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Categorization and category effects in normal object recognition A PET Study

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Abstract

To investigate the neural correlates of the structural and semantic stages of visual object recognition and to see whether any effects of category could be found at these stages, we compared the rCBF associated with two categorization tasks (subjects decided whether pictures represented artefacts or natural objects), and two object decision tasks (subjects decided whether pictures represented real objects or nonobjects). The categorization tasks differed from each other in that the items presented in the critical scan window were drawn primarily from the category of artefacts in the one task and from the category of natural objects in the other. The same was true for the object decision tasks. The experiment thus comprised a two-by-two factorial design. The factors were Task Type with two levels (object decision vs. categorization) and Category also with two levels (natural objects vs. artefacts). The object decision tasks were associated with activation of areas involved in structural processing (fusiform gyri, right inferior frontal gyrus). In contrast, the categorization tasks were associated with activation of the left inferior temporal gyrus, a structure believed to be involved in semantic processing. In addition, activation of the left premotor cortex was found during the categorization of artefacts compared with both the categorization of natural objects and object decision to artefacts. These findings suggest that the structural and semantic stages are dissociable and that the categorization of artefacts, as opposed to the categorization of natural objects, is based, in part, on action knowledge mediated by the left premotor cortex. However, because artefacts and natural objects often caused activation in the same regions within tasks, processing of these categories is not totally segregated. Rather, the categories differ in their weight on different forms of knowledge in particular tasks. © 2000 Elsevier Science Ltd. All rights reserved.

Keywords: Artefactural objects; Action knowledge; Cascade processing; Natural objects; rCBF; Semantics

1. Introduction

In the last 15 years evidence has accumulated suggesting that different categories of objects are not processed in the same way. This evidence has primarily come from cases with category-specific recognition or naming impairments. Recently, converging evidence has come from imaging studies that all demonstrate some degree of specialization within the brain for the processing of different categories of objects [31]. The exact findings in these studies, however, are rather inconsistent. Thus, natural objects have been found to activate the left hemisphere from the point of the calcarine sulcus [29] over the fusiform gyrus [33] and the inferior temporal lobe [5] to the anterior temporal lobe [31]. In contrast, Gerlach et al. [18] found that natural objects caused increased processing in the posterior part of the right inferior temporal gyrus. With respect to artefacts the picture is somewhat clearer as the left premotor area has been found activated in many studies [19,20,29] as has the left middle temporal gyrus [5,29,31,32]. Although these imaging studies take us some way in understanding the neural correlates of category effects, there are two major obstacles in relating the findings from most of these studies to models of category-specificity. The first is that the stimulus material used has usually not been adequately matched across categories. This is unfortunate as it has been

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known for some time that factors like visual complexity and familiarity may lead to spurious category-effects if not controlled for [15,41]. Accordingly, some of the category-specific activations reported may be artifacts [31]. The second obstacle is that the brain regions found activated cannot often be linked to particular stages in visual object processing because of the tasks used. Thus, there is often no way of knowing whether the activations observed arose at a structural, a semantic, or a phonological stage in visual object processing.

In the present study we tried to overcome these problems by using adequately matched stimulus material and tasks intended to tap particular stages in visual object recognition. The purpose of the present PET-study was to investigate the neural correlates of the structural and semantic stages of visual object recognition and to see whether any effects of category (natural objects vs. artefacts) could be found at these stages. This was done by using categorization tasks, where subjects decided whether pictures represented artefacts or natural objects, and object decision tasks where subjects decided whether pictures represented real objects (natural or artefact) or nonobjects.

2. Method

2.1. Subjects

Fifteen right-handed healthy volunteers (seven female, eight 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).

2.2. PET scanning

PET scans were obtained with an eighteen-ring GE-Advance scanner (General Electric Medical Systems, Milwaukee, WI, USA) operating in 3D 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 [7].

Each subject received 12 intravenous bolus injections of 200 MBq (5.7 mCi) of $H_2^{15}O$ 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 [9].

2.3. MRI scanning

For accurate anatomical localization of activated foci structural magnetic resonance imaging (MRI) scanning was performed on every subject with a 1.5 T Vision scanner (Siemens, Erlangen, Germany) using a 3D 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.

2.4. Image analysis

For all the 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) [10]. All intra-subject images were aligned on a voxel-by-voxel basis using a 3D automated six parameters rigid body transformation and the anatomical MRI scans were co-registered 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 [42] using the PET template defined by the Montreal Neurological Institute [12]. The stereotactically normalized images consisted of 68 planes of $2 \times 2 \times 2$ 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 [11]. 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 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 $P < 0.05$ ($Z > 4.5$) after correction for multiple non-independent comparisons. The voxel significance threshold was estimated according to Friston et al. [13,14] using the

theory of Gaussian fields. The resulting foci were then characterized in terms of peak Z-scores above this level.

2.5. Cognitive tasks

The experiment consisted of 12 different tasks, although only a subset will be reported here. This subset includes a pattern discrimination task, two object decision tasks and two categorization tasks. In the pattern discrimination task the subjects saw two different patterns (see 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 two object decision tasks the subjects were presented with pictures that represented either real objects or nonobjects (see Fig. 1b). In these tasks the subjects were instructed to press the 'real object'-key (index finger) if the picture represented a real object and the 'nonobject'-key (middle finger) if it represented a nonobject. Although object decision tasks may cause access to semantic and phonological knowledge, especially if information processing operates in cascade [28], evidence suggests that the object decisions are primarily based on access to structural knowledge [4,18,38]. In the categorization tasks the subjects were presented with pictures of natural objects and artefacts (see Fig. 1c) 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). In contrast to the object decision tasks, this kind of task does require access to semantics. In all tasks the subjects were encouraged to respond as fast and as accurately as possible. Before the actual experiments started the subjects performed a practice version of each task while in the scanner. Stimuli used in these practice versions were not used in the actual experiments.

The two object decision tasks differed from each other in that the real objects were drawn entirely from the category of natural objects in the one task and entirely from the category of artefacts in the other. The two categorization tasks differed from each other in that the items presented in the critical scan window were drawn predominantly from the category of natural objects in the one task and predominantly from the category of artefacts in the other (cf. Section 2.6). The pattern discrimination task was included as a low-level baseline task because it matched the object decision tasks and the categorization tasks with respect to sensoric processing and response mode, while it differed from them in that pattern discrimination does not require access to structural knowledge or semantics.

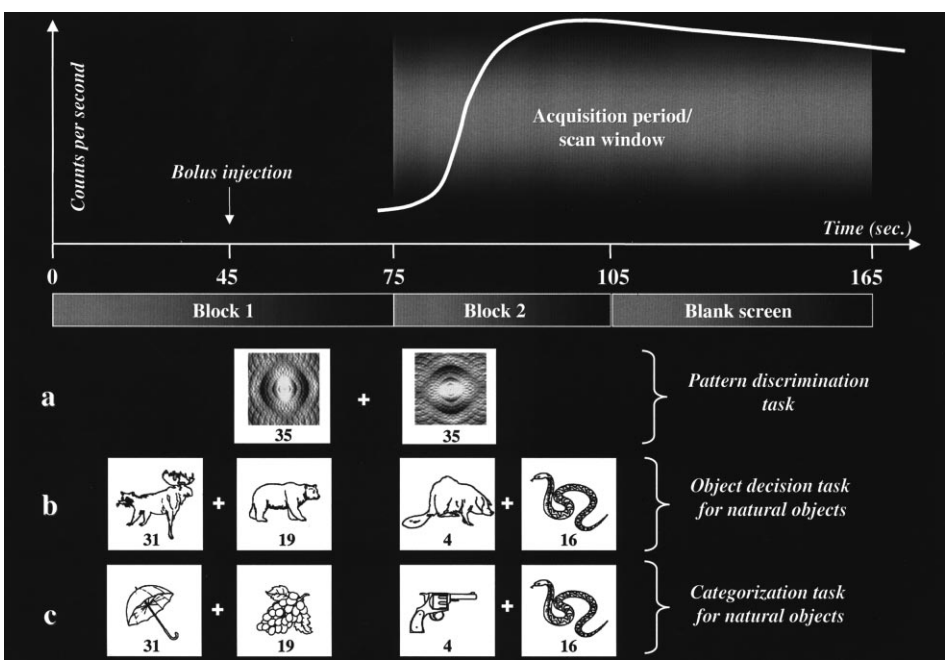

Fig. 1. Illustration of the relationship between PET data acquisition and the task design for three tasks: (a) the pattern discrimination task, (b) the object decision task for natural objects, and (c) the categorization task for natural objects. For the object decision tasks and the categorization tasks 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 object decision task for artefacts, the categorization task for artefacts, and the pattern discrimination task were arranged in a similar manner except for the fact that the pattern discrimination task was not blocked.

2.6. Design

Seventy stimuli were presented in each task. All stimuli were presented on a white background on a PC-monitor hanging 60 cm in front of the subjects. The stimuli subtended between 3–5° of visual angle and were presented in the center of gaze. Each stimulus was displayed for 180 ms, with an inter stimulus interval of 1320 ms, making each task last 1 min and 45 s. All the tasks were initiated at 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 subjects viewed a blank screen for the next 60 s, yielding a total acquisition time of 90 s (Fig. 1). By reducing isotope washout and improving counting statistics this protocol optimizes the signal-to-noise ratio from activated regions [3,21,39].

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

Each object decision task consisted of line-drawings of 35 real objects and 35 nonobjects. However, the presentation was blocked in two so that the first block consisted of 19 real objects (either natural objects or artefacts) + 31 nonobjects whereas the second block consisted of 16 real objects (either natural objects or artefacts) + four nonobjects.

Each categorization task consisted of line-drawings of 35 natural objects and 35 artefacts. These tasks were blocked in the same way as the object decision tasks. Accordingly, in one of the categorization tasks the first block consisted of 19 natural objects and + 31 artefacts, whereas the second block consisted of 16 natural objects + four 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 + four natural objects.

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 (Fig. 1). Due to this arrangement, the activation seen during the four tasks should primarily reflect structural or semantic processing of either real natural objects or real artefacts depending on the particular task.

The order of the pictures (real vs. nonobject/natural vs. artefact) was randomized within each block. The order of tasks was randomized across subjects except for a simple reaction time task that was always presented first.

2.7. Stimuli

The nonobjects used in the object decision tasks were selected from the set made by Lloyd-Jones [28]. These nonobjects are chimeric line-drawings of closed figures constructed by exchanging single parts belonging to objects from the same category. Since these nonobjects are composed of parts of objects from the same category, they could be considered either 'natural' or 'artefactual'. One set of 'natural' nonobjects was used in the object decision task with real natural objects and one set of 'artefactual' nonobjects was used in the object decision task with real artefacts.

The line-drawings of real objects were selected from various sources but mainly from the standardized set of Snodgrass and Vanderwart [40]. Care was taken to insure that the pictures looked similar overall regardless of source. The pictures used in the second block were all selected from the pool of Snodgrass and Vanderwart [40]. Ten sets of real objects (five sets of natural objects and five sets of artefacts), with 16 items in each set, were selected.

Snodgrass and Vanderwart supply ratings, on a scale from one to five, of the pictures along three dimensions, visual complexity, familiarity, and image agreement. Visual complexity reflects the subject's 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 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, $P > 0.1$).

Since ten sets of real objects were selected, these sets could be rotated across tasks. Accordingly, the same set of natural objects would appear in both an object decision 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 the particular selection of stimuli but rather are caused by true differences between tasks.

3. Results

3.1. Behavioral results

Only reaction times (RTs) to the 16 pictures presented in the second block (in the critical scan window) of the object decision tasks and the categorization tasks were subjected to analysis. A two-way ANOVA was carried out. The factors were Task Type with two levels (object decision vs. categorization) and Category with

Table 1
Mean error rate and mean correct RTs (ms) and S.D. for the 16 objects presented in the second block of the object decision tasks and the categorization tasks

	M error rate	*M* RT	S.D.
Natural objects in the object decision task	1.8	667	85
Artefacts in the object decision task	2.2	581	61
Natural objects in the categorization task	0.7	588	78
Artefacts in the categorization task	0.9	590	87

two levels (artefacts vs. natural objects). There was a significant main effect of Task Type [$F(1, 15) = 5.9$, $P < 0.03$] with slower RTs to objects in the object decision tasks, a significant main effect of Category [$F(1, 15) = 5.8$, $P < 0.03$] with faster responses to artefacts, and a significant interaction between Task Type and Category [$F(1, 15) = 14.7$, $P < 0.002$] with the difference between the object decision task and the categorization task being larger for natural objects. There was a significant difference in the number of errors in the four tasks (Friedman $P < 0.001$) with the error rate being highest in the object decision tasks. This finding suggests that there was no tradeoff between RT and accuracy. The mean error rate and the mean correct RTs and standard deviations (S.D.) are given in Table 1.

Post-hoc analyses (Tukey's HSD tests) of the main effects revealed a significant difference ($P < 0.05$) in responses to natural objects versus artefacts in the object decision tasks and between responses to natural objects in the object decision task vs. the categorization task. There were no significant differences in responses to natural objects vs. artefacts in the categorization tasks nor in responses to artefacts in the object decision task vs. the categorization task.

3.2. PET results

The results from the object decision tasks and the categorization tasks were subjected to a two-by-two factorial analysis. The factors were Task Type with two levels (object decision vs. categorization) and Category also with two levels (natural objects vs. artefacts). The adoption of a factorial approach makes it possible to evaluate activation effects that are context-sensitive, that is activations that reflect the interaction between Task Type and Category. As will be shown shortly interactions were found, and this makes the evaluation of the main effects more difficult. This difficulty can to some extent be overcome by use of conjunction analysis in which main effects are discounted when there is evidence for an interaction [34]. In what follows all main effects have been identified by creating an SPM of the sum of two simple contrasts and subsequently eliminating voxels where differences between the two simple contrasts were significant. As an example, the main effect of categorization was computed by (a) contrasting the categorization task for artefacts with the object decision task for artefacts, (b) contrasting the categorization task for natural objects with the object decision task for natural objects and (c) finding areas of activation that were common for both contrasts and in which the rCBF did not differ significantly between the two contrasts. To ensure that each contrast contributed to the conjunction we further excluded all voxels from the analysis that were not significant in each simple main effect at a threshold of $P < 0.01$. This was done using the masking option in SPM. A second problem in the interpretation of imaging data concerns whether differences between conditions reflect areas of activation or areas of deactivation. To overcome this problem we excluded all voxels from the conjunction analyses where the activation did not exceed that found during a low-level baseline task (the pattern discrimination task). This was done by masking each conjunction with the low-level baseline task at a threshold of $P < 0.01$. Thus, the conjunction constituting the main effect of categorization was computed by masking the conjunction with (a) the contrast between categorization and object decision to artefacts, (b) the contrast between categorization and object decision to natural objects, (c) the contrast between categorization of artefacts and the pattern discrimination task and (d) the contrast between categorization of natural objects and the pattern discrimination task. Areas associated with this conjunction, therefore, reflect areas where activation increases significantly during the categorization tasks relative to both the low-level baseline task and the object decision tasks regardless of category. The approach described here was also used to establish the main effect of object decision, artefacts and natural objects using the appropriate contrasts.

To identify areas where activation depended on both category and task type (areas associated with interactions), the approach was somewhat different. As an example, to identify areas specific to categorization of artefacts, the contrast between categorization of artefacts and categorization of natural objects was masked with (a) the contrast between categorization and object decision to artefacts, (b) the contrast between categorization of artefacts and the low-level baseline task, and (c) the interaction (between artefacts versus natural objects and categorization versus object decision). This was done using the masking option in SPM with the threshold for each mask set at $P < 0.01$. The procedure described here was also used to identify areas specific to the categorization of natural objects, object decision to artefacts and object decision to natural objects.

3.2.1. Areas associated with the main effect of object decision

The object decision tasks were associated with activation of (a) the right inferior temporal gyrus (Brodmann area (BA) 37) where the activation extended into the fusiform gyrus (BA 37 and 20) and the precuneus (BA 19 and 31); (b) the left fusiform gyrus (BA 19) of the occipital lobe; (c) the left middle occipital gyrus (BA 18); (d) the right inferior frontal gyrus (45); and, (e) the right inferior occipital gyrus (BA 18) (Table 2 and Fig. 2A).

3.2.2. Areas associated with the main effect of categorization

The only area associated with the categorization tasks regardless of category was the left inferior temporal gyrus (BA 20) ($Z = 4.81$). The peak of this activation corresponded to the following coordinates in Talairach space ($x = -52$, $y = -16$, $z = -40$).

3.2.3. Areas associated with the main effect of artefacts

The only area associated with the processing of artefacts regardless of task type was the left inferior temporal gyrus (BA 20) ($Z = 4.63$). The peak of this activation corresponded to the following coordinates in Talairach space ($x = -56$, $y = -24$, $z = -30$).

3.2.4. Areas associated with the main effect of natural objects

No areas were associated with the processing of natural objects regardless of task type.

3.2.5. Task specific activations

There were no areas specifically activated during the categorization of natural objects, object decisions to natural objects or object decisions to artefacts compared with the other tasks. However, areas with significantly increased rCBF during the categorization of artefacts relative to the categorization of natural objects, object decision to artefacts and the low-level baseline task were found in (a) the ventral and lateral part of the left frontal lobe including the middle frontal gyrus (BA 11), the inferior frontal gyrus (BA 46 and 47) and the ventral part of the left premotor cortex (BA 6); and (b) the left anterior cingulate gyrus (BA 32) (Table 3, Fig. 2B).

4. Discussion of PET results

4.1. Areas associated with the main effect of object decision

The object decision tasks were associated with increased rCBF bilaterally in the ventral parts of the brain (Fig. 2A and Table 2). The activated area, however, was considerably larger in the right hemisphere including both the right inferior temporal gyrus (BA 37) and the right precuneus (BA 19 and 31), suggesting that the right hemisphere may dominate in structural processing (also see [18]). This activation pattern is in good agreement with the finding that object recognition tasks primarily activate the ventral parts of the brain (e.g. [23]).

The object decision tasks were also associated with activation of the right inferior frontal gyrus (BA 45). This result has been reported earlier by Gerlach et al. [18], comparing four different object decision tasks (including the present ones) with a pattern discrimination task (which serves as a low-level baseline task in the present experiment). Since the important difference between the object decision tasks and the pattern discrimination task seems to be that the former tasks require access to stored visual knowledge (structural

Table 2
Areas associated with the main effect of object decision[a]

Region	Coordinates (x, y, z)			BA	Z-score
R. Inferior temporal gyrus	**50**	**−64**	**−12**	**37**	**6.75**
R. Fusiform gyrus	50	−52	−20	37	6.28
R. Precuneus	32	−72	52	19	5.44
R. Precuneus	30	−76	28	31	5.27
R. Fusiform gyrus	50	−32	−30	20	4.96
R. Fusiform gyrus	56	−40	−24	20	4.84
R. Fusiform gyrus	42	−28	−30	20	4.55
L. Fusiform gyrus	**−46**	**−72**	**−18**	**19**	**6.28**
L. Middle occipital gyrus	**−40**	**−88**	**10**	**18**	**6.20**
R. Inferior frontal gyrus	**48**	**42**	**8**	**45**	**5.18**
R. Inferior occipital gyrus	**26**	**−96**	**−16**	**18**	**4.49**

[a] Coordinates are in millimetres, relative to the anterior commissure. *L*, left, *R*, Right. Regions written in boldface 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 ($Z > 4.4$).

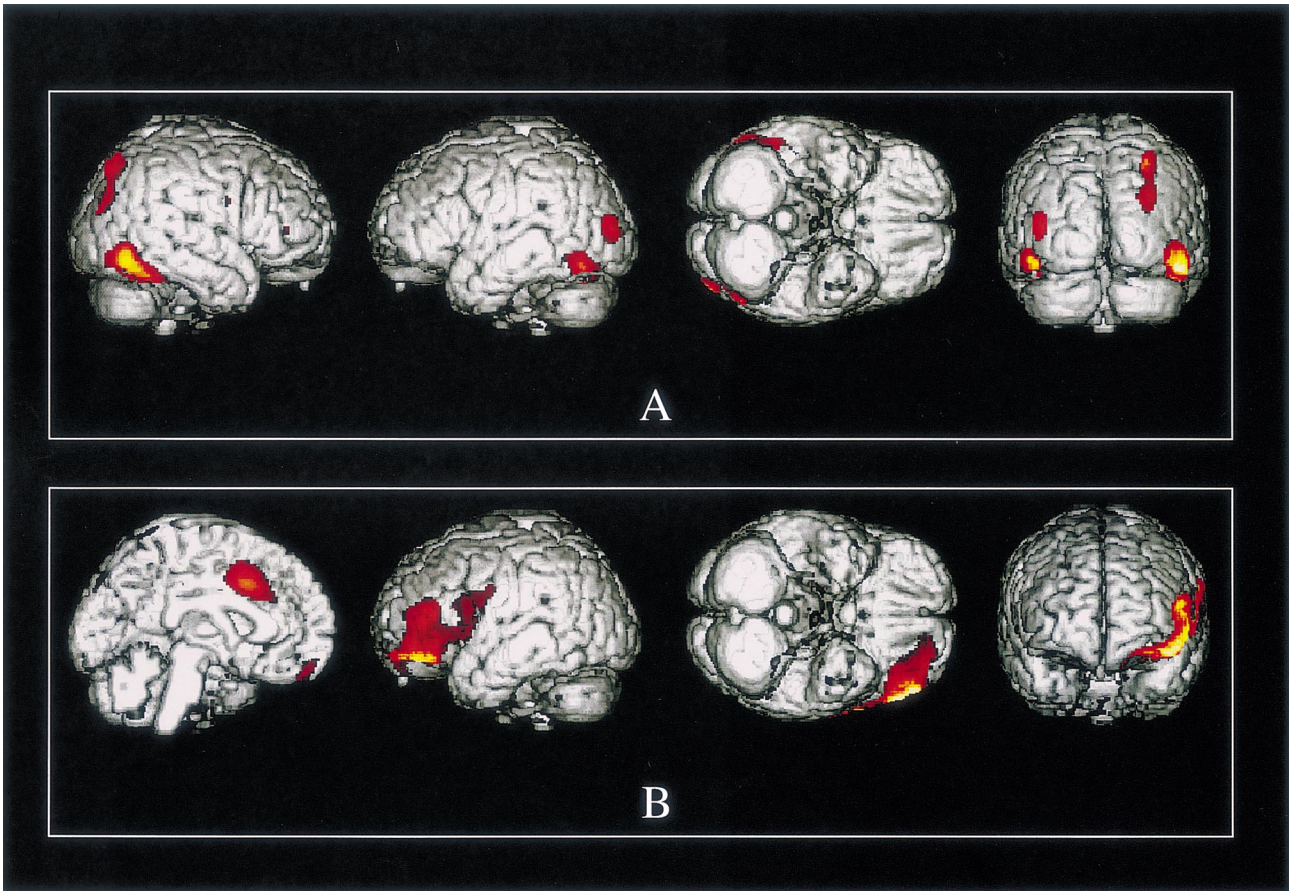

Fig. 2. Two renderings showing the areas activated during: (A) the object decision tasks, and (B) the categorization task for artefacts relative to all other tasks. The activated areas are projected onto a template anatomical MRI scan in coregistration with the Talairach atlas. All areas shown were significant at $P < 0.05$ corrected for multiple comparisons ($Z > 4.4$).

descriptions) whereas the latter task does not, it was concluded by Gerlach et al. [18] that this activation might reflect the involvement of the right inferior frontal gyrus in the retrieval of stored visual knowledge. Since the present data suggest that more structural processing is demanded by object decisions than by categorizations, this interpretation also holds for the present comparison. Thus, the observation that the right inferior frontal gyrus is associated with the object decision tasks, even when these tasks are contrasted with categorization tasks, supports the interpretation that this activation could reflect the retrieval of structural knowledge.

4.2. Areas associated with the main effect of categorization

The categorization tasks were associated with activation of the left inferior temporal gyrus (BA 20). Activation of this region has earlier been associated with a common semantic system for pictures and words [1,44]. The finding that this area is associated with the contrast between the categorization tasks and the object decision task supports a role for the left inferior temporal gyrus in semantic processing.

4.3. Areas associated with the main effect of artefacts

The activation found in the left inferior temporal gyrus (BA 20) during the processing of artefacts is very near the activation found during the categorization tasks compared with the object decision tasks. Since there is no evidence of any interaction between task type and category in this area it appears as if the effects of category and task type are additive (Fig. 3). In other words, the activation of the left inferior temporal gyrus is higher during the categorization tasks than during the object decision tasks but in both types of task the rCBF is higher during the processing of artefacts than during the processing of natural objects. If the left inferior temporal gyrus does play a role in the mediation of semantic knowledge, this activation pattern suggests that semantic knowledge contributes more to the categorization of artefacts than to the categorization of natural objects.

Table 3
Areas specifically activated during the categorization of artefacts[a]

Region	Coordinates (x, y, z)			BA	Z-score
L. Middle frontal gyrus	**−44**	**38**	**−20**	**11**	**6.81**
L. Middle frontal gyrus	−30	52	−18	11	6.64
L. Middle frontal gyrus	−32	44	−20	11	6.60
L. Inferior frontal gyrus	−54	36	16	46	6.25
L. Inferior frontal gyrus	−58	26	0	47	6.19
L. Precentral gyrus	−64	6	20	6	6.03
L. Anterior cingulate gyrus	**−12**	**16**	**38**	**32**	**6.75**

[a] See footnote to Table 2 for details.

4.4. Areas specifically activated during the categorization of artefacts

The most interesting area associated with the categorization of artefacts compared with all the other tasks was the left premotor cortex. This activation could reflect the processing of action knowledge. Evidence in favor of this suggestion comes from a study by Grafton et al. [20] in which silent naming of tool-use caused greater activation in the ventral part of the left premotor area (BA 6 and 44) than did silent tool naming. It seems reasonable to assume that the difference between these conditions is that silent naming of tool-use requires greater access to knowledge of tool function than does silent naming of tools. As argued by Grafton et al. [20] this knowledge could very well be related to the motor valence of the objects presented. Given that the left ventral premotor cortex does serve a role in mediating action knowledge, and given that this area was activated more during the categorization of artefacts than during any other task, this suggests that the categorization of artefacts is based, in part, on action knowledge. This suggestion seems to concur with the everyday experience where artefacts are often grouped together according to what kind of action applies to them (e.g. chairs are for sitting, knives are for cutting), whereas natural objects are often not. A similar conclusion was reached by Miller and Johnson-Laird [30]. In their view an artefact, as opposed to a natural object, is assigned to a category not because of any intrinsic aspect of its three-dimensional shape, but because its form is perceived as appropriate for a particular function. This 'function' could very well be related to what kind of action applies to the object. It is also interesting to note that this interpretation is compatible with psycholinguistic evidence suggesting that categorization begins at the level of distinctive or characterizing actions [26].

Besides the ventral part of the left premotor cortex the categorization of artefacts was also associated with activation of left anterior cingulate gyrus (BA 24). If action knowledge is accessed during the categorization of artefacts although no movement is required, movement might need to be suppressed. Since the anterior cingulate gyrus has been associated with motor inhibition [8], we propose that it serves just this purpose during the process of categorization. A similar account

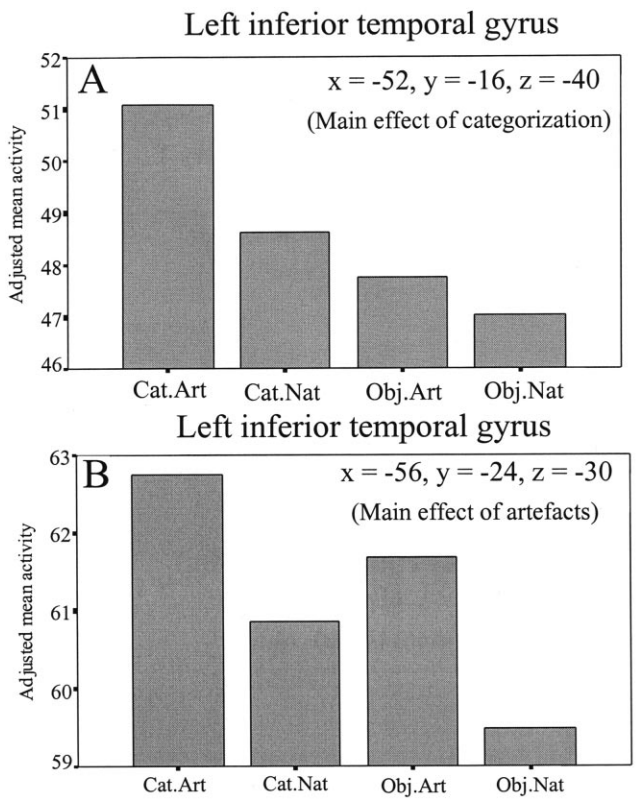

Fig. 3. The figures show the adjusted mean activity in: (A) the inferior temporal gyrus associated with the main effect of categorization, and (B) the inferior temporal gyrus associated with the main effect of artefacts for the following four conditions: Cat. Art., the categorization task for artefacts; Cat. Nat., the categorization task for natural objects; Obj. Art., the object decision task for artefacts; and Obj. Nat., the object decision task for natural objects. As can be seen, the rCBF is generally higher in the left inferior temporal gyrus during the categorization tasks compared with the object decision tasks but in both kinds of task the rCBF reaches its highest value during the processing of artefacts suggesting that the effects of category and task type are additive.

may be given for the activation of the orbitofrontal parts of the cortex (BA 11 and 47) because these regions have also been associated with motor inhibition [6,27].

The last area associated with the categorization of artefacts was the left inferior frontal gyrus (BA 46). Activation of this site has previously been associated with the processing of semantic knowledge (e.g. [22]). However, the activation of the left dorsolateral prefrontal cortex in the present study was associated with the interaction between category and task type rather than the main effect of categorization. How can we account for this interaction if activation of the dorsolateral prefrontal cortex reflects semantic processing? One possibility might be that the left dorsolateral prefrontal cortex is involved in the retrieval of action knowledge in much the same way as we have argued that the right dorsolatral prefrontal cortex is involved in the retrieval of structural knowledge. This proposal would fit with the suggestion that (a) action knowledge plays an important part in the categorization of artefacts, and (b) that action knowledge is primarily stored in the left hemisphere whereas the right hemisphere seems to dominate in structural processing [18].

5. General discussion

5.1. Evidence for dissociable stages in visual object processing: structure versus semantics

The object decision tasks were associated with increased rCBF in both the right and left fusiform gyri and the right inferior temporal gyrus regardless of category. Since these areas apparently play a role in the storage of structural knowledge [36], this finding supports the notion that object decision tasks are based on structural rather than semantic knowledge [4,35,38]. In contrast, the categorization tasks were associated with increased rCBF in the left inferior temporal gyrus regardless of category. These findings suggest that the left hemisphere plays a dominant role in semantic processing, even the semantic processing of pictures [37]. In addition to these areas, which are probably all involved in the storage of knowledge, the inferior frontal gyri were also found to be activated. These dorsolateral prefrontal areas have previously been suggested to be involved in the retrieval of knowledge. In the present study the right inferior frontal gyrus was activated more during the object decision tasks than during the categorization tasks, supporting a more specific role for this structure in the retrieval of visual/structural knowledge [18,24,25]. In contrast, the left inferior frontal gyrus was activated more during the categorization of artefacts than during any other task, supporting a more specific role for this structure in the retrieval of semantic/action knowledge [16,22].

The finding that the object decision tasks and the categorization tasks activated quite different structures supports the hypothesis that semantic knowledge and structural knowledge are in fact functionally dissociable.

5.2. Evidence for cascade processing in visual object processing

The finding that natural objects were categorized faster than they were accepted as real objects in the object decision task can be explained in two ways. On one hand it could be argued that this finding supports a cascade account because it would otherwise be difficult to explain how semantic information can be made available before structural processing has completed. On the other hand it could be argued that the categorization of natural objects is not performed on a truly semantic level but rather is performed on a structural level. Thus, because objects with similar physical form tend to belong to the same super-ordinate category [2], it might be that super-ordinate structural descriptions exist for objects with highly correlated features (i.e. natural objects [43]). The finding that semantic knowledge was accessed during the categorization of natural objects supports the former account because semantic access during this condition would not be expected if natural objects could be categorized entirely on a structural level. Accordingly, the PET data and the behavioural data combined seem to suggest that semantic information can be made available before structural processing has completed corresponding to the selection of a particular structural representation, and these data favor a cascade account.

Although a cascade account can explain why objects can be categorized faster than they can be accepted as real objects in an object decision task, it cannot explain why this difference between tasks depends on category. To explain this we must assume that a difference exists between these categories. One such difference might be that natural objects tend to be globally more visually similar and share more common parts with other members of their categories than artefacts, making natural objects harder to differentiate perceptually [17,18,28]. If this is the case we can account for the behavioural results in the following way. On the object decision tasks, natural objects are disadvantaged compared with artefacts because natural objects, due to their visual similarity, are harder to differentiate perceptually. However, because information processing operates in cascade, this disadvantage does not necessarily cause a disadvantage on the categorization tasks, because evidence for super-ordinate category membership accumulates (at a semantic level) while structural processing takes place, compensating for the difference between the two categories with respect to perceptual differentiation.

5.3. Evidence for a role of action knowledge in visual object processing

The categorization of artefacts was associated with increased rCBF in structures that have been suggested to play a role in action. These areas include, the ventral part of the left premotor cortex [19,20], the left anterior cingulate gyrus [8], and the left orbitofrontal cortex [6,27]. We believe that these activations can most easily be accounted for if it is assumed (a) that the ventral part of the left premotor cortex mediates action knowledge; (b) that action knowledge comprises information regarding the 'distinctive' actions that apply to different objects; (c) that the categorization of artefacts is based, in part, on what kind of distinctive actions apply to them [26], and (d) that the left anterior cingulate gyrus and orbitofrontal cortex are involved in motor suppression required during the categorization of artefacts because action knowledge is accessed but no actions are to be performed. Given these assumptions we can account for the finding that (i) the increase in rCBF in the ventral part of the premotor cortex was highest during the categorization of artefacts compared with any other task and (ii) the increase in rCBF in the left anterior cingulate gyrus and in the orbital parts of the left prefrontal cortex was highest during the categorization of artefacts compared with any other task. In general these findings lend support to the suggestion by Warrington and McCarthy [45] that action knowledge probably plays a more significant role during the processing of artefacts than during the processing of natural objects. The present data, however, takes this suggestion further by showing that action knowledge is not equally important across processing stages because it plays a more important part during categorization than during object decision.

5.4. Category-specificity

In the object decision tasks both natural objects and artefacts were associated with increased rCBF bilaterally in the ventral parts of the occipito-temporal cortex, areas suggested to contain structural knowledge. In the categorization tasks both the categories were associated with increased rCBF in the left inferior temporal gyrus. Accordingly, due to this overlap, the processing of the respective categories cannot be said to be totally segregated. On the other hand, the data do suggest that the categories differ with respect to how important different types of knowledge are for their processing. Thus, action knowledge seems more important for the categorization of artefacts than for the categorization of natural objects. Based on these findings, we suggest that the processing of these categories is not totally segregated, but rather that the categories differ in their weight on different forms of knowledge in particular tasks.

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