

Large, colourful or noisy? Attribute- and modality-specific activations during retrieval of perceptual attribute knowledge

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ABSTRACT

PET was used to investigate whether retrieval of perceptual knowledge from long-term memory activates unique cortical regions associated with the modality and/or attribute type retrieved. Knowledge about the typical colour, size and sound of common objects and animals was probed, in response to written words naming the objects. Relative to a non-semantic control task, all attribute judgements activated similar left temporal and frontal regions. Visual (colour, size) knowledge selectively activated right posterior inferior temporal (PIT) cortex, while sound judgements elicited selective activation in left posterior superior temporal gyrus and adjacent parietal cortex. All of the attribute judgements activated a left PIT region, but colour retrieval generated more activation in this area. Size judgements activated right medial parietal cortex. These results indicate that the retrieval of perceptual semantic information activates not only a general semantic network but also cortical areas specialised for the modality and attribute type of the knowledge retrieved.

INTRODUCTION

Stored knowledge about object concepts is generally described as comprising both functional/associative information such as what an object is used for and where it is found, and perceptual/sensory information such as what the object looks like (e.g. colour, size, shape), any sound it makes, its smell, taste, and texture, and so on. It has been further proposed that the cortical regions subserving different aspects of semantic representations might be located in or near the sensory or motor cortices through which the knowledge is acquired and experienced (e.g. Allport, 1985; Gainotti, Silveri, Daniele & Giustoli, 1995; Pulvermüller, 1999). While direct evidence for separable neural systems contributing to the representation and processing of different types of perceptual knowledge has been provided by a small number of neuropsychological studies, attempts to localise perceptual attribute knowledge using neuro-imaging techniques have either been restricted to

a single type of visual attribute (colour), or have examined a range of broadly defined visual attributes (e.g. (relative) size/shape judgements, feature/part identification). If the retrieval of different perceptual attributes engages non-identical and sensorily relevant cortical regions, then careful definition of the attribute(s) of interest and comparison across a variety of attributes is critical. The PET study reported here was designed to investigate the distinctiveness of the neural substrates involved in various types of perceptual attribute knowledge, both within and between modalities.

Neuropsychological data: Few neuropsychological studies have reported selective impairment or sparing of the knowledge of various perceptual attributes; and the insights provided by even these few studies are limited by a lack of systematicity in the range of attributes tested. Localisation of the critical underlying neural structures has also been problematic because most reported cases

involve extensive and/or diffuse cortical damage. Nonetheless the specific perceptual attribute dissociations reported in those few studies which have investigated a range of relevant attributes provide some support for fractionation of perceptual semantic attributes and their separate cortical localisations. Several studies have reported relative sparing of knowledge pertaining to the perceptual attribute of size, in the context of impaired knowledge about other visual perceptual attributes (e.g. the colour, overall shape, and parts of objects: Forde, Francis, Riddoch, Rumiati, & Humphreys, 1997; Coltheart, Inglis, Cupples, Michie, Bates, & Budd, 1998; Sartori & Job, 1988; see also Sheridan & Humphreys, 1993). This dissociation has led to suggestions that size information may be a non-perceptual semantic attribute rather than a visual perceptual attribute (Sartori & Job, 1988; see also Coltheart et al., 1998), or represent a 'higher' level of visual representation which may be spared when more specific knowledge is impaired (Sartori & Job, 1988). Alternatively, size knowledge can be viewed as distinct from other visual object properties in that it is more spatially defined. In the absence of clear empirical evidence favouring any of these alternatives, the present study takes the last possibility as the working hypothesis to be investigated. To our knowledge no patient has yet been reported with a selective *impairment* of size knowledge relative to other visual attributes. Of course not all perceptual attributes are visual, and two neuropsychological studies have shown that auditory information may be spared in patients with impaired knowledge about visual attributes (excluding size) (Sartori & Job, 1988; Coltheart et al., 1998). A selective impairment of auditory relative to visual knowledge has not yet been reported.

Although extremely limited, these neuropsychological data suggest that the visual attribute of colour may be dissociable from both size (another visual attribute) and sound knowledge, and provide support for the general proposal that

knowledge about the perceptual attributes of objects involves a cortical network comprised of functionally and neuroanatomically distinct regions.

Neuroimaging data: Functional imaging has enabled investigation of the neural regions associated with different types of semantic knowledge in normal participants. Only four neuroimaging studies to date, however, have directly compared the retrieval of non-perceptual and (visual) perceptual knowledge (Thompson-Schill, Aguirre, D'Esposito, & Farah, 1999; Cappa, Perani, Schnur, Tettamanti, & Fazio, 1998; Mummery, Patterson, Hodges, & Price, 1998; Martin, Haxby, Lalonde, Wiggs, & Ungerleider, 1995). While all four studies have reported increased activation in the temporal lobe (as well as a number of frontal and parietal regions) for visual perceptual knowledge relative to functional attributes and non-semantic control tasks, various regions of temporal lobe were implicated. Both the Cappa et al. (1998) and Thompson-Schill et al. (1999) studies reported activation of (somewhat different) regions of left or bilateral posterior inferior temporal (PIT) cortex, but Mummery et al. (1998) found that left anteromedial temporal cortex was uniquely associated with the retrieval of visual semantic knowledge (colour). These inconsistencies can perhaps be explained by the variety of tasks utilised and the diverse nature of what comprised a visual perceptual attribute across these studies.

A small number of functional imaging studies have specifically investigated the neural substrates supporting colour knowledge, with rather more consistent findings. In three overlapping studies, Martin and colleagues (Martin et al., 1995; Chao & Martin, 1999; Wiggs, Weisberg, & Martin, 1999) compared object naming with object colour naming of achromatic line drawings and observed increased rCBF associated with colour naming in left lateralised (bilateral in Martin et al., 1995) PIT cortex, including areas of parahippocampal gyrus, fusiform gyrus and/or inferior temporal

gyrus. The retrieval of colour attribute knowledge in these studies also consistently activated left inferior and superior parietal regions, and numerous frontal areas (most notably left middle and inferior frontal gyri), although these latter activations have been observed in a large range of semantic retrieval tasks and are therefore not unique to colour knowledge (e.g. Martin et al., 1995; Frith, Friston, Liddle, & Frackowiak, 1991; Mummery, Patterson, Hodges, & Wise, 1996; Mummery et al., 1998; Peterson, Fox, Posner, Mintun, & Raichle, 1988; Wise, Chollet, Hadar, Friston, Hoffner, & Frackowiak, 1991). Using a very different approach, Paulesu and colleagues (Paulesu, Harrison, Baron-Cohen, Watson, Goldstein, Heather, Frackowiak, & Frith, 1995) investigated the cortical regions engaged when people with word-colour synaesthesia experienced colours in response to hearing words and also reported a left PIT activation.

Vandenberghe and colleagues (Vandenberghe, Price, Wise, Josephs, & Frackowiak, 1996) compared knowledge of semantic association and object size in a matching task using triads of pictures or words, and found no cortical areas uniquely activated during the processing of size information. This (null) result at least does not contradict the hypothesis that size information may be more similar to verbal/semantic knowledge than to visual semantic knowledge, as has been suggested on the basis of the neuropsychological data, but does not directly address the question of how the neural substrates of size knowledge compare to those of other perceptual attributes.

Given the sparse functional imaging data on the cortical representation of visual perceptual knowledge, it is perhaps not surprising that perceptual attributes in other modalities, such as auditory and olfactory knowledge, remain unexplored. The functional imaging evidence for involvement of the ventral visual processing route associated with tasks requiring the retrieval of colour knowledge suggests that other types of

perceptual attribute information may also engage processing regions specialised for modality- and/or attribute type. Evidence tangentially supportive of this hypothesis comes from the results from two recent studies of episodic memory for stimuli comprised of paired visual and auditory components (Wheeler, Peterson, & Buckner, 2000; Nyberg, Habib, McIntosh, & Tulving, 2000). Secondary auditory cortex was activated during the recall of sounds which were cued by a verbal or visual cue with which the sound was paired at encoding, and secondary visual processing areas were activated by the recall of pictures. Nyberg et al. (2000) also reported activation of auditory association cortex in response to words which had earlier been paired with a sound, even when the retrieval task was a simple old/new discrimination during which the recall of the paired sound was incidental. In these studies, the tasks required retrieval of episodic information from the time of encoding, so the results can only be suggestive with regard to the issue addressed here: whether modality-specific activations apply to the retrieval of perceptual attribute knowledge from long-term semantic memory.

The current study: The PET study reported here was designed to investigate the modality- and attribute-specificity of the PIT activations previously reported to be associated with colour knowledge, and to determine whether retrieval of other types of perceptual knowledge similarly activates unique regions of cortex. No differences between the activations elicited by the retrieval of a range of perceptual attributes would be consistent with all semantic knowledge residing in a single shared network, whereas differential activations associated with retrieving the various attributes would support the hypothesis proposed here: that different types of perceptual knowledge recruit additional areas of sensorily relevant cortex in a distributed semantic processing network. Written words referring to objects were used, and the perceptual attributes examined were

object colour, size and sound. These particular attributes were chosen because neuropsychological evidence suggests that both size and sound knowledge are dissociable from colour knowledge, and because this range of attributes allows the investigation of the neural correlates of perceptual attribute knowledge both within (visual: colour, size) and between (visual, auditory) modalities.

Several specific predictions were made. First, given the consistent results reported by Martin and colleagues, and the role of ventral cortical areas in the processing of non-spatial visual object properties (e.g. Corbetta, Meizin, Dobmeyer, Shulman, & Peterson, 1991), retrieval of colour knowledge was expected to activate PIT regions, with a left hemisphere predominance. Second, on the basis that size judgements are likely to require a degree of spatial processing we predicted that retrieval of size knowledge would engage dorsal parietal regions comprising part of the dorsal visual processing system (e.g. Corbetta et al., 1991). Activations in line with these predictions would indicate attribute-specific cortical activation during semantic retrieval. It was less clear whether to expect ventral as well as dorsal activation in response to size judgements. Third, we predicted that retrieval of knowledge about an object's sound would selectively engage cortical regions responsive to auditory processing located in or near posterior regions of auditory association cortex (posterior superior temporal gyrus, temporoparietal junction). Such activation would constitute an example of modality-specific cortical activation associated with semantic retrieval.

METHOD

Participants

Ten males (mean age 28.3 years, range 22-43 years) who were right-handed, had English as their first language, and with normal or corrected-to-normal vision were paid for their participation. All were comprehensively screened for medical and other exclusion criteria and provided informed consent prior to scanning.

Design and Materials

Three experimental conditions were designed to require selective access to colour, size and sound knowledge about familiar objects. Yes/no questions were used to probe each of these types of knowledge selectively (see Table 1). The questions were further clarified for the participants in the following manner: 'coloured' was defined as 'not black and/or white'; for the 'sound' question, the object could either make noise spontaneously (e.g. a dog barking) or noise could be associated with use of the object (e.g. a drill); for the 'size' condition objects were either obviously large (e.g. bus) or obviously small (e.g. coin), with no medium-sized objects included (e.g. chair). No reference object was suggested for making the size judgements. The participants' understanding of the tasks was consolidated by using examples and through practice runs prior to the commencement of scanning.

Attribute probed	Question	'yes' response object	'no' response object
Colour	Is it coloured?	Banana	Skunk
Sound	Does it make a noise?	Drill	Pillow
Size	Is it small?	Coin	Bus

Table 1: Question posed for each experimental condition, with examples of objects designed to elicit positive and negative responses to these questions.

Seventy-two nouns were selected for each of the experimental conditions, with 36 chosen to elicit a positive response and 36 to elicit a negative response. Of these, half were from natural categories and half from manmade categories, with a similar number of tools included in each semantic condition. The nouns were matched for mean word length (number of letters) and concept familiarity (see below) across conditions and response type (Table 2). While the use of unique stimuli in each condition leaves open the

possibility that any observed effects could be interpreted as stimulus-specific rather than condition-specific, this possibility is minimised by the stimuli being well matched across conditions. Furthermore, by avoiding stimulus repetitions the current design precludes contamination of activations across conditions associated with an attribute which has been the focus of selective retrieval being ‘primed’ in subsequent conditions where that attribute is irrelevant for the same stimulus.

Condition	Positive Response		Negative Response		Total	
	Familiarity	Word length	Familiarity	Word length	Familiarity	Word length
Colour	2.2 (1.1)	8.0 (2.7)	1.9 (1.0)	7.3 (2.6)	2.1 (1.1)	7. (2.7)
Sound	2.1 (1.0)	7.0 (2.8)	2.0 (1.0)	6.8 (2.1)	2.0 (1.0)	7.1 (2.3)
Size	2.3 (1.1)	6.3 (2.0)	1.8 (1.0)	6.3 (1.9)	2.0 (1.1)	6.3 (2.1)

Table 2: Mean familiarity (on a 5-point scale) and word length in letters (standard deviations in parentheses) for each attribute condition, split by expected positive and negative responses.

The 216 (72x3) experimental stimuli were selected from a set of 522 concepts for which familiarity ratings had previously been obtained from 36 paid volunteers. Familiarity was rated on a 5-point scale and, following Snodgrass and Vanderwart (1980), volunteers were asked to rate ‘the degree to which you *come into contact with* or *think about* each of the objects referred to by the words’: Volunteers were reminded to rate their familiarity with the object rather than the word itself, and were given three examples with a range of responses. A correlation was performed on the ratings for those items for which Snodgrass and Vanderwart (1980) familiarity ratings were also available, yielding a robust correlation coefficient of 0.87.

A control condition was also constructed which was visually similar to the experimental conditions (comprised of uppercase letters) while having no semantic content. This condition

comprised consonant letter strings (a single consonant *per* string) which were matched to the experimental conditions on mean number of letters. Half of the letter strings contained an ‘X’ (e.g. VVVXV), while the other half did not. The position of the ‘X’ in the letter string, when present, was varied randomly with the exclusion of the first and last positions. For this condition the question posed was ‘Does it contain an X?’.

Procedure

Participants were instructed and given examples of the tasks before being positioned in the PET scanner. Once in the scanner they were also given a short practice for each condition to familiarise them with both the tasks and the scanner set-up. The stimuli were presented on a monitor suspended over the scanner, which was 100 cm from the participant’s eyes and positioned so he

had an unobstructed view. Behavioural responses were recorded via a two-button mouse, and responses were made with the middle ('no') and index ('yes') fingers of the left hand. Speed and accuracy of responses were given equal weighting in the instructions.

Each participant was scanned 12 times, with three scans for each of the four conditions, and a different set of 24 stimuli presented during each condition repetition. The scan order of the conditions was counterbalanced across participants, while within each scan the order of the stimuli was randomised for each participant.

Prior to image acquisition, condition and response instructions were displayed for seven seconds, and four unique lead-in items appropriate to the condition were presented. Onset of the 24 experimental stimuli coincided with the onset of image acquisition. Stimulus words were presented for 1800 ms each, with an ISI of 200 ms. After the presentation of the experimental stimuli (48 sec), participants viewed a fixation point (colon) for the remainder of the scanning period (42 sec). This technique of switching from the task of interest shortly after the count rate reaches its peak has been used to improve the signal-to-noise ratio by reducing isotope washout from activated regions (e.g. Cherry, Woods, Doshi, Banerjee, & Mazziotta, 1995; see also Gerlach, Law, Gade, & Paulson, 1999; Kanwisher, Woods, Iacoboni, & Mazziotta, 1997; Simons, Graham, Owen, Patterson, & Hodges, in press).

PET scanning and data analysis

A GE Advance scanner was used to obtain 12 scans for each participant, each comprising 35 image slices at an intrinsic resolution of approximately 4.0 x 5.0 x 4.5 mm. Each participant received twelve 20 sec intravenous bolus injections of 300 MBq ml⁻¹ H215O, at a flow rate of 10 ml min⁻¹, through a forearm cannula. This method results in images of rCBF

integrated over a 90 sec period from the time the tracer enters cerebral circulation. Head movements were restricted through the use of foam padding.

We used SPM99 software for image analysis (Wellcome Department of Cognitive Neurology, London, UK). The twelve scans for each subject were first realigned using the first scan as a reference. Inspection of the realignment parameters indicated that none of the ten participants had head movements exceeding 8mm. For each subject, we spatially normalized the mean of the PET images to a template matching the Montreal Neurological Institute (MNI) standard template. Each of the individual realigned PET images were then resliced using the same transformations to give 12 scans per subject matched to the MNI brain. These images were smoothed with a 16mm FWHM isotropic Gaussian kernel to increase signal to noise. As is standard for SPM99, the effect of global signal in each scan was removed with subject specific global signal covariates in the statistical analysis. Task related differences in rCBF were estimated for each voxel using SPM 99 with reaction time entered as a covariate of interest; time (scan order) and head movement (three planes of rotation, three dimensions of translation) were set as confounding factors in the analysis (Brett, Bloomfield, Brooks, Stein & Grasby 1999). Peak activations outside specified regions of interest (see below) were thresholded with the conservative criterion of $p < .05$ corrected for multiple comparisons across the entire brain volume. In addition, in line with our *a priori* hypotheses, significance thresholds for a number of brain regions were adjusted using two regions of interest (ROIs). An experienced neurologist blind to the PET data defined a bilateral ROI encompassing the inferior and middle temporal gyri and the ventral surface of the temporal lobe, using MRICro (Rorden & Brett, in press). This ROI corresponds to our hypotheses regarding specific PIT activation in association with visual

knowledge. We used a second ROI to look at the differences between PIT activations between the various semantic conditions. We defined the ROI by taking a sphere of 10mm radius around the voxel with the maximum activation in this area when the three semantic conditions were contrasted with the control condition.¹ This voxel had coordinates -58, -45, -19 (X,Y and Zmm) (see the top panel of Figure 1). Finally, when the condition of interest concerned the object's sound, although no clearly relevant data yet exist to define a precise ROI, we report activations in posterior temporal auditory association areas and the temporal-parietal junction at a lower threshold, as we had hypothesised *a priori* that this auditory processing region might be involved in the retrieval of sound knowledge.

We have presented results as SPM maximum intensity projections, tables giving coordinates with statistics and brain slices through selected regions. The SPM maximum intensity projections (see Figure 1), or "glass brain" views, have white pixels where any voxel in a line perpendicular to the plane of the page, passing through that pixel location, has a *t* statistic above threshold. The intensity of the image at that point is relative to the maximum *t* statistic on that line. Thus, for a lateral projection, a white pixel could reflect a high *t* statistic in either left or right temporal lobe, or intervening structures. The tables give results abstracted from the SPM results output. Coordinates are in terms of the MNI brain to which the data have been spatially normalized. To estimate the Brodmann areas of each activation focus, we have used the Talairach atlas (Talairach & Tournoux 1988). The brain in this

atlas is not the same shape or size as the MNI brain, so that we have used a simple transform of the MNI coordinates (<http://www.mrc-cbu.cam.ac.uk/Imaging/mnispace.html>) to estimate their locations in the Talairach atlas. Lastly, Figures 2 and 3 use colour intensity overlaid on the MNI brain template to show activation in various key regions. The colour intensity represents the size of effect at each voxel, in terms of estimated ml/min/dl blood flow change. The outlined areas show where this change is significant at the given threshold, and therefore where the *t* statistic (which is the size of effect divided by an estimate of its standard error) is above the threshold given by random field theory (Worsley, Marrett, Neelin, Vandal, Friston & Evans 1996).

RESULTS

Behavioural data

Reaction time: Reaction times (RT) differed between the four conditions [$F(3,27) = 22.69$, $p < 0.001$](Table 3). Predictably, responses were significantly faster in the control condition than in any of the semantic retrieval conditions [$t(1,9) = 5.82-7.13$, all $p < 0.0001$], while none of the semantic retrieval conditions differed significantly from each other [Bonferroni corrected $\alpha = 0.008$: $t(1,9) = 1.54-2.70$, all $p > 0.02$]. Note that RT was included as a covariate in the analysis of the PET data, making it possible to interpret the neuroimaging data having adjusted for differences in RT.

Condition	Reaction Time (ms)		Errors (%)	Misses (%)
	Mean	Std. Deviation		
Colour	991.93	159.00	9.4	1.5
Size	936.46	107.29	4.4	0.6
Sound	898.47	115.79	2.6	0.8
Control	764.62	99.67	1.5	0.0

Table 3: Mean reaction times, standard deviations, error rates, and miss rates for each attribute condition.

Accuracy: Note that the error rates are dependent on the agreement of the subjects' and experimenters' judgements as to whether the objects fit the criteria in question (i.e. that a pearl is not usually coloured), and that high levels of accuracy were not critical to the aims of the current study –selective retrieval of the specified type of knowledge was the crucial aspect. Error rates differed between the four conditions [$F(3,27) = 12.47$, $p < 0.001$](Table 3). The error rate for the colour retrieval condition was higher relative to the other three conditions, although only significantly higher than that of the size and control conditions [Bonferroni corrected $\alpha = 0.008$: $t(1,9) = 3.89$ & 4.27 , $p = 0.004$ & 0.002]. The higher error rate in the colour condition probably reflects the somewhat subjective nature of the decisions for some stimuli in this condition. While the error rates for the colour and sound retrieval conditions did not differ significantly, the sound condition had a higher error rate than the control condition only [Bonferroni corrected $\alpha = 0.008$: $t(1,9) = 3.71$, $p = 0.005$]. Misses were determined by use of a cut-off response time of 1950 ms. Although the miss rate differed between conditions [$F(3,27) = 3.65$, $p = 0.025$], the experimental conditions did not differ significantly when compared individually to each other.

PET data

The rCBF data were analysed in two steps. Firstly, in order to identify activity associated with processes such as orthographic and phonological decoding, word identification, and more general aspects of object knowledge, as well as areas uniquely activated by retrieval of each

semantic attribute type, each of the experimental conditions (colour, size and sound) was compared to the same pre-lexical control condition ('X' detection task) (see Table 4). Very similar cortical regions were more highly activated by each of the attribute retrieval conditions relative to the control condition. All of the experimental conditions elicited the same left lateralised regions of inferior temporal and fusiform gyri (BA 37 & 20), and inferior frontal lobe (Fig. 1).² In addition, regions of posterior left middle/superior temporal gyrus, left medial frontal cortex at the level of the superior frontal gyrus, and right cerebellum were activated above threshold in the sound minus control comparison only.

Although comparisons between the experimental and control conditions are useful for identifying areas associated with lexical decoding and general semantic retrieval, it is direct comparisons between the experimental conditions which address the central questions pertaining to modality- and attribute-specific activations in a controlled manner. The second series of rCBF analyses involved two sets of contrasts between the semantic retrieval conditions. First, modality-specific activations were investigated by contrasting the two visual conditions (colour and size together) to sound retrieval. A second set of analyses investigated attribute-specific activations within the visual modality by comparing the colour and size retrieval conditions. In addition, each of the two visual conditions was also compared individually to the sound condition to verify that a) any observed effects of modality were robust for both visual conditions and b) any activations identified as specific to a particular visual attribute were not also elicited by sound judgements.

Anatomical localisation (estimated Brodmann Area)	Coordinates x y z	T	Uncorr	Corr	ROI corr
Colour-Control					
<i>Frontal lobe</i>					
L inferior frontal/orbital gyrus (11/47)	-34 36 -16	6.08	.000	.001	
<i>L medial inferior frontal gyrus/insula (44)</i>	<i>-32 12 16</i>	<i>5.41</i>	<i>.000</i>	<i>.006</i>	
<i>L inferior frontal gyrus (45/47)</i>	<i>-46 38 04</i>	<i>5.13</i>	<i>.000</i>	<i>.017</i>	
<i>Temporal lobe</i>					
L inferior temporal gyrus (37)	-60 -44 -18	5.38	.000	.007	.000 (IT)
<i>L fusiform gyrus (20)</i>	<i>-28 -06 -46</i>	<i>5.05</i>	<i>.000</i>	<i>.023</i>	<i>.003 (IT)</i>
<i>L inferior temporal gyrus (20)</i>	<i>-52 -12 -30</i>	<i>4.20</i>	<i>.000</i>	<i>.303</i>	<i>.023 (IT)</i>
<i>L fusiform gyrus (20)</i>	<i>-34 -38 -20</i>	<i>4.10</i>	<i>.000</i>	<i>.382</i>	<i>.031 (IT)</i>
Size-Control					
<i>Frontal lobe</i>					
L inferior frontal gyrus (44)	-32 12 16	6.42	.000	.000	
<i>L inferior frontal gyrus (11/47)</i>	<i>-32 40 -18</i>	<i>5.43</i>	<i>.000</i>	<i>.006</i>	
<i>Temporal lobe</i>					
L fusiform gyrus (20)	-38 -08 -46	4.58	.000	.104	.007 (IT)
<i>L inferior temporal gyrus (20)</i>	<i>-40 -32 -20</i>	<i>3.94</i>	<i>.000</i>	<i>.530</i>	<i>.049 (IT)</i>
L inferior temporal gyrus (37)	-58 -46 -18	3.97	.000	.500	.045 (IT)
Sound-Control					
<i>Frontal lobe</i>					
L superior frontal gyrus (9)	-12 52 34	5.37	.000	.007	
L inferior frontal gyrus (11/47)	-38 34 -14	8.36	.000	.000	
<i>L inferior frontal gyrus (45)</i>	<i>-46 16 16</i>	<i>5.39</i>	<i>.000</i>	<i>.007</i>	
<i>L inferior frontal gyrus (8/9)</i>	<i>-36 12 28</i>	<i>5.34</i>	<i>.000</i>	<i>.008</i>	
<i>L inferior frontal gyrus (47)</i>	<i>-56 20 06</i>	<i>5.08</i>	<i>.000</i>	<i>.020</i>	
<i>Temporal lobe</i>					
<i>L inferior temporal gyrus (20)</i>	<i>-52 -12 -36</i>	<i>5.37</i>	<i>.000</i>	<i>.002</i>	<i>.000 (IT)</i>
<i>L inferior temporal/fusiform gyrus (20)</i>	<i>-36 -34 -22</i>	<i>5.64</i>	<i>.000</i>	<i>.003</i>	<i>.000 (IT)</i>
<i>L inferior temporal/parahippocampal gyrus (20)</i>	<i>-34 -08 -48</i>	<i>5.50</i>	<i>.000</i>	<i>.004</i>	<i>.000 (IT)</i>
<i>L inferior temporal gyrus (37)</i>	<i>-56 -44 -20</i>	<i>4.41</i>	<i>.000</i>	<i>.173</i>	<i>.012 (IT)</i>
<i>L middle/superior temporal gyrus (21/22)</i>	<i>-50 -48 04</i>	<i>4.28</i>	<i>.000</i>	<i>.245</i>	<i>(TP)</i>
Cerebellum					
R cerebellum	16 -86 -32	5.25	.000	.011	
	<i>44 -80 -34</i>	<i>4.79</i>	<i>.000</i>	<i>.054</i>	

Table 4: Brain regions activated by each of the semantic retrieval conditions compared to the control condition. Anatomical localisation of maximal t-values are in stereotaxic coordinates in mm (R = right, L = left). Activations in bold type indicate region maxima, while region size is in voxels. T = t-value, uncorr = uncorrected p-values, corr = p-values corrected for entire brain volume, ROI = p-values corrected for relevant region of interest as indicated in parentheses (see text for details): IT = inferior temporal lobe, sphere = left PIT 10mm radius spherical ROI, TP = temporoparietal.

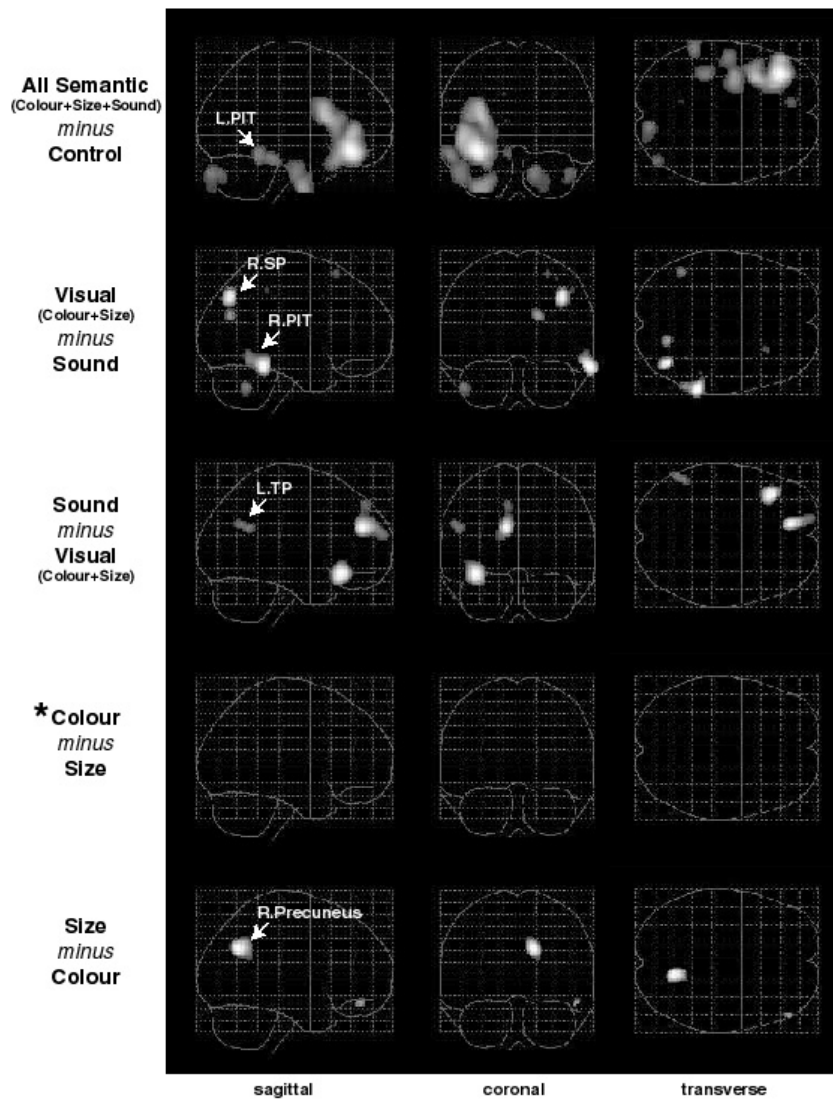


Figure 1: SPM maximum intensity projections ('glass brain' views) showing regions of increased blood flow for the main comparisons of interest. The figures are thresholded to t -values ≥ 3.94 , which is the maximum t -value corresponding to the inferior temporal lobe ROI. *Colour retrieval showed increased blood flow relative to both size and sound retrieval conditions in left PIT lobe when a more specific ROI was applied (Tables 5 & 6, Fig. 3A).

Modality-specific activations

Activations specific to visual attributes (colour & size): Relative to the sound condition, retrieval of visual (colour and size) knowledge activated right PIT areas (BA 37/20) and a region of the superior parietal lobule (BA 7) also in the right hemisphere (see Table 5, Fig. 1, Fig. 2A & B). While the right PIT activation was significant for both colour and size relative to sound, the superior parietal lobule activation failed to reach corrected

significance when colour judgements were compared to sound knowledge ($t=4.46$, $p=0.146$: Table 6).

Activations specific to sound: The retrieval of sound knowledge relative to visual (colour and size) knowledge yielded activation of a posterior area of the left superior temporal gyrus at the junction of the parietal lobe (BA 22/39/40: Table 5, Fig. 1, Fig. 2C). Although this activation did not reach significance when corrected for the

number of voxels across the whole brain, we consider it valid to report this result because of its close proximity to the posterior temporal auditory association areas, which is the region in which we hypothesised *a priori* that activity would be associated with the retrieval of sound knowledge.

Further comparisons between the sound condition and the colour and size judgements separately indicated that this temporoparietal activation was evident relative to both types of visual knowledge (Table 6).

Anatomical localisation (estimated Brodmann Area)	Coordinates x y z	T	Uncorr	Corr	ROI corr
Modality-specific activations					
(Colour+Size)-Sound					
<i>Temporal lobe</i>					
R inferior temporal gyrus (37/20)	64 -42 -20	5.29	.000	.010	.001 (IT)
	60 -52 -14	4.44	.000	.157	.011 (IT)
<i>Parietal lobe</i>					
R superior parietal lobule (7)	38 -70 42	5.22	.000	.012	
Sound-(Colour+Size)					
<i>Temporal & Parietal lobes</i>					
L inferior parietal lobule (40)	-52 -54 26	4.32	.000	.217	(TP)
<i>L superior temporal gyrus (22/39)</i>	-52 -62 30	4.24	.000	.272	(TP)
<i>Frontal lobe</i>					
L superior/medial frontal gyrus (9)	-10 46 26	5.25	.000	.011	
L inferior frontal gyrus (11/47)	-38 28 -14	5.25	.000	.011	
(Visual) Attribute-specific activations					
Colour-Size					
<i>Temporal lobe</i>					
L inferior temporal gyrus (37)	-62 -42 -16	3.60	.000	.847	.149 (IT)
	-62 -42 -16	3.60	.000		.009 (sphere)
Size-Colour					
<i>Parietal lobe</i>					
R precuneus (7)	14 -64 30	4.85	.000	.044	

Table 5: Modality- and (visual) attribute-specific activations. Anatomical localisation of maximal t-values are in stereotaxic coordinates in mm (R = right, L = left). Activations in bold type indicate region maxima, while region size is in voxels. T = t-value, uncorr = uncorrected p-values, corr = p-values corrected for entire brain volume, ROI = p-values corrected for relevant region of interest as indicated in parentheses (see text): IT = inferior temporal lobe, sphere = left PIT 10mm radius spherical ROI, TP = temporoparietal.

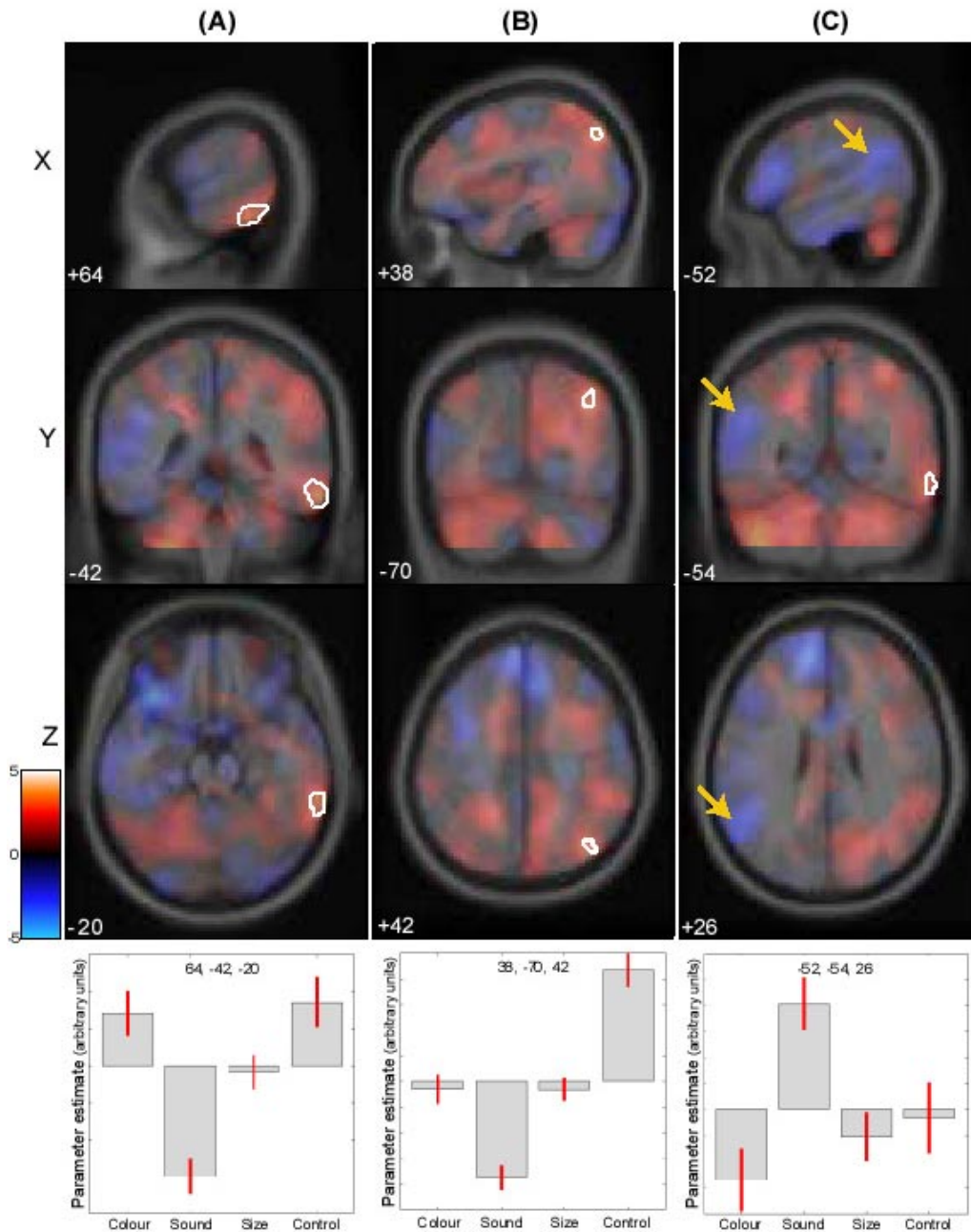


Figure 2: Differential activation when visual (colour and size) judgements were contrasted with sound judgements (red) and when sound judgements were contrasted with visual (colour and size) judgements (blue). Colour intensity is overlaid on the MNI brain template to show activation in various key regions. The colour intensity represents the effect size at each voxel, in terms of estimated ml/min/dl blood flow change. The outlined areas show where this change is significant at the given threshold, and therefore where the t statistic (which is the size of effect divided by an estimate of its standard error) is above the threshold given by random field theory (Worsley et al. 1996). (A) *Top*: outlined region indicates activation at $p < .05$ corrected for the inferior temporal lobe ROI – left PIT activated more strongly by visual judgements than sound judgements. *Bottom*: Parameter estimate plot for each condition at the local maxima corresponding to the outlined region. (B) *Top*: outlined region indicates activation at $p < .05$ corrected for the entire brain volume – right superior parietal cortex activated more strongly by visual judgements than sound judgements. *Bottom*: Parameter estimate plot for each condition at the local maxima corresponding to the outlined region. (C) *Top*: arrow indicates activation in temporoparietal ROI activated more strongly by sound judgements than visual judgements. *Bottom*: Parameter estimate plot for each condition at the local maxima corresponding to the indicated region.

Anatomical localisation (estimated Brodmann Area)	Coordinates x y z	T	Uncorr	Corr	ROI corr
Colour-Sound					
<i>Temporal lobe</i>					
R inferior temporal gyrus (37/20)	64 -42 -22	5.38	.000	.007	.000 (IT)
L inferior temporal gyrus (37)	-64 -48 -18	3.07	.001		.036 (sphere)
<i>Parietal lobe</i>					
R superior parietal lobule (7)	40 -70 44	4.46	.000	.146	
Size-Sound					
<i>Temporal lobe</i>					
R inferior temporal gyrus (37)	62 -54 -12	4.05	.000	.427	.036 (IT)
	66 -60 -4	3.73	.000	.745	
<i>Parietal lobe</i>					
R precuneus (31/7)	16 -68 28	5.95	.000	.001	
<i>R precuneus (7)</i>	12 -58 36	5.61	.000	.003	
<i>R superior parietal lobule (7)</i>	38 -72 40	4.76	.000	.059	
Sound-Colour					
<i>Temporal lobe</i>					
L superior temporal gyrus (22)	-54 -56 24	4.24	.000	.275	(TP)
	-64 -44 22	3.52	.000	.903	<i>(TP)</i>
Sound-Size					
<i>Temporal & Parietal lobes</i>					
L inferior parietal lobule (40)	-46 -50 28	3.76	.000	.717	(TP)
<i>L superior temporal gyrus (22/39)</i>	-56 -62 30	3.45	.000	.935	<i>(TP)</i>
<i>Frontal lobe</i>					
L inferior frontal gyrus (11/47)	-38 30 -14	6.07	.000	.001	
L superior/medial frontal gyrus (9)	-10 46 28	5.81	.000	.001	
<i>L superior frontal gyrus (9)</i>	-16 64 20	4.79	.000	.053	

Table 6: Brain regions activated by remaining direct comparisons between the semantic retrieval conditions. Anatomical localisation of maximal t-values are in stereotaxic coordinates in mm (R = right, L = left). Activations in bold type indicate region maxima, while region size is in voxels. T = t-value, uncorr = uncorrected p-values, corr = p-values corrected for entire brain volume, ROI = p-values corrected for relevant region of interest as indicated in parentheses (see text for details): IT = inferior temporal lobe, sphere = left PIT 10mm radius spherical ROI, TP = temporoparietal.

(Visual) attribute-specific activations

Activations specific to colour: No brain regions were specifically associated with colour knowledge using a significance criterion controlling for the whole brain. When a ROI

(10mm radius sphere) was applied to the centre of the left PIT area (BA 37: -58, -45, -19) activated by all the semantic retrieval conditions relative to the control condition (as explained above), colour judgements elicited relatively more activation

compared to both size and sound knowledge (-62, -42, -16; $t=3.60$, $p=0.009$ & -64, -48, -18; $t=3.07$, $p=0.036$ respectively – ROI corrected), while size and sound did not differ from one another at this threshold (ROI maximum t -value = 2.93: Fig. 1, Fig. 3A).³

Activations specific to size: Judgements about object size resulted in enhanced activation of a medial right parietal area (precuneus: BA 7) relative to conditions requiring retrieval of either colour or sound knowledge (Tables 5 & 6, Fig. 1, Fig. 3B).

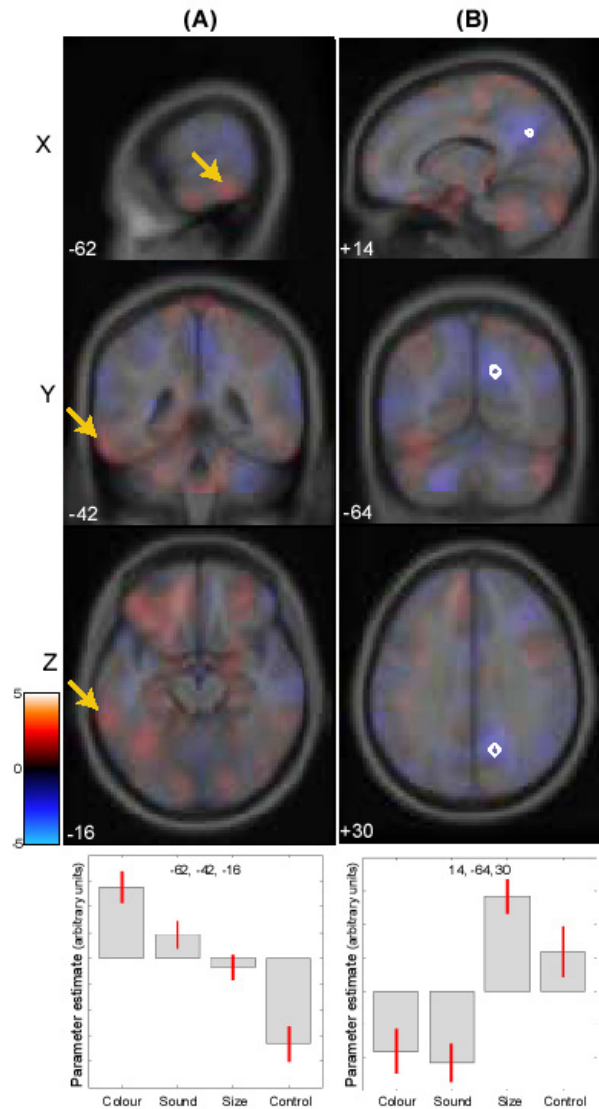


Figure 3: Mean differential activation when colour judgements were contrasted with size judgements (red) and when size judgements were contrasted with colour judgements (blue). Colour intensity is overlaid on the MNI brain template to show activation in various key regions. The colour intensity represents the effect size at each voxel, in terms of estimated ml/min/dl blood flow change. The outlined areas show where this change is significant at the given threshold, and therefore where the t statistic (which is the size of effect divided by an estimate of its standard error) is above the threshold given by random field theory (Worsley et al. 1996). (A) *Top*: arrow indicates activation in 10mm radius spherical ROI of left PIT activated more strongly by colour judgements than size judgements. *Bottom*: Parameter estimate plot for each condition at the local maxima corresponding to the indicated region. (B) *Top*: outlined region indicates activation at $p<.05$ corrected for the entire brain volume – right medial parietal cortex activated more strongly by size judgements than colour judgements. *Bottom*: Parameter estimate plot for each condition at the local maxima corresponding to the outlined region.

Activations not specific to modality or attribute

Relative to the non-semantic control condition, retrieval of colour, size and sound knowledge activated left temporal and inferior frontal regions largely compatible with the results of previous neuroimaging studies probing the retrieval of semantic knowledge (e.g. Vandenberghe et al., 1996; Mummery et al., 1998; Price, Moore, Humphreys, & Wise, 1997). The present study confirms that this network is engaged by tasks requiring access to highly specific semantic attributes, as well as more general judgements of semantic categorisation or association. The activation of left inferior frontal regions by all three attribute retrieval tasks is consistent with a generalised (non-attribute-specific) role for this region and accords with recent proposals that left inferior frontal cortex participates in the selection of semantic information (Thompson-Schill et al., 1997; Fiez, 1997; Mummery, Patterson, Wise, Vandenberghe, Price, & Hodges, 1999; see also Gabrieli, Brewer, & Poldrack, 1998). Focusing on or selecting a specific semantic attribute was clearly a critical mechanism required by the three experimental tasks in the current study.

Unlike the studies reported by Martin and colleagues (Martin et al., 1995; Chao & Martin, 1999; Wiggs et al., 1999), an anterior region of temporal lobe was activated in the present study. This anterior temporal lobe activation seems likely to reflect the particular demands of the semantic attribute judgements in the current paradigm rather than cognitive operations such as associative semantic access which should also have occurred in the Wiggs et al. (1999) study which similarly compared colour knowledge retrieval to a lower level control condition. The exact conditions under which the left anterior temporal lobe is recruited by semantic tasks remains unclear, but the association is strongly supported by the consistent finding of significant atrophy in this region in semantic dementia, a neurodegenerative condition that results in

relatively selective deterioration of semantic memory (Hodges, Patterson, Oxbury, & Funnell, 1992; Mummery, Patterson, Price, Ashburner, Frackowiak, & Hodges, 2000; Snowden, Neary, & Mann, 1996). This area has also been implicated in the processing of natural relative to manmade objects (e.g. see Moore & Price 1999; Mummery et al., 1996). The current study was not designed to shed new light on this issue.

The region of left PIT lobe which has previously been specifically associated with colour knowledge (Chao & Martin, 1999; Martin et al., 1995; Wiggs et al., 2000) was also elicited by all the attribute retrieval conditions relative to the control task, although the current activation had a somewhat more lateral focus. This left temporal region thus seems to be involved in the retrieval of perceptual semantic information more generally, rather than colour information *per se*, which is compatible with the evidence that this area forms part of a cortically distributed network contributing to semantic processing over a range of tasks (e.g. Vandenberghe et al., 1996; Mummery et al., 1998; Price et al., 1997). Nonetheless, consistent with previous reports that this PIT region plays a critical role in colour knowledge processing, we were able to show that colour judgements activated this region more strongly than either size or sound knowledge retrieval (see below for further discussion of this result).

Modality-specific activations

Visual attributes (colour and size): Both colour and size judgements, relative to the sound condition, activated a region of PIT lobe in the right hemisphere, which was homologous to the left lateralised PIT focus observed when each of the semantic attribute retrieval conditions was compared to the control condition (see above). This suggests that this area on the right is selectively involved in representation and/or processing of *visual* semantic attributes, rather

than semantic attributes more generally which engage this region in the left hemisphere.

One interpretation of the functional role of the right PIT area is in terms of visual imagery. Although the present study did not explicitly require the use of mental imagery, it has previously been suggested that performing a colour knowledge task involves creating and inspecting a coloured mental image of the object (De Vreese, 1991; Farah, 1984). Consistent with this proposal, a number of neuroimaging studies on the processing of explicit visual object/shape imagery have implicated a region of PIT lobe, in some cases right lateralised, comparable to that observed during visual attribute retrieval in the current study (D'Esposito, Detre, Aguirre, Stallcup, Alsop, Tippet, & Farah, 1997; Mellet, Tzourio, Crivello, Joliot, Denis, & Mazoyer, 1996; Mellet, Tzourio, Denis, & Mazoyer, 1998a; Mellet, Petit, Mazoyer, Denis, & Tzourio, 1998b; Mellet, Tzourio-Mazoyer, Bricogne, Mazoyer, Kosslyn, & Denis, 2000; Kosslyn, Alpert, Thompson, Maljkovic, Weise, Chabris, Hamilton, Rauch, & Buonanno, 1993; Roland & Gulyas, 1995; see also Goldenberg, Podreka, Steiner, Willems, Suess, & Lüder, 1989).

It is noteworthy that the studies by Martin and colleagues have also reported bilateral PIT activations associated with retrieval of colour knowledge (Martin et al., 1995; Wiggs et al., 1999; Chao & Martin, 1999), although in two of these studies the activation on the right was only significant when colour naming was compared to a lower control task, not when compared to object naming (Wiggs et al., 1999; Chao & Martin, 1999). Martin et al. (1995) also reported right hemisphere PIT activations for colour naming relative to action naming, again consistent with a hypothesis of visual attribute specificity for this right PIT activation. Further compatible with the current findings, Gerlach et al. (1999) reported a similar right PIT activation in a task comparison proposed to index stored knowledge about the visual forms of objects.

Visual knowledge retrieval in our study was also associated with increased activity in a region of the right superior parietal lobule, although this activation was only reliable at our conservative statistical threshold for the comparison between size and sound judgements, making it difficult to draw general conclusions about the role of this region in the retrieval of visual knowledge.

Sound: Retrieval of knowledge about object sounds relative to colour and size judgements activated left posterior superior temporal gyrus/sulcus and contiguous regions of inferior parietal cortex. This selective activation of regions adjacent to auditory association cortex is consistent with our prediction that accessing and retrieving sound knowledge would elicit modality-specific activations in and/or near to auditory association cortex. These activations elicited by sound judgements were somewhat more posterior (~1cm) to the regions associated with the episodic recall of auditory information (Wheeler et al., 2000; Nyberg et al., 2000) or imagery for music (Zatorre, Halpern, Perry, Meyer, & Evans, 1996; Halpern & Zatorre, 1999), but were almost identical to the cortical area activated when subjects passively listen to auditorily presented words or pseudowords, relative to fixation (Peterson et al., 1988, 1989; Fiez, Raichle, Balota, Tallal, & Peterson, 1996).⁴ As this activation is not generally elicited by non-linguistic auditory stimuli it has been hypothesised to index speech-specific auditory processing and perhaps to reflect speech-based short-term auditory storage mechanisms (Fiez et al., 1996; see also Paulesu et al., 1993; Binder, Frost, Hammeke, Cox, Rao, & Prieto, 1997; Wise et al., 2001). The current result indicates that this area can play a role in the processing of (meaningful) non-speech sounds, and that these need not be externally generated. The limited evidence available does not provide sufficient basis for any clear conclusion regarding the functional significance of this activation, although previous suggestions that this region subserves

auditory working memory are at least not incompatible with the idea that it may be supporting a form of auditory imagery engaged during object sound judgements in the current experimental context.

When compared to the control condition, the sound condition uniquely generated additional activation in the left posterior middle/superior temporal gyrus which was slightly more anterior and inferior to the regions activated in the direct contrasts between the sound and visual retrieval conditions. It therefore appears that auditory association cortex may have been activated by sound judgements, although not evident in the comparisons with the visual retrieval conditions. This pattern might be expected if weak activation of auditory association areas occurred automatically in response to sound information associated with the objects during the visual judgement conditions.

(Visual) attribute-specific activations

Colour: A region of left PIT cortex activated by all the semantic retrieval conditions (relative to the control) was also significantly more activated by object colour judgements. Although the focus was slightly less medial (~1cm) than the activations reported by Martin and colleagues it seems likely that similar aspects of colour knowledge are being indexed, and the small difference in activation foci may reflect differences in the tasks used. The proximity of this activation to colour perception areas is consistent with the hypothesis that retrieval of specific perceptual knowledge engages cortical regions near to the relevant sensory cortex, and is in keeping with engagement of a visual mental imagery process which does not activate primary sensory cortex (D'Esposito et al., 1997; Mellet et al., 1993); as noted above, performing a colour knowledge task has been proposed to entail creating and inspecting a coloured mental image of the object (De Vreese, 1991; Farah, 1984). The only study which has explicitly examined the

neural substrates of colour imagery reported activation in PIT cortex (although this activation was right lateralised: Howard, Ffytche, Barnes, McKeefry, Ha, Woodruff, Bullmore, Simmons, Williams, David, & Brammer, 1998), while Paulesu et al. (1995) have shown that word-colour synesthetes activate left PIT lobe while experiencing colour images in response to words. Object-based imagery has also been reported to activate this left PIT region (D'Esposito et al., 1997; Mellet et al., 1996, 1998a, 1998b, 2000; Kosslyn et al., 1993; Roland & Gulyas, 1995; see also Goldenberg et al., 1989; Nakamura, Honda, Okada, Hanakawa, Toma, Fukuyama, Konishi, & Shibasaki, 2000). In our study, however, this region was also activated by size and sound knowledge relative to the control condition, suggesting that this area is not only specialised for colour knowledge processing but also plays a more general role in word processing and/or semantic retrieval. One possibility is that knowledge about the visual appearance of objects is activated by all the tasks, although this does not account for the enhanced activation in the colour attribute retrieval condition. Alternatively, colour imagery is automatically activated during retrieval of perceptual information about objects regardless of the task but the requirement to make an explicit judgement regarding this aspect of knowledge results in increased activation.

Intriguingly, while the left PIT region was associated particularly with retrieval of colour knowledge, the homologous region of right PIT gyrus responded equally strongly when either type of visual (colour or size) knowledge was retrieved (see above: plots in Figs 1B & 2A), suggesting that right and left PIT cortex play somewhat specialised roles in perceptual (and particularly visual) knowledge.

Size: Relative to both the colour and sound conditions, size judgements were uniquely associated with increased activity in a right hemisphere medial parietal structure (precuneus). Returning to our earlier hypothesis that the right

PIT activations associated with visual (colour and size) semantic judgements might reflect object/shape-based visual imagery, it is less clear whether this argument can be extended to explain the right medial parietal activations selectively activated during retrieval of size knowledge. While the dorsal visual processing system plays a primary role in the spatial processing of external visual stimuli (e.g. Haxby, Horwitz, Ungerleider, Maisog, Pietrini, & Grady, 1994), and parietal activations have been consistently obtained in visual imagery tasks with a spatial element (Mellet, Tzourio, Denis, & Mazoyer, 1995; Mellet et al., 1996, 2000; Kosslyn, DiGirolamo, Thompson, & Alpert, 1998; Kosslyn et al., 1993; Cohen, Kosslyn, Breiter, DiGirolamo, Thompson, Anderson, Brookheimer, Rosen, Belliveau, 1996; Harris, Egan, Sonkkila, Tochon-Danguy, Paxinos, & Watson, 2000; see also Carpenter, Just, Keller, Eddy, & Thulborn, 1999), these activations have generally been reported as in and around the intraparietal sulcus, and therefore lateral and superior to that found in the current study. This is not, however, true for all preceding studies (Wheeler et al., 2000; Mellet et al., 1995), although these particular studies utilised memory-based paradigms. Consistent with this observation, precuneus activations have most often been reported in the context of episodic retrieval tasks. Activation of this region was initially thought to reflect visual imagery processes during retrieval (e.g. Fletcher, Frith, Baker, Shallice, Frackowiak, & Dolan, 1995), although this interpretation has subsequently been challenged (e.g. Buckner et al., 1996; Krause et al., 1998; Maguire et al., 1999) and the functional role of this structure is the subject of current investigation and debate. Interestingly, Mummary et al. (1998) reported (right) precuneus involvement in a semantic retrieval task requiring judgements about where objects are typically found, which was argued to involve a spatial element. Taken in conjunction with the current finding, this result may suggest that medial parietal cortex is activated in semantic retrieval

tasks with a spatial component as well as during episodic retrieval.

Although size judgements apparently failed to elicit a similar parietal activation in the study reported by Vandenberghe et al. (1996), various differences between their paradigm and ours could account for the lack of correspondence in results. For example, the main experimental condition in the previous study was a difficult associative matching task, while their size matching task was also extremely demanding (both tasks elicited reaction times around 2.6-2.9 seconds), making it difficult to derive a clear definition of the processes being indexed.

The enhanced activation of this medial parietal region in conjunction with the right PIT (and superior parietal lobule) activation observed during the retrieval of both size and colour information indicates that size knowledge may involve several processes or mechanisms. We have hypothesised that the right PIT and parietal activations index visual imagery mechanisms engaged during the retrieval of visual attribute information requiring internal inspection prior to a decision. This interpretation suggests that size knowledge judgements engage both object-based and perhaps more spatially specific visual imagery processes, in keeping with the intuitive assumption that this task requires both knowledge of what the object in question looks like, and how large it is relative to some criterion.

Conclusions

These results support the hypothesis that, in addition to a general cortical network activated by all semantic tasks, the retrieval of perceptual semantic knowledge engages modality- and attribute-specific cortical processing areas. Consistent with our predictions for modality-specific activations, (a) retrieval of visual attribute knowledge (colour and size) activated a right lateralised PIT region associated with the processing of visual object properties, and (b) judgements about the sounds that objects make

engaged left lateralised posterior superior temporal and temporoparietal regions adjacent to auditory association cortex. In agreement with previous reports and our predictions based on these, retrieval of colour knowledge elicited more left PIT activation than either size or sound knowledge. This latter region was also activated by size and sound judgements relative to the control task, however, suggesting that this cortical area is not exclusively engaged by the retrieval of colour information. In addition to the general semantic network, judgements about object size uniquely recruited medial dorsal parietal structures (precuneus), the functional role of which is underspecified.

The evidence for the recruitment of distinct neural areas during the retrieval of object size, sound and colour is consistent with the limited neuropsychological data which have revealed dissociations between knowledge of these particular attributes. These findings do not necessarily indicate neuroanatomically separate subsystems supporting the long-term representation of various perceptual attributes and modalities. Rather, we propose that the data are consistent with the idea that a distributed network of cortical regions specialised for the processing of the particular sensory aspects of a multisensory stimulus is engaged both during the acquisition of perceptual knowledge about objects, and during the retrieval of such knowledge (Allport, 1985; see also Ishai, Ungerleider, Martin, Schouten, & Haxby, 1999). Within this framework, the interrelation of multiple sensory representations into an integrated whole presumably involves one or more additional cortical regions (e.g. medial temporal lobe structures: Cohen, Ryan, Hunt, Romine, Wszalek, & Nash, 1999).

While we have speculated that the attribute- and modality-specific activations observed here may reflect the operation of sensorily specific imagery mechanisms, the precise role played by imagery in these processes remains an important and unresolved issue. It will be difficult to

differentiate between this interpretation and the proposal that retrieval of semantic knowledge involves (re-) representations in/near the sensory and motor cortical regions through which the knowledge is acquired and experienced (e.g. Gainotti et al., 1995; Allport, 1985). Indeed the difficulty in distinguishing between these two accounts perhaps indicates that these conceptualisations are largely overlapping.

NOTES

1. We centred this ROI on the PIT activations elicited in our own study. An alternative might be to centre the ROI on the activations elicited in earlier studies by Martin and colleagues, but this was considered a less optimal option both because we used a very different paradigm and because the structural correspondences between the SPM95 templates used by Martin and colleagues, the Talairach and Tournoux (1988) brain, and the brain templates from the Montreal Neurological Institute (MNI) employed here, are unclear.
2. While the ventral extension of the anterior temporal activation in Figure 1 suggests that the activations associated with the contrasts between the semantic and control conditions may have been contaminated by some artefact (such as movement: Brett et al., 1999). Analysis of the movement parameters showed no statistically significant differences between any of the conditions, however. Furthermore, the critical left PIT activation appears unaffected in that the direct contrasts between the semantic attribute conditions show no evidence of any similar contamination (Figure 1).
3. While the plot in Figure 3A does not correspond to the centre of the spherical ROI described here, it corresponds to the focus of the observed enhancement of activation associated with colour knowledge.
4. Auditory presentation of verbal stimuli also often activates slightly more anterior regions of left superior temporal gyrus (e.g. Belin, Zatorre, Lafaille, Ahad, & Pike, 2000; Wise et al., 1991; Howard, Patterson, Wise, Brown, Friston, Weiller, & Frackowiak, 1993; Demonet, Wise, &

Frackowiak, 1993; Wise, Scott, Blank, Mummery, Murphy, & Warburton, 2001; Scott, Blank, Rosen, & Wise, 2000), and although often described together with the temporoparietal activations focused on here, it remains to be shown whether activations of these areas are functionally distinct.

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