A functional neuroimaging study of the variables that generate category-specific object processing differences

Caroline J. Moore and Cathy J. Price

Wellcome Department of Cognitive Neurology, Institute of Neurology, London, UK

Correspondence to: Dr Cathy Price, Wellcome Department of Cognitive Neurology, 12 Queen Square, London WCIN 3BG, UK
E-mail: cprice@fil.ion.ucl.ac.uk

Summary
Brain damage can cause remarkably selective deficits in processing specific categories of objects, indicating the high degree of functional segregation within the brain. The neuroimaging study presented here investigates differences in the neural activity associated with two categories of natural objects (animals and fruit) and two categories of man-made objects (vehicles and tools). Stimuli were outline drawings and the tasks were naming and word–picture matching. For man-made objects, the only category-specific effect was in the left posterior middle temporal cortex, which was most active for drawings of tools, as previously reported. For natural objects, drawings of animals and fruit (relative to drawings of man-made objects) enhanced activity in bilateral anterior temporal and right posterior middle temporal cortices. Critically, these effects with natural objects were not observed when the stimuli were coloured appropriately to facilitate identification. Furthermore, activation in the same right hemisphere areas was also observed for viewing and matching unfamiliar non-objects relative to naming and matching man-made objects. These results indicate that, in the right hemisphere, differences between processing natural relative to man-made objects overlap with the effects of increasing demands on object identification. In the left hemisphere, the effects are more consistent with functional specialization within the semantic system. We discuss (i) how category-specific differences can emerge for multiple reasons and (ii) the implications of these effects on the interpretation of functional imaging data and patients with category-specific deficits.

Keywords: category specificity; object identification; temporal lobe; functional neuroimaging

Abbreviations: AC = anterior commissure; BA = Brodmann area; PC = posterior commissure; rCBF = regional cerebral blood flow

Introduction
We investigated how different categories of objects are processed in the brain. Evidence supporting the existence of category-specific processing comes from patients who show selective difficulties when processing particular classes of objects. Category-specific disorders can result from brain damage following stroke, head injury, herpes simplex viral encephalitis or dementia of the Alzheimer type. Impairments can be as specific as an inability to identify fruit and vegetables (Hart et al., 1985; Farah and Wallace, 1992) or animals (Hart and Gordon, 1992). However, the most common dissociation reported in patients is an impairment with natural (living) objects relative to man-made (non-living) objects (e.g. Warrington and Shallice, 1984; Basso et al., 1988; Pietrini et al., 1988; Sartori and Job, 1988; Silveri and Gainotti, 1988; Farah et al., 1991; Hillis and Caramazza, 1991; Mazzoni et al., 1991; Silveri et al., 1991; Funnel and Sheridan, 1992; Giustolisi et al., 1993; Sartori et al., 1993; DeRenzi and Lucchelli, 1994; Damasio et al., 1996; Forde et al., 1997; Tranel et al., 1997a). The reverse dissociation, where the greatest impairment is with man-made objects, occurs less frequently (though see Warrington and McCarthy, 1983, 1987; Hillis and Caramazza, 1991; Sacchett and Humphreys, 1992; Tippett et al., 1996a), and normal subjects take longer to name and discriminate natural objects than man-made objects (Humphreys et al., 1988; Gaffan and Heywood, 1993; Capitani et al., 1994), with more errors to natural objects when naming-to-deadline (Vitkovitch et al., 1993). The patient and normal literature, therefore, are consistent in showing a greater proportion of deficits with natural
objects, an observation that must be accounted for by theoretical explanations of category-specific effects.

**Theoretical perspectives**

Explanations for category-specific deficits vary, but there are three main approaches. One view is that object knowledge is compartmentalized according to category, and localized brain damage can cause selective impairments within this modular system (Hart et al., 1985; Hillis and Caramazza, 1991; Caramazza and Shelton, 1998). A second view is that identification of natural objects relies more on perceptual properties, whereas identification of man-made objects relies more on functional properties (Warrington and Shallice, 1984; Warrington and McCarthy, 1987; Farah and McClelland, 1991). The first view relates to a semantic system organized by category, while the second relates to a semantic system organized by different types of knowledge. The third view does not involve segregated semantic representations, but proposes that different types of objects place different demands on a shared processing system. For instance, identifying natural objects is relatively demanding due to the high degree of similarity between category exemplars and the many levels of overlapping and intercorrelated features (Gelman, 1988; Keil, 1989; Tyler et al., 1996; Durrant-Peatfield et al., 1997; Gommerman et al., 1997; McRae et al., 1997; Devlin et al., 1998). In contrast, man-made objects tend to have more distinct visual and semantic attributes, resulting in fewer ‘competing neighbours’ that need to be dismissed prior to identification (for behavioural evidence for these differences, see Humphreys et al., 1988; McRae et al., 1997). Differences in response competition from visually and semantically similar neighbours will generate category-specific effects when stimuli are real objects, pictures of objects or the written versions of objects. However, for real objects and pictures of objects, there will also be differences in the demands placed on visual, pre-semantic processing (Damasio et al., 1982, 1993; Humphreys et al., 1988, 1995; Damasio, 1990; Gaffan and Heywood, 1993; Tanel et al., 1997b). Indeed, deficits with natural kinds of objects can arise even in the absence of semantic knowledge. For instance, Gaffan and Heywood (1993) observed a dissociation between discriminating line drawings of natural and man-made objects in monkeys who ‘cannot plausibly be assumed to know anything about the items tested, except for their arbitrary association with food reward or its absence’ (for a critique, see Shallice, 1996).

**Anatomical coordinates**

**Lesion data**

Deficits in processing man-made objects are usually associated with damage to left frontoparietal areas (see Gainotti et al., 1995). However, the pathology associated with deficits in processing natural kinds of objects is not consistent. Single case studies presenting deficits in processing natural objects have been reported primarily in patients who have recovered from herpes simplex viral encephalitis, which typically causes bilateral damage to the anterior–medial (temporolimbic structures) and inferior temporal cortices (for a review, see Gainotti et al., 1995). Data from groups of patients with dementia of the Alzheimer type (where damage to temporolimbic structures often occurs early in the course of the disease) have also produced some evidence for deficits in processing natural objects (Mazzoni et al., 1991; Silveri et al., 1991; Giustolisi et al., 1993; Montanes et al., 1995), although this has not been shown consistently in other studies (see Tippett et al., 1996b; Gonnerman et al., 1997; Garrard et al., 1998). Data from groups of patients with other aetologies are also inconsistent; Damasio et al. (1996) demonstrated correlations of lesion site and abnormal lexical retrieval for faces in the left temporal pole, animals in the left inferior (mostly anterior) temporal cortex and tools in the left posterolateral inferior temporal and lateral tempo-occipital cortices. Tanel et al. (1997a) demonstrated maximal overlap of lesion site with abnormal concept retrieval for faces in the right temporal pole, animals in the right mesial occipital/ventral temporal cortex (with a smaller overlap in the left mesial occipital cortex) and tools in the left lateral occipital–temporal–parietal junction. In summary, lesion data have associated damage with several different regions of the brain with category-specific deficits.

**Neuroimaging studies**

Five neuroimaging studies investigating natural–man-made category dissociations have been published to date (Perani et al., 1995; Damasio et al., 1996; Martin et al., 1996; Mummery et al., 1996, 1998), the findings of which are summarized in Table 1. Taken together, there are few consistencies. Martin et al. (1996) and Perani et al. (1995) both report activation of the extrastriate cortex when pictures of animals are contrasted with pictures of tools. However, this area was not reported by Damasio et al. (1996) who had a priori regions of interest (from $z = -30$ to $z = 0$) which may have excluded extrastriate activations, or by Mummery et al. (1996, 1998) who used words rather than pictures of objects. All but the Perani et al. (1995) study showed differential activation in the left posterior temporal cortex. On the lateral surface ($x = -57$), Damasio et al. (1996) and Mummery et al. (1998) report activation for man-made objects. On the medial surface ($x = -36$), the results are conflicting: Damasio et al. (1996) report activation for animals, Martin et al. (1996) report activation for tools and Mummery et al. (1996, 1998) report activation for man-made categories. Similarly, in the left medial frontal cortex, Martin et al. (1996) report activation for animals and Perani et al. (1995) report activation for tools.

Despite the single case neuropsychological findings that bilateral anterior temporal regions are associated with
Table 1 Previous neuroimaging findings

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Visual areas:</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Left extrastriate</td>
<td>A–T –04 –80 +08</td>
<td>–</td>
<td>A–T –02 –94 00</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Left fusiform</td>
<td>–</td>
<td>–</td>
<td>A–T –32 –82 –20</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Posterior temporal areas:</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Anterior temporal areas:</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Frontal areas:</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Left precentral</td>
<td>T–A –48 00 +20</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Left medial inferior frontal*</td>
<td>A–T –26 +28 +16</td>
<td>–</td>
<td>T–A –28 +34 +12</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Other areas:</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Right inferior parietal</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>NAT–MAN +44 –64 +40</td>
<td>–</td>
</tr>
</tbody>
</table>

The areas reported in previous functional neuroimaging studies that have compared animals (A) with tools (T), faces (F) with animals and tools, and natural (NAT) with man-made (MAN) categories. Three of the studies investigated object processing differences: (i) Martin et al. (1996) compared animal and tool naming in normal subjects using line drawings and silhouettes; (ii) Damasio et al. (1996) contrasted face, animal and tool naming in patients with naming impairments and in normal subjects; and (iii) Perani et al. (1995) investigated the differences between animals and tools with a picture–picture matching task. In the other two studies, Mummery et al. (1996, 1998) investigated category effects without the use of pictorial stimuli during: (i) production of category exemplars in response to verbal cues such as ‘land animals’ and ‘tools’ (Mummery et al., 1996); and (ii) semantic similarity judgements on words (Mummery et al., 1998). Inconsistencies between findings (e.g. where an area is activated for animals relative to tools and also tools relative to animals) are marked with ‘*’. Coordinates correspond to the stereotactic atlas of Talairach and Tournoux (1988) and are reported in the order of $x$ (where + is right and – is left), $y$ (where – is posterior to the anterior commissure line and + is anterior to the anterior commissure line) and $z$ (where – is inferior to the AC–PC line and + is superior to the AC–PC line).
processing natural stimuli (see above), the only neuroimaging study that has reported differential activation in the anterior temporal cortices for natural relative to man-made stimuli is that by Mummery et al. (1996). In the studies by Martin et al. (1996) and Perani et al. (1995), this region may not have been investigated fully.¹ In the study by Damasio et al. (1996), left anterior temporal activation was observed for naming faces, animals and tools (relative to an orientation judgement on faces), but the only differential activation reported in the anterior temporal regions was for faces.

Interpreting the neuroimaging literature is problematic because some of the differential activations may relate to uncontrolled differences in object processing that are not related directly to category-specific effects. For instance, in studies that have used pictures of objects as stimuli (Perani et al., 1995; Damasio et al., 1996; Martin et al., 1996), there are differences between categories in the configuration of visual features and number of component parts. Animals, for example, have more complex structures than tools; therefore, the increased activation in the medial extrastriate cortex for animals (Perani et al., 1995; Martin et al., 1996) might reflect greater demands on visual processing due to animals having a more complex configuration of visual features than tools. Martin et al. (1995) dismissed this explanation because the medial extrastriate cortex remained more active for animals relative to tools when the stimuli were silhouettes. However, although silhouettes remove differences in internal visual configuration, differences between categories remain for (i) the number of component parts (animals have more component parts than tools) and (ii) the area covered by the visual stimuli (animals tend to have broader shapes, tools tend to be long and thin). Further, because direct comparisons between categories primarily have compared animals and tools, it is not possible to know whether the effects generalize to all natural relative to man-made categories of object.

In this functional neuroimaging study, we attempt to segregate differences due to object category from differences due to (i) the visual configurations of objects and (ii) the demands placed on object identification. Differences relating to the visual configurations of objects were evaluated by contrasting activity evoked by complex, multicomponent objects (e.g., animals and vehicles) with activity evoked by objects with simple shapes (e.g., fruit and tools). Differences relating to the demands on object identification were evaluated by contrasting (i) black and white outline drawings relative to the same stimuli filled with appropriate colour and (ii) drawings of non-objects relative to drawings of real objects. The rationale behind these manipulations is described below.

Colour facilitates object identification, particularly for stimuli such as fruit and vegetables which have unique colours despite similar shapes (Price and Humphreys, 1989; Humphrey et al., 1994; Mapelli and Behrmann, 1997). By looking at the effect of colour at the level of individual items, effects due to the demands placed on object identification can be assessed independently of object category. Our hypothesis concerning non-objects was as follows: when viewing non-objects (see Fig. 1), object identification processes will be engaged to find structural coherence and meaning (for similar arguments concerning pseudowords, see Price et al., 1996a; Rumsey et al., 1997). Non-objects may therefore challenge pre-semantic, structural processing (and possibly the semantic system) to a greater degree than real objects. However, since there are no specific meanings associated with non-objects, we would not expect selective retrieval of semantic attributes. In other words, if knowledge relating to different categories of objects is segregated anatomically (Hart et al., 1985; Hillis and Caramazza, 1991; Caramazza and Shelton, 1998), then we would not expect non-objects to show differential activation of category-specific regions.

Our prediction regarding the previous association of the extrastriate cortex in comparisons of animals relative to tools (Perani et al., 1995; Martin et al., 1996) is that if activation relates to the visual differences between these categories, then objects with complex visual configurations relative to objects with simple shapes will activate the extrastriate cortex. Our predictions regarding category effects are as follows. First, if the semantic system is segregated by category, then we would expect to see the same effect of category for black and white objects and coloured objects. Further category-specific effects should be observed regardless of the baseline used. For example, activation associated with natural objects should be over and above that seen for all types of man-made objects, and non-objects. Secondly, if category effects arise because natural objects place increased demands on object identification, then we would expect the observed effects to be less when the stimuli are coloured appropriately to facilitate identification.

Methods

Data acquisition

The study comprised two experiments. In each, subjects were scanned with PET which measured rCBF (regional cerebral blood flow) using bolus infusion of radiolabelled water (H₂¹⁵O) and MRI to obtain structural images for co-registration with the PET images. Each subject underwent 12 PET scans, performed on a Siemens/CPS Ecat HR+ (962) head scanner with a total field of view of 15 cm. A bolus of H₂¹⁵O at a concentration of 55 MBq/ml and a flow rate of 10 ml/min was administered as an intravenous cannula. For each scan, ~10–15 mCi of H₂¹⁵O in 3 ml of normal saline was flushed into the subject over 20 s, at a rate of 10 ml/min by an automatic pump. Data acquisition time lasted 90 s, and the interval between successive H₂¹⁵O administrations was 8 min. The effective dose equivalent for the PET scans was <5.0 mSv as approved

¹The anterior temporal cortex is a region rarely reported in functional neuroimaging studies. This is because (i) many previous PET studies have used cameras with a limited field of view, requiring an a priori decision of which areas to scan and (ii) use of image processing that excludes data >28 mm below the intercommisural line; with smoothing, this results in loss of signal 20 mm below.
Fig. 1 Examples of the stimuli used during (A) naming and (B) matching.

by the Administration of Radioactive Substances Advisory Committee of the Department of Health UK. The research ethics committee at the National Hospital for Neurology and Neurosurgery, Queen Square approved the protocol. T1 -weighted, structural MRI scans were performed on a Siemens 2 Tesla Magnetom Vision MRI camera (Erlargen, Germany).

Subjects
There were eight subjects in Experiment 1 [two female and six male with a mean age of 38 years (range 23–52 years)] and six subjects in Experiment 2 [all male with a mean age of 28 years and 6 months (range 23–34 years)]. All subjects were right handed, with English as their first language and no history of neurological, psychiatric or language disorders, and each gave informed consent to participate in the study.

Stimuli and tasks
Experiment 1—naming
There were 12 conditions in the first experiment in a 2 × 2 × 2 factorial design (eight activation conditions) with four control conditions. In the activation conditions, subjects named objects from four different categories. The four categories of objects were (i) multicomponent natural objects (animals); (ii) multicomponent man-made objects (e.g. vehicles, appliances: from here on referred to as complex man-made objects); (iii) natural objects with simple shapes (fruit and vegetables: from here on referred to as fruit); and (iv) man-made objects with simple shapes (e.g. tools and utensils: from here on referred to as simple man-made objects). Stimuli were outline drawings of objects that were presented either in black and white or filled with the appropriate colours. In the control conditions, subjects responded ‘okay’ when viewing black and white and coloured non-objects. Half of the conditions comprised non-objects with multicomponent shapes and the other half comprised non-objects with simple shapes. The resulting four non-object conditions were (i) black and white multicomponent non-objects; (ii) black and white simple shaped non-objects; (iii) coloured multicomponent non-objects; and (iv) coloured simple shaped non-objects. The factorial design described allowed us to examine the effects of (i) visual configuration (multicomponent versus simple shapes); (ii) category-specific effects; (iii) black and white versus coloured outline drawings; and (iv) objects versus non-objects.

The objects were selected for their colour associations (see Price and Humphreys, 1989) and colours were matched across natural and man-made categories (e.g. a red tomato and a red bus). Stimuli were divided into two groups so that half of the subjects saw Set 1 presented as black and white outline drawings and Set 2 presented in colour. The other half of the subjects saw Set 2 presented as black and white outline drawings and Set 1 presented in colour. All pictures were equated as far as possible for size (~7.7 cm × 7.7 cm). All stimuli were presented on a 43 cm monitor suspended on a movable gantry that was a distance of ~45 cm from the subject. The names of the objects were matched across conditions for word frequency (Kucera and Francis, 1967) and across natural or man-made categories for number of syllables and colour. Non-objects were drawn maintaining the size, basic shape and visual configuration of the range of objects. Ten subjects (who did not participate in the PET study) piloted the baseline stimuli to ensure that they were not associated with a specific real object. Examples of stimuli are given in Fig. 1.

For the first 45 s of the 90 s scan when the uptake of radioactivity occurs, 15 novel items were presented successively for 500 ms each at a rate of one stimulus per 3 s. In the remaining 45 s, the same 15 items were presented again to maintain attention to the task. There were no stimulus repetitions between scans. Subjects were instructed to mouth the names silently to eliminate the effects of hearing the sound of their own voice (see Price et al., 1994, 1996b). Stimuli were randomized within each condition, and conditions were fully counterbalanced.

Experiment 2—matching
There were six conditions in the second experiment, with each condition repeated once. Subjects performed a word-
picture matching task and a non-object matching task. There were two categories of natural objects (i) animals and (ii) fruit and vegetables (from here on referred to as fruit); and two categories of man-made objects: (i) vehicles and (ii) tools. This experiment allowed us to investigate whether there are consistent category effects for naming and word–picture matching for natural relative to man-made objects. It also allowed us to examine whether there were areas specialized for processing tools or vehicles.

A word was presented on the left (lower-case Helvetica font, size 36, ranging from $\approx 2.5\, \text{cm} \times 1.3\, \text{cm}$ to $7.4\, \text{cm} \times 1.3\, \text{cm}$) and a picture ($\approx 7.7\, \text{cm} \times 7.7\, \text{cm}$) was presented simultaneously on the right. As in Experiment 1, all stimuli were presented on a 43 cm monitor suspended on a movable gantry that was a distance of $\approx 45\, \text{cm}$ from the subject. Subjects were instructed to read the word on the left and make a mouse key response if it matched the large false font on the right of the screen. Subjects were instructed to read the word on the left and make a mouse key response if it had the same meaning as the picture on the right. All conditions were matched for word frequency (Kucera and Francis, 1967), and syllable length and conditions were counterbalanced across subjects. The non-object matching task comprised strings of false font letters presented on the left of the screen, with a large false font presented simultaneously on the right of the screen. The length and size of false font strings were matched to the number of letters constituting the words in word–picture matching conditions. The task was to look at the shapes of false fonts on the left of the screen and make a mouse key response if they matched the large false font on the right of the screen. In each scan, there were eight individual stimulus items, resulting in 14 different stimulus pairs displayed for 2 s at a rate of one per 3 s. Subjects did not see the same stimulus pair more than once, but individual items were presented three times: (i) once as a word with a different picture; (ii) once as a picture with a different word; and (iii) once as a matching word–picture pair. Examples of stimuli are given in Fig. 1.

**Reaction time data**

Sixteen new volunteers [eight males and eight females with a mean age of 30.5 years (range 22–44 years)] participated in a complementary naming reaction time study. Stimuli were presented under the same parameters as for Experiment 1, except that subjects were instructed to name aloud, allowing voice onset times to be measured. For word–picture matching (Experiment 2), reaction times were recorded during scanning.

For both these experiments, responses were collated for each trial, and any score $\pm 2.5$ SD away from the mean was replaced by the ceiling/floor score for that particular trial. A factorial ANOVA identified main effects of category and colour and any interactions between these variables. Bonferroni post hoc testing identified differences (i) between individual conditions (colour and black and white) and (ii) averaged for natural objects (animals and fruit) and man-made objects (complex and simple).

**Data analysis**

The data were analysed with statistical parametric mapping (SPM 97) (Wellcome Department of Cognitive Neurology, London, UK: http://www.fil.ion.ucl.ac.uk/spm), implemented in Matlab (Mathworks Inc. Sherborn, Mass., USA). The PET scans from each subject were realigned using the first as a reference. The $T_1$-weighted, structural MRI scans were coregistered to the mean PET image for each subject and stereotactically transformed into Talairach and Tournoux space (Talairach and Tournoux, 1988). This transformation matrix was then applied to the PET images (Friston et al., 1995a). Finally, images were smoothed with a Gaussian filter of 16 mm. The resulting search volume was from $z = -48\, \text{mm}$ to $z = +60\, \text{mm}$ [where $-$ is inferior to the anterior commissure–posterior commissure (AC–PC) line and $+$ is superior to the AC–PC line].

The data were analysed using a blocked one-way ANCOVA (see Friston et al., 1990), and the design matrix included global activity as a subject-specific confounding covariate. Subject and covariate effects were estimated according to the general linear model at each voxel (see Friston et al., 1995b). To test the hypotheses about regionally specific condition effects, the estimates were compared using linear contrasts. The resulting set of voxel values for each contrast constitutes a statistical parametric map of the $t$ statistic SPM($t$). The SPM($t$) is transformed to the unit normal distribution (SPM($Z$)) at a threshold of 3.09 (or $P = 0.001$ uncorrected) for multiple comparisons.

In this study, we were concerned with effects of category that are common to naming and word–picture matching. Combining the results of two experiments together was not only more powerful, but it also allowed us to look at the reliability of the results and reduce the effects of artefacts that might be introduced differentially in different experiments. The importance of replicating results is also highlighted by the lack of consistent replications in previous studies of category-specific object processing (see Table 1). The analysis therefore pooled data from both experiments into a single multistudy design matrix.

**Linear contrasts**

*For both naming and matching experiments*

Each category was contrasted to all others and all objects were contrasted to non-objects. Main effects were calculated using conjunction analysis (Price and Friston, 1997). Essentially, conjunction analysis calculates main effects by summing the simple main effects and excluding regions where there are significant differences between the simple main effects. In order to confirm that each simple main effect is contributing to the main effect, we took a more conservative approach. This involved excluding any voxels that were not significant in each simple main effect at a threshold of $P < 0.08$. In addition, we only report main effects that are significant at $P < 0.01$ in both Experiments 1 and 2 (see
Fig. 2 The graphs show mean reaction time responses. The first two graphs relate to stimuli from the naming reaction time study. First (i) shown are the naming response means for animals (A), fruit (F), complex man-made objects such as vehicles (V) and simple man-made objects such as tools (T). Second (ii), the naming response means are shown for natural (Nat) and man-made (Man) categories. The third graph shows the mean reaction times recorded during scanning for the word–picture matching task for non-objects (N), animals (A), fruit (F), vehicles (V) and tools (T). Standard error bars are shown on each graph. Stippled columns = black and white; open columns = colour.

Friston, 1997) and at $P < 0.001$ summed over experiments. Differences between experiments are listed in Appendix I.

The main effect of multicomponent versus simple shaped objects was calculated from the conjunction of (i) animals versus fruit and (ii) complex versus simple man-made objects (where each contrast was significant at $P < 0.08$). Similarly, the main effect of natural versus man-made was calculated from the conjunction of (i) animals versus complex man-made objects and (ii) fruit versus simple man-made objects (where each contrast was significant at $P < 0.08$). Effects that were specific to individual categories were calculated by the conjunction of contrasts for one category relative to all others (e.g. animals versus fruit, complex man-made objects and simple man-made objects) where each contrast was significant at $P < 0.08$.

For naming only (i) Black and white drawings of objects were contrasted with the same drawings appropriately coloured and (ii) the interaction between colour and object category was analysed. Activations are reported at $P < 0.001$.

**Results**

**Behavioural data**

**Reaction times (see Fig. 2)**

**Experiment 1.** An analysis of variance showed main effects of (i) category ($F = 5.7$, $P < 0.001$), with natural objects taking longer to name than man-made objects; and (ii) colour ($F = 6.8$, $P < 0.01$), with black and white objects taking longer to name than coloured objects. There was no significant interaction between these variables ($F = 1.7$, $P > 0.1$). Bonferroni post hoc tests show that black and white natural objects took significantly longer to name than (i) black and white man-made objects ($P < 0.05$); (ii) coloured natural objects ($P < 0.005$); and (iii) coloured man-made objects ($P < 0.005$). Further analysis also revealed that responses to black and white drawings of fruit were slower ($P < 0.05$) than all other categories (except coloured complex man-made objects), and colour drawings of tools were faster than coloured fruit, and black and white vehicles and animals ($P < 0.05$).

**Experiment 2.** For matching, there was no significant variance (as identified by an analysis of variance and Bonferroni post hoc testing) between responses either to any of the category groups: animals, fruit, vehicles, tools and non-objects; or between grouped categories of natural and man-made objects.

**Errors**

In Experiment 1, subjects made 11.2% errors when naming black and white stimuli (animals = 5.2%, fruit = 15.1%, complex man-made objects = 10.4%, simple man-made objects = 12.7%) and 7.8% errors when naming appropriately coloured stimuli (animals = 2.4%, fruit = 6.7%, complex man-made objects = 9.1%, simple man-made objects = 14.3%). Bonferroni post hoc tests showed that animal naming produced significantly less errors than fruit and tools irrespective of whether stimuli were black and white or appropriately coloured ($P = < 0.01$), and that the presence of appropriate colour reduced the number of errors produced for naming fruit ($P = < 0.01$).

Out of the total errors made, 37.2% were passes and hesitations, 34.5% were visual semantic (e.g. ‘lion’ for tiger), 12.4% were visual (e.g. ‘cup’ for thimble), 7.1% were semantic but not visual (e.g. ‘pear’ for carrot), 5.3% were phonological (e.g. ‘bushroom’ for mushroom), 1.8% were subordinate (e.g. ‘bird’ for chick) and 1.8% were unclassified responses (e.g. ‘beat’ for leaf).

The high error rates may relate to the brief presentation durations (500 ms). The influence of these errors on activation...
Table 2  Multicomponent relative to simple shaped objects

<table>
<thead>
<tr>
<th>Areas</th>
<th>All experiments</th>
<th>Naming</th>
<th>Matching</th>
</tr>
</thead>
<tbody>
<tr>
<td>Right medial extrastriate</td>
<td>+04 -80 -12</td>
<td>3.0</td>
<td>2.6</td>
</tr>
<tr>
<td>Right occipito-temporal</td>
<td>+38 -78 +18</td>
<td>3.5</td>
<td>3.6</td>
</tr>
<tr>
<td>Right fusiform</td>
<td>+38 -20 -24</td>
<td>3.5</td>
<td>2.4</td>
</tr>
</tbody>
</table>

The effects of multicomponent (black and white drawings of animals and complex man-made objects) relative to simple shaped objects (black and white drawings of fruit and simple man-made objects). Activations are shown that are common to both experiments (naming and matching), and maximal activations within these areas are also shown for each study, respectively. Coordinates correspond to the stereotactic atlas of Talairach and Tournoux (1988), see Table 1. Z-scores are shown in bold. Activations are reported at a significance level of $P < 0.001$ (Z-scores over 3.1), unless in an area of interest (e.g. the medial extrastriate cortex) where activation is reported at a significance level of $P < 0.01$ (Z-scores over 2.6).

Fig. 3  The regional cerebral blood flow (rCBF) of activations associated with black and white drawings of multicomponent relative to simple shaped objects. The graphs depicting right occipito-temporal and fusiform areas show an additive effect of complexity and category, with maximal activation for animals and least activation for tools. rCBF values are shown for complex non-objects (CN), simple non-objects (SN), matching non-objects (N), animals (A), fruit (F), complex man-made objects such as vehicles (V) and simple man-made objects such as tools (T). The point of origin (0) is the mean global blood flow for the selected voxel. Stippled columns = naming; open columns = matching.

Neuroimaging results

We report activations that are in common to both naming and matching tasks. This approach will reduce the influence of artefactual effects such as activation differences related to the differential error scores for particular naming conditions. Appendix I shows areas of activation specific to each task. In this study, we do not attempt to interpret these task-specific differences because each task was performed by a different group of subjects; therefore, any observed differences could reflect subject group rather than task differences.

Objects with multicomponent versus simple structures (see Table 2 and Fig. 3)

In common to both tasks, contrasts (i) animals relative to fruit and (ii) complex relative to simple man-made objects resulted in activation of the right medial extrastriate cortex (Brodmann area (BA) 18)), the right occipitotemporal cortex (BA 19/39) and the right fusiform (BA 20) (see Table 2 and Fig. 3). The reverse contrasts, (i) fruit relative to animals and (ii) simple relative to complex man-made objects, activated bilateral post-central gyri (BA 2/40: $x = -58$, $y = -28$, $z = +36$, Z-score = 4.2; $x = +28$, $y = -20$, $z = +28$, Z-score = 3.7).

Category effects

Man-made relative to natural objects (see Fig. 4).

In common to both tasks, contrasts (i) complex man-made objects relative to animals and (ii) simple man-made objects relative to fruit resulted in activation of the left medial extrastriate cortex (BA 18: $x = -8$, $y = -92$, $z = -14$;
Fig. 4 The regional cerebral blood flow (rCBF) of the left medial extrastriate cortex identified in a comparison of man-made relative to natural objects, and the tool area identified during matching. Note that the latter activation is not above that evoked by non-objects. rCBF values are shown for complex non-objects (CN), simple non-objects (SN), matching non-objects (N), animals (A), fruit (F), complex man-made objects such as vehicles (V) and simple man-made objects such as tools (T). The point of origin (0) is the mean global blood flow for the selected voxel. Activation is also shown projected onto a horizontal slice of a standardized MRI template brain. Stippled columns = naming; open columns = matching.

Table 3 Natural black and white relative to man-made black and white

<table>
<thead>
<tr>
<th>Areas</th>
<th>All experiments</th>
<th>Naming</th>
<th>Matching</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bilateral anterior temporal (BA 21/38)</td>
<td></td>
<td>3.7</td>
<td>3.0</td>
</tr>
<tr>
<td></td>
<td>−28 00 −14</td>
<td>−26 +02 −18</td>
<td>−28 +02 −14</td>
</tr>
<tr>
<td></td>
<td>+42 +10 −18</td>
<td>+38 +12 −18</td>
<td>+42 +10 −18</td>
</tr>
<tr>
<td>Right posterior temporal (BA 21/37)</td>
<td></td>
<td>3.7</td>
<td>4.1</td>
</tr>
<tr>
<td></td>
<td>+64 −56 00</td>
<td>+60 −62 +06</td>
<td>+64 −58 −06</td>
</tr>
</tbody>
</table>

The effects of comparing black and white outline drawings of natural (animals and fruit) relative to black and white drawings of man-made objects (complex and simple man-made objects, respectively). Activations are shown that are common to both experiments (naming and matching), and maximal activations within these areas are also shown for each study, respectively. Z-scores are shown in bold.

Z-score = 4.3). Maximum activity in this area was seen for vehicles (see Fig. 4).

There were no other areas that were activated specifically for either complex or simple man-made objects relative to all other categories including non-objects across experiments. However, we note that in the matching experiment, where simple man-made objects were always tools, the left posterior temporal cortex (BA 37/19: x = −58; y = −60, z = −6) was more activated for tools relative to all other object categories (Z-score = 3.0), except non-objects (see Fig. 4).

Natural relative to man-made objects (see Table 3 and Figs 5 and 6)

In common to both tasks, natural relative to man-made objects increased activation in bilateral anterior temporal cortices (BA 21/38) (extending into the insula) and the right posterior middle temporal cortex (BA 37/21).

Although these activations were common to (i) animals relative to complex man-made objects and (ii) fruit relative to simple man-made objects, the left anterior temporal/insula cortex was most active for fruit and the right posterior temporal cortex was most active for animals (see Fig. 6). We also note that for animals there was increased activation in the right fusiform gyrus relative to fruit and tools, but this did not reach significance (P = > 0.08) relative to non-objects or complex man-made objects. Similarly, in the right occipitotemporal cortex, there was maximal activity for animals and non-objects (see Fig. 3).

Effects of colour (naming experiment only) (see Table 4 and Fig. 7)

There was a main effect of black and white drawings versus coloured drawings in the right superior temporal cortex (BA 22: x = +50, y = +2, z = +4, Z-score = 3.4).2

2In the reverse contrast (colour relative to black and white), activation was demonstrated in the brainstem (x = −8, y = −32, z = −36; Z-score = 4.4). This activation may relate to enhanced arousal (e.g. see Steriade, 1996); since this contrast is not the focus of our study, it will be discussed no further. Although comparisons of colour relative to black and white objects did not activate V4, previous studies reporting V4 activation in response to coloured stimuli have only done so in the context of transient on/off presentation for each stimulus, where stimuli were alternated at a rate of 1 Hz with a plain background (McKeefry and Zeki, 1997).
Significant interactions between colour and object category were demonstrated in the right anterior temporal (BA 21/38), posterior temporal (BA 21/37) and occipitotemporal cortices (BA 19/39), the right cerebellum and the right putamen. At a lower significance threshold ($P < 0.05$), there was also a significant interaction in the left anterior temporal cortex (BA 21/38). The interactions arose because the differences seen between natural and man-made objects (see Table 3) were specific to black and white stimuli. This finding is critical because it demonstrates that there are areas more active for black and white drawings of natural objects irrespective of whether the baseline is the same items appropriately coloured, or black and white drawings of man-made objects (see Table 4).

Once identification had been facilitated by the presence of colour, the only difference observed for natural relative to man-made objects was in the right cerebellum ($x = +6, y = -76, z = -30, Z$-score = 3.4). Since this study is concerned
with effects of category that are replicated over experiments, we do not attempt to interpret the cerebellum activation here.

**Objects versus non-objects (see Table 5 and Fig. 7)**
The left inferior frontal gyrus (BA 47) was activated for objects relative to non-objects in both experiments (natural objects relative to non-objects: x = –38, y = +26, z = –12, Z-score = 3.4; man-made objects relative to non-objects: x = –42, y = +24, z = –8, Z-score = 2.9). Drawings of natural objects relative to non-objects additionally activated the left anterior temporal cortex (BA 21/38: x = –28, y = +2, z = –14, Z-score = 3.9).

Non-objects relative to both natural and man-made objects activated the cuneus (BA 19) and medial precuneus (BA 7) (see Table 5). Relative to natural objects, non-objects also activated the left occipitotemporal cortex (BA 19/39: x = –32, y = –82, z = +22, Z-score = 4.1). Relative to man-made objects, non-objects activated right hemisphere areas: the anterior (BA 21/38), posterior (BA 21/37), middle (BA 21) and superior (BA 22) temporal cortices, the occipitotemporal (BA 19/39), the anterior inferior parietal (BA 40), the middle/superior frontal cortex (BA 46), the precentral cortex (BA 6) and the cerebellum (see Table 5 and Fig. 7). Activation of the right anterior and posterior temporal cortices overlaps with the activations identified for natural relative to man-made objects, and for black and white relative to coloured natural objects (see Tables 4 and 5, and Fig. 7).

**Summary of results**
Replicated across two different experiments, this study has distinguished differential effects of object category in seven regions; the medial extrastriate, the right temporo-occipital, the right fusiform, the left posterior temporal, the left anterior temporal, the right anterior temporal and the right posterior middle temporal cortices.

(i) In the medial extrastriate cortex, there were two effects which dissociated the right and left hemispheres. In the right hemisphere, there was a main effect of visual configuration, with greater activation for multicomponent objects. In the left hemisphere, there was a main effect of man-made relative to natural objects, with maximal activation for complex man-made objects and no differences between animals and fruit. Despite the differential activations, Fig. 8 shows that there was substantial overlap between these areas. In previous studies (Martin et al., 1996; Perani et al., 1996), the medial extrastriate cortex was found to be more active for animals and tools. Our results demonstrate that a possible explanation for a response in this area is that it relates to the complexity of the visual configurations of objects (e.g. animals relative to fruit, and multicomponent relative to simple shaped man-made objects).

(ii) In the right temporo-occipital and fusiform cortices, there was a main effect of visual configuration (more activation for multicomponent objects), with an additive effect of natural relative to man-made objects. Maximum activity was detected for animals and least activity was detected for simple man-made objects, but there was not more activation for animals than non-objects.

(iii) In the left posterior temporal cortex, there was greatest activity for tools relative to all other object categories in the matching task (Experiment 2). Activation for tools relative to animals replicates previous findings (see Table 1). However, our study also demonstrates that non-objects activate this area as much as tools (see Fig. 4).

(iv) In bilateral anterior temporal and right posterior middle temporal cortices, there was greater activity for natural relative to man-made objects when the stimuli were black and white drawings, but these effects were not seen when stimuli were coloured appropriately. These category-specific areas can be dissociated in relation to non-objects. In the left anterior temporal cortex, more activity was observed for black and white drawings of natural objects relative to man-made objects and non-objects, and there was
no difference between non-objects and man-made objects. In the right anterior and posterior temporal cortices, there was more activity for non-objects than man-made objects, suggesting that these regions are particularly sensitive to the demands placed on object identification. There were also differences between these effects for animals and fruit. For fruit, activity was maximal (relative to all other conditions) in the left anterior temporal/insula cortex. For animals, activity was maximal (relative to all other conditions) in the right posterior temporal cortex (see Fig. 6).

Discussion
There were three overall aims of our study. First, we attempted to segregate effects due to object category from effects due to differences in the visual configuration of objects. Secondly,
we used colour to manipulate the demands placed on object identification at the level of single objects. Thirdly, we used non-objects as a baseline to evaluate whether category-specific effects represent a semantic system that is segregated by category (Hart et al., 1985; Hillis and Caramazza, 1991; Caramazza and Shelton, 1998). We discuss in turn (i) the effects of visual object configuration; (ii) activation associated with man-made relative to natural objects; (iii) activation associated with natural relative to man-made objects; and (iv) consistency with previous studies.

### Visual configuration areas

Drawings of multicomponent relative to simple shaped objects activated three areas: the right occipitotemporal, fusiform and the medial extrastriate cortices (see Table 2 and Fig. 3). In the right occipitotemporal and fusiform cortices, activity was strongest for animals and non-objects, and least for simple man-made objects. There was also an additive effect of visual configuration, with more activity for complex man-made objects such as vehicles than for simple man-made objects such as tools. The enhanced response to animals in the right fusiform corresponds to lesion data presented by Tranel et al. (1997a), where damage to this area was more likely to result in naming deficits for animals than for tools. We suggest, therefore, that the right occipitotemporal and fusiform cortices are engaged maximally by multicomponent objects, in particular those depicting animals.

Activity in the medial extrastriate cortex previously has been associated with animals relative to tools (Perani et al., 1995; Martin et al., 1996). In this study, we observed maximal activation for complex man-made objects such as vehicles. The most likely explanation for the differences in results is that the extrastriate activation reflects visual configuration differences between categories. Without a direct comparison of the stimuli used in different studies (Perani et al., 1995; Damasio et al., 1996; Martin et al., 1996; this study), it is not possible to say how the stimuli varied (e.g. the size of

<table>
<thead>
<tr>
<th>Areas</th>
<th>Interaction</th>
<th>BW–COL NAT</th>
<th>BW NAT–MAN</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bilateral anterior temporal (BA 21/38)</td>
<td>+30 +08 −24</td>
<td>3.3</td>
<td>2.3</td>
</tr>
<tr>
<td>Right posterior temporal (BA 21/37)</td>
<td>−26 00 −20</td>
<td>2.2</td>
<td>2.4</td>
</tr>
<tr>
<td>Right occipitotemporal (BA 19/39)</td>
<td>+62 −64 +08</td>
<td>3.5</td>
<td>3.0</td>
</tr>
<tr>
<td>Right cerebellum</td>
<td>+38 −78 +18</td>
<td>3.4</td>
<td>3.1</td>
</tr>
<tr>
<td>Right putamen</td>
<td>+28 −42 −40</td>
<td>4.0</td>
<td>2.6</td>
</tr>
<tr>
<td>Bilateral anterior temporal (BA 21/38)</td>
<td>+28 −10 +12</td>
<td>3.5</td>
<td>4.0</td>
</tr>
</tbody>
</table>

The interaction between colour and category (from Experiment 1 only). Z-scores are also given for the simple main effects of black and white outline drawings (BW) of natural objects (NAT) relative to: (i) appropriately coloured drawings (COL) of natural objects (NAT), and (ii) black outline drawings (BW) of man-made objects (MAN). Z-scores are shown in bold.

<table>
<thead>
<tr>
<th>Areas</th>
<th>NON–NAT</th>
<th>NON–MAN</th>
</tr>
</thead>
<tbody>
<tr>
<td>Non-objects–objects</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Precuneus (BA 7)</td>
<td>−16 −66 +56</td>
<td>4.8</td>
</tr>
<tr>
<td>Left cuneus (BA 19)</td>
<td>−08 −72 +54</td>
<td>4.0</td>
</tr>
<tr>
<td>Non-objects–man-made objects</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Right anterior temporal (BA 21/38)</td>
<td>NS</td>
<td>+36 +12 −18</td>
</tr>
<tr>
<td>Right posterior temporal (BA 21/37)</td>
<td>NS</td>
<td>+54 −60 +10</td>
</tr>
<tr>
<td>Right middle temporal (BA 21)</td>
<td>NS</td>
<td>+52 −38 −10</td>
</tr>
<tr>
<td>Right superior temporal (BA 22)</td>
<td>NS</td>
<td>+66 −18 −08</td>
</tr>
<tr>
<td>Right inferior parietal (BA 40)</td>
<td>NS</td>
<td>+70 −44 +16</td>
</tr>
<tr>
<td>Right occipitotemporal (BA 19/39)</td>
<td>NS</td>
<td>+48 −34 +42</td>
</tr>
<tr>
<td>Right middle/superior frontal (BA 46)</td>
<td>NS</td>
<td>+30 −46 +58</td>
</tr>
<tr>
<td>Right precentral (BA 6)</td>
<td>NS</td>
<td>+40 −80 +24</td>
</tr>
<tr>
<td>Right cerebellum</td>
<td>NS</td>
<td>+26 +28 +28</td>
</tr>
<tr>
<td>Right occipitotemporal (BA 19/39)</td>
<td>NS</td>
<td>+38 +38 +14</td>
</tr>
</tbody>
</table>

The effects of (i) non-objects relative to objects where areas are activated by non-objects relative to natural objects (NON–NAT) and non-objects relative to man-made objects (NON–MAN), and (ii) the additional areas activated by non-objects relative to man-made objects (NON–MAN) (areas that are not in regions of interest as defined in Table 3 are shown in italics). Z-scores are shown in bold. Differences between tasks in Appendix I.
animals relative to tools, texture differences, number of features, etc.). Nevertheless, the comparison between multicomponent and simple shaped objects highlights the importance of considering visual differences when comparing different categories of objects. Such differences are difficult to eliminate. For example, although Martin et al. (1996) attempted to control for visual differences between animals and tools by presenting stimuli as silhouettes, category effects are still confounded by shape and visual configuration.

**Man-made relative to natural objects**

The only area to show enhanced responses to man-made objects (other than the left medial extrastriate cortex, see above) was the left posterior temporal cortex, which responded more to tools than to any other category except non-objects. This finding is consistent with previous neuroimaging studies which have used both pictures and written words (see Table 1). Similar activations have also been associated with generating action words relative to object naming (Martin et al., 1995) and for the recognition of meaningful relative to meaningless actions (Decety et al., 1997). The left posterior middle temporal cortex, therefore, appears to respond to the representation of actions. The enhanced activation in this region for tools, therefore, is consistent with an interpretation of category effects in terms of a semantic system segregated by types of knowledge (Warrington and Shallice, 1984; Warrington and McCarthy, 1987; Farah and McClelland, 1991). However, we still need to account for why this region is as active for non-objects as it is for tools (see Fig. 4).

**Natural relative to man-made objects**

When the stimuli were black and white outline drawings, natural relative to man-made objects activated three areas: the bilateral anterior temporal and right posterior middle temporal cortices. The responses in these regions could be differentiated in relation to drawings of non-objects. In the left anterior temporal region, black and white drawings of natural objects (particularly fruit) resulted in more activity than all other conditions including non-objects, and there was no difference between non-objects and man-made objects. This pattern of effects is consistent with category specificity. In contrast, in the right hemisphere regions (both anterior and posterior), there was significantly more activity for non-objects than man-made objects, indicating that these regions do not respond specifically to semantic knowledge related to natural objects.

We also observed that when stimuli were coloured appropriately, differences between natural and man-made objects (seen with black and white drawings) were eliminated. Similarly, reaction time differences between natural and man-made objects were only observed for black and white items. The overlap in activation pattern for (i) black and white drawings of natural relative to man-made objects; (ii) black and white drawings of natural objects relative to the same stimuli appropriately coloured; and (iii) non-objects relative to man-made objects (in the right hemisphere only) suggests that the critical factor in determining response differences in the right hemisphere relates to the demands placed on object identification. Object identification is relatively more demanding because, in general (i) natural objects have more visually and semantically similar competing neighbours than man-made objects (e.g. see Humphreys et al., 1988; McRae et al., 1997); (ii) colour reduces the number of competing responses within category (Price and Humphreys, 1989; Humphrey et al., 1994; Mapelli and Behrmann, 1997); and (iii) object relative to non-object processing is constrained by familiarity. According to this theory, we would expect the right hemisphere regions to respond more to man-made items which have many, rather than few, visually and/or semantically similar neighbours. Likewise, we would expect animals or fruit with unique features to activate the right hemisphere regions less than animals and fruit with many similar neighbours.

In summary, responses in the left anterior temporal cortex show a preference for natural objects, in particular fruit and vegetables. Responses in the right anterior and posterior temporal cortices are enhanced when the demands placed on object identification increase. Greater activity for natural objects suggests that these items increase the demands placed on object identification (Damasio et al., 1982, 1993; Humphreys et al., 1988; Damasio, 1990; Gaffan and Heywood, 1993; Humphreys et al., 1995; Tranel et al., 1997b).
Consistency with previous studies

Lesion studies

The enhanced bilateral anterior temporal cortex activations reported in this study for natural objects are of particular interest because these areas are damaged in herpes simplex viral encephalitis, an infection that often results in a greater impairment for natural categories, and indeed accounts for the majority of the literature on deficits for natural categories of objects (for a review, see Gainotti et al., 1995). Gainotti et al. (1995) comment that the reported instances of category-specific deficits in herpes simplex virus encephalitis had ‘bilateral damage to the anteromedial parts of both temporal lobes’ and ‘an extension of the lesion to the inferior temporal lobes was evident in all of those cases in whom this structure could be visualised’. Further, Silveri et al. (1991) predicted that because bilateral temporolimbic structures are usually affected early on in the course of dementia of the Alzheimer type, a deficit for natural objects should be evident in Alzheimer’s patients similar to that observed in patients with herpes simplex viral encephalitis. They found that patients with both mild and moderate dementia of the Alzheimer type were impaired at naming and recognizing natural objects significantly more than normal controls (but see Tippett et al. 1996a; Gonnerman et al., 1997; Garrard et al., 1998).

Other neuropsychological findings have associated the anterior temporal cortex with semantic knowledge (e.g. Hodges et al., 1992; Breedin et al., 1994). In particular, Breedin et al. (1994) suggest that the anterior temporal cortex may be involved in processing ‘perceptual components of semantic representations’. These authors investigated patient D.M., who had damage to his anterior temporal cortices (particularly affected on the left) and was more impaired on tests of (i) concrete word knowledge than abstract word knowledge and (ii) perceptual knowledge than non-perceptual knowledge. Since natural object knowledge tends to be predominately perceptual (Warrington and Shallice, 1984; Warrington and McCarthy, 1987; Farah and McClelland, 1991), activation of the anterior temporal cortex, particularly for natural objects, could reflect access to perceptual knowledge. In the present study, anterior temporal activation (in the left hemisphere) was greatest for fruit.

The enhanced right fusiform and posterior middle temporal activations reported in this study for animals (and to a lesser extent for fruit) are consistent with the findings of Tanel et al. (1997a), who associated lesions to the right mesial occipital/ventral temporal cortex with deficits in the retrieval of conceptual knowledge for animals. These lesion sites spread from the right anterior temporal polar area to the right mesial occipital cortex for both animals and faces, although relatively more patients with animal deficits had damage to the right mesial occipital/ventral temporal cortex, and relativity more patients with face deficits had damage to the right temporal pole. Interpretation is not simple, as Tanel et al. (1997a) comment ‘each site should be seen as part of a multi-component system, each containing circuitry necessary for the process of optimal concept retrieval’. Our findings suggest that the right fusiform is responding to pre-semantic visual configuration differences, but the right posterior middle temporal cortex has a role that is independent of the number of visual features within a given object.

Srinivas et al. (1997), on the basis of neuropsychological findings, predicted that ‘patients with lesions limited to the anterior inferior temporal cortex will demonstrate semantic deficits without impairment to structural descriptions . . . whereas patients with more posterior involvement with relative sparing anteriorly will exhibit impairments to structural descriptions with relative preservation of semantic knowledge’. Consistent evidence for such a dissociation comes from primate studies, where lesions to the lateral middle temporal gyrus cause deficits in processing features of objects, such as colour discrimination tasks (Buckley et al., 1997). In contrast, lesions to the perirhinal cortex (on the medial surface of the anterior temporal cortex) result in deficits in (i) concurrent discrimination learning with multiple foils (Buckley and Gaffan, 1997) and objects presented in different views (Buckley and Gaffan, 1998a); (ii) visual association learning (Murray et al., 1993; Buckley and Gaffan, 1998b); (iii) configural learning (Buckley and Gaffan, 1998b); and (iv) identification of new views of familiar objects, and of familiar objects presented in the context of unfamiliar scenes (Buckley and Gaffan, 1998c). A role for the perirhinal cortex in primates, therefore, has been suggested in processing component parts of objects together with non-visual object information in order to produce ‘coherent concepts of multiple individual objects’ (Buckley and Gaffan, 1998a). In relation to our study, this would suggest that the right posterior middle temporal activation is involved in pre-semantic structural differentiation, whereas the anterior regions (particularly in the left hemisphere, see above) are involved in accessing semantic knowledge.

Functional neuroimaging

In functional neuroimaging studies, bilateral anterior temporal cortex activations have been associated with object naming (Price et al., 1996c), face identification (Sergent et al., 1992; Damasio et al., 1996), visual discrimination tasks on faces and words (Gorno Tempini et al., 1998) and subordinate relative to basic level classification of objects (Gauthier et al., 1997). Bilateral posterior inferior temporal activations (in particular within the basal temporal, fusiform area, BA 37) have been reported for faces relative to objects (Kanwisher et al., 1997) and faces relative to words (Gorno Tempini et al., 1998), subordinate relative to basic level classification of objects (Gauthier et al., 1997), non-canonical relative to canonical views of objects (Kosslyn et al., 1994), objects relative to words (Menard et al., 1996; Moore and Price, 1997), objects relative to non-objects (Schacter et al., 1995; Martin et al., 1996) and objects relative to visual lines (Bookheimer et al., 1995). Activation in the right hemisphere is generally stronger than in the left (e.g. Gauthier et al., 1997; Kanwisher et al.,
1997; Gorno Tempini et al., 1998). For example, Kanwisher et al. (1997) showed that of the 10 right handed subjects who showed fusiform activations for faces relative to objects, half of these subjects activated the right hemisphere only, while the other half had bilateral activations.

The enhanced involvement of bilateral anterior temporal and right posterior temporal cortices in face processing is particularly interesting in light of the increased activity in these areas for natural relative to man-made categories of objects and when the demands placed on object identification are increased. Face identity requires a high degree of differentiation to discriminate between subtle feature differences (e.g. see Damasio, 1990). Consistent with this, Gauthier et al. (1997) showed that bilateral anterior temporal and posterior temporal cortices are activated for subordinate (e.g. ‘sparrow’) relative to basic level (e.g. ‘bird’) object tasks to a greater extent than the same tasks with words. Gauthier et al.’s (1997) findings suggest that these regions may be involved in differentiating between similar objects. However, the role of the anterior temporal cortices appears to be of a higher order than that driven by purely visual input because in a category fluency study by Mummery et al. (1996), where no visual stimuli were involved, bilateral medial anterior temporal activation was observed in response to natural category cues (e.g. ‘fruit’ and ‘land animals’) relative to man-made cues (e.g. ‘tools’ and ‘furniture’) (see Table 1). The left anterior temporal cortex has also been associated with semantic processing in electrophysiological (Nobre and McCarthy, 1995) and PET studies (Vandenbergh et al., 1996; Price et al., 1997). Consistent with the lesion data (see above), these findings suggest that the posterior temporal activations relate to structural processing of objects but the anterior temporal activations are involved in accessing semantic knowledge. Further studies are required to dissociate functional specialization within the anterior temporal cortex.

**Neuroimaging studies of category effects**

Areas previously identified in functional neuroimaging studies of category specificity are summarized in Table 1. There have been no areas that have been reported consistently across all studies. However, both Perani et al. (1995) and Martin et al. (1996) demonstrated activation of the left extrastriate cortex in comparisons of animals relative to tools. Our findings suggest that activation of the medial extrastriate cortex reflects visual differences between categories (see above). Both Damasio et al. (1996) and Mummery et al. (1998) demonstrated activation of the left lateral posterior temporal cortex for tools relative to animals. We also demonstrate activation for tools relative to animals and we note that non-objects activate this area as much as tools. It is not the case that the left posterior temporal responses are related specifically to object processing because the study by Mummery et al. (1998) showed differential activation of this region for man-made relative to natural categories during semantic similarity judgements on written words. As concluded above, the left lateral posterior middle temporal cortex appears to be responsive specifically during tasks involving action knowledge. Greater activation in this area for tools, therefore, supports the perceptual–functional account of category-specific effects introduced by Warrington and Shallice (1984).

Activation of the anterior temporal cortices in comparisons of pictures of animals relative to pictures of tools has not been reported by Perani et al. (1995), Damasio et al. (1996) or Martin et al. (1996). Damasio et al. (1996) report activation in the left anterior temporal cortex for animals and tools relative to the baseline, but the difference between animals and tools was not significant. Although Martin et al. (1996) and Perani et al. (1995) may not have investigated this region (see Footnote 1), another possibility for the absence of activation is that this area (particularly in the left hemisphere) responds more specifically to fruit (as in this study) or faces (as in the Damasio et al., 1996 study) than it does to animals. Indeed, in the only other study to show anterior temporal activity for natural kinds (Mummery et al., 1996), the stimuli included fruit and vegetables. If the anterior temporal regions are specialized for perceptual knowledge (Breedin et al., 1994, see above), our findings suggest that identification of fruit and vegetables is more reliant on perceptual attributes than are other object categories.

Regarding the right posterior temporal cortex, this area was not included in the regions of interest specified by Perani et al. (1995). Damasio et al. (1996) investigated activity in regions of interest only (the temporal pole/inferior temporal region: from $z = -30$ to $z = 0$), which would have excluded any right posterior temporal cortex activations above $z = 0$. Martin et al. (1996) demonstrated activation for animals and tools relative to baseline tasks, but no significant difference was reported in a direct comparison of animals relative to tools. In our study, the right posterior temporal cortex was more active for natural than man-made objects in two independent experiments. Further experiments are required to account for the discrepancy with Martin et al.’s (1996) findings. One possibility is that the pictures of animals used by Martin et al. (1996) were easier to identify than the pictures used in our study.

**Conclusions**

In this functional imaging study of category-specific object processing, we attempted to reduce the effect of visual processing differences by comparing drawings of animals with drawings of complex man-made objects (such as vehicles) and drawings of fruits with drawings of simple man-made objects (such as tools). These contrasts demonstrate that natural relative to man-made objects activate bilateral anterior temporal and right posterior middle temporal cortices, irrespective of whether the task is naming or word–picture matching. The left anterior temporal/insula cortex was activated maximally by fruit and the right posterior temporal cortex was activated maximally by animals. We also replicate other studies showing that the left posterior temporal cortex is activated maximally by tools.
Our critical question relates to whether these category-specific activations reflect neural specialization for different types of semantic knowledge or differential demands on a shared object processing system. This was addressed by using colour and non-objects to manipulate the demands placed on object processing. The right anterior and posterior temporal regions that showed differential activation for natural objects relative to man-made objects were also activated for non-objects relative to man-made objects. These right hemisphere activations, therefore, appear to reflect the demands placed on object recognition. In contrast, the left hemisphere activations are consistent with theories arguing that natural objects are more dependent on perceptual knowledge (in the anterior temporal cortex) and man-made objects are more dependent on functional knowledge (in the left posterior temporal cortex).

In the Introduction, we discussed three theoretical explanations for category-specific deficits. The first involved anatomical segregation on the basis of object category. The second involved anatomical segregation on the basis of the type of semantic knowledge (perceptual and functional). The third involved a shared processing system that was weighted differentially by natural kinds of objects. Our findings support the latter two interpretations of category specificity: (i) the perceptual–functional theory; and (ii) the theory that natural objects increase the demands placed on object processing and semantic differentiation (see Introduction). Deficits with natural objects may be more common than deficits with man-made objects because the former items will be sensitive to lesions in both left and right hemispheres.

These conclusions require further investigation using written words as stimuli rather than drawings of objects. We also need to evaluate the effect of task on category-specific activations. The emphasis of this study, however, is to highlight the many variables that need to be explored in functional imaging studies that compare natural and man-made objects.

Acknowledgements

We would like to thank Professors L. K. Tyler and G. W. Humphreys for their invaluable comments on this manuscript, the radiographers at the Functional Imaging Laboratory and the volunteers who participated in the studies. C.J.M. is funded by the Brain Research Trust and C.J.P. is funded by the Wellcome Trust.

References


Category-specific object effects

accepted January 18, 1999


Appendix I. Differences between tasks

Objects with multicomponent versus simple structures

Additional activation for naming:
left middle temporal cortex (BA 21) \((x = -46, y = 0, z = -20; \text{Z-score} = 4.0)\)
caudate \((x = 0, y = -2, z = +16; \text{Z-score} = 3.7)\)

**Natural–man-made**

Additional activation for naming:
right cerebellum \((x = +24, y = -48, z = -30; \text{Z-score} = 4.0)\)

Additional activation for matching:
right thalamus \((x = +4, y = -4, z = +2; \text{Z-score} = 4.8)\)
left anterior cingulate \((x = -14, y = +32, z = +14; \text{Z-score} = 3.7)\)
right postcentral gyrus \((x = +48, y = -22, z = +24; \text{Z-score} = 3.9)\)

More extensive activation for matching:
right posterior temporal cortex \((x = +40, y = -46, z = -18; \text{Z-score} = 3.8)\)
\(x = +70, y = -42, z = +8; \text{Z-score} = 3.9)\)

**Natural–non-objects**

Additional activation for naming:
bilateral fusiform (BA 37) bordering cerebellum \((x = -30, y = -50, z = -16; \text{Z-score} = 3.8)\)
\(x = -42, y = -70, z = -20; \text{Z-score} = 3.7)\)
\(x = +34, y = -64, z = -20; \text{Z-score} = 3.6)\)
cerebellum \((x = +2, y = -74, z = -24; \text{Z-score} = 3.8)\)
\(x = -6, y = -70, z = -12; \text{Z-score} = 3.2)\)
left insula \((x = -42, y = 0, z = -4; \text{Z-score} = 3.6)\)
left thalamus \((x = -14, y = -22, z = +8; \text{Z-score} = 3.2)\)
[these areas have been associated with name retrieval; Price et al. (1997)]
right hippocampus \((x = +34, y = -10, z = -16; \text{Z-score} = 3.4)\)

Additional activation for matching:
left inferior temporal cortex (BA 20) \((x = -56, y = -14, z = -18; \text{Z-score} = 3.7)\)
[this area has been associated with semantic processing; Vandenbergh et al. (1996)]

**Manmade–non-objects**

Additional activation for naming:
left fusiform (BA 37) \((x = -38, y = -50, z = -14; \text{Z-score} = 3.1)\)
cerebellum \((x = +2, y = -74, z = -24; \text{Z-score} = 3.6)\)

Additional activation for matching:
Left medial extrastriate \((x = -4, y = -92, z = -10; \text{Z-score} = 3.6)\)