placed in front of their right hand if the pattern was vertical and the “horizontal”-key (middle finger) if the pattern was horizontal. In the categorization tasks the subjects were presented with pictures of natural objects and artefacts and had to press the “natural”-key (index finger) if the picture represented a natural object and the “artefact”-key (middle finger) if the picture represented an artefact (the keys were not counterbalanced across subjects). The two categorization tasks differed from each other in the number of items from each category presented in the critical scan window. In the one task they were drawn predominantly from the category of natural objects, whereas they were drawn predominantly from the category of artefacts in the other (Fig. 1b). In the two naming tasks the subjects were presented with pictures of either artefacts or natural objects (Fig. 1c). In these tasks the subjects were instructed to silently name the pictures and to press a key (index finger) as

soon as they knew their name. The pattern discrimination task was included as a low-level baseline task needed for the evaluation of whether potential differences in rCBF between the naming tasks and the categorization tasks reflected decreases or increases in rCBF.

In all tasks the participants were instructed to respond as fast and accurately as possible. Before the actual experiments started the subjects performed a practise version of each task while in the scanner. Stimuli used in these practise versions were not used in the actual experiments.

Design. Seventy stimuli were presented in the pattern discrimination task and the categorization tasks whereas 56 stimuli were presented in the naming tasks. All stimuli were presented on a white background on a PC-monitor hanging 60 cm in front of the subjects. The stimuli subtended between 3° and 5° of visual angle and were presented in the centre of gaze. In the pattern discrimination task and in the categorization tasks each stimulus was displayed for 180 ms with an interstimulus interval of 1320 ms. In the naming tasks each stimulus was displayed for 180 ms with an interstimulus interval of 1695 ms. Thus, all tasks lasted 1 min and 45 s. All tasks were initiated approximately 1 min and 15 s prior to isotope arrival to the brain and continued during the first 30 s of acquisition corresponding to the delivery of radiotracer to the brain. From the point of task offset, the participants viewed a blank screen for the next 60 s, yielding a total acquisition time of 90 s (see Fig. 1). By reducing isotope washout and improving counting statistics this protocol optimizes the signal-to-noise ratio from activated regions (Cherry *et al.*, 1995; Hurtig *et al.*, 1994; Silbersweig *et al.*, 1993).

The pattern discrimination task consisted of 35 horizontal patterns and 35 vertical patterns. The order of horizontal and vertical patterns was randomized.

Each categorization task consisted of line-drawings of 35 artefacts and 35 natural objects. However, the presentation was blocked in two. In one of the categorization tasks the first block consisted of 19 natural objects +31 artefacts whereas the second block consisted of 16 natural objects +4 artefacts. In the other categorization task the first block consisted of 19 artefacts and +31 natural objects whereas the second block consisted of 16 artefacts +4 natural objects. The order of the pictures (natural vs artefact) was randomized within each block.

Each naming task consisted of line-drawings of either 56 artefacts or 56 natural objects. These tasks were also blocked in two so that the first block consisted of 40 pictures, whereas the second block consisted of 16 pictures. The order of the pictures was randomized within each block.

In the blocked tasks the two blocks were presented

sequentially but arranged so that the first block would be initiated approximately 45 s before injection and last until the bolus was estimated to reach the brain. The second block was displayed in the actual uptake phase of the tracer and ended before washout was likely to begin (see Fig. 1). Because of this arrangement, the activation seen during the tasks should primarily reflect naming or categorization of either natural objects or artefacts depending on the particular task.

Stimuli. The line-drawings of objects were selected from various sources but mainly from the standardized set of Snodgrass and Vanderwart (1980). Care was taken to insure that the pictures looked similar overall regardless of source. The pictures used in the second block were all taken from the pool of Snodgrass and Vanderwart (1980). Ten sets of objects (five sets of natural and five sets of artefacts), with 16 items in each set, were selected (see Appendix A).

Snodgrass and Vanderwart supplied ratings, on a scale from one to five, of the pictures along three dimensions: visual complexity, familiarity, and image agreement. Visual complexity reflects the subjects' judgement of how detailed the picture is. Familiarity reflects how often the subject came into contact with or thought about the concept associated with the picture. Image agreement reflects how closely the picture resembled the subjects' mental image of the object. The relevance of these measures has been emphasized by several authors (Funnell and Sheridan, 1992; Stewart *et al.*, 1992), because spurious effects of category can arise due to differences between categories along these dimensions alone. The ten sets of objects were matched with respect to familiarity, visual complexity and image agreement so that they did not differ significantly along any of these dimensions (Kruskal-Wallis, $P > 0.1$).

Because ten sets of objects were selected, these sets could be rotated across tasks. Accordingly, the same set of natural objects would appear in both a naming task and in a categorization task. The same was true of the artefacts. This procedure ensures that any potential differences observed between the tasks are unlikely to be caused by a particular selection of stimuli, but are rather caused by true differences between tasks.

RESULTS

Behavioral Results

Only reaction times (RTs) to the 16 pictures presented in the critical scan window of the categorization tasks and the naming tasks were subjected to analysis. A two-way analysis of variance was carried out. The factors were task type with two levels (naming vs categorization) and category also with two levels (artefacts vs natural objects). There was a significant main

TABLE 1

Mean Correct RTs (ms) and SDs (in Brackets) for Stimuli Presented in the Second Block of the Categorization Tasks and the Naming Tasks

	Natural objects	Artefacts
Naming task	928 (281)	884 (266)
Categorization task	588 (78)	590 (87)

effect of task type, $F(1, 14) = 24$, $P < 0.001$, with slower responses to objects presented in the naming tasks. No other significant effects were found. The mean correct RTs and standard deviations (SDs) are given in Table 1. The mean correct RT and SD for items in the pattern discrimination task were 497 and 80 ms, respectively.

Physiological Results

To test whether activation of the left premotor area is common for all tasks involving the semantic processing of artefacts or whether it is specific for tasks involving the categorization of artefacts, three main comparisons were made.

(i) In the first comparison we identified areas that were specifically activated by the categorization task for artefacts relative to the other tasks. This was achieved in two steps. In the first step we made a contrast between the categorization task for artefacts and the categorization task for natural objects. In the next step we ensured that the areas associated with this contrast were indeed more activation by the categorization task for artefacts than by any other task. This was done using SPM's masking option, where we masked the contrast between the categorization task for artefacts and the categorization task for natural objects with: (a) a contrast between the categorization task for artefacts and the naming task for artefacts, (b) a contrast between the categorization task for artefacts and the pattern discrimination task, and (c) a contrast involving the interaction between category (artefacts vs natural objects) and task type (categorization vs naming) (See Appendix B for areas associated with the interaction). The threshold for each mask was set at $P < 0.001$. Activation associated with this comparison should reveal areas, where activation depends on both category and task type and the rCBF increased more during the categorization task for artefacts than during the other tasks. The purpose of this comparison was to establish whether the activation of the left PMv reported by Gerlach *et al.* (2000) could also be found when the categorization task for artefacts was compared with a naming task for artefacts instead of an object decision task for artefacts.

(ii) In the second comparison we tested whether activation of the left PMv could be established during

naming of artefacts relative to naming of natural objects. This was achieved in two steps. In the first step we made a contrast between the naming task for artefacts and the naming task for natural objects. In the next step we ensured that the areas associated with this contrast were also more activated during the naming task for artefacts than during the pattern discrimination task. This was done using SPM's masking option, where we masked the contrast between the naming task for artefacts and the naming task for natural objects with a contrast between the naming task for artefacts and the pattern discrimination. The threshold for the mask was set at $P < 0.001$. If the left PMv is indeed activated by all tasks involving the semantic processing of artefacts, we should expect to find the left PMv associated with this comparison.

(iii) In the third comparison we looked for areas that were activated in common by the categorization task and the naming task for artefacts compared with the same two tasks for natural objects. This was achieved in four steps. In the first step we made two contrasts: (a) one between the categorization task for artefacts and the categorization task for natural objects, and (b) one between the naming task for artefacts and the naming task for natural objects. In the next step we looked for areas that were common for these two contrasts and in which the rCBF did not differ significantly between the two contrasts. This was done using conjunction analysis (Price and Friston, 1997). Thus, the activations associated with this comparison should reveal areas where the processing of artefacts does not differ significantly as a function of task type (naming vs categorization). In the third step we ensured that each of the two contrasts contributed to the activation identified by the conjunction analysis. This was done by excluding all voxels from the analysis that were not significant in each contrast at a threshold of $P < 0.1$ uncorrected for multiple comparisons, using the masking option in SPM. In the fourth step we further ensured that the areas associated with the conjunction analysis were also activated more by the categorization task and the naming task for artefacts than by the pattern discrimination task. This was done using SPM's masking option, where we masked the conjunction with: (a) a contrast between the categorization task for artefacts and the pattern discrimination task and (b) a contrast between the naming task for artefacts and the pattern discrimination task. The threshold for these masks was also set at $P < 0.1$ uncorrected for multiple comparisons. This comparison is in a sense less conservative than the second comparison because it allows any area associated with the conjunction to be driven primarily by one of the contrasts.

For all comparisons, effects of condition order were removed as confounds using linear regression.

TABLE 2

Areas More Activated by the Categorization Task for Artefacts Than by the Categorization Task for Natural Objects, the Naming Task for Artefacts, and the Pattern Discrimination Task

	Region Coordinates (x, y, z)			Brodman area	Z score
L. Middle frontal gyrus	-42	36	-22	11	5.98
L. Inferior frontal gyrus	-58	28	0	47	5.91
L. Middle frontal gyrus	-36	54	-14	10	5.30
L. Inferior frontal gyrus	-52	38	16	46	5.28
L. Precentral gyrus	-66	6	22	6	5.16
L. Inferior frontal gyrus	-58	34	8	45	5.01
L. Inferior frontal gyrus	-56	34	-8	47	4.94

Note. Coordinates are in millimeters, relative to the anterior commissure. L, left. Within each region, the anatomical location of the voxel with the maximum Z score is indexed by the measures established in the *MNI-SPM96 Implementation of the Stereotatic Atlas of Talairach and Tournoux* (1988). Regions written in bold designate the main peak activation within an area whereas regions written in roman designate associated peaks. Threshold was set at $P < 0.05$ corrected for multiple comparisons ($Z > 4.4$).

Areas more activated by the categorization task for artefacts than by the categorization task for natural objects, the naming task for artefacts and the pattern discrimination task. The main peak activations associated with this comparison were found in the left middle frontal gyrus (Brodmann area (BA) 11) from where activation extended upwards and backwards into the precentral gyrus (BA 6/44) covering also the inferior frontal gyrus (BA 44, 45, 46, and 47). (See Table 2 and Fig. 2.)

Areas more activated by the naming task for artefacts than by the naming task for natural objects and the pattern discrimination task. No voxels were associated with this comparison when the threshold was set at $P < 0.05$ corrected for multiple comparisons. However, to see whether any activation of the left premotor area could be established at a lower threshold, we lowered the threshold to $P < 0.1$ uncorrected for multiple comparisons. Although this did reveal some areas of activation none of these were located in the dorso-lateral or ventral part of the left frontal cortex.

Areas more activated by the processing of artefacts than by the processing of natural objects regardless of task type. No voxels were associated with this comparison when the threshold was set at $P < 0.05$ corrected for multiple comparisons. To see whether any activation of the left premotor area could be established at a lower threshold, we lowered the threshold to $P < 0.1$ uncorrected for multiple comparisons. Again this did reveal some areas of activation, but none of these were located in the dorsolateral or ventral part of the left frontal cortex.

DISCUSSION

The left middle frontal gyrus (BA 11), the left inferior frontal gyrus (BA 44, 45, 46, and 47), and the left PMv (BA 6/44) were more activated by the categorization

task for artefacts than by the categorization task for natural objects, the naming task for artefacts and the pattern discrimination task. It should be noted though, that the left PMv was not associated with the interaction between category and task type when the threshold was set at $P < 0.05$ corrected for multiple comparisons ($Z > 4.4$) (see Appendix B). However, the area was associated with the interaction when the threshold was lowered to $P < 0.001$ uncorrected for multiple comparisons ($Z > 3.09$), suggesting that the left PMv was in fact more activated by the categorization task for artefacts than by any other task (see Fig. 3). Accordingly, given that the left PMv seems to be associated with the categorization task for artefacts, regardless of whether this task is contrasted with object decision tasks or naming tasks, strongly suggest that this area is specifically involved when artefacts are categorized and thus that activation of this area is both category- and task-specific.

The positive finding that the left PMv was more activated by the categorization task for artefacts than by the naming task for artefacts of course does not exclude the possibility that it was also activated by the latter task, although less so. This possibility, however, is unlikely because the left PMv was not associated with the contrast between the naming task for artefacts and the naming task for natural objects or the comparison involving areas activated in common by the categorization task for artefacts and the naming task for artefacts. Although it might be argued that interpretation of such null effects is ill-advised because of the conservative criterion adopted for defining an activation difference, it should be noted the left PMv was not associated with any of these comparisons even when the criterion was lowered to $P < 0.1$ uncorrected for multiple comparisons.

The pattern of activation described above is very similar to the one reported by Gerlach *et al.* (2000)

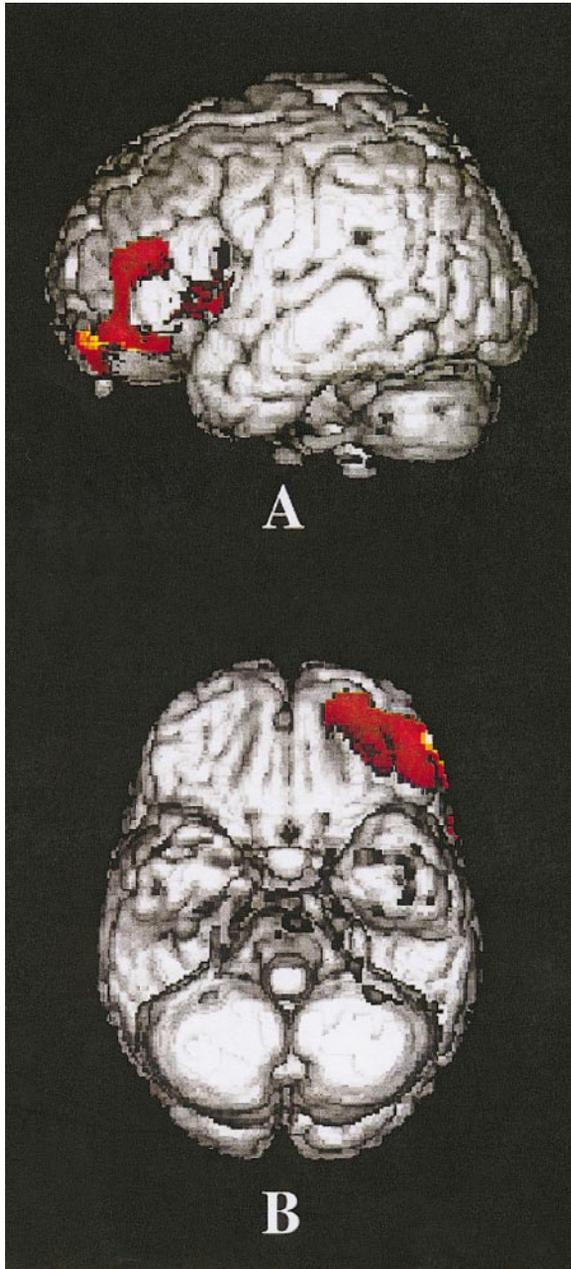


FIG. 2. A rendering showing the areas more activated by the categorization task for artefacts than by the categorization task for natural objects, the naming task for artefacts, and the pattern discrimination task. The activated areas are projected onto a template anatomical MRI scan in coregistration with the Talairach atlas (Talairach and Tournoux, 1988). All areas shown were significant at $P < 0.05$ corrected for multiple comparisons ($Z > 4.4$). (A) The left side of the brain showing activation of the left middle frontal gyrus (BA 11), the left inferior frontal gyrus (BA 44, 45, 46, and 47), and the left premotor cortex (BA 6). (B) The ventral part of the brain showing activation of the left middle frontal gyrus (BA 11) and the left inferior frontal gyrus (BA 47).

comparing the present categorization tasks with object decision tasks instead of naming tasks. In keeping with our earlier interpretation (Gerlach *et al.*, 2000), we

suggest that the PMv activation (BA 6/44) reflects that the act of categorizing objects may rely on motor-based knowledge of action equivalency (Lakoff, 1987) and that artefacts are more tightly associated with aspects of handling (action knowledge) than natural objects (for a similar suggestion see Miller and Johnson-Laird, 1976). The same interpretation may apply to the activation of the left inferior frontal gyrus (BA 44) as this area has been associated with both naming of tool use vs naming of tools (Grafton *et al.*, 1997), observation of object-related actions (Buccino *et al.*, 2001), as well as with tactile manipulation/recognition of complex objects (Binkofski *et al.*, 1999). This greater use of action knowledge is mirrored by an increased need for motor inhibition, demanded because action knowledge is retrieved though no action is to be performed, explaining the activation of the left middle frontal gyrus, a structure previously associated with motor inhibition (Fuster, 1997; Lhermitte *et al.*, 1986).

The finding that action knowledge is not accessed in all tasks demanding semantic processing of artefacts suggests that action knowledge is not important for the comprehension of artefacts per se (though it may support the processing of artefacts in other contexts—in this case categorization). This is in keeping with the

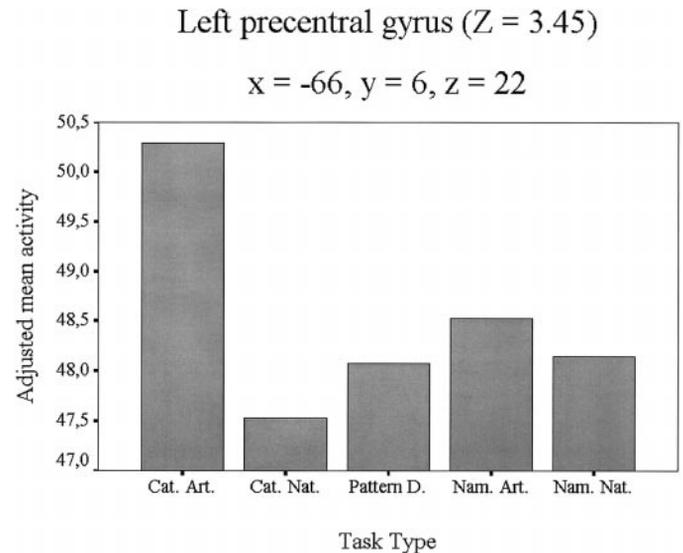


FIG. 3. The figures show the adjusted mean activity in the left precentral gyrus associated with the interaction between category (artefacts vs natural objects) and task type (categorization vs naming) for the following five conditions: Cat. Art., the categorization task for artefacts; Cat. Nat., the categorization task for natural objects; Pattern D., the pattern discrimination task; Nam. Art., the naming task for artefacts; and Nam. Nat., the naming task for natural objects. As can be seen, the rCBF is higher during the categorization task for artefacts compared with any other task. Note also that the rCBF level associated with the naming task for artefacts is not much higher than the rCBF level associated with the pattern discrimination task. This observation speaks against a strong involvement of the premotor area in the comprehension of artefacts.

long-standing conception that action knowledge and semantics are dissociable (Heilman *et al.*, 1997)—a conception that can be dated back to Pick in 1902 who reported a few patients who often misused objects they could both recognize and name (De Renzi, 1989). However, if action knowledge plays no necessary part in the comprehension of artefacts, how can we account for the finding that many patients with category-specific disorders for artefacts have lesions of left frontoparietal structures (Gainotti *et al.*, 1995)? If knowledge representations are distributed and interactive, with each part of an object's representation providing collateral activation to the other parts, damage of one part may affect the activation of other parts. Accordingly, to the degree that action knowledge provides input to the semantic system, the activation level of the representations in this system may be lowered following damage to action knowledge. This will affect artefacts more than natural objects if the link between semantics and action is tighter for artefacts than for natural objects. Thus, if the semantic system is impaired in cases with category-specific disorders for artefacts, as evidence suggests is the case (Sacchett and Humphreys, 1992; Warrington and McCarthy, 1983; Warrington and McCarthy, 1987), this semantic processing deficit will be exacerbated for artefacts following additional damage to action knowledge (mediated by structures including the left PMv). In this way damage to action knowledge may impair the comprehension of artefacts although action knowledge per se is not necessary for the comprehension of these objects.

The suggestion that action knowledge plays no necessary part in the comprehension of artefacts diverges from the conclusion reached by Martin *et al.* (1996) and Chao and Martin (2000). In these studies the left PMv was found to be more activated during naming of tools compared with animals, a finding that led these investigators to conclude that the ability to recognize and identify tools may depend on retrieval of knowledge of tool use (action knowledge). It should be noted though, that just because the naming of tools caused greater activation of the left PMv than did the naming of animals in these studies, this does not necessarily imply that access to action knowledge is directly important for naming or comprehending tools (although it may be for naming tool use (Grafton *et al.*, 1997), but that is a different aspect). In fact, such an interpretation would seem to conflict with the observed dissociation between action knowledge and semantics (Heilman *et al.*, 1997; Moreaud *et al.*, 1998). Thus, the premotor activation found in these studies could reflect a motor priming effect caused by tools being more manipulable than animals. This possibility, however, is unlikely in the present study because it was the same items that caused strong activation of the left PMv in the categorization task and little such activation in the nam-

ing task. Accordingly, the activation of the left PMv associated with the categorization task for artefacts is genuinely task- and category-specific and cannot be explained as a motor priming effect. Nevertheless, even if the interpretation offered by Martin *et al.* (1996) and Chao and Martin (2000) is questioned we still need to account for the fact that left PMv was found more activated during the naming of tools than during the naming of animals in these studies but not in the present study. We can probably rule out any explanation in terms of the present study lacking statistical power to identify category-specific effects because such effects were obtained in the categorization tasks using a rather conservative criterion ($P < 0.05$ corrected for multiple comparisons) but not in the naming tasks using a very liberal criterion ($P < 0.1$ uncorrected for multiple comparisons). Rather, the most likely explanation for the discrepancy lies in the stimuli used. Thus, in the studies of Martin *et al.* (1996) and Chao and Martin (2000) only tools and animals were used whereas in the present study a much broader range of artefacts and natural objects was included. Accordingly, if the activation of the left PMv found by Martin *et al.* (1996) and Chao and Martin (2000) reflects a motor priming effect such an effect may fail to show up in the present study because some of the artefacts used here are not directly associated with simple hand-movements (e.g., a bike), whereas some of the natural objects might be (e.g., fruits and vegetables) canceling potential motor priming effects related to simple hand-movements.³ Whether or not this explanation for the discrepancy turns out to be valid, the present findings suggest that the left PMv is critically involved in the categorization of artefacts as a broad class but not in naming the very same items. We believe that this finding can most easily be explained by the notion that the categorization of artefacts is based in part on action knowledge but that the comprehension of these objects on the other hand is not contingent on access to action knowledge—an interpretation which is compatible with the observed dissociation between action knowledge and semantics (Heilman *et al.*, 1997).

CONCLUSION

We report positive evidence that the left PMv (BA 6/44) is more activated during categorization of artefacts than during both categorization of natural objects and naming of artefacts. In addition we report negative evidence, suggesting that the left PMv is not activated

³ This explanation may also account for the fact that the left middle temporal gyrus was not associated with artefacts in the present study whereas it has been in studies using only tools as stimuli (Martin *et al.*, 1996; Moore and Price, 1999).

more during naming of artefacts than during naming of natural objects nor is involved in the semantic processing of artefacts in general. Provided that the left PMv is involved in the mediation of action knowledge these findings suggest that action knowledge contributes to the categorization of artefacts but that action knowledge is not important for the comprehension of artefacts per se.

APPENDIX A

Set 1	Set 2	Set 3	Set 4	Set 5
Beetle	Sheep	Dog	Lettuce	Melon
Pear	Peanut	Pineapple	Cherry	Carrot
Penguin	Bee	Ant	Spider	Caterpillar
Kangaroo	Banana	Lemon	Grapes	Squirrel
Ostrich	Sparrow	Monkey	Seal	Racoon
Owl	Cock	Horse	Rabbit	Mouse
Artichoke	Deer	Flower	Peach	Fly
Tomato	Apple	Pumpkin	Tortoise	Giraffe
Fox	Eagle	Asparagus	Skunk	Snail
Strawberry	Potato	Butterfly	Zebra	Maize
Three	Snake	Grasshopper	Donkey	Goat
Camel	Onion	Leaf	Crocodile	Orange
Fish	Seahorse	Frog	Pig	Mountain
Swan	Duck	Rhinoceros	Chicken	Cow
Gorilla	Polar bear	Lobster	Pepper	Peacock
Lion	Leopard	Cat	Mushroom	Celery
Set 6	Set 7	Set 8	Set 9	Set 10
Cigar	French loaf	Watch	Jacket	Arrow
Envelope	Hammer	Helmet	Bat	Broom
Wheel	Basket	Boat	Barn	Crown
Chain	Ball pen	Stool	Umbrella	Racket
Spinning wheel	Rolling pen	Trumpet	Top	Windmill
Flute	Revolver	Kitchen range	Bell	Snowman
Roller skate	Bowl	Church	Bow	Helicopter
Ruler	Motor cycle	Swing	Accordion	Toboggan
French horn	Hat	Wood chisel	Kite	Canon
Glove	Harp	Bus	Violin	Iron
Wristwatch	Ladder	Piano	Axe	Handcart
Plane	Well	Glasses	Vase	Waistcoat
Screw	Fence	Clothes-peg	Nail file	Drum
Nut	Barrel	Anchor	Padlock	Layer cake
Thimble	Water jug	Rocking chair	Reel	Train
Suitcase	Needle	Record player	Tie	Bike

APPENDIX B

Areas associated with the interaction between category (artefacts vs natural objects) and task type (categorization vs naming)

	Region Coordinates (x, y, z)			Brodman area	Z score
L. inferior frontal gyrus	-60	20	0	47	5.24
L. inferior frontal gyrus	-52	36	18	46	4.80
L. middle frontal gyrus	-46	36	-20	11	4.63
L. middle frontal gyrus	-16	56	-20	11	4.49

Note. See footnote to Table 2 for details.

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