Perceptual differentiation and category effects in normal object recognition
A PET study

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Summary
The purpose of the present PET study was (i) to investigate the neural correlates of object recognition, i.e. the matching of visual forms to memory, and (ii) to test the hypothesis that this process is more difficult for natural objects than for artefacts. This was done by using object decision tasks where subjects decided whether pictures represented real objects or non-objects. The object decision tasks differed in their difficulty (the degree of perceptual differentiation needed to perform them) and in the category of the real objects used (natural objects versus artefacts). A clear effect of task difficulty was found in both the behavioural and in the PET data. In the PET data, the increase in task difficulty was associated with increased regional cerebral blood flow in the posterior part of the right inferior temporal gyrus and
in the anterior part of the right fusiform gyrus. This may be the neural correlate of matching visual forms to memory, and the amount of activation in these regions may correspond to the degree of perceptual differentiation required for recognition to occur. With respect to behaviour, it took significantly longer to make object decisions on natural objects than on artefacts in the difficult object decision tasks. Natural objects also recruited larger parts of the right inferior temporal and anterior fusiform gyri compared with artefacts as task difficulty increased. Differences in the amount of activation in these regions may reflect the greater perceptual differentiation required for recognizing natural objects. These findings are discussed in relation to category-specific impairments after neural damage.

Keywords: object recognition; perceptual differentiation; category-specificity; object decision; PET

Abbreviations: MPRAGE = magnetization prepared rapid acquisition gradient echo; rCBF = regional cerebral blood flow; SPM = statistical parametric mapping

Introduction
In recent years several patients with category-specific problems in recognition or naming of natural objects or artefacts have been described. It has been claimed that impaired recognition of natural objects co-occurs with impaired visual knowledge and that impaired recognition of artefacts co-occurs with impaired functional knowledge (Warrington and McCarthy, 1983, 1987; Warrington and Shallice, 1984; Hart and Gordon, 1992; Gainotti and Silveri, 1996). In accord with these observations it has been argued that impaired recognition or naming of natural objects might reflect an impaired visual semantic system, whereas the impairment for artefacts might reflect an impaired functional/verbal semantic system. Although plausible, this account is difficult to reconcile with at least two sets of observations: (i) patients with category-specific recognition deficits for

natural objects may be equally impaired on visual and functional knowledge (Laiacona *et al.*, 1993; Caramazza and Shelton, 1998), and (ii) patients with impaired recognition of natural objects may perform successfully on tasks that demand access to stored visual knowledge (Riddoch and Humphreys, 1987*b*; Sheridan and Humphreys, 1993). However, even though there is no one to one correspondence between category-specific deficits for natural objects and impaired visual knowledge, cases have been reported in which the underlying deficit seems attributable to impaired pre-semantic visual processing (Sartori and Job, 1988; Etcoff *et al.*, 1991; Sirigu *et al.*, 1991; Sartori *et al.*, 1993*a*, *b*; De Renzi and Lucchelli, 1994; Mauri *et al.*, 1994; Arguin *et al.*, 1996). Different accounts for these cases have been advanced. This paper is primarily concerned with the account proposed

by Humphreys and colleagues (Lloyd-Jones and Humphreys, 1997), who argue that deficits for living/natural objects may sometimes be attributed to differences that occur in normal object recognition.

In the account by Humphreys and colleagues, normal object naming may be characterized by three general stages. In stage one, the visual information activates associated structural representations specifying the object's form (the structural description system). In stage two, activation of structural descriptions spreads to associated semantic representations specifying functional/associative knowledge (the semantic system). In stage three, activation of semantic representations spreads to phonological representations specifying object names. It is assumed that the representations of many stimuli can be activated in parallel within any given level (structural, semantic or phonological). Moreover, information processing is thought to be transmitted continuously from one level to the next, i.e. in cascade.

The relevance of this model in the present context stems from the suggestion that natural objects tend to be globally more visually similar and share more common parts with other members of their categories than artefacts (Riddoch and Humphreys, 1987b; Humphreys et al., 1988). If items from the category of natural objects share more common parts than items from the category of artefacts and if many representations can be activated in parallel, competition within the structural description system (and subsequent processing systems) will be larger for natural objects compared with artefacts. Natural objects will simply be more difficult to differentiate than artefacts when matched to memory, yielding artefacts an advantage. Hence, damage at a level corresponding to the structural description system could lead to a category-specific deficit for natural objects.

The suggestion that artefacts are differentiated more easily than natural objects at the structural level has found support in a study by Lloyd-Jones and Humphreys (Lloyd-Jones and Humphreys, 1997). In this study subjects had to perform an object decision task (distinguish between real objects and non-objects), a task believed to require access to structural descriptions but not necessarily to semantics (Riddoch and Humphreys, 1987a; Chertkow et al., 1992; Sheridan and Humphreys, 1993). It was found that responses were significantly slower to natural objects compared with artefacts. This finding has also been obtained in a computational simulation (Humphreys et al., 1995). Additional evidence in favour of the notion that artefacts are differentiated more easily than natural objects comes from Gaffan and Heywood (Gaffan and Heywood, 1993) who found that normal observers make more errors while identifying living as opposed to non-living things under degraded viewing conditions (the stimuli were presented for only 20 ms). Moreover, Gaffan and Heywood found that the same was true for monkeys trained to discriminate between objects from the same set of items. Together these findings suggest that category-specific effects can indeed arise at the structural level.

The purpose of the present PET study was to investigate the neural correlates of perceptual differentiation and to see whether any evidence of category-specific brain activation(s) could be found at this level. This was done by using object decision tasks varying in difficulty and so requiring relatively more or less differentiation between stimuli at a structural level.

The aim of this study was twofold. (i) To test the notion that object decisions are based on structural rather than semantic knowledge. If this is so, increased regional cerebral blood flow (rCBF) during object decisions should be found in areas believed to be involved in visual rather than semantic processing. (ii) Though category-specific effects in object recognition have been investigated previously (e.g. Perani et al., 1995; Martin et al., 1996; Grabowski et al., 1998) these studies have often not directly addressed the level of processing where effects occurred. The present study provides such an attempt, because the tasks used were aimed at directly assessing potential category effects at the structural level, as defined in the model proposed by Humphreys and colleagues (Lloyd-Jones and Humphreys, 1997).

Methods
Subjects
Fifteen right–handed healthy volunteers (seven female, eight male) ranging in age from 22 to 30 (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 Medical Systems, Milwaukee, Wis., 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 (DeGrado et al., 1994).

Each subject received 12 intravenous bolus injections of 200 MBq (5.7 mCi) of $H_2^{15}O$ with an inter-scan 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 from 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).
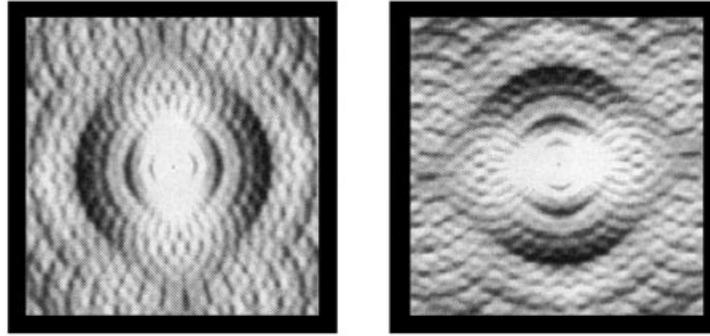
Fig. 1 The patterns displayed in the pattern discrimination task.

MRI scanning

Structural MRI scanning was performed with a 1.5 T Vision scanner (Siemens, Erlangen, Germany) using a 3D MPRAGE 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 was 170 and the in-plane matrix dimensions were 256 × 256.

Image analysis

For all subjects the complete PET brain volume was sampled. Image analysis was performed using Statistical Parametric Mapping software (SPM96, 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 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 were subsequently transformed into the standard stereotactic atlas of Talairach and Tournoux (Talairach and Tournoux, 1988) using the PET template defined by the Montreal Neurological Institute (Friston *et al.*, 1995*a*). 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 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 and colleagues (Friston *et al.*, 1991, 1995*b*) using the theory of Gaussian fields. The resulting foci were then characterized in terms of peak *Z*-scores above this level.

Cognitive tasks

The experiment consisted of 12 different tasks, although only a subset will be reported here. This subset includes a pattern discrimination task and four different object decision tasks. In the pattern discrimination task the subjects saw two different patterns (see Fig. 1). The subjects were instructed to press the 'vertical' key on a serial response box placed in front of their right hand if the pattern was vertical and the 'horizontal' key if the pattern was horizontal. In the four object decision tasks the subjects were presented with pictures that represented either real objects or non-objects (see Fig. 2). In these tasks the subjects were instructed to press the 'real object' key if the picture represented a real object and the 'non-object' key if it represented a non-object. 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 four object decision tasks differed from each other along two variables: (i) type of real object used (natural versus artefact), and (ii) type of non-object used (novel versus chimeric, where the novel non-objects were completely unknown to the subjects, whereas the chimeric non-objects were composed by exchanging single parts belonging to real objects). This created four conditions: (a) novel non-objects + natural objects, (b) novel non-objects + artefacts, (c) chimeric non-objects + natural objects and (d) chimeric non-objects + artefacts. Examples of the real objects and the non-objects used are given in Fig. 2.

Because object decision tasks with novel non-objects are generally performed significantly faster and more accurately than those with chimeric non-objects (pilot study/behavioural results), the former task will be referred to as *easy*, whereas the latter will be referred to as *difficult*.
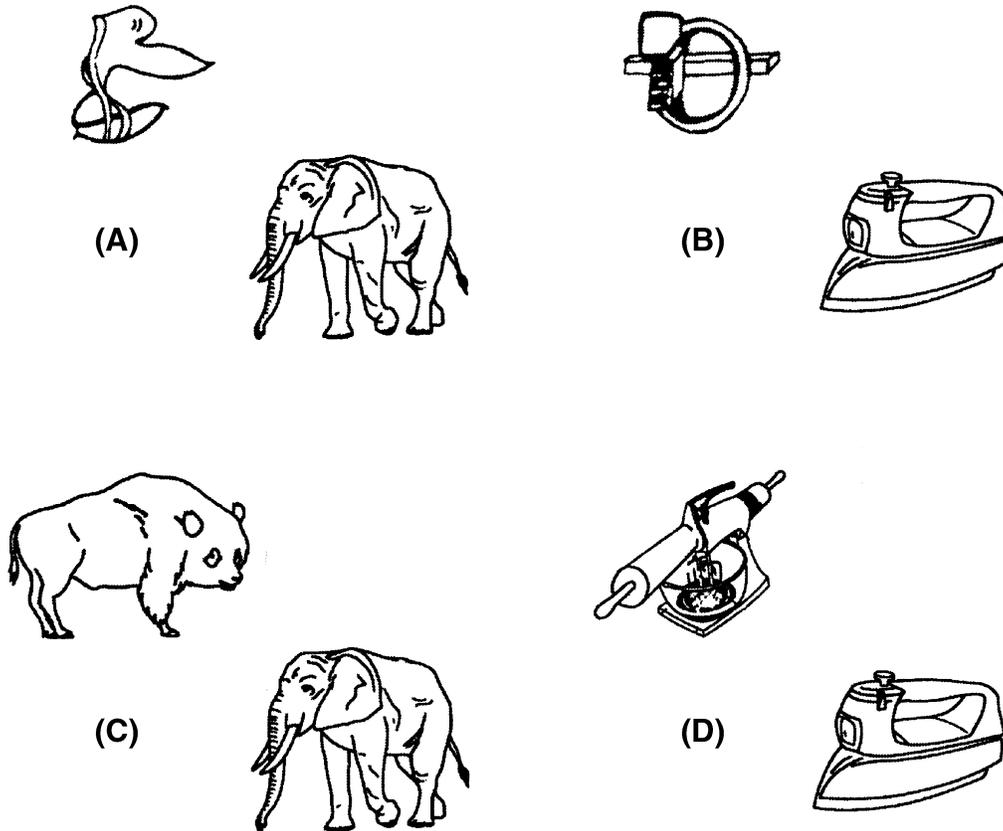
Fig. 2 Examples of the stimuli displayed in the four object decision tasks. (**A**) Novel non-objects + natural objects; (**B**) novel non-objects + artefacts; (**C**) chimeric non-objects + natural objects; and (**D**) chimeric non-objects + artefacts.

The rationale for using the tasks is as follows. The pattern discrimination task was chosen as a baseline task because it matched the object decision tasks with respect to sensoric processing and response mode, while it differed from them in that pattern discrimination does not require access to stored visual knowledge. Accordingly, a comparison between the pattern discrimination task and the object decision tasks should reveal the areas important for visual object recognition. The potential activation associated with this comparison, however, cannot be uniquely attributed to access to stored visual knowledge; activation could also reflect the fact that pictures of objects, as opposed to patterns, are subjected automatically to semantic or phonological processing. A further measure of perceptual differentiation therefore involves a comparison between the easy versus the difficult object decision tasks. Any automatic access to semantic or phonological knowledge from objects should occur in both tasks. What differs across tasks is the degree of perceptual processing required to reject distractors at the structural level.

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 and 5° of visual angle and were presented in the centre of

gaze. Each stimulus was displayed for 180 ms, with an inter-stimulus interval of 1320 ms, making each task last 105 s. All tasks were initiated at approximately 75 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 this point of task offset, the subjects viewed a blank screen for the next 60 s, yielding a total acquisition time of 90 s. By reducing isotope washout and improving counting statistics this protocol optimizes the signal-to-noise ratio from activated regions (Silbersweig *et al.*, 1993; Hurtig *et al.*, 1994; Cherry *et al.*, 1995).

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 black and white line-drawings of 35 real objects and 35 non-objects. However, the presentation was blocked in two so that the first block consisted of 19 real objects + 31 non-objects, whereas the second block consisted of 16 real objects + 4 non-objects. 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. Accordingly, the second block was displayed in the actual uptake phase of the tracer and ended before washout was likely to begin. Because of this arrangement, the activation seen during the object decision tasks should

primarily reflect the processing of real objects. The delay from injection to isotope delivery to the brain and the estimate of the duration of the critical uptake phase was based on each individual's first scanning (a simple reaction time task). However, correct timing was monitored throughout the scanning sessions and corrections in task onset were made if a change occurred.

The order of the pictures (real versus non-object) 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. Reaction times were recorded during scanning by use of a serial response box.

Stimuli

The novel non-objects used in the two easy object decision tasks were selected randomly from the set made by Kroll and Potter (Kroll and Potter, 1984). These non-objects are line-drawings of closed figures with an object-like appearance. They were created by tracing parts of drawings of real objects and regularizing the resulting figures. The chimeric non-objects used in the difficult decision tasks were selected from the set made by Lloyd-Jones and Humphreys (Lloyd-Jones and Humphreys, 1997). These chimeric non-objects are line-drawings of closed figures constructed by exchanging single parts belonging to objects from the same category. Because these non-objects are composed of parts of objects from the same category, they could be considered either 'natural' or 'artefactual'. One set of 'natural' non-objects was used in the difficult object decision task with real natural objects, and one set of 'artefactual' non-objects was used in the difficult 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 (Snodgrass and Vanderwart, 1980). Care was taken to ensure 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. 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 1 to 5, 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 parameters has been emphasized by several authors (e.g. 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 10 sets of objects were matched with respect to familiarity, visual complexity and image agreement so that

Table 1 *Mean error rate and mean correct reaction times (ms) and standard deviations for real objects presented in the second block of the four object decision tasks*

	Mean error rate	Mean reaction time	SD
Novel non-objects + natural objects	1.3	556	78
Novel non-objects + artefacts	1.3	564	80
Chimeric non-objects + natural objects	1.8	667	85
Chimeric non-objects + artefacts	2.2	581	61

they did not differ significantly along any of these dimensions (Kruskal-Wallis, $P > 0.1$).

Because 10 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 easy and a difficult object decision task. The same was true of the artefacts. This procedure ensures that any potential differences observed between the two categories (natural objects versus artefacts) are unlikely to be caused by the particular selection of stimuli but rather are caused by true differences between tasks (easy versus difficult object decisions) and categories.

Results
Behavioural results

Only reaction times to real objects presented in the second block (in the actual scan window) of the four object decision tasks were subjected to analysis. A two-way ANOVA (analysis of variance) was carried out. The factors were task type, with two levels (novel versus chimeric non-objects), and category, with two levels (artefacts versus natural objects). There was a significant main effect of task type [$F(1,15) = 48.6$, $P < 0.001$] with slower reaction times to real objects in tasks with chimeric non-objects, a significant main effect of category [$F(1,15) = 8.1$, $P < 0.02$], with faster responses to artefacts, and a significant interaction between task type and category [$F(1,15) = 15.8$, $P < 0.001$], with the difference between artefacts and natural objects being larger in tasks with chimeric non-objects. There was no significant difference in the number of errors in the four tasks (Friedman, $P > 0.1$), suggesting that there was no trade-off between reaction time and accuracy. The mean error rate and the mean correct reaction times and standard deviations are given in Table 1.

Post hoc analyses (Tukey honest standard deviation tests) of the main effects revealed significant differences ($P < 0.05$) in responses to natural objects versus artefacts in the tasks with chimeric non-objects, and in responses to natural objects in tasks with novel versus tasks with chimeric non-objects. There was no significant difference in either responses to natural objects versus artefacts in tasks with novel non-objects, or in responses to artefacts in the task with novel versus the task with chimeric non-objects.

Discussion of behavioural results

The advantage for artefacts found by Lloyd-Jones and Humphreys (Lloyd-Jones and Humphreys, 1997) is replicated. However, the difference between natural objects and artefacts was shown to depend on task difficulty because it only appeared on the difficult tasks. At first hand this finding questions the explanation advanced by Lloyd-Jones and Humphreys, who argue that the response to artefacts is faster than to natural objects in the object decision task because they are more structurally dissimilar than natural objects and therefore differentiated more easily. If this was the case, it might be expected that an advantage for artefacts would be found in both tasks. It is, however, quite likely that the easy object decision tasks were so easy that only a minimal degree of perceptual differentiation was required in order to perform them, preventing any differences between categories from emerging. Thus, given that the non-objects are novel in the easy tasks it might be sufficient to identify just some recognizable part of an object to judge it as a real object. This strategy will not do in the difficult tasks because the non-objects are also composed by parts of real objects. Accordingly, as opposed to a real object in the difficult task, a real object in the easy object decision task might be judged as real before there is a complete match between the stimulus and a stored structural representation corresponding to the stimulus.

The suggestion that the subjects adopt different strategies in the easy and the difficult object decision tasks is compatible with the account offered by Lloyd-Jones and Humphreys who argue that natural objects are more difficult to differentiate than artefacts because they are more visually similar and share more common parts with other members of their categories than artefacts. From this it might be predicted that natural objects are only disadvantaged compared with artefacts when the demand on perceptual differentiation is high, as it is in difficult object decision tasks. If the demand on perceptual differentiation is low, as it might be in the easy object decision tasks, no prediction is made.

PET results

To identify the areas activated during the four object decision tasks relative to the pattern discrimination task a contrast was made between each object decision task and the pattern discrimination task. A conjunction analysis was then performed on these contrasts. Because the conjunction analysis sums up the four contrasts and removes voxels where there is a significant difference between the contrasts (Price and Friston, 1997) this analysis should identify areas that are activated to the same extent during each of the four object decision tasks compared with the pattern discrimination task. The analysis revealed extensive bilateral activation of the ventral parts of the brain as well as activation of the right inferior frontal gyrus during object decisions (Fig. 3). The peak activations were found in the fusiform gyri, the parahippocampal gyri, the limbic lobes, the right inferior occipital gyrus, the right superior parietal lobe, the right inferior frontal gyrus, the left middle occipital gyrus and the left inferior temporal gyrus (Table 2).

The results from the four different object decision tasks were subjected to a two-by-two factorial analysis. The factors were task type, with two levels (easy versus difficult), and category, also with two levels (natural objects versus artefacts). There was no interaction between task type and category and no main effect of category. There was, however, a significant main effect of task type associated with increased rCBF in the posterior part of the right inferior temporal gyrus including the anterior part of the fusiform gyrus during the difficult object decision tasks ($Z = 5.23$) (Fig. 4). The activation had its peak in the extreme posterior part of the right inferior temporal gyrus corresponding to the following coordinates in Talairach space: $x = 54$, $y = -62$, $z = -12$.

Discussion of PET results

Compared with the pattern discrimination task, all four object decision tasks caused extensive bilateral activation of the posterior and ventral parts of the brain. This pattern of activation is in good agreement with the finding that object recognition tasks generally activate the ventral parts of the brain (e.g. Kohler *et al.*, 1995). The activation found in the right inferior frontal gyrus, on the other hand, is not usually associated with object recognition but rather with working memory (e.g. Blaxton *et al.*, 1996; Coull *et al.*, 1996). It is difficult, however, to see why the object decision tasks should engage working memory to a greater extent than the pattern discrimination task. Alternatively, it has been suggested that areas in the dorsolateral prefrontal cortex may be involved in the retrieval of stored knowledge. Moreover, activations found in the left dorsolateral prefrontal cortex have usually been associated with the retrieval of verbal/semantic knowledge (e.g. Kapur *et al.*, 1994; Gade *et al.*, 1997), whereas activations of the right dorsolateral prefrontal cortex have been associated with the retrieval of more visual/spatial knowledge (Kosslyn, 1994; Kosslyn *et al.*, 1995). In keeping with these suggestions, we would like to argue that the activation of the right inferior frontal gyrus probably reflects that this area is engaged in the retrieval of stored visual knowledge. This interpretation makes sense because (i) the important difference between the object decision tasks and the pattern discrimination task seems to be that the former tasks can only be performed by accessing stored visual knowledge, and (ii) the area associated with increased task difficulty was located in the right hemisphere.

It is worth noting that object decisions in this comparison were associated with neither activation of the anterior part of the left inferior temporal gyrus nor of the left middle temporal gyrus—regions proposed to be involved in semantic processing (Sergent *et al.*, 1992; Gainotti *et al.*, 1995; Vandenberghe *et al.*, 1996; Caramazza and Shelton, 1998).
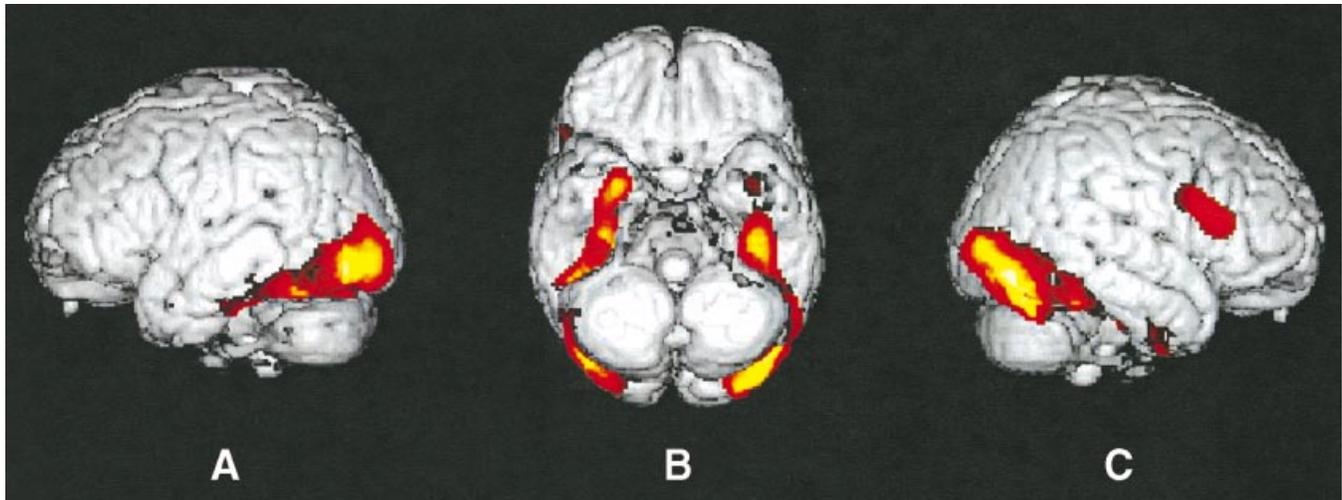
Fig. 3 A rendering showing the activated areas common for the four object decision tasks relative to the pattern discrimination task. The activated areas are projected onto a template anatomical MRI scan in co-registration with the Talairach atlas. All areas shown were significant at $P < 0.05$, corrected for multiple comparisons ($Z > 4.5$). (**A**) The left side of the brain showing activation of the middle occipital gyrus, the inferior occipital gyrus and the inferior temporal gyrus. (**B**) The ventral part of the brain showing activation of the inferior occipital gyri, the fusiform gyri, the inferior temporal gyri, the parahippocampal gyri and the limbic lobes. (**C**) The right side of the brain showing activation of the inferior occipital gyrus, the middle occipital gyrus, the inferior temporal gyrus and the inferior frontal gyrus.

Table 2 *Brain regions associated with significantly increased peak activation in the four object decision tasks compared with the pattern discrimination task*

Region	Coordinates			Z–score
	x	y	z	
Right fusiform gyrus	**38**	**–62**	**–12**	**9.16**
Right fusiform gyrus	42	–46	–18	8.49
Right inferior occipital gyrus	34	–86	2	7.70
Right parahippocampal gyrus	36	–28	–22	7.16
Right limbic lobe	30	0	–36	6.42
Right superior parietal lobe	30	–68	48	4.51
Left middle occipital gyrus	**–36**	**–58**	**–10**	**8.14**
Left fusiform gyrus	–42	–74	–14	7.73
Left fusiform gyrus	–36	–40	–18	7.38
Left parahippocampal gyrus	–36	–26	–24	7.20
Left fusiform gyrus	–36	–48	–16	6.98
Left fusiform gyrus	–44	–50	–18	6.85
Left middle occipital gyrus	–28	–90	–6	6.61
Left inferior temporal gyrus	–52	–72	–6	6.40
Left fusiform gyrus	–54	–58	–18	5.29
Left limbic lobe	–34	0	–26	5.12
Right inferior frontal gyrus	**44**	**10**	**26**	**6.54**
Right inferior frontal gyrus	50	24	16	5.79

Coordinates are in millimetres, relative to the anterior commissure. Regions written in bold indicate the main peak activation within an area, whereas regions written in roman indicate associated peaks. Threshold was set at $P < 0.05$, corrected for multiple comparisons ($Z > 4.4$).

In addition, retrieval of verbal/semantic knowledge is usually associated with left dorsolateral prefrontal activations, whereas a right dorsolateral prefrontal activation was found in the present contrast. It therefore appears that the object decision tasks used in the present study are performed without necessarily accessing semantic knowledge.

This assumption is further strengthened by the finding that increasing the difficulty of the object decisions causes increased rCBF in the extreme posterior part of the right inferior temporal gyrus including the anterior part of the fusiform gyrus. The site of this activation is very similar to the one found by Schacter and colleagues (Schacter *et al.*, 1995) in a PET study where subjects decided whether 3D geometrical figures could exist in the 3D world or not. Because the stimuli used in the study by Schacter and colleagues are unlikely to be associated with semantic knowledge, the observed activation at this site appears to relate to pre-semantic visual processing.

Based on this evidence, the present finding suggests a role for the extreme posterior part of the right inferior temporal gyrus and the anterior part of the right fusiform gyrus in the processing of structural knowledge, and the activation seen in these areas may be the neural correlate of the process of matching visual forms to memory, akin to accessing the structural description system in models of object recognition. This interpretation is in accord with, and supports the proposal that object decisions are based on pre-semantic visual knowledge regarding the form of objects (i.e. structural descriptions) (Riddoch and Humphreys, 1987*a*; Chertkow *et al.*, 1992; Sheridan and Humphreys, 1993). Accordingly, the increase in task difficulty in this study probably reflects an increased demand on perceptual differentiation. It is interesting, in this context, that some researchers have proposed that the lateral part of the right fusiform gyrus is activated specifically by faces (Kanwisher *et al.*, 1997; McCarthy *et al.*, 1997). Although the proposal of face
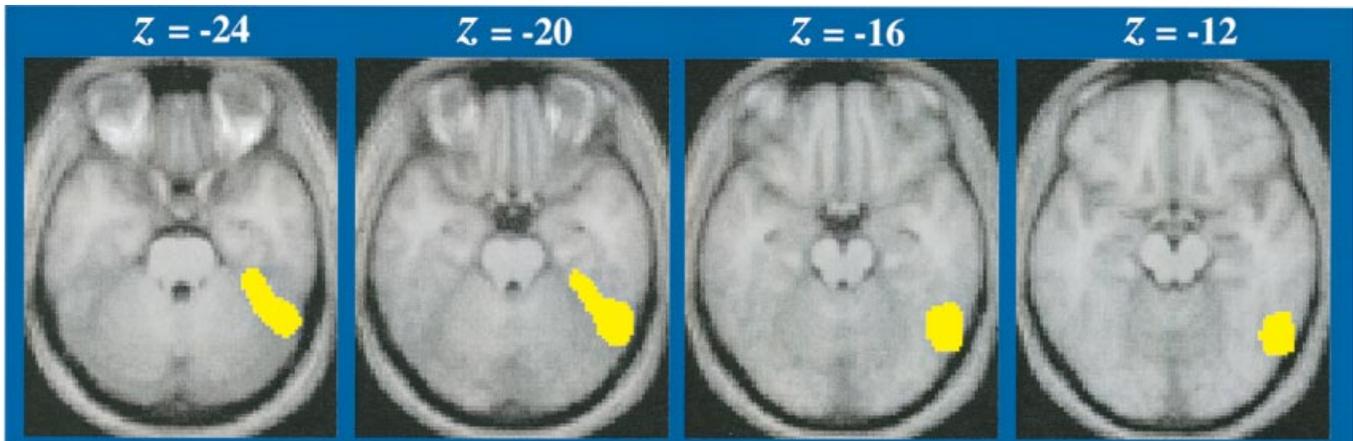
Fig. 4 Four horizontal sections showing the area associated with the main effect of increased task difficulty. The activated area is superimposed on the average image of the stereotactically normalized anatomical MRI scans for each subject. The SPM{Z} was thresholded at a level of $P < 0.001$, uncorrected ($Z > 3.09$). In each slice the left cerebral hemisphere is displayed to the left. The peak activation was located at $x = 54$, $y = -62$, $z = -12$, $Z = 5.23$, in Talairach space. The cluster shown was significant at $P = 0.006$.

selective activation in this area cannot be rejected, the present finding does raise the possibility that the activation seen during face perception might simply reflect increased demand on perceptual differentiation, a process that could very well take more effort among faces than among other categories, rather than face specific processing *per se* (for similar findings, see Chao *et al*., 1998).

General discussion

Compared with the pattern discrimination task, the object decision tasks caused increased rCBF bilaterally in the ventral parts of the brain and in the right inferior frontal gyrus. In addition, the increase in the difficulty of the object decision tasks caused increased rCBF in the posterior part of the right inferior temporal gyrus. Thus, the activation pattern associated with the object decision tasks is predominantly right-sided and it does not include areas that have previously been associated with semantic processing in imaging studies (e.g. Sergent *et al*., 1992; Vandenberghe *et al*., 1996) or in lesion studies (e.g. Gainotti *et al*., 1995; Caramazza and Shelton, 1998). However, it has been suggested that the right inferior temporal gyrus stores structural representations of objects (Schacter *et al*., 1995) and that the right inferior frontal gyrus plays a role in the retrieval of visual/spatial knowledge (Kosslyn, 1994; Kosslyn *et al*., 1995). The present findings therefore support the notion that object decisions are performed by accessing structural rather than semantic knowledge (Riddoch and Humphreys, 1987*a*; Chertkow *et al*., 1992; Stewart *et al*., 1992; Sheridan and Humphreys, 1993).

Comparing the PET data with the behavioural data from the four object decision tasks, the immediate finding seems to be a lack of correspondence. Thus, in the behavioural data the change in task type (easy versus difficult) seemed to affect results for the category of natural objects only, whereas it appeared to affect the results for both categories in the PET data. How can we account for this discrepancy?

Given that the PET data suggest that the difference in results obtained as a function of task type is related to the degree of perceptual differentiation needed to perform the tasks, and given that the behavioural data suggest that the change in task type affects the results for natural objects more than for artefacts, we would have expected to find interactions between category and task type in the areas associated with the main effect of increased task difficulty. The absence of such interactions could conceivably be due to insufficient statistical power in the analysis of the PET data. We consider this possibility unlikely because there was no evidence of interactions in these areas even when the threshold was lowered to $P < 0.05$, uncorrected.

Although the failure to find interactions in the PET data seems to imply that there is no simple one-to-one correspondence between performance measures and measures of rCBF, we would still expect some neural correlate of the increased reaction times to natural objects in the difficult object decision task. In an attempt to find this correlate we explored the simple main effects of increased task difficulty in the PET data. Although this sort of analysis is usually performed in an attempt to establish the source of an interaction, an interaction that is missing in the present PET data, we find this approach warranted because the PET data did show effects of task type and because an interaction between task type and category was evident in the behavioural data.

The analysis of the simple main effects revealed that only the difference between the difficult versus the easy object decision task for natural objects was significant. The contrast, however, was only significant at the cluster level ($P = 0.028$) with the maximum peak value being just marginally significant ($P < 0.08$, corrected). The activation had its centre in the extreme posterior part of the right inferior temporal gyrus corresponding to the following coordinates in Talairach space ($x = 52$, $y = -62$, $z = -14$), but it also included the anterior part of the right fusiform gyrus (Fig. 5).
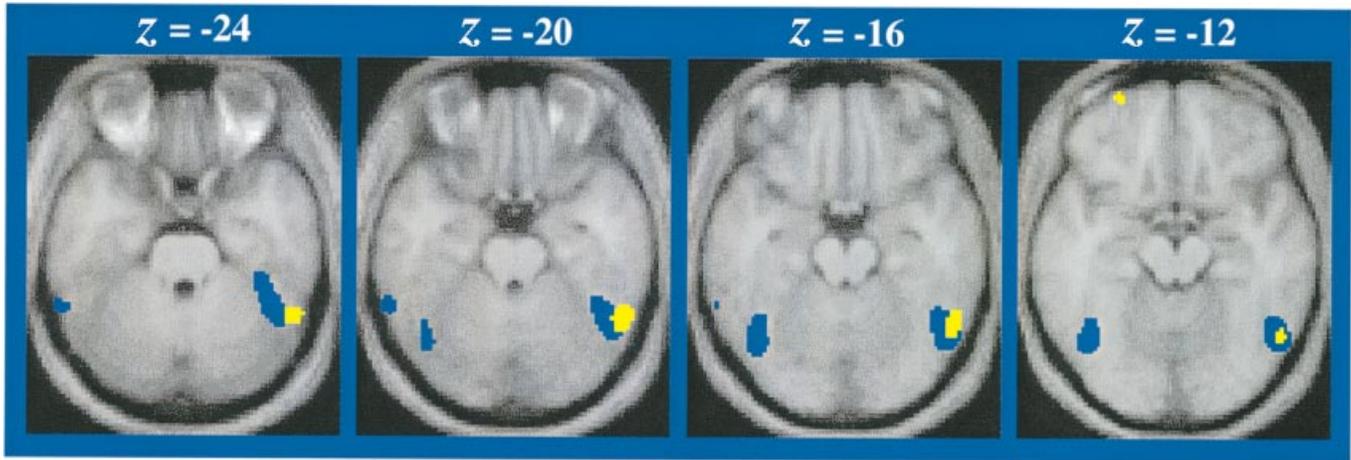
Fig. 5 Four horizontal sections showing the areas associated with the simple main effect of increased task difficulty for natural objects (blue) and the simple main effect of increased task difficulty for artefacts (yellow). The activated areas are superimposed on the average image of the stereotactically normalized anatomical MRI scans for each subject. The SPM{Z} was thresholded at a level of $P < 0.001$, uncorrected ($Z > 3.09$). In each slice, the left cerebral hemisphere is displayed to the left. The largest peak activation associated with natural objects was located at $x = 52$, $y = -62$, $z = -14$, $Z = 4.33$ in Talairach space and the activated area covered 661 voxels. The second peak activation was located at $x = -44$, $y = -64$, $z = -14$, $Z = 4.14$ in Talairach space. The peak activation associated with artefacts was located at $x = 56$, $y = -54$, $z = -20$, $Z = 3.73$ in Talairach space and the activated area covered 166 voxels. Although there is an overlap between the activation associated with processing natural objects and artefacts, the activated area associated with natural objects is considerably larger than the activation associated with artefacts and it also includes the anterior part of the right fusiform gyrus. In addition, natural objects are associated with activation of the posterior part of both inferior temporal gyri, whereas artefacts are only associated with activation of the right inferior temporal gyrus.

The finding that only the contrast between the difficult versus the easy object decision task for natural objects was significant (and *only* at the cluster level) suggests that the processing of natural objects activates a larger region of the brain compared with artefacts as task difficulty increases. The existence of a tendency in this direction is supported by the observation that the activated region associated with the contrast between the difficult versus the easy object decision task for natural objects was approximately four times larger than the activated region associated with the contrast between the difficult versus the easy object decision task for artefacts (Fig. 5). Note, however, that because the difference between the difficult versus the easy object decision task for artefacts was not significant at a level corresponding to $P < 0.05$, corrected, this comparison was performed by lowering the threshold to $P < 0.001$, uncorrected. Another notable difference between the simple main effects of increased task difficulty seems to be that the simple main effect for natural objects is associated with activation of the posterior part of *both* right and left inferior temporal gyri ($x = 52$, $y = -62$, $z = -14$, $Z = 4.33$; $x = -44$, $y = -64$, $z = -14$, $Z = 4.14$), whereas the simple main effect for artefacts is only associated with activation of the right inferior temporal gyrus ($x = 56$, $y = -54$, $z = -20$, $Z = 3.73$) (Fig. 5).

Even though the exploration of the simple main effects reveals a tendency only, it does suggest that the interaction between task type and category observed in the behavioural data may be reflected in the PET data as an increase in the size of the activated region and in the number of regions activated by natural objects compared with artefacts as task difficulty increases. Thus, the difference in the amount of activation in these regions may reflect the difference in the degree of perceptual differentiation required for matching items from the respective categories to memory. We find this interpretation reasonable because we would expect to find the neural correlate of increased reaction times during difficult object decisions to natural objects in the areas where the rCBF increased as a function of task difficulty.

Based on the data presented above, we suggest that the discrepancy between the behavioural data and the PET data regarding the interaction between task type and category may arise because increased task difficulty for natural objects causes increased activation in two regions rather than one. In neither of these regions in isolation, however, is the activation large enough to cause an interaction.

If the interpretation offered here for the interaction between task type and category is correct, we should expect to find lesions in the posterior portions of the right inferior temporal gyrus or anterior portions of the fusiform gyrus in cases where the category-specific impairment for natural objects appears to be confined to a pre-semantic level. Although lesion data are often not reported in great detail, at least three cases seem to satisfy both the criteria for the lesion(s) and for the cognitive deficit (Etcoff *et al.*, 1991; De Renzi and Lucchelli, 1994; Arguin *et al.*, 1996). Accordingly, the present findings seem to concur with the lesion data. It should be mentioned, however, that there is also evidence for category-specific impairments for natural objects following unilateral left hemisphere damage (e.g. Sheridan and Humphreys, 1993). However, in these cases the impairment

may be more related to object naming than to object recognition.

It is difficult to directly compare the functional imaging data of this study with previous studies because of the different tasks used. However, Martin and colleagues found that naming animals compared with tools caused increased rCBF in the left calcarine sulcus (Martin *et al.*, 1996). They suggest that this finding could reflect 'top-down' reactivation necessary for identifying animals because animals compared with tools are more visually similar. Whether or not this interpretation is correct, the finding remains obscure as there are no reports of category-specific impairments following lesions in this area. In another relevant study by Perani and colleagues where subjects judged whether a pair of pictures represented the same concept (e.g. a cow), living things were associated with activation of the left lingual and fusiform gyri (Perani *et al.*, 1995). If anything, this finding is quite the opposite to what was found in the present experiment. Given that the task used by Perani and colleagues was conceptual in nature it might be that the activation found was related to semantic processing. However, although semantic processing has been associated with the left hemisphere it has usually been associated with more anterior structures (e.g. Sergent *et al.*, 1992). In any case it should be mentioned that the left lingual gyrus in the study by Perani and colleagues was found to be activated in both the living versus baseline contrast and in the non-living versus baseline contrast, and that it was probably only found to be activated in the direct contrast between the living versus non-living conditions because the threshold was lowered to $P < 0.01$, uncorrected. Accordingly, their finding might not be reliable.

In conclusion the present study lends support to the hypothesis that performance on object decision tasks primarily reflects perceptual differentiation and that this stage in object recognition is distinct from semantic processing. It also suggests that category effects in object recognition can arise at this level and that they are probably not solely a consequence of neurological impairments. Rather, neurological impairments are likely to produce clear category-specific impairments by exacerbating such pre-existing processing differences between categories in normal object recognition. Finally, the present study suggests a role for the right inferior temporal gyrus in storing visual knowledge and for the right inferior frontal gyrus in the retrieval of visual knowledge.

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