

## Conceptual Structure Modulates Anteromedial Temporal Involvement in Processing Verbally Presented Object Properties

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**Recent research has indicated that anteromedial temporal cortex (including the perirhinal cortex) may function as the endpoint of a hierarchically organized visual object-processing network providing the basis for fine-grained discrimination among objects. The present study examines whether the same system is involved in processing conceptual information when concepts, and their properties, are denoted by words. A lesion-behavior correlational study was conducted in which cortical damage in 21 brain-damaged patients was correlated with behavioral scores in a verbally presented property verification task. Results indicated that the neural correlates of conceptual processing depend on the dynamic interaction between the content of a conceptual representation and the specific demands of the task and that the role of anteromedial temporal cortex in this process is not limited to the visual input modality. The results are consistent with the claim that anteromedial temporal cortex provides the neural structure necessary for the emergence of fine-grained conceptual knowledge about objects, although the region is strongly weighted toward processing of visually based object features.**

**Keywords:** category specificity, conceptual knowledge, feature conjunctions, integration, object processing

### Introduction

How conceptual knowledge is processed and represented in the brain remains a key issue in cognitive neuroscience. In terms of the neural representation and organization of conceptual knowledge, accounts have ranged from the view that category, domain, or type of semantic property (e.g., visual, motor, etc) provide organizing principles (Warrington and McCarthy 1983; Caramazza and Shelton 1998; Martin and Chao 2001) to the claim that conceptual knowledge is represented in a distributed neural system with category and domain structure emerging from the structure and content of concepts (Durrant-Peatfield and others 1997; Gonnerman and others 1997; Tyler and others 2000, 2003; Tyler and Moss 2001; Devlin and others 2002).

Recent research has attempted to relate representational accounts of conceptual knowledge to claims about how concepts—in this case concrete concepts in the form of objects—are processed in the human ventral temporal cortex (Tyler and others 2004; Moss and others 2005; Taylor and others 2006). This research takes as its basic assumption that concepts are represented as sets of coactivated features within a distributed network, with the structure of concepts varying as a function of factors, such as number and type of semantic properties, the distinctiveness of properties and the strength of the correlations between different types of property (Gonnerman and others 1997; Tyler and others 2000; McRae

and Cree 2002; Moss and others 2002, 2006). These differences in conceptual structure generate category effects in the sense that concepts within living thing categories, such as animals, tend to differ in their conceptual structure from concepts in categories such as tools. For example, living thing concepts tend to have many shared properties that are strongly correlated with each other (e.g., legs, eyes, movement) and few, weakly correlated distinctive properties (e.g., mane, hump, pouch), making living thing concepts more difficult to differentiate one from another. In contrast, nonliving concepts (such as vehicles and tools) have fewer shared properties and more distinctive correlated properties, making them less confusable with each other. Evidence for this conceptual structure account (CSA) of category-specific semantic deficits (Tyler and others 2000; Tyler and Moss 2001; Moss and others 2002) comes from a mixture of property norm data, behavioral studies with healthy subjects and brain-damaged patients, and computational modeling (Moss and Tyler 2000; Greer and others 2001; Moss and others 2002, 2006; Randall and others 2004; Taylor and others 2006).

Tyler and others (2004) following claims made by Simmons and Barsalou (2003) have argued that these differences in the structure of concepts have consequences for how they are processed in the human ventral temporal cortex. Simmons and Barsalou (2003), integrating earlier accounts by Damasio (1989) and models of object processing in the nonhuman primate (Gross and others 1972; Buckley and Gaffan 1998; Murray and Bussey 1999; Murray and Richmond 2001), suggested that objects are processed in a hierarchical processing stream in ventral temporal cortex with simple properties of objects processed in more posterior temporal sites, with increasingly more complex features and conjunctions of features processed more anteriorly, culminating in the perirhinal cortex where different types of sensory properties are integrated. Moss, Tyler and others have shown that processing within this ventral stream is modulated by the conceptual structure of objects. In a functional magnetic resonance imaging (fMRI) study, they asked subjects to silently name pictures of objects (either living or nonliving things) at either a basic level or a domain level. Basic level naming, which involves identifying the object itself (e.g., cat, apple, spoon), requires access to more detailed information so that one object can be differentiated from another, whereas domain level naming (i.e., to identify the object is either “living” or “man-made”) only requires access to general properties of objects. They found that both basic and domain level naming activated the posterior inferior temporal cortex bilaterally (Tyler and others 2004), whereas basic level naming additionally activated more anterior regions including perirhinal cortex. Importantly, this region was activated more strongly for living compared with nonliving things (Moss and

others 2005). These results were interpreted as evidence for hierarchical object processing along the ventral temporal stream in humans, with more posterior temporal sites involved in combining the more simple features of objects and more anterior sites involved in processing object features into the complex feature conjunctions necessary for a more detailed analysis of objects. This interpretation was strengthened by the finding that living things, which have more shared features and are more difficult to differentiate from one another, activated the anteromedial temporal cortex more strongly than did nonliving things when objects had to be processed at a more specific level (in basic level naming). These claims were further supported by data from brain-damaged patients (Moss and others 2005). Patients with damage to anteromedial temporal cortex, including the perirhinal cortex, with a category-specific deficit for living things had a disproportionate deficit for the distinctive features of living things, whereas patients with a similar degree of semantic impairment but who did not have perirhinal damage neither had a category-specific living things deficit nor were they especially impaired on knowledge of their distinctive properties.

These claims about the processing of object concepts in the ventral temporal cortex are based upon data from visual stimuli in the form of pictures of objects. This raises the question of the extent to which object processing along this pathway is restricted to the visual properties of objects. Is the same system involved in processing conceptual information when concepts, and their properties, are denoted by words? There is reason to believe that at least some regions along the ventral processing stream may process nonvisual as well as visual properties of concepts. Unlike most other regions of the ventral visual stream, the perirhinal cortex has reciprocal links with areas processing nonvisual sensory information, including superior temporal gyrus (audition) and posterior insula (somatosensory), and with multimodal regions (parahippocampal gyrus, superior temporal sulcus, orbitofrontal cortex, and cingulate cortex) (Mishkin and others 1997; Buckley and Gaffan 1998; Murray and Bussey 1999; Taylor and others 2005, 2006). On the basis of these extensive links, Murray and Richmond (2001) have suggested that perirhinal cortex may bind together both visual and other sensory properties. This claim has been substantiated by a recent fMRI study in humans, in which the perirhinal cortex was associated with integration of information across different sensory modalities (Taylor and others 2006). Furthermore, this region was also sensitive to the “meaningfulness” of objects, suggesting it may provide the basis for the construction of conceptual object representations (Tyler and others 2004; Bright and others 2005; Moss and others 2005; Taylor and others 2006). If this is the case, this region may be involved in conceptual processing, regardless of the format of stimulus presentation. For example, both words denoting objects and pictures of objects should recruit these anteromedial regions.

We tested this prediction in the present study asking whether 1) referring to concepts and their properties by verbal labels engages the ventral processing stream and 2) this stream is modulated by the same variables (e.g., distinctiveness of properties) as have been shown to modulate the processing of pictures of objects.

We addressed these questions in a lesion-behavior correlational study in which we correlated cortical damage in 21 brain-damaged patients with their behavioral scores in a property verification task. We used this method in order to relate the

sensitivity of brain tissue integrity to performance on different conditions of the verbal property verification task. Specifically, this method uses 2 continuous measures—signal intensity values for each voxel across the entire brain of each patient (a measure of tissue integrity) and continuous scores on a behavioral test. In this way, we avoid binarising either the structural data as damaged or healthy or the behavioral results as impaired or preserved (for a detailed description of the methodology and its rationale, see Tyler and others 2005a, 2005b). As the approach is sensitive to lesion sampling, it is necessary that all correlations are derived from the “same” patient group and that, across these patients, the anatomical regions of interest (ROIs) are adequately sampled (the more variability in signal intensity at a particular voxel the greater the sensitivity at that voxel to any potential relationship). Thus, any brain region unaffected in all patients is less likely to show correlations with any behavioral task due to a narrower range of signal intensities in that location. For this reason, it is important that patients are not selected on the basis of a priori assumptions about lesion location or related behavioral deficits. The sensitivity of the method for identifying brain-behavior correlations also depends on there being sufficient variability in performance on the behavioral task entered into the analysis and that there is roughly equal variability across any task conditions being compared. As is the case with signal intensities, a narrow range of behavioral scores (for instance, due to ceiling or floor effects) will reduce the likelihood of identifying brain-behavior correlations.

With this method, we explored the pattern of correlations between signal intensities across the brain and knowledge of different types of properties—visually based and nonsensory-based distinctive and shared features of living things and artefacts as determined by performance on a verbal property verification task. In this task, patients were presented with spoken questions about properties of objects (e.g., do cats have whiskers?) to which they made a yes/no decision. The nature of the property questions was manipulated across conditions. Half of the questions were about visually based properties (e.g., are pigs pink?) and half were about nonsensory properties (e.g., are pigs kept on farms?). If anteromedial temporal regions support both sensory and nonsensory conceptual information, we would expect equal involvement for both types of property. However, if the role of this region is strongly weighted toward visual processing, which might be predicted given that more than 60% of inputs originate in visual areas (Suzuki and Amaral 1994), we would expect a significantly greater correlation of anteromedial temporal damage with performance on visually based questions than with nonvisually based questions. Finally, if this region is selectively involved in processing complex conjunctions of features from the visual object-processing pathway and has no nonsensory semantic role, then we might expect little or no correlation between performance and damage in these regions. To determine the role of category and property distinctiveness, half the questions were about living things (animals and fruits) and half were about nonliving things (tools and vehicles), and within each category, half the questions probed knowledge of distinctive properties (e.g., do brooms have bristles?), whereas half probed shared properties (e.g., do brooms have handles?). If conceptual structure modulates anteromedial temporal involvement as predicted by the CSA, then we would expect to see the stronger correlations for distinctive than shared properties and for questions about living things rather than nonliving things.

## Materials and Methods

### Patients

The subjects were 21 brain-damaged patients who ranged in age from 29 to 71 years (mean age 53 years; standard deviation 13.5), and were all right-handed native English speakers (see Table 1 for details). All the patients were members of our long-term pool of neuropsychological patients, and none of them were significantly cognitively impaired on the Ravens measure of fluid intelligence (mean Ravens score = 32, range = 27–36). Performance on backward digit span was more variable, with 3 patients able to recall only 2 digits. We included patients in this study according to 2 criteria: They had 1) a  $T_1$ -weighted 3-dimensional magnetic resonance imaging (MRI) scan and 2) could reliably perform the property verification task. Patients were not selected on the basis of their either lesion location or pattern of behavioral scores (Table 1). The group consisted of different etiologies, including herpes simplex encephalitis, haemorrhage, meningioma excision, and abscess. We also included 2 semantic dementia patients, for which the behavioral data were collected within 6 weeks of the MRI scan used in the present analysis. In the majority of patients, the lesions were predominantly restricted to the left hemisphere ( $N = 15$ ), but there were also 2 right hemisphere cases, and 4 in which damage was represented equally in both hemispheres. Left anteromedial temporal cortex was clearly implicated in 9 of the 21 cases.

### Behavioral Task

We developed a property verification task, previously used in a study of category-specific semantic deficits (Moss and others 2002 see also Moss HE and Tyler LK, submitted). In this task, we asked participants to verify properties of concepts in different semantic categories. The concepts came either from a living (animals and fruits) or nonliving (vehicles and tools) category, and properties were either visually (e.g., has eyes) or nonvisually based (e.g., used for cutting). Within each category, we also manipulated whether the property was distinctive (true of few concepts in the category—e.g., has a mane, has bristles) or shared (true of many or all members of the category—e.g., has eyes, has a handle).

Ten concepts were selected for each of 4 categories. The concepts in the living (animals and fruits) and nonliving domains (tools and vehicles) were matched for word frequency, imageability, and age of acquisition. Eight properties for each of 10 concepts in each category were selected. Each concept was paired with 4 visually based properties (e.g., has eyes) and 4 nonvisually based properties (e.g., used for cutting), divided equally into true and false trials. The true properties were selected from an earlier normative property generation study in which healthy adult

participants ( $N = 45$ ) listed properties for a large set of concepts (Randall and others 2004). This allowed us to determine the distinctiveness and “sharedness” of each property. For example, the property “used for milk” (for the concept COW) was given for only 2 of 31 animal concepts and was therefore rated as distinctive. Conversely, “can eat” was provided for all animals and was therefore rated as shared. To create a binary division of distinctive versus shared properties for this study, we counted properties given for fewer than half the items in a category as distinctive and those given for more than half as shared. An equal number of false trials in each condition was created by re-pairing the properties and concepts. For the distinctive conditions, properties were exchanged within a category (e.g., the distinctive perceptual property “is pink” for the concept PIG was re-paired with camel to give the false distinctive perceptual trial “Is a camel pink?”). Shared properties were re-paired with a concept in the opposing domain (animal properties were exchanged with vehicle properties, whereas fruit properties were exchanged with tool properties). For example, the shared perceptual property “made of metal” for SHIP was paired with COW to give the false shared perceptual property “Is a cow made of metal?”. The mean sharedness of shared properties was matched across the domains, as was the mean distinctiveness of the distinctive properties. Thus, there were a total of 80 property conditions per category presented in a fully counterbalanced design (living/nonliving  $\times$  visual/nonvisual  $\times$  distinctive/shared  $\times$  true/false).

Each property was presented as a spoken question (e.g., do cats have fur?) to the patients, and they were required to produce a “yes” or “no” response. In this way, the style of presentation for each trial remained constant across all conditions and was designed to be as straightforward as possible. All patients attempted every trial and at no time appeared to show any difficulty understanding the nature of the task. In fact, chance level performance was very rare, and every patient correctly verified all trials in at least 1 of the 16 conditions (see Table 2). All 8 verification trials for a concept were administered sequentially. Percent correct scores were calculated for each subject in each of the conditions, and these values constituted the behavioral data entered into the correlational analysis. From Table 2, it can be seen that variability in performance on the vehicles category is low, with a high frequency of maximum scores. This means that there is relatively low sensitivity for finding brain-behavior correlations for this category. However, the level of variability across the remaining 3 categories is relatively similar, suggesting that any regional differences in the size of brain-behavior correlation with signal intensities among these categories cannot simply reflect different sensitivities among the statistical analyses.

A recent neuroimaging study has found that the relationship between true and false trials can modulate cortical activity during object property verification (Kan, Barsalou, Solomon, Minor and Thompson-Schill 2003). Specifically, significantly more left fusiform activation was found when true trials were intermixed with associated false trials (in which the property was not a physical part of the object, e.g., “stapler-paper”) than with nonassociated false trials (e.g., stapler-vegetable). An implication of this research for the present study is that differences in the results may, at least in part, be explained by differences in the relative difficulty of rejecting the false trials across task conditions. In order to explore this possibility, we subtracted percent correct scores for the true trials from the false trials for the visually based properties and compared these difference scores across the 4 categories. The results show that the true and false trials were similar in terms of the difficulty in correctly accepting or rejecting a trial, particularly for the shared properties (shared: animals = 2.1, fruits = 0, vehicles = 2.1, tools = -2.9; distinctive: animals = 10.7, fruits = 6.4, vehicles = 8.5, tools = 11.4). On distinctive properties, and for all categories, a greater proportion of true trials were failed than false trials, with a range of just 5% between the largest (tools) and smallest (fruits) difference scores. We can conclude, therefore, that it is therefore very unlikely that differential difficulty on true and false trials across the categories can underlie the category differences reported below.

### Brain-Behavior Correlational Analysis

#### Preprocessing

The  $T_1$  images were spatially normalized to the Montreal Neurological Institute (MNI) template using SPM99 (Wellcome Institute of Cognitive

**Table 1**

Patient details

Patient	Age	Sex	Etiology	Lesion	Ravens (/36)	Digit F/B
1	48	M	HSE	Bilateral temporal (>L)	35	5/5
2	38	F	HSE	Bilateral temporal (=)	30	4/4
3	71	F	HSE	Right temporal	34	—
4	65	M	HSE	Bilateral temporal (>L)	27	—
5	43	M	HSE	Bilateral temporal (>L)	33	—
6	70	M	HSE	Left temporal	36	6/4
7	70	F	HSE	Bilateral temporal (=)	33	6/5
8	57	M	HSE	Bilateral temporal (=)	34	7/4
9	29	F	Haemorrhage	Left temporal	—	—
10	43	F	Aneurysm	Left frontal	34	6/6
11	68	M	CVA	Left temporo-occipital	21	5/2
12	67	M	SD	Right temporal	32	6/4
13	60	F	SD	Bilateral temporal (=)	30	6/4
14	35	F	Infarct	Left frontotemporal	31	7/2
15	37	M	Abscess (drained)	Left temporal	36	7/6
16	50	M	CVA	Left frontotemporal	36	—
17	41	F	Meningioma (excised)	Left temporal	34	6/4
18	65	M	Infarct	Left temporal/frontal	29	2/2
19	44	F	Infarct	Left temporal	31	6/5
20	48	F	Aneurysm	Left frontotemporal	29	6/3
21	64	M	Infarct	Left temporoparietal	32	5/3

Note: HSE, herpes simplex encephalitis; SD, semantic dementia; CVA, cerebrovascular accident; Ravens, Ravens Colored Progressive Matrices (Raven 1965). F, forward digit span; B, backward digit span. Lesion labels summarise the main effects of damage. (>L), greater lesion extent in left hemisphere; (=), lesion extent approximately equal in both hemispheres.

**Table 2**

Scores (percent correct) for all test conditions by each patient

Patient	Visually based: distinctive				Visually based: shared				Nonvisually based: distinctive				Nonvisually based: shared			
	A	T	F	V	A	T	F	V	A	T	F	V	A	T	F	V
1	40	75	75	72	100	95	80	100	67	100	69	95	95	100	80	100
2	45	40	85	67	95	100	95	100	70	85	64	90	85	100	84	90
3	95	100	95	100	95	100	100	94	93	100	93	100	100	100	100	95
4	75	90	85	94	85	90	100	89	84	95	64	100	90	100	95	100
5	30	45	32	44	100	80	45	94	53	90	36	55	63	95	65	95
6	60	80	95	94	100	90	100	94	87	75	92	100	95	89	100	100
7	70	70	74	67	95	95	85	100	67	95	71	95	84	100	95	90
8	75	90	74	83	95	100	90	94	87	100	57	100	95	100	100	100
9	70	50	95	100	75	55	95	100	67	65	92	100	63	68	100	100
10	95	95	95	100	100	100	95	100	100	95	79	95	100	100	100	95
11	70	80	65	94	90	85	90	100	100	95	69	95	100	100	100	100
12	60	65	70	67	100	85	90	100	87	80	69	85	95	89	100	95
13	40	55	65	67	95	80	85	100	73	90	77	80	100	95	90	95
14	80	80	90	89	100	90	90	94	74	90	71	95	100	95	85	95
15	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100
16	95	80	70	100	100	100	80	100	87	95	77	95	84	95	85	100
17	100	95	100	100	95	100	95	100	100	95	100	100	100	100	100	100
18	80	90	80	94	95	100	100	94	100	85	85	100	89	100	85	100
19	100	100	95	94	100	100	100	94	100	100	92	100	100	100	100	100
20	90	100	95	94	100	100	95	100	100	95	100	100	100	100	100	100
21	100	100	100	100	95	100	100	100	100	100	100	100	100	100	100	100

Note: A, animals; T, tools; F, fruits; V, vehicles.

Neurology, London, UK). This involved both linear (12 affine transformations) and nonlinear ( $7 \times 8 \times 7$  basis functions) transformations, with lesion masks applied to avoid lesion-related deformation of images (Brett and others 2001). Segmentation into gray and white matter was not included, as this procedure often fails when brains contain large lesions (Stamatakis and Tyler 2005). The skull was excluded from each analysis, using the brain mask provided with SPM99, and the images were smoothed with a 10-mm Gaussian kernel to account for small-scale anatomical variations and to increase the signal-to-noise ratio (Friston and others 1994).

### Statistical Analysis

Covariate analyses were carried out in the context of the general linear model (Friston and others 1995) as implemented in SPM99. We correlated property verification scores for each of the experimental conditions with signal intensity across each of the patient scans. Global mean signal from each scan was included in the model as a confounding covariate. We tested regional effects for each of the behavioral measures using *t*-statistics. Gaussian random field theory was used to correct for the search volume in terms of *P* values. In 4 separate models (visual distinctive, visual shared, nonvisual distinctive, nonvisual shared), behavioral scores (percent correct) for each patient for each of the 4 categories (animals, fruits, vehicles, and tools) were correlated with signal intensity at each voxel (Tyler and others 2005a, 2005b). Each of the models revealed the cortical regions in which there was a significant correlation between signal intensity and behavioral scores for the experimental condition. We report the coordinates of the peak significant voxels in MNI space and as Talairach and Tournoux labels after correction for differences between the Talairach and the MNI stereotactic coordinate systems. We threshold the statistical parametric maps at the standard threshold of  $P < 0.001$  uncorrected at the voxel level and report maxima for clusters that survive a random field corrected *P* value of  $P < 0.05$ , adjusted for the entire brain. Results are also reported from a lower threshold ( $P < 0.01$  uncorrected at the voxel level) to determine the extent to which areas of correlation below the standard statistical cutoff are shared across categories and conditions (see Fig. 1A).

### Results

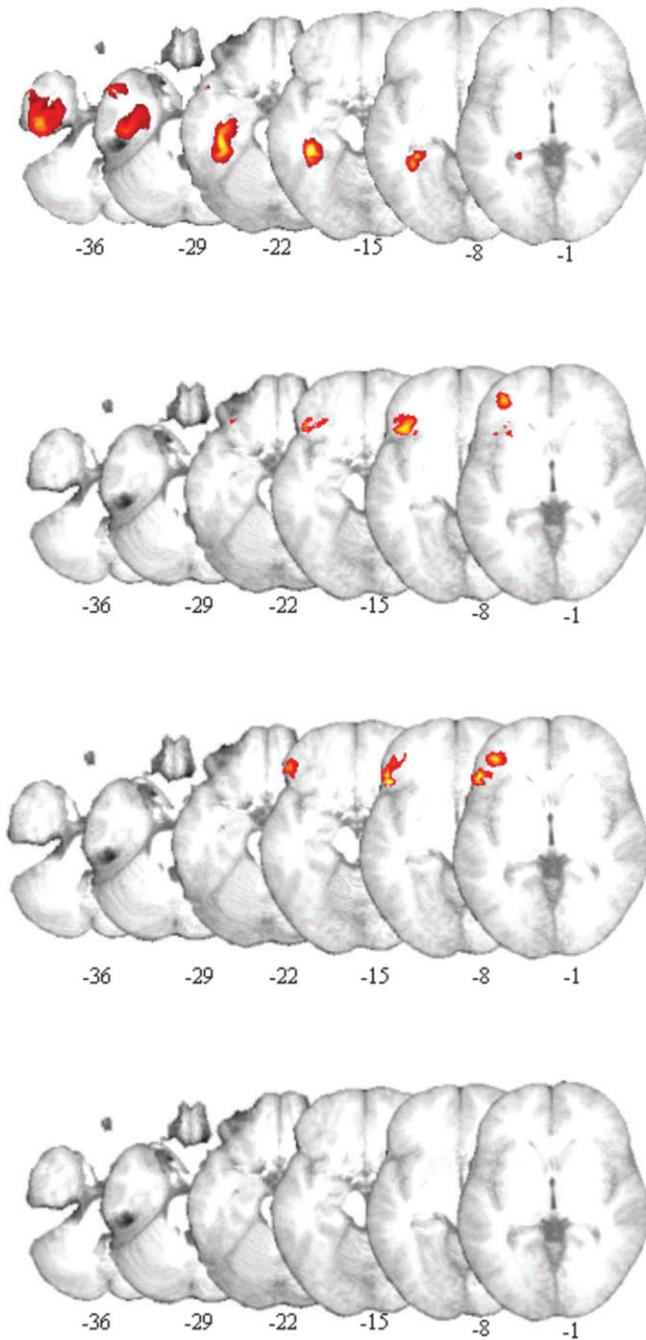
We first report results for distinctive properties. If the processing of verbally presented information about object properties shares the same ventral processing stream as has been shown for visually presented pictures of objects, we would expect

distinctive properties to be strongly associated with left anteromedial temporal cortex. Moreover, on the basis of the CSA, we would predict that the greater similarity among animals renders this category especially dependent on the integrity of this brain region. For the visually based distinctive properties, this is what we found. The verification scores for the visually based distinctive properties of animals were significantly correlated with signal intensity in anteromedial temporal cortex, specifically the parahippocampal gyrus (Brodmann area [BA] 36), with a peak correlation at  $(-39 -35 -18)$ , the cluster extending to include left fusiform gyrus (BA 20/37). A second cluster was located in inferior temporal gyrus (BA 20)  $(-45 -18 -34)$ , extending into parahippocampal gyrus (BA 36) and perirhinal cortex (BA 35) at  $P < 0.01$  (Fig. 1A). At this lower threshold, we also found significant correlations with signal intensity in middle temporal gyrus (BA 21) and temporal pole (BA 38).

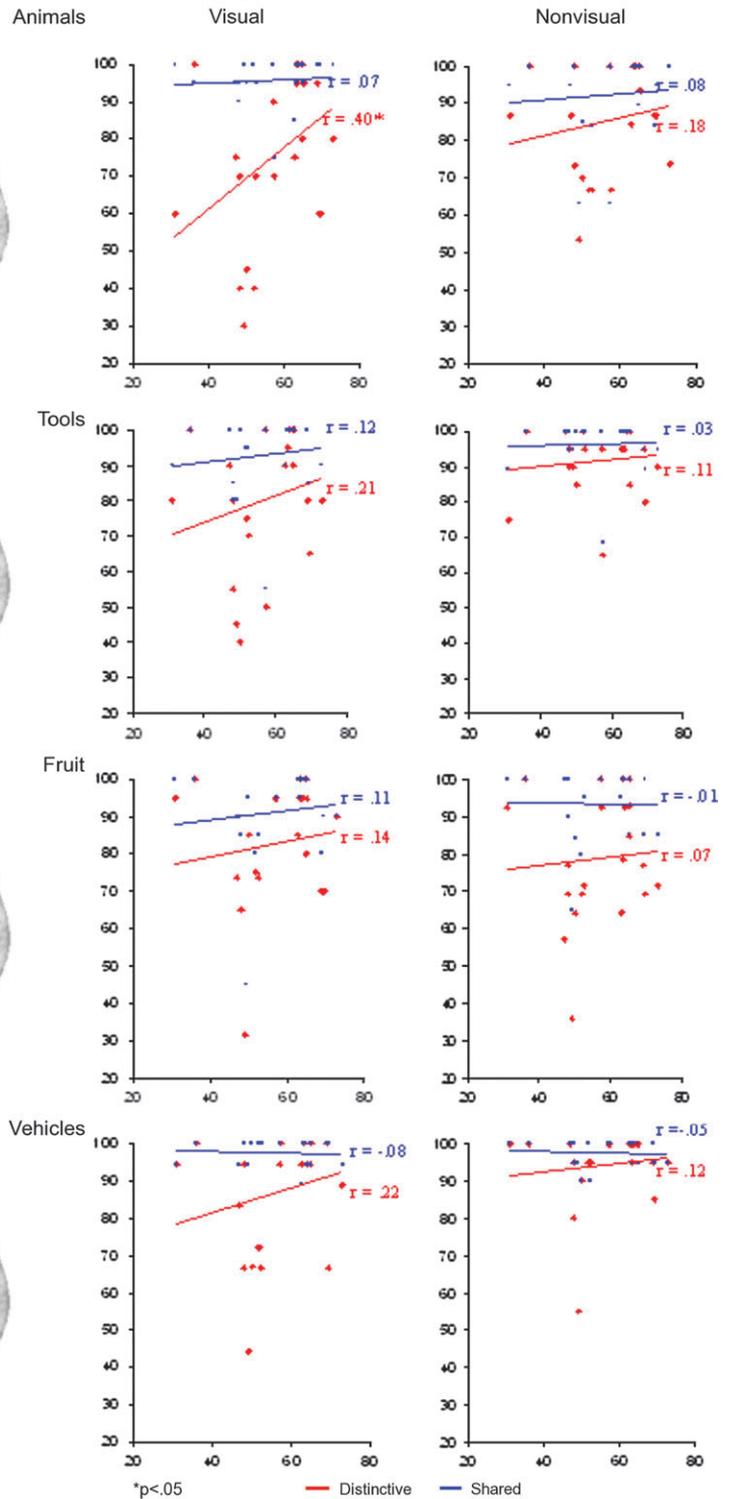
Only at the lower threshold were effects found for the visual distinctive properties of concepts in other categories: for fruits and tools, significant correlations were observed in left frontal cortex (BA 45/47/10) with a peak correlation in BA 47 (fruits:  $-50 25 -8$ ; tools:  $-44 27 -11$ ). No areas of significant correlation were observed for vehicles (see Fig. 1A). This finding, that the processing of verbally presented, visually based distinctive properties of animal concepts are related to anteromedial temporal lobe integrity, is consistent with the view that conceptual representations of objects can be accessed via verbal inputs.

As a precaution against the possibility that the strong correlations found for verification of visually based distinctive properties of animals may have been influenced by the presence of damage in homologous areas of the contralateral hemisphere, we conducted a second analysis, excluding any patients with bilateral lesions ( $N = 7$ ). Although there was less power for identifying brain-behavior correlations, the results were very highly consistent with the full sample analysis. The distinctive visually based properties of animals were significantly correlated (at  $P = 0.01$ ) with left anteromedial temporal cortex (including left fusiform gyrus, parahippocampal gyrus, and

A) Correlations between signal intensity and visual distinctive properties



B) Plots showing correlations in perirhinal cortex (-25 -20 -20) for visual and nonvisual properties



**Figure 1.** (A) Representative axial slices showing  $T_1$ -signal correlations with verification scores for the distinctive visually based properties of objects (animals, tools, fruits, and vehicles). The correlations are superimposed on a  $T_1$ -weighted image and slices are shown in neurological convention where left = left. Talairach z-values (mm) are shown below each slice. (B) Scatter plots of filtered intensity values (x axis) of every patient scan plotted against performance (y axis) on shared and distinctive properties, separately for visually based and nonvisually based property types.

perirhinal cortex BA 35), fruits and tools were correlated with left frontal cortex, and with no areas of correlation identified for vehicles.

We next examined the relationship between signal intensity and “nonsensory”-based distinctive properties in order to test the possibility that, if anteromedial temporal cortex supports the processing of nonsensory conceptual information, damage in this region may be correlated with distinctive properties that are not rooted in any sensory modality. In fact, knowledge of nonvisually based distinctive properties were not associated with anteromedial temporal cortices for any object category, nor did these properties correlate significantly with any region for any category. Thus, the role of left anteromedial temporal cortex appears to be strongly weighted toward processing of visually based features of objects.

With respect to shared properties, which we would predict not to be associated with anteromedial temporal cortex (or at least less associated than was found for distinctive properties), the visually based shared properties of animals were correlated with an area of the right lateral temporal cortex (middle temporal gyrus, BA 20/21) with a peak at (57 -16 -27). No left hemisphere effects for visually based shared properties were observed for any category, even at the reduced threshold ( $P = 0.01$ ). At this lower threshold, the nonvisually based shared properties of tools correlated with left lenticular nucleus (-26 -9 -3) and occipital cortex (-23 -73 -1), and vehicles correlated with right inferior frontal gyrus (BA 47) (21 20 -10). The data are thus consistent with the claim that referring to shared object properties is not sensitive to damage in left anteromedial temporal regions because this level of conceptual representation does not require fine-grained within-category discriminations among objects to be made.

Finally, in order to directly compare the correlations between each type of feature for each category in the perirhinal cortex, we plotted the correlation of signal intensity ( $x$  axis) and performance ( $y$  axis) for each condition and each category. To be sure that the observed effects were within the perirhinal cortex, we selected a voxel on the basis of neuroanatomical data that was centrally located within the perirhinal area (BA 35) (-25 -20 -20). In each of the models, we plotted the filtered signal (i.e., after adjustment for global mean) against the behavioral scores at this perirhinal voxel. We extracted the filtered signal at the voxel using the Marsbar ROI toolbox (Brett and others 2002) and calculated correlation coefficients, testing for significant differences between them using Williams' (1959) test for significant differences between dependent correlations. These plots are shown in Figure 1B. For visual properties, the only significant correlation in the perirhinal voxel was for the visual distinctive properties of animals ( $r = 0.40$ ,  $P < 0.05$ ). This was greater than the size of the effect for the distinctive properties of fruits ( $P = 0.05$ ), vehicles ( $P = 0.07$ ), or tools ( $P = 0.06$ ). No other comparisons among categories, either for shared visually based properties or for shared or distinctive nonvisually based properties, approached significance ( $P > 0.1$ ).

## Discussion

These results demonstrate that correlating a measure of neural integrity—that is, signal intensity—with behavioral data from a verbally presented property verification task can reveal differential sensitivity to manipulations of semantic category, to property distinctiveness, and also to whether verification of

visually or nonvisually based properties is required. To the extent that anteromedial temporal cortex provides the neural basis for fine-grained modality-general conceptual knowledge, we predicted that performance on the distinctive properties of living things (which have greater within-category similarity than nonliving things) would be particularly sensitive to damage in this region, irrespective of whether the task required verification of visually or nonvisually based properties. We found that the “visually” based distinctive properties of “animals” were correlated with integrity of left anterior inferior temporal regions, including anterior fusiform gyrus, parahippocampal gyrus, and perirhinal cortex—indicating that the involvement of these regions are not restricted to object processing from the visual input modality. However, this effect was not replicated for the “nonvisually” based distinctive properties of any category, a finding seemingly inconsistent with the claim that this region supports modality-general semantic knowledge within an amodal semantic memory system (see below for further discussion of this point).

The anteromedial temporal brain areas, sensitive to the visually based distinctive properties of animals, did not correlate with performance on the shared properties in any category, whether visually or nonvisually based. The insensitivity of damage in these regions to knowledge of relatively coarse-grained conceptual knowledge (of the same concepts) fits with our recent studies combining fMRI data in healthy subjects with behavioral data from patients with damage to temporal cortex. These studies argued for a process-driven view of anteromedial temporal involvement in object processing (Tyler and others 2004; Moss and others 2005). The fMRI data showed increased activation in anteromedial temporal cortex when the task required access to the fine-grained, defining properties of a concept (e.g., knowledge that a lion has a mane) and damage in the perirhinal cortex and neighboring areas predicted poor performance under similar conditions.

On the basis of our earlier functional neuroimaging object-processing study (Moss and others 2005), we predicted that performance on distinctive properties of animals and fruits might be more associated with anteromedial temporal regions than for vehicles and tools. This is because members of both living thing categories have a greater proportion of highly correlated shared properties and relatively few distinctive properties, whereas the artifactual categories have a larger proportion of distinctive relative to shared features and are therefore more easily distinguished from each other. In a large scale normative study of object properties generated by a group of unimpaired participants (Moss and others 2002), we found that the claims about living and nonliving domains set out in the CSA are most faithfully represented by the categories of animals and tools because animals have many shared, correlated properties but few distinctive properties, whereas tools have relatively limited shared information and strong correlations among pairs of highly distinctive form and function properties. Concepts in the category of fruits have fewer properties overall than other living things, such as animals. Whether the lack of sensitivity of damage in left anterior temporal regions to performance on fruits relates to the relatively simple structure of fruits than animals is unknown and requires further investigation.

Why is the left perirhinal cortex and neighboring anteromedial temporal cortex sensitive only to verification of the visually based distinctive properties of animals? Although the perirhinal

cortex receives inputs from all sensory modalities (Murray and Bussey 1999), in nonhuman primates the majority of inputs are from visual cortex (area TE). Thus, it is possible that words denoting visual features of objects are particularly likely to require the preserved functioning of neurons in perirhinal cortex if these are especially tuned to the processing of visual input. For example, according to Barsalou and others (2003), the conceptual system is “grounded in” through a process of “re-enactment”. That is, when an object (e.g., a car) is perceived visually, a corresponding set of neurons in the visual system is activated, and the active features are then conjoined in association areas and stored in memory. At a later time, and in the absence of visual input, these conjunctive neurons partially reactivate the earlier sensory representation of the car, even though the relevant physical stimulus is not presented. This provides a framework to explain how semantic knowledge about objects in the world can be built up on the basis of controlled reactivation of sensorimotor regions. The left anteromedial temporal cortex may play a critical role in the interface between conceptual knowledge and object processing, but it may be the knowledge of visually based properties about an object that map most directly onto its conceptual representation. We must also note, however, that there was less overall variability in performance on the nonvisually based properties, so it is possible that the lack of significant effects were in part due to less overall power to detect a relationship. The presence of ceiling effects in some patients may also have contributed to the lack of any significant correlations being identified for the shared properties across all categories (both visually and nonvisually based).

Overall, the data provide evidence that the role of left anteromedial temporal cortex observed in earlier studies of visual object processing (Tyler and others 2004; Moss and others 2005; Taylor and others 2005, 2006) may extend to include information not limited to the visual input modality. In addition to being the endpoint of the ventral visual object-processing stream, polymodal neurons in anteromedial temporal cortex may process and integrate information from different sensory input modalities and provide the basis for the emergence of nonsensory, fact-like knowledge and associations among objects (Murray and Richmond 2001; Simmons and Barsalou 2003; Bright and others 2004; Moss and others 2005; Taylor and others 2005, 2006). These regions, rather than being critical just for visual object recognition, may also support fine-grained semantic processing more generally, although there was no evidence for their sensitivity to nonvisually based property knowledge. The finding that damage in anteromedial temporal cortex predicts fine-grained semantic knowledge of animals, but not tools, is consistent with the neuropsychological literature (e.g., Damasio and others 1996, 2004), which links category-specific semantic deficits for living things with damage to these regions. Thus, although we acknowledge the potential caveats of our methodology outlined in the Introduction (particularly ceiling effects and lesion sampling issues), the results provide important, corroborative evidence for a crucial role of this brain region in conceptual level processing.

In summary, these findings support our claim that the neural correlates of conceptual processing depend on the dynamic interaction between the content of a conceptual representation and the specific demands of the task and that the role of anteromedial temporal cortex in this process is not limited to the visual input modality. A key claim of the hierarchical object-

processing account is that polymodal neurons in this region integrate information across a range of sensory modalities. Damage impacts on the conceptual processing of animals (which have greater within-category similarity than artifacts such as tools and vehicles and require greater differentiation of object properties) but only when access to the defining visually based properties is required. The results are consistent with the claim that this region may provide the neural structure necessary for the emergence of fine-grained conceptual knowledge, although further work is needed to clarify the extent to which processing may encompass conceptual knowledge that is not rooted in the visual modality.

## Notes

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## References

- Barsalou LW, Kyle Simmons W, Barbey AK, Wilson CD. 2003. Grounding conceptual knowledge in modality-specific systems. *Trends Cogn Sci* 7:84-91.
- Brett M, Anton J-L, Valabregue R, Poline J-B. 2002. Region of interest analysis using an SMP toolbox, paper presented at: 8th International Conference on Functional mapping of the Human Brain [Sendai, Japan: Neuroimage 16(2)].
- Brett M, Leff AP, Rorden C, Ashburner J. 2001. Spatial normalization of brain images with focal lesions using cost function masking. *Neuroimage* 14:486-500.
- Bright P, Moss H, Tyler LK. 2004. Unitary vs multiple semantics: PET studies of word and picture processing. *Brain Lang* 89:417-432.
- Buckley MJ, Gaffan D. 1998. Perirhinal cortex ablation impairs visual object identification. *J Neurosci* 18:2268-2275.
- Caramazza A, Shelton JR. 1998. Domain-specific knowledge systems in the brain: the animate-inanimate distinction. *J Cogn Neurosci* 10:1-34.
- Damasio AR. 1989. The brain binds entities and events by multi regional activation from convergence zones. *Neural Comput* 1:123-132.
- Damasio H, Grabowski TJ, Tranel D, Hichwa RD, Damasio AR. 1996. A neural basis for lexical retrieval. *Nature* 380:499-505.
- Damasio H, Tranel D, Grabowski T, Adolphs R, Damasio A. 2004. Neural systems behind word and concept retrieval. *Cognition* 92:179-229.
- Devlin JT, Russell RP, Davis MH, Price CJ, Moss HE, Fadili MJ, Tyler LK. 2002. Is there an anatomical basis for category-specificity? Semantic memory studies in PET and fMRI. *Neuropsychologia* 40:54-75.
- Durrant-Peatfield MR, Tyler LK, Moss HE, Levy JP. 1997. The distinctiveness of form and function in category structure: a connectionist model. In: Shafto MG, Langley P, editors. *Proceedings of the 19th annual conference of the cognitive science society*. Stanford, CA: Lawrence Erlbaum Associates. p 193-198.
- Friston KJ, Jezzard P, Turner R. 1994. Analysis of functional MRI time series. *Hum Brain Mapp* 1:153-171.
- Friston KJ, Holmes AP, Worsley KJ, Poline JP. 1995. Statistical parametric maps in functional imaging: a general linear approach. *Hum Brain Mapp* 2:189.
- Gonnerman LM, Andersen ES, Devlin JT, Kempler D, Seidenberg MS. 1997. Double dissociation of semantic categories in Alzheimer's disease. *Brain Lang* 57:254-279.
- Greer M, van Casteren M, McLellan S, Moss H, Rodd J, Rogers T, Tyler L. 2001. The emergence of semantic categories from distributed featural representations. In: Moore JD, Stenning K, editors. *Proceedings of the 23rd annual conference of the cognitive science society*. Edinburgh, UK: Lawrence Erlbaum Associates. p 358-363.

- Gross CG, Rocha-Miranda C, Bender D. 1972. Visual properties of neurons in the inferotemporal cortex of the macaque. *J Neurophysiol* 35:96-111.
- Kan IP, Barsalou LW, Solomon KO, Minor JK, Thompson-Schill. 2003. Role of mental imagery in a property verification task: fMRI evidence for perceptual representations of conceptual knowledge. *Cogn Neuropsychol* 20:525-540.
- Martin A, Chao LL. 2001. Semantic memory and the brain: structure and processes. *Curr Opin Neurobiol* 11:194-201.
- McRae K, Cree GS. 2002. Factors underlying category-specific semantic deficits. In: Forde JD, Humphreys GW, editors. *Category-specificity in brain and mind*. Hove, UK: Psychology Press. p 291-314.
- Mishkin M, Suzuki WA, Gadian DG, Vargha-Khadem F. 1997. Hierarchical organization of cognitive memory. *Philos Trans R Soc Lond B Biol Sci* 352:1461-1468.
- Moss HE, Rodd JM, Stamatakis EA, Bright P, Tyler LK. 2005. Anteromedial temporal cortex supports fine-grained differentiation among objects. *Cereb Cortex* 15:616-627.
- Moss HE, Tyler LK. 2000. A progressive category-specific semantic deficit for non-living things. *Neuropsychologia* 38:60-82.
- Moss HE, Tyler LK, Devlin J. 2002. The emergence of category specific deficits in a distributed semantic system. In: Forde E, Humphreys GW, editors. *Category-specificity in brain and mind*. Sussex, UK: Psychology Press. p 115-148.
- Murray EA, Bussey TJ. 1999. Perceptual-mnemonic functions of the perirhinal cortex. *Trends Cogn Sci* 3:142-151.
- Murray EA, Richmond BJ. 2001. Role of perirhinal cortex in object perception, memory, and associations. *Curr Opin Neurobiol* 11:188-193.
- Randall B, Moss HE, Rodd JM, Greer M, Tyler LK. 2004. Distinctiveness and correlation in conceptual structure: behavioral and computational studies. *J Exp Psychol Learn Mem Cogn* 30:393-406.
- Raven JC. 1965. *Guide to using the colored progressive matrices*. London, UK: HK Lewis.
- Simmons WK, Barsalou LW. 2003. The similarity-in-topography principle: reconciling theories of conceptual deficits. *Cogn Neuropsychol* 20:451-486.
- Stamatakis EA, Tyler LK. 2005. Identifying lesions on structural brain images: Validation of the method and application to neuropsychological patients. *Brian Lang* 94:167-177.
- Suzuki WA, Amaral DG. 1994. Perirhinal and parahippocampal cortices of the macaque monkey: cortical afferents. *J Comp Neurol* 350:497-533.
- Taylor KI, Moss HE, Stamatakis EA, Tyler LK. 2005. Cross-modal integration and the perirhinal cortex. *J Cogn Neurosci* 17(Suppl):F299.
- Taylor KI, Moss HE, Tyler LK. 2006. The conceptual structure account: a cognitive model of semantic memory and its neural instantiation. In: Hart J, Kraut M, editors. *The neural basis of semantic memory*. Cambridge, CA: Cambridge University Press.
- Tyler LK, Bright P, Dick E, Tavares P, Pilgrim L, Fletcher P, Greer M, Moss H. 2003. Do semantic categories activate distinct cortical regions? Evidence for a distributed neural semantic system. *Cogn Neuropsychol* 20:541-560.
- Tyler LK, Marslen-Wilson W, Stamatakis EA. 2005a. Dissociating neurocognitive component processes: voxel-based correlational methodology. *Neuropsychologia* 43:771-778.
- Tyler LK, Marslen-Wilson WD, Stamatakis EA. 2005b. Differentiating lexical form, meaning, and structure in the neural language system. *Proc Natl Acad Sci USA* 102:8375-8380.
- Tyler LK, Moss HE. 2001. Towards a distributed account of conceptual knowledge. *Trends Cogn Sci* 5:244-252.
- Tyler LK, Moss HE, Durrant-Peatfield MR, Levy JP. 2000. Conceptual structure and the structure of concepts: a distributed account of category-specific deficits. *Brain Lang* 75:195-231.
- Tyler LK, Stamatakis EA, Bright P, Acres K, Abdallah S, Rodd JM, Moss HE. 2004. Processing objects at different levels of specificity. *J Cogn Neurosci* 16:351-362.
- Warrington E, McCarthy R. 1983. Category specific access dysphasia. *Brain* 106:859-878.