Category differences in brain activation studies: where do they come from?

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Differences in the neural processing of six categories of pictorial stimuli (maps, body parts, objects, animals, famous faces and colours) were investigated using positron emission tomography. Stimuli were presented either with or without the written name of the picture, thereby creating a naming condition and a reading condition. As predicted, naming increased the demands on lexical processes. This was demonstrated by activation of the left temporal lobe in a posterior region associated with name retrieval in several previous studies. This lexical effect was common to all meaningful stimuli and no category-specific effects were observed for naming relative to reading. Nevertheless, category differences were found when naming and reading were considered together. Stimuli with greater visual complexity (animals, faces and maps) enhanced activation in the left extrastriate cortex. Furthermore, map recognition, which requires greater spatio-topographical processing, also activated the right occipito-parietal and parahippocampal cortices. These effects in the visuo-spatial regions emphasize inevitable differences in the perceptual properties of pictorial stimuli. In the semantic temporal regions, famous faces and objects enhanced activation in the left antero-lateral and postero-lateral cortices, respectively. In addition, we showed that the same posterior left temporal region is also activated by body parts. We conclude that category-specific brain activations depend more on differential processing at the perceptual and semantic levels rather than at the lexical retrieval level.

Keywords: neural processing; naming; reading; visual complexity; object processing; category differences

1. INTRODUCTION

Questions concerning how the human brain stores and retrieves semantic and lexical information about the world have been debated for more than two decades. One question relates to whether such memories are categorically organized, a notion derived from neuropsychological patients who demonstrate selective impairment and/or preservation for processing one or more categories of stimuli. The most frequently reported pattern of impairment is a deficit with living things (naturally occurring species such as animals and fruit and vegetables) with relative preservation of non-living (man-made objects) stimuli (e.g. Warrington & Shallice 1984). Further work revealed that category-specific impairments could be far more specific. For example, cases were described with selective deficits/preservation for animals only (Caramazza & Shelton 1998), body parts and man-made objects (Sacchett & Humphreys 1992), man-made objects only (Cappa *et al*. 1998*a*), maps (Incisa della Rocchetta *et al*. 1998; Cipolotti 2000), famous faces (Kapur *et al*. 1986; Semenza & Zettin 1989) and colours (De Renzi *et al*. 1987).

The impairment of specific categories of knowledge seems to occur at different stages of the object-naming processes. In most cases a clear disorder at the semantic level also causes a name retrieval deficit (Warrington & Shallice 1984). However, in a few cases, there is little semantic impairment despite a noticeable lexical retrieval deficit (e.g. Cappa *et al*. 1998*a*). The interpretation of these last cases is a matter of debate. Categorical effects at the lexical level only may be consistent with a categorical

organization of the lexical output systems and/or with differential access to it from semantic storage (Caramazza & Hillis 1990; Farah & Wallace 1992; Damasio *et al*. 1996). Alternatively, the effects could arise from a top-down phenomenon caused by name retrieval at prior levels of the identification process (Humphreys *et al*. 1997).

Despite these reports, we still do not have a plausible neuro-cognitive explanation for categorical effects. The most commonly held views fall into three camps (Caramazza 1998). First, there is evolutionary value for segregating the neural systems dedicated to different types of objects (Caramazza 1998). Second, category differences arise because there are different neural systems for perceptual and functional attributes. Identification of natural objects relies more on perceptual differentiation while identification of man-made objects relies more on functional attributes (Warrington & Shallice 1984). Third, the category effects need not always reflect segregation within the semantic system but can arise because different categories of object place differential demands on a single processing system. More specifically, natural kinds of objects, which tend to have many similar visual neighbours, place greater demands on perceptual processing than man-made objects (Humphreys *et al*. 1988; Gaffan & Heywood 1993).

The existence of patients with category-specific deficit/preservation implies that neurological damage can selectively impair particular aspects of object processing. Functional neuroimaging can be used to place anatomical and neurophysiological constraints on the theoretical explanations of these effects and, thereby, contribute to

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the evaluation of the different psychological models. Several neuroimaging studies have now been performed investigating language processing and category-specific effects (Perani *et al*. 1995, 1999; Damasio *et al*. 1996; Martin *et al*. 1996; Mummery *et al*. 1996, 1998; Cappa *et al*. 1998*b*; Moore & Price 1999*a*; Thompson-Schill *et al*. 1999). Despite the difficulties in designing these experiments, some of the experimental variables and cognitive components underlying specific language- and category-related activations have now been established. For instance, while it was observed that the extrastriate cortex responds more to pictures of living than non-living stimuli (Perani e*t al*. 1995; Martin *et al*. 1996), it was only in a recent positron emission tomography (PET) experiment (Moore & Price 1999*a*) that these effects were attributed to differences in the visual configuration between the two categories. Furthermore, other recent studies have outlined the role of the left temporal cortex in semantic processing (Gorno-Tempini *et al*. 1998; Mummery *et al*. 1998) and the specific involvement of the left fusiform gyrus in lexical retrieval (Price & Friston 1997; Moore & Price 1999*b*).

In the present paper, we contrast the neural activation elicited by six different object categories (maps, body parts, man-made objects, animals, famous faces and colours). There were two main aims of the experiment: (i) to study whether category-specific brain activations will be influenced by increasing lexical retrieval processes, and (ii) to identify the neural correlates of maps and body parts, which to our knowledge have not yet been investigated. Contrasting a naming condition with a reading condition (where the same pictorial stimuli were presented along with their written name) controlled for differences in the perceptual properties and allowed us to evaluate categorical effects which were influenced by the greater lexical retrieval effort required in the naming task. When categorical differences were found in common to naming and reading, the perceptual differences between categories were not controlled and interpretation required reference to previous studies of functional anatomy.

2. MATERIAL AND METHODS

(a) *Task and stimuli*

Twelve experimental conditions were arranged in a 2×6 factorial design. One level was the task, i.e. to read or retrieve the name of visually presented pictorial stimuli. In the reading condition the name of the object was written in capital letters below the figure. In the naming condition a string of Xs was presented below the same picture, with the number of Xs corresponding to the number of letters in the written words (figure 1). In all conditions the subjects had to articulate the word silently and the responses could be checked through a video camera. The second level was the stimulus category: maps of countries, body parts, objects, animals, famous faces and colours. The maps, body parts, objects and animals were black and white line drawings. The famous faces were black and white photographs and the colours were coloured rectangles. The size of the stimuli was *ca.* 10 cm × 15 cm. In the map-naming condition, the subject had to name the country, which was highlighted within the map (see figure 1). The stimuli names were of high frequency (Thorndike and Lorge 1968) and were matched for the number
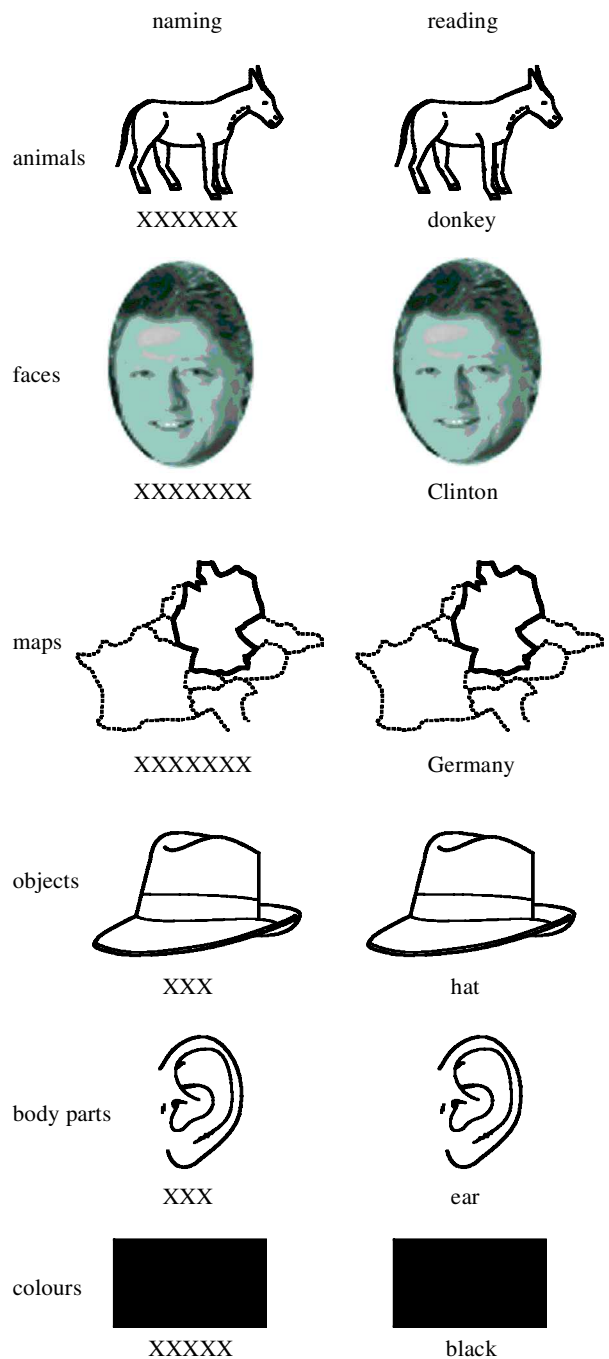

Figure 1. Examples of the stimuli used in the naming and reading conditions for all six categories.

of syllables across categories. During each scanning session 12 different stimuli were presented at the centre of a Macintosh computer screen (distance 40 cm) for 1.5 s, at a rate of one per 4 s starting 10 s before data acquisition. Each picture was seen twice, once during the naming condition and once during the reading condition, with a different order within scans and the order of naming and reading counterbalanced over subjects.

(b) *Subjects*

Eight subjects, four males and four females (age range 42–60 years), participated. All were right-handed, native English speakers on no medication and free from any history of neurological or psychiatric illness. The study was approved by the

local hospital ethics committee and the Administration of Radioactive Substances Advisory Committee (UK) (ARSAC).

(c) *PET scanning*

The 12 PET scans were obtained using a SIEMENS/CPS ECAT EXACT HR + (model 962) PET scanner (Siemens/CTI, Knoxville, TN, USA). The participants received a 20 s intravenous bolus of $H_2^{15}O$ at a concentration of 55 Mbq ml^{-1} at a flow rate of 10 ml min^{-1} through a forearm cannula. For each subject, a T1-weighted structural magnetic resonance (MR) image was obtained with a 2 T Magnetom VISION scanner (Siemens, Erlangen, Germany).

(d) *Data analysis*

The data were analysed with statistical parametric mapping (SPM97, Wellcome Department of Cognitive Neurology, London, UK, http://www.fil.ion.ucl.ac.uk/spm) implemented in Matlab (Mathworks Inc., Sherborn, MA, USA) using standardized procedures (Friston *et al.* 1995). The condition and subject effects were estimated according to the general linear model at each voxel. To test the hypotheses about regionally specific condition effects, these estimates were compared using linear compounds or contrasts. The resulting set of voxel values for each contrast is an SPM of the *t*-statistic.

In this experiment, we were interested in category-specific effects, which were either greater in the naming task (i.e. naming versus reading), independent of task (naming and reading) or task dependent (naming only). We were also interested in the main effect of the naming task irrespective of category (naming common to all categories) in order to confirm that naming placed greater demands on lexical retrieval. The contrasts were as follow.

(i) *Effects of category*
Single category effects

Each category was contrasted to each of the other five for the following.

(i) Naming versus reading. This comprised a series of interaction terms for each category (e.g. name–read faces versus name–read animals, name–read faces versus name–read objects, etc.). Conjunction analysis (Price & Friston 1997) and the inclusive masking option in SPM were used to generate main effects where voxels were eliminated, if there was a significant difference between the simple main effect of category ($p < 0.05$) or when one or more of the contrasts did not reach a significance level of $p < 0.08$.
(ii) Naming and reading. In these contrasts we identified areas where there was a category-specific effect common to the name and read conditions, i.e. name and read faces versus name and read animals, name and read faces versus name and read objects, etc. As with the naming versus reading contrasts, category-specific effects were calculated using conjunction analysis and inclusive masking.
(iii) Naming only. Finally, we used the same procedure in order to check whether there were any effects for the naming condition only that were not detected either for naming versus reading or naming and reading.

Group of category effects

Items that weighted functional properties such as objects and body parts were contrasted to items that weighted perceptual properties and/or were visually more complex such as animals, faces and maps (Sacchett & Humphreys 1992; Warrington &

Shallice 1984). The effects were identified for naming versus reading, naming and reading, and naming only, as described above.

(ii) *Effects of naming irrespective of category*

Conjunctions and masking (as described above) were used to find the common effects of 'naming versus reading' for all six categories. The same analysis was also performed excluding the colour category, which is not strongly associated with form and semantics.

Increases as well as decreases were considered for each of the above effects. By category-specific increases we mean that there was greater activation for one category relative to all others. For category-specific decreases, we mean that there was less activation for one category than for all others.

We report activations that reached significance at $p < 0.05$ corrected for multiple comparisons. A level of significance of $p < 0.001$ non-corrected was accepted for regions of interest defined by previous neuroimaging and neuropsychological data. The *a priori* areas of interest were the occipital and temporal regions, which have previously been shown to be activated in neuroimaging studies of category specificity (Perani *et al.* 1995, 1999; Damasio *et al.* 1996; Martin *et al.* 1996; Mummery *et al.* 1996, 1998; Cappa *et al.* 1998*b*; Thompson-Schill *et al.* 1999) and face processing (Gorno-Tempini *et al.* 1998). Moreover, areas previously involved in visuo-spatial processing were hypothesized to be more involved for the map stimuli (Incisa della Rocchetta *et al.* 1998; Cipolotti 2000).

3. RESULTS

(a) *Effects of category*

(i) *Single category effects*

Naming versus reading

No areas showed a significant category-specific increase or decrease when naming was compared to reading.

Naming and reading (table 1 and figure 2)
(i) Maps. With increases, naming and reading maps compared to naming and reading all other categories activated an extensive region in the posterior part of the right hemisphere, which included the right middle and superior occipital gyri (BA 19). When a non-corrected level of significance was applied, the occipital activation extended superiorly to the intraparietal sulcus (BA 7) and anteriorly to the parahippochampal gyrus (BA 30). With decreases, the left putamen showed an activation decrease specific for maps.
(ii) Faces. Retrieving the name and reading the name of photographs of famous faces activated a region in the left anterior middle temporal gyrus (BA 21) when compared to all other categories. The right fusiform gyrus, which has previously been associated with perceptual processing of faces (Gorno-Tempini *et al.* 1998), was more active for all shaped stimuli relative to colours (see § 3). There were no face-specific decreases.
(iii) Objects, body parts, animals and colours. No areas showed a specific increase or decrease effect for naming and reading any of these categories more than all the others (but see the effect of grouping below).

Table 1. *Category effects for naming and reading*

(The table presents the areas, coordinates and Z-scores of areas which show category-specific effects for either one category compared to all others or for a group of categories compared to all others.)

|	areas	coordinates	Z-score
categories			
faces only	left anterior temporal (BA 21)	$-66, -14, -8$	4.5
maps only	right superior/mid-occipital (BA 19)	$24, -80, 32$	5.7
		$38, -86, 18$	4.5
	right parahippocampus (BA 30)	$40, -36, -8$	3.8
	right intraparietal sulcus (BA 7)	$26, -54, 46$	3.6
group of categories			
faces, animals, maps	left cuneus (BA 18/19)	$-4, -62, 20$	5.3
		$-10, -94, 8$	3.9
objects and body parts	left mid-/inferior temporal (BA 21/37)	$-54, -56, 0$	4.1
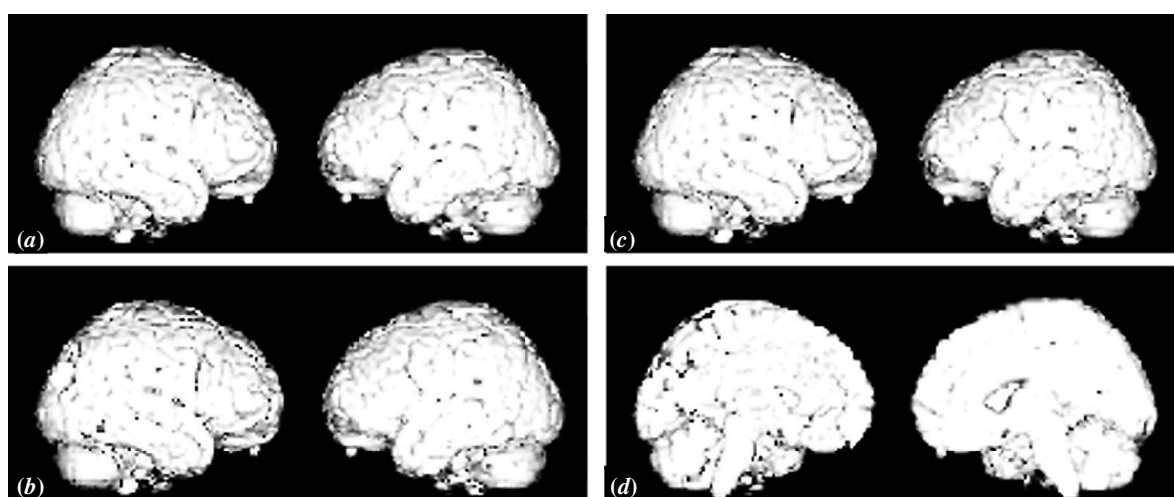
Figure 2. Category-specific effects on naming and reading for (*a*) faces more than all other categories, (*b*) maps more than all other categories, (*c*) objects and body parts more than animals, faces and maps, and (*d*) animals, faces and maps more than objects and body parts. The activations are superimposed on a three-dimensional reconstruction of the Montreal Neurological Institute standard brain.

Naming only

The only region that revealed a category-specific effect for naming was the right fusiform gyrus, which showed a decrease for colour naming more than for naming all other categories ($38, -82, -8$ and $Z = 5.0$, and 42, $-58, -20$ and $Z = 3.9$). Faces and animals showed maximum activation, although the difference did not reach significance.

(ii) *Group of category effects*

The only significant activations were found when naming and reading were considered together.

Faces, animals and maps activated an extensive region in the left extrastriate visual cortex (BA 18/19). This activation was most extensive for maps.

When compared to all other categories, objects and body parts activated a region in the posterior middle/inferior temporal gyri (BA 21/37). A non-corrected

level of significance ($Z = 4.1$ and $p < 0.0001$ non-corrected) was accepted since this area has previously been shown to be more active for object than for animal processing (Perani *et al*. 1995; Cappa *et al*. 1998*b*; Mummery *et al*. 1998) and in the generation of action words more than in the generation of colour words (Martin *et al*. 1995).

(b) *Effects of naming irrespective of category*

No area was found to be specific for naming all categories. However, when the same analysis was performed excluding the colour conditions a significant effect of naming was found in the left fusiform gyrus ($-46, -66, -18$, BA 37). This activation did not reach a corrected level of significance ($Z = 4.3$ and $p < 0.07$ corrected), but it has previously been shown to be involved in naming and reading tasks irrespective of category or modality of input (Price & Friston 1997; Moore &

Price 1999*b*). No area showed a specific increase in activation for naming relative to reading colours.

4. DISCUSSION

Six different object categories were investigated in order to identify (i) category-related effects which are greater at the lexical retrieval level, and (ii) the neural substrate for recognizing maps and body parts. Two tasks were performed on the same pictorial stimuli, either name the object or read its name printed below the figure.

In the naming versus reading contrast, all meaningful categories activated a left middle fusiform region, which has previously been associated with name retrieval when perceptual and semantic properties are controlled for (Price & Friston 1997; Moore & Price 1999*b*). Any category-related effect for naming relative to reading could then be attributable to differences at the lexical retrieval level. However, no such category-specific differences were found in the naming versus reading contrasts, not even for categories grouped by perceptual and functional properties. The present results confirm that the left middle fusiform gyrus becomes involved when a meaningful stimulus has to be linked to its specific lexical label and show that this region does not seem to be category specific but instead common to all meaningful stimuli.

However, category-specific effects were found when both the naming and reading conditions were considered together. Naming and reading maps activated the right occipito-parietal and parahippocampal regions which have previously been associated with visuo-spatial (Haxby *et al*. 1994) and topographical (Aguirre *et al*. 1998) tasks. Our findings are reasonably explained by the fact that map identification and learning relies greatly on visuo-spatial processes (Cipolotti 2000). In fact, maps are abstract shapes that, to be identified, need an evaluation of their absolute and reciprocal positions in the world map.

Body parts as well as manipulable objects activated an area in the posterior temporal cortex. This region has been associated with semantic tasks (Mummery *et al*. 1996) and man-made object recognition, even when perceptual and phonological processing were carefully controlled for (Mummery *et al*. 1998; Moore & Price 1999*a*). Furthermore, activation in this region is enhanced when retrieving actions linked to the usage of an object (Martin *et al*. 1995; Phillips *et al*. 1999). Consistent with neuropsychological studies, these results confirm the association of action knowledge with the recognition of objects and body parts.

The current study also confirms the role of the anterior temporal cortex in the identification of famous faces. This area has previously been observed in studies that compared famous faces to other categories of objects (Damasio *et al*. 1996), and famous to non-famous faces and buildings (Gorno Tempini *et al*. 1998, 1999). Previous and present evidence suggests that this area is involved in the identification of items that are linked to unique semantic attributes (see also Ellis *et al*. 1989).

Finally, the left extrastriate cortex was activated more for visually complex stimuli, i.e. maps, animals and faces. As discussed in § 1, these effects are attributable to the differences in perceptual properties such as the configuration of visual features and the number of component parts (Moore & Price 1999*a*).

In conclusion, although differential activations between naming and reading were identified in common to all meaningful stimuli, category differences predominantly arose from different demands on visuo-spatial processing and semantic associations. In particular, the right occipito-parietal and parahippocampal activation elicited by maps indicates enhanced visuo-topographical analysis, and the posterior temporal focus shown for body parts and objects indicated the involvement of action retrieval.

REFERENCES

Aguirre, G. K., Zarahn, E. & D'Esposito, M. 1998 Neural components of topographical representation. *Proc. Natl Acad. Sci. USA* **95**, 839–846.

Cappa, S. F., Frugoni, M., Pasquali, P., Perani, D. & Zorat, F. 1998*a* Category-specific naming impairment for artifacts: a new case. *Neurocase* **4**, 391–397.

Cappa, S. F., Perani, D., Schnur, T., Tettamanti, M. & Fazio, F. 1998*b* The effects of semantic category and knowledge type on lexical–semantic access: a PET study. *NeuroImage* **8**, 350–359.

Caramazza, A. 1998 The interpretation of semantic category-specific deficits: what do they reveal about the organization of conceptual knowledge in the brain? *Neurocase* **4**, 265–272.

Caramazza, A. & Hillis, A. E. 1990 Where do semantic errors come from? *Cortex* **26**, 95–122.

Caramazza, A. & Shelton, J. R. 1998 Domain-specific knowledge systems in the brain: the animate–inanimate distinction. *J. Cogn. Neurosci.* **10**, 1–34.

Cipolotti, L. 2000 Sparing of country and nationality names in a case of modality specific oral output impairment: implications for theories of speech production. *Cogn. Neuropsychol.* (In the press.)

Damasio, H., Grabowski, T. J., Tranel, D., Hichwa, R. D. & Damasio, A. R. 1996 A neural basis for lexical retrieval. *Nature* **380**, 499–505.

De Renzi, E., Zambolin, A. & Crisi, G. 1987 The pattern of neuropsychological impairment associated with left posterior cerebral artery infarcts. *Brain* **110**, 1099–1116.

Ellis, A. W., Young, A. W. & Critchley, E. M. R. 1989 Loss of memory for people following temporal lobe damage. *Brain* **112**, 1469–1483.

Farah, M. J. & Wallace, M. A. 1992 Semantically-bounded anomia: implications for the neural implementation of naming. *Neuropsychologia* **30**, 609–621.

Friston, K. J., Worsley, K. J., Poline, J. B., Frith, C. D. & Frackowiak, R. S. J. 1995 Statistical parametric maps in functional imaging: a general linear approach. *Hum. Brain Mapp.* **2**, 189–210.

Gaffan, D. & Heywood, A. 1993 A spurious category-specific visual agnosia for living things in normal human and nonhuman primates. *J. Cogn. Neurosci.* **5**, 118–128.

Gorno-Tempini, M. L., Price, C. J., Josephs, O., Vandenberghe, R., Cappa, S. F., Kapur, N., Frackowiak, R. S. & Tempini, M. L. 1998 The neural systems sustaining face and proper-name processing. *Brain* **121**, 2103–2118.

Gorno-Tempini, M. L., Price, C. J. & Frackowiak, R. S. J. 1999 Recognition of unique items. *Soc. Neurosci. Abstr.* **25**, 100.

Haxby, J. V., Horwitz, B., Ungerleider, L. G., Maisog, J. M., Pietrini, P. & Grady, C. L. 1994 The functional organization of human extrastriate cortex: a PET-rCBF study of selective attention to faces and locations. *J. Neurosci.* **14**, 6336–6353.

Humphreys, G. W., Riddoch, M. J. & Quinlan, P. T. 1988 Cascade processes in picture identification. *Cogn. Neuropsychol.* **5**, 67–104.

Humphreys, G. W., Riddoch, M. J. & Price, C. J. 1997 Top-down processes in object identification: evidence from experimental psychology, neuropsychology and functional anatomy. *Phil. Trans. R. Soc. Lond.* B **352**, 1275–1282.

Incisa della Rocchetta, A., Cipolotti, L. & Warrington, E. 1998 Countries: their selective impairment and preservation. *Neurocase* **4**, 99–109.

Kapur, N., Heath, P., Meudell, P. & Kennedy, P. 1986 Amnesia can facilitate memory performance: evidence from a patient with dissociated retrogade amnesia. *Neuropsychologia* **24**, 215–221.

Martin, A., Haxby, J. V., Lalonde, F. M., Wiggs, C. L. & Ungerleider, L. G. 1995 Discrete cortical regions associated with knowledge of color and knowledge of action. *Science* **270**, 102–105.

Martin, A., Wiggs, C. L., Ungerleider, L. G. & Haxby, J. V. 1996 Neural correlates of category-specific knowledge. *Nature* **379**, 649–652.

Moore, C. J. & Price, C. J. 1999*a* A functional neuroimaging study of the variables that generate category-specific object processing differences. *Brain* **122**, 943–962.

Moore, C. J. & Price, C. J. 1999*b* Three distinct ventral occipitotemporal regions for reading and object naming. *NeuroImage* **10**, 181–192.

Mummery, C. J., Patterson, K., Hodges, J. R. & Wise, R. J. 1996 Generating 'tiger' as an animal name or a word beginning with T: differences in brain activation. *Proc. R. Soc. Lond.* B **263**, 989–995.

Mummery, C. J., Patterson, K., Hodges, J. R. & Price, C. J. 1998 Functional neuroanatomy of the semantic system: divisible by what? *J. Cogn. Neurosci.* **10**, 766–777.

Perani, D., Cappa, S. F., Bettinardi, V., Bressi, S., Gorno-Tempini, M., Matarrese, M. & Fazio, F. 1995 Different neural systems for the recognition of animals and man-made tools. *NeuroReport* **6**, 1637–1641.

Perani, D., Schnur, T., Tettamanti, M., Gorno-Tempini, M., Cappa, S. F. & Fazio, F. 1999 Word and picture matching: a PET study of semantic category effects. *Neuropsychologia* **37**, 293–306.

Phillips, J., Humphreys, J. & Price, C. 1999 Different routes to action from words and pictures: evidence from neuroImaging. *NeuroImage* **6**, S1042.

Price, C. J. & Friston, K. J. 1997 Cognitive conjunctions: a new approach to brain activation experiments. *NeuroImage* **5**, 261–270.

Sacchett, C. & Humphreys, G. W. 1992 Calling a squirrel a squirrel but a canoe a wigwam: a category-specific deficit for artifactual objects and body parts. *Cogn. Neuropsychol.* **5**, 105–132.

Semenza, C. & Zettin, M. 1989 Evidence from aphasia for the role of proper names as pure referring expressions. *Nature* **342**, 678–679.

Thompson-Schill, S. L., Aguirre, G. K., D'Esposito, M. & Farah, M. J. 1999 Aneural basis for category and modality specificity of semantic knowledge. *Neuropsychologia* **37**, 671–676.

Thorndike, E. L. & Lorge, I. 1968 *The teacher's word book of 30 000 words.* New York: Teacher College Press.

Warrington, E. K. & Shallice, T. 1984 Category specific semantic impairments. *Brain* **107**, 829–854.