Complementary hemispheric asymmetries in object naming and recognition: A voxel-based correlational study

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ABSTRACT

Cognitive neuroscientific research proposes complementary hemispheric asymmetries in naming and recognising visual objects, with a left temporal lobe advantage for object naming and a right temporal lobe advantage for object recognition. Specifically, it has been proposed that the left inferior temporal lobe plays a mediational role linking conceptual information with word forms and vice versa, while the right inferior temporal lobe supports the retrieval of conceptual knowledge from visual input. To test these hypotheses, we administered four behavioural tasks to fifteen patients with temporal lobe brain damage, and correlated their behavioural scores with voxel-based measures of neuronal integrity (signal intensities) in whole-brain analyses. The behavioural paradigms included four tasks. Two were verbal tasks: (a) picture naming requiring the mapping of conceptual knowledge to word forms, (b) semantic categorisation of words requiring the reverse mapping of word forms to conceptual knowledge, and two were visual object tasks with no verbal component, both of which required the retrieval of conceptual information from visual objects, i.e., (c) visual object categorisation and (d) normal and chimera object decisions. Performance on the verbal tasks correlated with the neural integrity of partially overlapping left inferior and anterior temporal lobe regions, while performance on the object tasks correlated with the neural integrity of overlapping regions in right inferior and anterior temporal lobe. These findings support the notion of complementary hemispheric advantages for object naming and recognition, and further suggest that the classical language model emphasising posterior regions in the mapping between word forms and conceptual knowledge should be extended to include left inferior temporal lobe.

1. Introduction

Neuropsychological research has suggested that there are complementary hemispheric asymmetries in the naming and recognition of visual objects. While object naming is thought to critically involve the left inferior temporal cortex, object recognition is thought to engage the right anterior temporal cortex. Evidence in support of this proposal comes from both lesion-behaviour correlations with brain-damaged patients and from neuroimaging studies of healthy participants (Damasio, Tranel, Grabowski, Adolphs, & Damasio, 2004; Tranel, Damasio, & Damasio, 1997).

The seminal studies defining this issue are reported by Damasio, Tranel and colleagues in a pair of papers identifying the neural bases for visual object naming (Damasio et al., 2004), and for the retrieval of conceptual knowledge necessary for object recognition (Tranel et al., 1997). In the object naming study (Damasio et al., 2004), brain-damaged patients were classified as having impairments in naming

pictures of people, animals and/or tools, and the areas of maximal lesion overlap within each group were identified. Picture naming errors were defined as such only if patients showed evidence of intact object recognition (i.e., they were able to define an object but failed to retrieve the correct name). Areas of lesion overlap were found in the left inferior temporal lobe, with distinct areas for persons, animals and tools located in progressively more posterior regions ranging from anterior temporal (temporal pole) to posterior (tempero-occipito-parietal junction) regions. Corresponding left temporal lobe regions were also activated in a companion PET study in which healthy participants named the same objects.

Findings from other neuroimaging studies indicate that the posterior to anterior distribution may reflect the degree of specificity of lemma and/or semantic property retrieval rather than the stimulus category per se, in line with a hierarchical model of object processing (Gorno-Tempini & Price, 2001; Grabowski et al., 2001). Nevertheless, Damasio et al. (2004) suggested that these left temporal areas form convergence zones that play a "mediational role in lexical retrieval", enabling the mapping from conceptual knowledge to the phonemic representations of words. Thus, these structures may represent the neural counterpart of the lemma level of repre-

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sentation (and/or its connections with semantic and phonological representational levels) proposed in many cognitive models of word production (Garrett, 1992; Indefrey & Levelt, 2004; Levelt, 1992, 1999). Importantly, Damasio, Grabowski, Tranel, Hichwa, and Damasio (1996) proposed that the mediational function supported by the left inferior temporal lobe also operates in reverse, allowing conceptual knowledge to be accessed from word form information, although, this hypothesis was not tested in their study.

In a companion paper, Tranel et al. (1997) used the same methodology to identify the maximal lesion overlap associated with object recognition rather than object naming. Patients' errors were now defined as a failure to recognise the pictured object as determined by ratings of the patients' verbal responses. In sharp contrast to the naming study, the areas of lesion overlap were typically located in the right temporal lobe, with retrieval of conceptual knowledge related to persons, animals and tools associated with right temporopolar, right ventral temporal, and medial occipital and the left temporo-parietal-occipital junction, respectively. Tranel et al. (1997) argued that these mainly right hemisphere (RH) regions play an intermediary role in the retrieval of conceptual knowledge from visual input, whereby the processing of visual properties of the picture stimulus evokes information about that object in other sensory-motor modalities.

There are a number of outstanding issues with respect to the differential roles of the hemispheres in naming and recognising visual objects. First, it is unclear whether left inferior temporal lobe regions support both the mapping of conceptual knowledge to lexical word forms, as well as the reverse process whereby lexical word forms are mapped onto conceptual representations (i.e., language comprehension). A second unresolved issue concerns the nature of the processes involved in the object recognition tasks employed in previous studies. Tranel et al. (1997) assessed their patients' ability to recognise pictured objects with respect to their lesion location, and the resulting regions of lesion-behaviour overlaps were interpreted as areas necessary for the retrieval or evocation of conceptual knowledge from the picture stimulus. However, the measure of object recognition that Tranel et al. (1997) used was entirely verbal. Patients were considered to have correctly recognised the object if they were able to name it correctly or were able to provide a definition of the object which was sufficiently precise to enable independent raters to correctly judge the object's identity, a procedure for distinguishing naming and recognition ability similar to that used in other studies (e.g., Glosser, Salvucci, & Chiaravalloti, 2003). Thus, performance on the recognition task could have been impaired by word production deficits. Given this aspect of the paradigm, it is perhaps surprising that the areas correlated with task performance were not more similar to the naming study (Damasio et al., 1996). However, right temporal lobe atrophy has been associated with poor performance on a word–picture matching task that also involved a verbal component (Lambon Ralph, McClelland, Patterson, Galton, & Hodges, 2001). It is therefore possible that the right temporal regions implicated in object recognition in these studies are in fact specific to the association of the object stimulus with the language system, either to name or describe the picture, or to match it with a given word form. If this is the case, different regions may be found to be critical for object recognition when no verbal processing is required.

In this paper we use a recently developed voxel-based correlational method which relates brain damage to behavioural data to address these outstanding issues. The first issue concerns the role of left inferior temporal regions in object naming; are these regions involved specifically in mapping conceptual knowledge to lexical word forms, or are they also involved in the reverse process whereby lexical word forms are mapped onto conceptual representations (i.e., language comprehension)? To address the issue of whether left inferior temporal damage correlates with both object

naming ability as well as mapping from lexical form to conceptual knowledge, we correlated brain damage with performance on two behavioural tasks. One task involved object naming where patients viewed pictures of common objects and were asked to name each object aloud. The second task involved categorisation, where patients read three written words and were asked to decide whether or not a fourth target word belonged to the same semantic category. Successful performance on this task requires the retrieval of conceptual information from the written words. If left temporal cortex is primarily involved in the naming process, then only naming responses should be correlated with damage in left temporal regions. However, if left temporal cortex is involved in the mapping between concepts and word forms, irrespective of whether a verbal output is required, behaviour on both tasks should correlate with damage to left temporal cortex.

To address the second issue of the role of the right temporal lobe in accessing conceptual knowledge from visual input in the absence of verbal task demands, we examined the relationship between brain damage and performance on two non-verbal object recognition tasks. The first was an object categorisation task in which patients viewed three pictures and decided whether a fourth picture belonged to the same category. Although it is possible that patients may silently name the pictures (a recurrent difficulty in contrasting recognition and naming processes, cf. Grabowski et al., 2001), there is no requirement to do so, and no overt naming response is measured. The second task required object decisions, a widely used task (Fleischman, Gabrieli, Reminger, Vaidya, & Bennett, 1998; Gerlach, Law, Gade, & Paulson, 1999; Hovius, Kellenbach, Graham, Hodges, & Patterson, 2003; Liu & Cooper, 2001; Rogers et al., 2004) in which patients are shown line drawings which depict either a real object or a chimera formed by pairing halves of two different objects, and are asked to indicate which pictures are "real" and which are not. The object decision task provides a means for probing object recognition in the absence of verbal processing. However, there is some dispute as to whether this type of object recognition task taps into conceptual representations (Rogers, Hodges, Lambon Ralph, & Patterson, 2003) or merely reflects access to a "pre-semantic" level of structural descriptions (Gerlach et al., 1999; Riddoch & Humphreys, 1987a, 1987b). By examining the overlap of lesion-performance correlations between the object decision task and the picture categorisation task (which clearly does require conceptual processing), it should be possible to determine the extent to which performance on these tasks depend on similar cognitive processes.

2. Methodological issues

The current study uses a recently developed voxel-based correlational method (Bright, Moss, Longe, Stamatakis, & Tyler, 2007; Stamatakis & Tyler, 2005; Tyler, Marslen-Wilson, & Stamatakis, 2005a; Tyler, Marslen-Wilson, & Stamatakis, 2005b) to address the issues outlined above. This method avoids some of the methodological limitations of previous studies of lesion-deficit relationships which have typically been investigated by testing large numbers of brain-damaged patients and grouping them on the basis of their behavioural deficit (impaired or normal; Adolphs, Damasio, Tranel, Cooper, & Damasio, 2000; Damasio et al., 1996), or their lesion location (Chao & Knight, 1998). This strategy has a number of limitations. First, the binarisation of patients' performance ignores potentially meaningful variation within the two groups. Patients who fail the behavioural criterion may range from those who were very close to passing to those that performed at chance. Ignoring this variation and averaging the behavioural results reduces the magnitude of the difference between groups and thus may reduce power to detect an effect. Some studies have tried to resolve this

Table 1
Details of patients included in the study (SD = semantic dementia, HSE = Herpes Simplex Encephalitis).

Patient	Gender	Age at testing	Aetiology
P1	F	40	Excised meningioma
P2	F	43	Excision of arteriovenous malformation
P3	M	63	Excision of capillary haemangioma, cerebral haemorrhage
P4	M	47	HSE
P5	F	76	HSE
P6	F	38	HSE
P7	M	57	HSE
P8	M	43	HSE
P9	M	71	HSE
P10	F	61	HSE
P11	M	73	Infarct
P12	M	47	Partial lobectomy for medial sclerosis
P13	M	48	Resection for epilepsy
P14	M	68	SD
P15	F	61	SD

problem by analysing only the lesions of the patients with best and worst performance (Damasio et al., 1996), but this requires a very large number of patients as much of the data is discarded. The second problem relates to the way in which brain damage is defined. Most methods make a binary distinction between whether an area is damaged or undamaged, leading to a loss of potentially informative variation. The third problem with current techniques is that the methods for determining whether an area is damaged typically involve non-automated procedures and thus are vulnerable to inconsistencies (Stamatakis & Tyler, 2005).

In an attempt to circumvent these problems, the present study uses a technique that has been shown to be sensitive to the relationships between lesion location and performance on a variety of behavioural tasks, e.g., the differentiation of neural systems underlying the processing of regularly and irregularly inflected words (Tyler et al., 2005b), the different neurocognitive processes in auditory word recognition (Tyler et al., 2005a) and the processing of different aspects of a verbal concept's conceptual structure (Bright et al., 2007). This method correlates the signal from a T1-weighted structural MR image to the behavioural scores for each patient, on a whole brain, voxel-by-voxel basis. The advantages of this technique are: (i) patients are not grouped by either behavioural scores or brain damage, maximising the sensitivity of the correlational technique; (ii) human input is not used to define a lesion, thereby removing problems of subjectivity; and (iii) correlations are calculated at a voxel level, maximising the spatial resolution.

3. Methods

3.1. Participants

Fifteen patients with damage to various parts of the temporal lobes were included in the study. These patients were selected on the basis of two main criteria: they had a T1-weighted structural MR scan and they could perform the experimental tasks. The location of their damage within the temporal lobes and their level of performance on the tasks were irrelevant for selection. Details of these patients are summarized in Table 1. Patients' damage stemmed from a variety of aetiologies: Herpes Simplex Encephalitis (HSE, diagnosed on the basis of CT, MRI and virological studies), semantic dementia (SD) and focal lesions including resections for epilepsy and tumour removal (see Table 1). The patients with progressive degenerative con-

ditions (i.e., semantic dementia) were tested within 1 month of the acquisition of the brain scan used in the analysis. Excluding the patients with semantic dementia, who had progressive damage, the patients were in a stable and chronic stage. Fig. 1 shows the distribution of damage across the patients and is included for illustrative reasons: these lesion definitions were not used in the voxel-based correlational analyses. Damage was concentrated in the anterior sections of the temporal lobe, but was evenly distributed between the left and right hemispheres.

3.2. Behavioural tests

Four behavioural tests were administered. As discussed above, the object naming and semantic categorisation of words tasks were included to investigate the difference between verbal production (naming) and verbal comprehension. The semantic categorisation of pictures and object decision tasks were included as visual recognition tasks with no linguistic demands.

3.2.1. Naming coloured pictures

Patients were asked to produce a unique name (e.g., dog, hammer) to each of 115 colour photographs of common everyday objects (subset from Bunn, Tyler, & Moss, 1998). The visual and psycholinguistic characteristics of these stimuli are (mean ± standard deviations, ranges in parentheses): rated visual complexity (5-point scale, where 5 = very complex) = 2.6 ± 0.7 (1.3–4.1), lemma frequency (Baayen, Piepenbrock, & van Rijn, 1993) = 38.2 ± 92.3 (0–724), rated familiarity (5-point scale, where 5 = very familiar) = 3.5 ± 0.9 (1.3–4.7), naming agreement = 94.8 ± 7.2% (72.5–100%) and syllable length = 2.0 ± 0.9 (1.0–4.0). If patients provided a category name (e.g., animal for dog), they were prompted for a more specific response. Picture naming requires processing of low-level visual features, the combination of these visual features in order to recognise the object and then retrieval and production of the name of that object.

3.2.2. Semantic categorisation of words

In this task (Devlin et al., 2002), subjects were presented with three written words and asked to judge whether a fourth target word belonged to the same or different category. For example, the sequence *plum, melon, apple* followed by the target CROW required a "different" response, whereas the sequence *tulip, daisy, rose*, DAFFODIL required a "same" response. There were 96 trials. The word triad and target words were matched on mean number of letters, frequency, and familiarity (number of letters: word 1 = 5.7 ± 1.6, word 2 = 5.3 ± 1.5, word 3 = 5.3 ± 1.5, target word = 5.3 ± 1.5; lemma frequency (Baayen et al., 1993): word 1 = 16 ± 24, word 2 = 17 ± 18, word 3 = 18 ± 21, target word = 19 ± 25; rated familiarity (Coltheart, 1981): word 1 = 495 ± 38, word 2 = 511 ± 52, word 3 = 511 ± 57, target word = 502 ± 58). To successfully determine whether the fourth word belonged in the same category, patients had to access the concepts from the words, correctly categorise them, compare the fourth stimulus to the category generated from the first three, and make a decision as to whether it belonged to the same category.
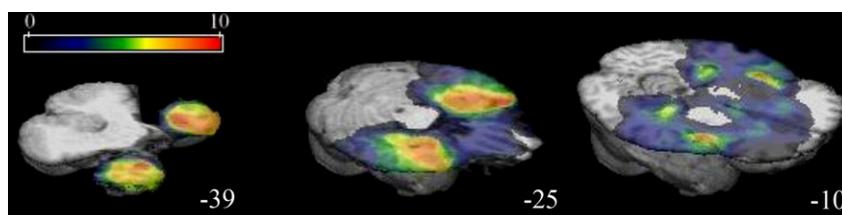
Fig. 1. Areas of lesion overlap in the patient group, where the colour bar indicates the number of patients with damage to a given region (MNI z-coordinates).

3.2.3. Semantic categorisation of pictures

This task (Tyler et al., 2003) was identical to the word semantic categorisation task, except that the stimuli were coloured pictures of objects instead of written words. There were 48 items in the task. The picture triad and target pictures were matched on rated visual complexity and familiarity (visual complexity (5-point scale, where 5 = very complex): Picture 1 = 2.60 ± 0.78, Picture 2 = 2.63 ± 0.79, Picture 3 = 2.73 ± 0.75, target picture = 2.53 ± 0.87; rated familiarity (5-point scale, where 5 = very familiar): Picture 1 = 3.23 ± 0.64, Picture 2 = 3.29 ± 1.02, Picture 3 = 3.39 ± 0.92, target picture = 3.51 ± 0.82). Successful performance on this task depended on the ability to extract the visual features of the object, then to generate a category from the first three objects and determine if the fourth object fits within that category.

3.2.4. Object decision test

This task required the patient to decide whether a line drawing depicts a real or an unreal object. This was the object decision test from the Birmingham Object Recognition Battery subtest "A: hard" (Riddoch & Humphreys, 1993). There were 32 items in the test, of which 28 were based on animals and 4 were based on tools. Half of the items were real objects and half were unreal. Unreal objects were composed of parts of two real objects. In order to correctly identify each object as real or not, the patient must be able to make a judgement based on the entire object, as each individual feature belongs to a real object.

3.3. Imaging analysis

All preprocessing and analysis of the structural images was performed using SPM5 (Wellcome Institute of Cognitive Neurology, www.fil.ion.ucl.ac.uk), implemented in Matlab (Mathworks Inc., Sherborn, MA, USA). T1-weighted Structural scans for the patients in the present study were spatially normalised to the SPM T1 template based on the Montreal Neurological Institute (MNI) template brain, using 12 parameter affine transformations and 7 × 8 × 7 non-linear basis functions. A hand-drawn mask of each lesion was used to prevent distortion of the lesion areas by the non-linear part of the spatial normalisation algorithm, and a brain mask was used to disregard all non-brain voxels during the spatial normalisation procedure. The scans were resliced to the same x, y, z dimensions and voxel size (182 × 218 × 128 voxels, with 1 mm × 1 mm × 1 mm voxel size). Images were smoothed using an isotropic 10 mm full-width half-maximal Gaussian kernel. The Gaussian kernels used to smooth anatomic images for voxel-based morphometric analyses are typically larger than those used to smooth functional magnetic resonance images because smoothing with larger kernels accounts for differences in sulcal and gyral anatomy across participants and reflects the size of the expected regional differences (Good et al., 2001; Stamatakis & Tyler, 2005). Non-brain voxels (i.e., skull and other tissues) were set to zero by multiplying them with the SPM

Table 2
Individual patient and mean behavioural scores (% correct) on the four experimental tasks.

Patient	Verbal tasks		Non-verbal tasks	
	Word categorisation	Naming	Picture categorisation	Object decision
P1	88	100	98	91
P2	78	42	92	59
P3	99	97	98	78
P4	65	30	77	75
P5	67	37	75	63
P6	85	80	88	69
P7	67	61	90	59
P8	96	60	96	91
P9	93	97	94	88
P10	90	64	77	59
P11	63	35	72	63
P12	95	89	98	91
P13	67	25	90	66
P14	85	73	88	59
P15	96	100	100	84
Chance	50	–	50	50
Mean	82	66	89	73
SD	13	27	9	13

brain mask. The cerebellum was removed using a hand-drawn mask because this structure was not hypothesised to be involved in the present tasks. Since there was substantial ventricular enlargement in some patients, in order to avoid erroneous findings in these regions resulting from misalignment, a ventricular mask was created to remove the ventricles from the statistical modelling. The outcome of each normalisation procedure was carefully visually inspected to ensure that there were no anatomical distortions.

The preprocessed images were used for statistical modelling in SPM5 using the general linear model. Each patient's performance on each of the tasks was scored as percent correct (see Table 2) and entered into separate covariate type analyses in SPM which were used to correlate the behavioural scores for each patient with the signal intensity at each voxel across the set of brain images. The global mean voxel value for each scan was included as a confounding covariate in order to normalise for global signal variation. The t-statistic was employed to test for regional effects
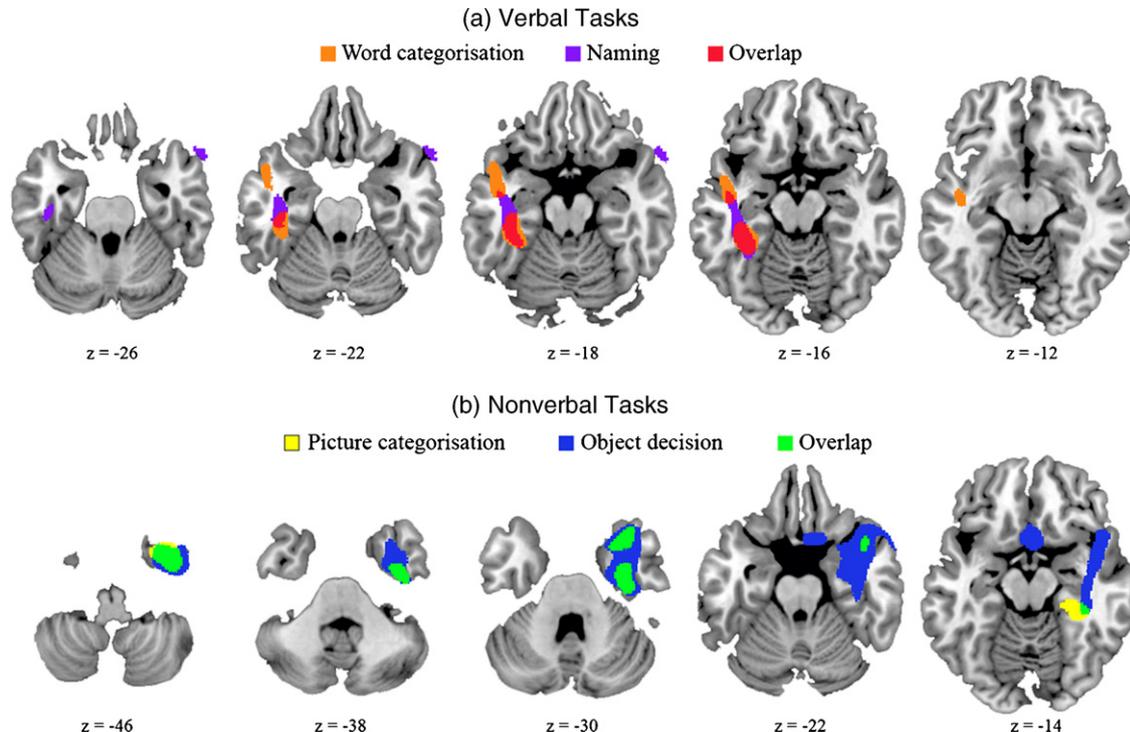
Fig. 2. Representative slices where voxel signal intensities significantly correlated with behavioural performance on the (a) verbal tasks of word categorisation (orange) and naming (purple; overlap shown in red) and (b) non-verbal tasks of picture categorisation (yellow) and object decision (blue; overlap shown in green). MNI coordinates are reported.

Table 3
Results of voxel-based correlation analyses of voxel signal intensities across the entire brains of 15 patients with performance measures on each behavioural task (MNI coordinates are reported).

	Cluster level		Voxel level		Co-ordinates of peak voxel		
	$p_{corrected}$[a]	Extent[b]	t[c]	z[d]	x	y	z
Verbal tasks							
Word categorisation							
L inferior temporal lobe (BA 37)	0.000	2,125	0.874	4.5	−36	−38	−15
L superior temporal lobe (BA 20)	0.000	1,868	1.000	3.63	−45	−9	−14
			1.000	3.48	−49	6	−20
Naming							
L inferior temporal lobe (BA 37)	0.000	3,040	1.000	4.06	−39	−34	−14
			1.000	3.96	−35	−41	−15
			1.000	3.89	−40	−26	−17
R superior temporal pole (BA 38)	0.008	791	0.994	4.22	59	19	−21
			1.000	3.27	59	16	−32
			1.000	3.1	64	20	−13
Non-verbal tasks							
Picture categorisation							
R fusiform gyrus (BA 20)	0.000	3,779	1.000	3.88	37	−15	−35
			1.000	3.44	32	6	−48
			1.000	3.41	37	−4	−46
R superior temporal pole (BA 20)	0.000	2,079	1.000	3.66	34	14	−31
R fusiform gyrus (BA 37)	0.042	590	1.000	3.42	32	−36	−15
			1.000	3.31	25	−29	−15
			1.000	3.15	21	−35	−9
Object decision							
R superior temporal pole (BA 38)	0.000	22,075	0.836	4.54	43	10	−20
			0.855	4.52	32	−1	−48
			0.893	4.48	40	16	−26
R olfactory sulcus (BA 25)	0.000	2,390	0.157	5.18	6	10	−19
			0.787	4.59	2	15	−14

[a] Cluster-level p-value corrected for search volume.
[b] Number of voxels in cluster.
[c] t-Score.
[d] z-Score.

in each analysis, and associated cluster p-values were corrected for search volume with the Gaussian random field theory. Significant results therefore represent brain regions (i.e., clusters of voxels) in which voxel-level signal intensities in the cluster were significantly correlated with the behavioural scores. Statistical parametric maps were thresholded at the standard $p < .001$ uncorrected at the voxel level and the coordinates of the peak significant voxels in clusters surviving a random field corrected p-value of <.05 adjusted for the entire brain are reported. To confirm that the results of the whole-brain correlation analyses were not driven by outlying datapoints, we generated scatterplots for each significantly correlated cluster where mean signal intensity in the cluster was plotted against the corresponding percent correct performance. Pearson's correlation analyses of these data were conducted.

4. Results

4.1. Behavioural results

Percent correct on each of the 4 tests for each subject were recorded (see Table 2). There was a wide range of performance for each of the tests with some patients performing close to chance and some achieving nearly perfect scores. The scores for the word categorisation and naming tasks ranged from 65% to 99% and 25% to 100%, respectively, and the picture categorisation and object decision scores ranged from 75% to 100% and 59% to 91%, respectively.

4.2. Structural image correlational analysis

For each of the four correlational analyses, brain regions where behavioural scores were significantly correlated with voxel signal intensities are shown in Fig. 2. Performance on the verbal word categorisation an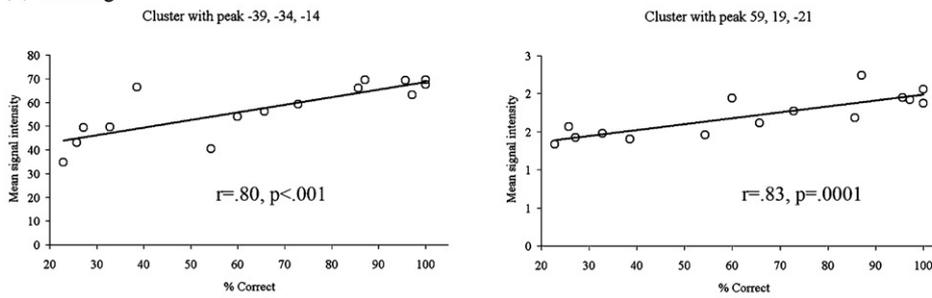d naming tasks correlated significantly with areas in the left anterior temporal cortex (see Table 3 and Fig. 2a, where overlapping regions of significant correlation are shown in red). Word categorisation scores correlated with two large clusters of voxels, one centered in the left inferior temporal lobe extending into the left fusiform gyrus (BAs 20, 37) and the second centered in the left anterior superior temporal lobe (BA 20) including the anterior middle temporal lobe (BA 20/21) and middle and superior temporal pole (BA 38). Naming scores correlated with a large cluster located mainly in the left inferior temporal lobe and left fusiform gyrus (BAs 20, 37) which extended into the left anterior middle and superior temporal lobes (BA 21) and medially into the hippocampus. Signal intensities in a smaller cluster bordering the right superior and middle temporal poles were also correlated with naming performance. These results suggest that performance on the two verbal tasks relies at least partly on the same, strongly left-lateralised temporal lobe regions, i.e., that the mapping of form to meaning relies on similar neural structures as the reverse mapping of meaning to word form.

Performance on the picture categorisation and object decision tasks correlated with voxel signal intensities in the right anterior temporal cortex (see Table 3 and Fig. 2b, where overlapping regions of significant correlation are shown in green). Picture categorisation scores correlated with three clusters, one centered in the right fusiform gyrus (BA 20) extending into the right parahippocampal gyrus (BA 36) and amygdala, a second centered in the right superior temporal pole (BA 20) extending into the middle temporal pole (BAs 20, 38), parahippocampal gyrus (BAs 28, 38) and amygdala, and a third centered in a more posterior portion of the right fusiform gyrus (BA 37) which included the parahippocampal gyrus (BAs 20,
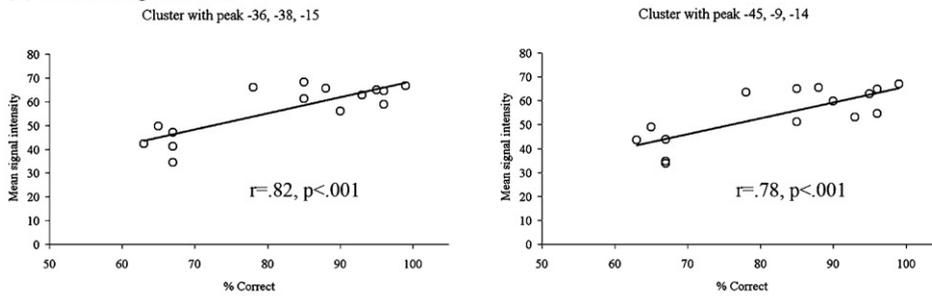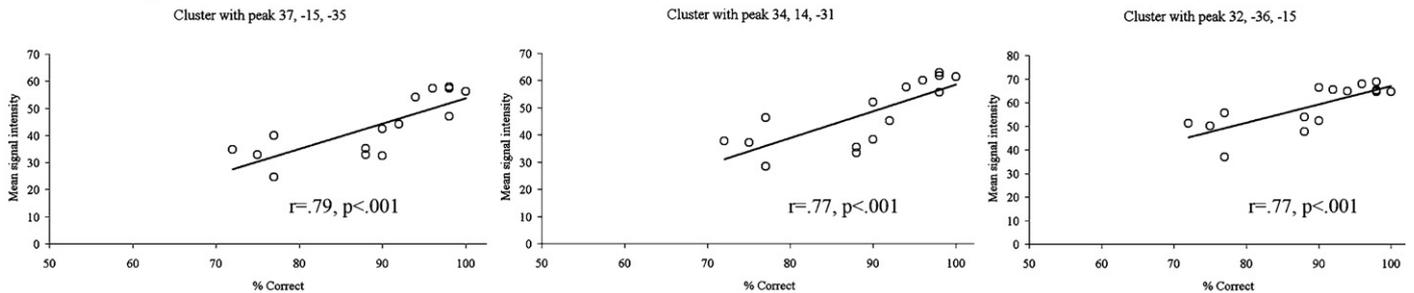
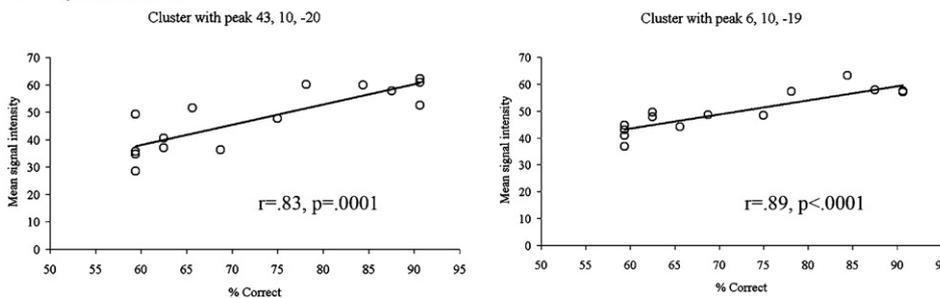**Fig. 3.** Scatterplots of mean signal intensity against corresponding behavioural (percent correct) performance on the (a) word categorisation, (b) naming, (c) picture categorisation and (d) object decision tasks. Clusters are identified with peak voxel coordinates in MNI space (cf. Table 3). Pearson's correlations and associated significance levels are reported.

30). Object decision scores correlated with a large cluster of right hemisphere voxels centered in the right superior temporal pole (BA 38) which included the middle temporal pole (BAs 20, 36, 38), fusiform gyrus (BA 20), inferior temporal lobe (BAs 20, 36), middle temporal lobe (BAs 20, 21), parahippocampal gyrus (BAs 20, 28, 36, 38), hippocampus, amygdala, and insula. A second, smaller cluster was located in the bilateral olfactory sulci and rectus gyri.

To confirm that the above results were not driven by outlying datapoints, we generated scatterplots for each significantly correlated cluster where mean signal intensity in the cluster was plotted against the corresponding percent correct performance. As illustrated in Fig. 3, mean signal strengths across all clusters and ranges of performance were regularly distributed, suggesting that the correlation findings reported above are robust.

5. Discussion

Using a novel voxel-based correlational method, three main issues were addressed. First, we asked whether the same left inferior temporal lobe regions underlie the mapping from a picture to conceptual knowledge to a word form as for the mapping from a word form to conceptual knowledge. We found that poor performance on a task requiring the mapping from visual object information to conceptual knowledge to word forms was associated with damage to left inferior and anterior temporal lobe regions which overlapped with those associated with performance on a task requiring the mapping from word forms to conceptual knowledge. These results are consistent with the hypothesis that left temporal lobe areas play a mediational role in linking concepts

with their associated word forms (Damasio et al., 1996), akin to the lemma level in cognitive models of word production (Garrett, 1992; Indefrey & Levelt, 2004; Levelt, 1992, 1999). This account predicts that if object naming is impaired, the opposite mapping (from word form to conceptual representation) should also show a deficit because both rely on the same mediational system in the left hemisphere.

This proposal contrasts with the predictions of other models of language processing. The Wernicke–Geschwind model of language processing emphasises the role of regions surrounding Wernicke's area, most notably the left inferior parietal lobule, in the retrieval of semantic knowledge from verbal input (Geschwind, 1965; Wernicke, 1874). The role of posterior superior temporal and inferior parietal regions in linking verbal input with semantic content to support verbal comprehension has enjoyed a wide body of support, including lesion-deficit studies (Hart & Gordon, 1990; Kreisler et al., 2000), cortical function mapping findings in epilepsy patients (Boatman et al., 2000) and functional imaging studies with healthy individuals (Gernsbacher & Kaschak, 2003; Kuest & Karbe, 2002), and the results of computational simulations (Weems & Reggia, 2006). The dorsal and ventral stream language model forwarded by Hickok and Poeppel (2000, 2004) also emphasises the importance of posterior regions in the temporo-parietal-occipital junction in the mapping of sound to meaning (ventral stream of language processing), primarily based on lesion-behaviour findings from transcortical sensory aphasia. However, increasingly more evidence, most notably from functional imaging studies in healthy individuals, support the involvement of left-lateralised inferior temporal and temporopolar regions during semantic processing of visual and auditory word forms for concrete concepts (Binder et al., 1997; Demonet, Thierry, & Cardebat, 2005; Marinkovic et al., 2003; Noppeney & Price, 2002; Tyler & Marslen-Wilson, 2008; Vandenberghe, Price, Wise, Josephs, & Frackowiak, 1996). Taken together, these findings suggest that the models of language processing emphasising left perisylvian structures in the mapping between concrete word forms and the conceptual system should be extended to reflect a larger network including the left inferior and anterior temporal lobe.

A potential limitation of the present study is that the word categorisation task requires processes that the naming task does not, e.g., extracting category information from four exemplars and matching the category of the target against the other three. Since it is possible that one of these additional processes is associated with left anterior temporal integrity, rather that the mapping between conceptual and word form information, a picture categorisation task was included as a control condition. This task included the same task components as the word categorisation task but, unlike both naming and word categorisation, did not require retrieval of a concept's name. Scores on the object categorisation task did not correlate with damage in left anterior temporal areas, supporting the claim that this area is involved in the retrieval of object names rather than specific components of the categorisation task.

A second main aim of the present study was to clarify the relationship between object recognition and right temporal lobe regions, which have been associated with the ability to recognise visually presented objects (Damasio et al., 1996; Glosser et al., 2003; Tranel et al., 1997). A problem with some object recognition tasks is that they require verbal responses, potentially confounding object recognition and naming abilities. The present study aimed to identify the neural areas that underlie object recognition in tasks that are entirely non-verbal, namely a picture categorisation task and an object decision task, neither of which required the comprehension of words nor verbal responses. Despite the lack of a language component to the task or the response, scores on both tasks were associated with the same areas in right inferior and anterior temporal cortex that had been previously linked with object recognition using tasks which included linguistic components. These findings suggest that right inferior and anterior temporal lobe involvement in these previous studies reflected recognition processes and is unlikely to be due to an underestimation of recognition abilities in patients with word-finding deficits, as suggested in Section 1.

Finally, areas that correlated with object decision scores were compared with those that correlated with scores on semantic categorisation of pictures, to determine whether object decision depends on the same neural areas associated with semantic tasks. Some authors have claimed that object decision taps into presemantic structural knowledge about object form, and decisions can then be made without access to semantic knowledge (Gerlach et al., 1999; Riddoch & Humphreys, 1987a, 1987b), whereas others argue that object decisions require access to conceptual representations (Rogers et al., 2003). In the present study, performance on the object decision task correlated with areas in the right anterior temporal cortex, including the inferior temporal gyrus and the fusiform gyrus. Furthermore, these areas overlapped with those found to be associated with scores from the picture categorisation task. Although performance on the picture categorisation task can be supported by comparing the pictures' structural visual features, we argue that access to semantic information is required to successfully complete this task. Therefore, it seems that object decisions are adversely affected by damage to areas that underlie semantic tasks and thus that object decision requires access to conceptual information.

The associations between left and right anterior temporal damage and the ability to name and recognise visual objects, respectively, are also supported by findings from patients with progressive temporal lobe atrophy. Patients with left-lateralised anterior temporal lobe atrophy typically show a pattern of progressive anomia (e.g., Graham, Patterson, & Hodges, 1995; Kay & Ellis, 1987; Snowden & Neary, 2003), with relatively intact conceptual knowledge, lexical word forms and phonology, but difficulty mapping between the two, known as "classical anomia" (Geschwind, 1967). In contrast, predominantly right-lateralised temporal lobe atrophy has been associated with progressive agnosia, sometimes limited to the recognition of unique objects such as faces (Evans, Heggs, Antoun, & Hodges, 1995; Gainotti, Barbier, & Marra, 2003; Snowden, 1999). Similar complementary hemispheric differences in naming and recognising objects have been observed in longitudinal studies of patients with semantic dementia, a syndrome characterised by progressive temporal lobe atrophy accompanied by both progressive anomia and object recognition impairments (Neary et al., 1998; Snowden, Goulding, & Neary, 1989; Warrington, 1975). Some patients showed a more rapid decline for naming objects than recognising them, a pattern associated with predominately left temporal atrophy, while others showed parallel declines in both naming and comprehension in association with greater right temporal involvement (Lambon Ralph et al., 2001). Taken together with the present findings, these studies highlight the importance of anterior inferior temporal lobe regions in conceptual processing, and offer additional confirmation for the verbal-visuospatial dichotomy proposed over a century ago (Taylor, 1958).

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