Objects and Categories: Feature Statistics and Object Processing in the Ventral Stream

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Abstract

■ Recognizing an object involves more than just visual analyses; its meaning must also be decoded. Extensive research has shown that processing the visual properties of objects relies on a hierarchically organized stream in ventral occipitotemporal cortex, with increasingly more complex visual features being coded from posterior to anterior sites culminating in the perirhinal cortex (PRC) in the anteromedial temporal lobe (aMTL). The neurobiological principles of the conceptual analysis of objects remain more controversial. Much research has focused on two neural regions—the fusiform gyrus and aMTL, both of which show semantic category differences, but of different types. fMRI studies show category differentiation in the fusiform gyrus, based on clusters of semantically similar objects, whereas category-specific deficits, specifically for living things, are associated with damage to the aMTL. These category-specific deficits for living things have been attributed to problems in differentiating between highly similar objects, a process that involves the PRC. To determine whether the PRC and the fusiform gyri contribute to different aspects of an object's meaning, with differentiation between confusable objects in the PRC and categorization based on object similarity in the fusiform, we carried out an fMRI study of object processing based on a feature-based model that characterizes the degree of semantic similarity and difference between objects and object categories. Participants saw 388 objects for which feature statistic information was available and named the objects at the basic level while undergoing fMRI scanning. After controlling for the effects of visual information, we found that feature statistics that capture similarity between objects formed category clusters in fusiform gyri, such that objects with many shared features (typical of living things) were associated with activity in the lateral fusiform gyri whereas objects with fewer shared features (typical of nonliving things) were associated with activity in the medial fusiform gyri. Significantly, a feature statistic reflecting differentiation between highly similar objects, enabling object-specific representations, was associated with bilateral PRC activity. These results confirm that the statistical characteristics of conceptual object features are coded in the ventral stream, supporting a conceptual feature-based hierarchy, and integrating disparate findings of category responses in fusiform gyri and category deficits in aMTL into a unifying neurocognitive framework. ■

INTRODUCTION

Recognizing an object involves not only an analysis of its visual properties but also the computation of its meaning. The neural system supporting visual analysis has been characterized as a hierarchical neurobiological system of increasing feature complexity in occipitotemporal cortex. Simple visual features are integrated into more complex feature combinations from visual cortex to anterior temporal regions along ventral occipitotemporal cortex (Tanaka, 1996; Ungerleider & Mishkin, 1982). At the apex of this stream, perirhinal cortex (PRC) is claimed to perform the most complex visual feature integrations required to discriminate between highly similar objects (Murray, Bussey, & Saksida, 2007; Bussey, Saksida, & Murray, 2002; Murray & Bussey, 1999).

The neurobiological principles of the conceptual analysis of objects remain more controversial, with studies primarily focusing on category structure (Mahon & Caramazza, 2009; Martin, 2007; Tyler & Moss, 2001; Chao, Haxby, & Martin, 1999; McRae, de Sa, & Seidenberg, 1997; Warrington & Shallice, 1984; Warrington & McCarthy, 1983) and its organizing principles. These are claimed to include domain or category membership or different property types that are shared among members of a category (e.g., visual, functional, and motor properties). Object categories have been associated with two neural regions in the ventral stream: the fusiform gyrus and the anteromedial temporal cortex (Martin, 2007; Moss, Rodd, Stamatakis, Bright, & Tyler, 2005; Tyler et al., 2004; Humphreys & Forde, 2001; Chao et al., 1999; Warrington & Shallice, 1984). Evidence for category differentiation in the fusiform gyrus comes from fMRI studies with healthy volunteers in which different parts of the fusiform preferentially respond to different object categories such as tools

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and animals (Chao et al., 1999) whereas neighboring regions of the lateral occipital complex show little category selectivity (Op de Beeck, Torfs, & Wagemans, 2008).

Category effects in the ventral stream have also been observed in studies of neuropsychological patients who show category-selective deficits. The most frequently reported findings are for category-specific deficits for living things in response to damage in anteromedial temporal lobe (aMTL; Moss et al., 2005; Tyler et al., 2004; Humphreys & Forde, 2001; Warrington & Shallice, 1984). In contrast, patients with anterolateral temporal lobe damage have a generalized semantic impairment and no category-specific impairment (Noppeney et al., 2007; Rogers et al., 2006; Moss et al., 2005). This distinction between anteromedial and anterolateral involvement has been further supported by neuroimaging studies with healthy volunteers, which show that living things preferentially engage the aMTL (Taylor, Moss, Stamatakis, & Tyler, 2006; Moss et al., 2005; Tyler et al., 2004).

Category-specific deficits for living things following damage to the anteromedial temporal cortex have been attributed to patients' difficulties in differentiating between highly similar objects (Taylor et al., 2006; Moss et al., 2005; Tyler et al., 2004). Although patients with aMTL damage have no difficulty in determining the category of an object, they are exceptionally poor at differentiating between similar objects, and this pattern is most marked for living things, especially animals (Moss et al., 2005; Tyler et al., 2004; Moss, Tyler, & Jennings, 1997), which are among the most highly confusable objects according to property norm data (Randall, Moss, Rodd, Greer, & Tyler, 2004; McRae et al., 1997; Keil, 1986; Malt & Smith, 1984). In patients with category-specific deficits, aMTL damage tends to be extensive, but one region within it— the PRC—may be the primary contributor to the deficit (Kivisaari, Tyler, Monsch, & Taylor, 2012; Tyler et al., 2004) because this region provides the neural infrastructure for complex feature integration that enables the fine-grained differentiation required for distinguishing between highly similar objects (Barense, Henson, & Graham, 2011; Moss et al., 2005; Tyler et al., 2004). Other findings support this suggestion: PRC lesions in nonhuman primates are associated with deficits in the ability to differentiate between highly ambiguous objects (Saksida, Bussey, Buckmaster, & Murray, 2007; Bussey et al., 2002) and patients with aMTL damage including the PRC have difficulty in complex feature ambiguity tasks (Barense, Gaffan, & Graham, 2007; Barense et al., 2005).

To determine whether the PRC and the fusiform gyri contribute to different aspects of an object's meaning with differentiation between confusable objects in the PRC and category differentiation in the fusiform, we carried out an fMRI study of object processing based on a feature-based model that characterizes the degree of semantic similarity and difference between objects and object categories. Feature-based models assume that conceptual representations are componential in nature:

that they are made up of smaller elements of meaning, referred to as features, properties or attributes. They account for categorization on the assumption that semantic categories are based on feature similarity, although models differ with respect to the nature of the attributes considered and the similarity computations they hypothesize (Smith & Medin, 1981). Componentiality, although not universally accepted, is now widely assumed in cognitive psychology (Mirman & Magnuson, 2008; Gotts & Plaut, 2004; Randall, Moss, Rodd, Greer, & Tyler, 2004; Cree & McRae, 2003; McRae et al., 1997) and accounts for behavioral aspects of processing the semantics of objects (Taylor, Devereux, Acres, Randall, & Tyler, 2012; Randall et al., 2004; Pexman, Holyk, & Monfils, 2003; McRae et al., 1997). This type of model also has the potential to capture the characteristics that distinguish objects from each other and thus enable individuation between similar objects. Although features that are shared by many objects provide the basis for categorization, those that are distinctive of a specific object enable similar objects to be differentiated from each other (Taylor et al., 2012; Taylor, Salamoura, Randall, Moss, & Tyler, 2008; Cree & McRae, 2003; McRae & Cree, 2002; Tyler & Moss, 2001).

The model used in this study was based on 2526 features derived from a large-scale norming study of 541 concepts (Taylor et al., 2012; McRae, Cree, Seidenberg, & McNorgan, 2005). In this study, participants generated verbal feature lists for each concept. Although the listed features (e.g., *has stripes*) are not intended to literally reflect all real features of a particular object, the statistical regularities of these features do reflect systematic statistical regularities we experience in the world that capture the content and structure of conceptual representations, provide a basis for categorization, and predict responses to semantic tasks using both words (Grondin, Lupker, & McRae, 2009; Randall et al., 2004; McRae et al., 1997) and pictures (Clarke, Taylor, Devereux, Randall, & Tyler, 2013; Taylor et al., 2012, Experiments 1 and 2). Two key aspects of conceptual representation have been tested and validated in these cognitive studies and form the basis of the current study. One important variable is the extent to which an object's features are shared by many (e.g., many animals *have fur*) or few concepts (e.g., few animals *have stripes*). The property norm statistics show that living things (e.g., animals) have many shared and few distinctive features, whereas nonliving things (e.g., tools) have fewer shared and relatively more distinctive features (Cree & McRae, 2003; Tyler & Moss, 2001). The issue is whether sharedness will be associated with activity in the fusiform, and if so, whether these property statistics will be associated with differentiation within the fusiform. Specifically, will the differential effects of sharedness overlap with the medial-lateral distinction in the fusiform such that the effects of greater sharedness will overlap with the lateral fusiform, known to be associated with animals (Chao et al., 1999), and effects of fewer shared features will overlap with tool-associated regions of the medial fusiform

(Chao et al., 1999)? That is, does the feature statistic variable of Sharedness explain fusiform gyrus activity as well as the living/nonliving variable?

A second feature statistic variable is that of correlational strength or feature co-occurrence, where highly correlated features (e.g., *has eyes* and *has ears*) co-occur frequently and mutually coactivate, facilitating feature integration (McRae et al., 1997; Rosch, Mervis, Gray, Johnson, & Boyes-Braem, 1976). Property norm statistics show that living things have more weakly correlated distinctive features compared with nonliving things (Taylor et al., 2008; Randall et al., 2004), making them more difficult to differentiate from other category members. As a consequence, living things are disadvantaged relative to nonliving things on those tasks that require differentiation between similar objects. One such task is basic level identification, which requires differentiating between similar objects by integrating a concept's distinctive features with its shared features. For example, a basic level naming response cannot be made on the basis of individual features such as the shared features *has legs* (dog?) or *lives in zoos* (elephant?), or the distinctive feature *has stripes* (shirt?). Instead, the individual shared and distinctive features must be integrated together (*has legs + lives in zoos + has stripes*) to know that the concept is, for example, a tiger. This process is facilitated by the correlational strength of a concept's distinctive features: Concepts with weakly correlated distinctive features, which are more difficult to integrate with the other object features, place greater demands on the complex feature integration computations required for basic level identification. In contrast, concepts with relatively highly correlated distinctive features are identified at the basic level more quickly than concepts with weakly correlated distinctive features (Taylor et al., 2012; Randall et al., 2004). The issue is whether the PRC, which is claimed to integrate the most complex feature conjunctions, will be preferentially engaged by these processes.

In the present fMRI study, we used a basic level naming task because it engages the entire ventral stream (Tyler et al., 2004) and therefore allows us to determine whether regions within the stream are involved in processing different aspects of an object's meaning. To determine whether feature statistic variables account for activity within different regions of the stream, we correlated activity with the two conceptual structure variables Sharedness and Correlation × Distinctiveness (see Task Design and Materials) after visual effects had been accounted for. We predicted that these two variables would differentiate between neural regions where activity is driven by (a) similarity of conceptual structure reflecting category structure (i.e., the relative amount of shared features within a concept) and (b) differentiation between similar concepts (Correlation × Distinctiveness, i.e., the relative extent to which the distinctive features critical to basic level differentiation are correlated with other features in the concept).

METHODS

Participants

Fifteen healthy, right-handed, native British English speakers participated in the fMRI study (nine men; mean age = 24 years, SD = 5 years). The major exclusion criteria were bilingualism; left-handedness; MR contraindications; neurological, psychiatric, or hormonal disorders; dyslexia; and color blindness. All participants had normal or corrected-to-normal vision, gave informed consent, and were paid for their participation. The study was approved by the East of England–Cambridge Central Research Ethics Committee.

Task Design and Materials

This fMRI study measured the influence of feature statistic variables on BOLD activity associated with basic level picture naming while controlling for visual variables. We selected all picturable concepts (n = 388) from an anglicized version (Taylor et al., 2012) of the McRae et al. (2005) property norm set. The pictures had high exemplarity (i.e., ratings on a 7-point Likert scale, which reflect the goodness with which the picture represented the written concept word, with seven reflecting a perfect representation). An independent group of 17 healthy individuals gave a mean rating ($\pm SD$) of 5.11 (± 0.88), ensuring that the object pictures are representative of the concept. The mean naming and concept agreement for the picture set was 76% and 82% based on a further independent sample of 20 healthy participants. The feature statistic variables were based on standard measures of "feature distinctiveness" (i.e., 1/[number of concepts the feature occurs in]) and the correlational strength of features (Taylor et al., 2012; Randall et al., 2004; Vigliocco, Vinson, Lewis, & Garrett, 2004; Tyler & Moss, 2001; McRae et al., 1997; Rosch et al., 1976) calculated based on the entire set of 517 anglicized feature norm concepts (Taylor et al., 2012; McRae et al., 2005). "Feature distinctiveness" has higher values for more distinctive features such as *has stripes*, but lower values for shared features such as *has fur*. We are interested in these shared features, since they provide the basis for categorization.

From these two standardly used measures, we calculated two feature statistic indices. The first measure, *Sharedness*, is a measure of the degree of sharedness of the features in a concept (i.e., how often a concept's features occur in other concepts). For each concept, Sharedness is defined as 1 minus the square root of the mean distinctiveness of the concepts' features (the square root transformation was applied to reduce the skew of the distribution). Sharedness has high values for concepts with proportionately more shared features (e.g., animals) and low values for concepts with proportionately more distinctive features (e.g., tools; see Table 1).

Second, we calculated *Correlation × Distinctiveness* as the slope of the regression of correlational strength

Table 1. Characteristics of All Stimuli and Separately for Living and Nonliving Objects: Key Feature Statistic Variables (C×D = Correlation × Distinctiveness; NOF = Number of Features; NODF = Number of Distinctive Features), Objective Visual Complexity (Size of JPEG Files), Naming and Concept Agreement, and Naming Latency for Correct Trials (RT)

	All		Living		Nonliving	
	Mean	SD	Mean	SD	Mean	SD
Sharedness	0.45	0.15	0.53	0.12	0.40	0.14
C×D	0.79	0.84	0.57	0.80	0.94	0.84
Correlational strength[a]	0.51	0.07	0.52	0.07	0.50	0.07
NOF	12.6	3.3	13.1	3.5	12.2	3.2
NODF	3.9	2.7	2.9	2.3	4.5	2.7
Visual complexity (JPEG file size)	10.5	0.6	10.7	0.5	10.4	0.6
Naming agreement (%)	76	28	71	32	79	25
Concept agreement (%)	82	25	75	30	87	20
RT (correct name, msec)	965	77	990	82	951	75

[a]Mean correlation of shared features within concept.

on distinctiveness values over all features in the concept, excluding highly distinctive features that occur in only one or two concepts because their correlational strength values may be spurious (Taylor et al., 2008, 2012; Cree, McNorgan, & McRae, 2006). This measure represents the relative correlational strength of shared versus distinctive features within a concept. Thus, concepts with low or negative Correlation × Distinctiveness values have relatively weakly correlated distinctive compared with shared features, generating greater demands on complex conceptual integration processes that bind distinctive with shared features to enable basic level identification (see Table 1).

We also constructed variables to represent the visual information present in the pictures using Gabor-filtered images to capture the spatial position and orientation of the objects. Related Gabor filter models have been used to model perceptual processing in the visual system (Nishimoto et al., 2011; Naselaris, Prenger, Kay, Oliver, & Gallant, 2009; Kay, Naselaris, Prenger, & Gallant, 2008). Gray-scale versions of the images were reduced to 153 × 153 pixels before applying Gabor filters with four orientations (0°, 45°, 90°, 130°) and five spatial frequencies (1, 2, 4, 8, 16 Hz [cycles/image]). Next, the set of 388 Gabor-filtered pictures were vectorized, and the 23,409 pixel × 388 picture matrix was entered into a PCA using the Matlab function "princomp" (Mathworks, Natick, MA). Each resulting component described part of the variance in pixel intensity across the set of pictures, with the first component describing the strongest common influence on variance (i.e., overall intensity) and subsequent components describing progressively more subtle components of the variance (difference in intensity between the top and bottom of the image, center and surround, etc.). The first eight components were selected, according to the

Scree test, and together explained 60% of the variance in image intensity. The loadings of these eight components on the 388 images were used to model the visual properties of the pictures.

All pictures, on a white background, were resized to fit comfortably on a computer screen with the longest axis spanning maximally 750 pixels horizontally or 550 pixels vertically (maximum visual angle 12.2° horizontally or 9.0° vertically) and were saved as JPEG images using identical compression settings. In addition to these 388 objects, the stimuli in the fMRI study included fixation crosses (n = 50) and phase-scrambled images of target stimuli (n = 54; scrambled using the Fourier method in Matlab) as low level visual baselines.

The items were presented in the same pseudorandomized order for each participant. The pseudorandomization ensured that no more than two items from the same semantic category (e.g., animal, furniture, vegetable) or beginning with the same phoneme followed one another. The pseudorandomization of pictures with fixation and scrambled images ensured a jittered, geometric distribution of stimulus onset asynchronies for the picture stimuli, which optimizes detection of BOLD activity.

fMRI Procedure

Pictures and baseline stimuli were pseudorandomized and presented in two blocks of approximately equal length. Each stimulus was displayed in the center of a projection screen in the scanner for 2000 msec followed by an intertrial interval of 1100 msec. Participants were instructed to name aloud each picture as quickly and accurately as possible, to respond to phase-scrambled images by saying "blur" aloud, and to fixate on a fixation

cross without responding. E-Prime software (Psychology Software Tools, Sharpsburg, PA) controlled presentation and timing of stimuli. Participants' spoken responses were collected during scanning using an OptiMRI noise-canceling microphone system (Optoacoustics Ltd., Moshav Mazoe, Israel). Stutters and no responses were scored as incorrect. Moreover, only object names that exactly corresponded to the concept name in the feature norm study (McRae et al., 2005) were scored as correct and thus included in the fMRI analyses to ensure that the corresponding feature statistic data were valid measures of the processed concept (e.g., although both "bread" and "loaf" could describe a given object, they may be associated with different nonperceptual and perceptual features).

Participants' response latencies were calculated using in-house software on the voice recordings made during the scan. Continuous scanner recordings were filtered to suppress frequencies over 700 Hz using a Chebyshev type I filter and split into segments containing naming responses to individual items. Naming onsets were determined relative to picture onset using custom software by finding the first time point where both (a) the root mean square power exceeded 5 standard deviations above a pre-object baseline period and (b) this root mean square power level was exceeded for at least 40 msec. Any naming latencies less than 500 msec were manually verified and corrected if necessary. To reduce the influence of outlying response latencies, we inverse-transformed the individual RTs (Ratcliff, 1993) then retransformed them after averaging for each participant to give the harmonic mean (msec).

Image Acquisition

Scanning was conducted on a 3T Siemens Tim Trio system at the MRC Cognition and Brain Sciences Unit, Cambridge, England. Continuous functional scans were collected using gradient-echo EPI with 32 slices, 3 mm isotropic voxel dimensions, repetition time = 2 sec, echo time = 30 msec, field of view = 192 × 192 mm, matrix = 64 × 64, flip angle = 78°. T1-weighted anatomical MPRAGE scans were acquired with repetition time = 2250 msec, echo time = 3 msec, inversion time = 900 msec, field of view = 256 mm × 240 mm × 160 mm, matrix size = 256 × 240 × 160.

Imaging Analyses

fMRI data were preprocessed and analyzed with SPM5 software (Wellcome Trust Centre for Neuroimaging, www.fil.ion.ucl.ac.uk/spm/software/spm5/) implemented in Matlab (Mathworks, Natick, MA). Preprocessing comprised slice time correction, within-subject realignment (motion correction), unified spatial normalization, and spatial smoothing with an 8-mm FWHM Gaussian smoothing kernel. Low-frequency noise was removed using a high-pass filter with a period of 128 sec in the SPM general linear model (GLM).

Each participant's data were analyzed with the GLM using the canonical haemodynamic response function. The correctly named pictures, incorrectly named pictures, and two baseline conditions were modeled as separate regressors. We also modeled the visual and feature statistic variables as parametric modulators of the regressor for correctly named pictures: First, the eight PCA components characterizing the Gabor-filtered images, then Sharedness and finally Correlation × Distinctiveness. Each modulator was orthogonalized with respect to previous modulators, ensuring that the effects of the feature statistic variables were not confounded with the visual variables. We confirmed that the Sharedness and C×D variables were not correlated with each other ($r = .06$, $p > .05$) and that there were no significant correlations between any of the eight Gabor PCA variables and either Sharedness or C×D (max $r < .14$, all family-wise error [FEW] $p > .05$). The model also included the six movement parameters produced by realignment (above) as nuisance variables.

The GLM in SPM includes implicit masking, which by default excludes voxels with signal below 80% of the mean signal over all voxels in the brain. This heuristic is used to avoid including brain regions with low BOLD signal because of variations in magnetic susceptibility, such as the anterior temporal regions under investigation. Because this heuristic approach may exclude voxels with low but reliable BOLD signal, we lowered the implicit masking threshold to 10% and then defined reliable voxels using a more specific measure of temporal signal-to-noise ratio (TSNR). We calculated TSNR maps for each participant by dividing the mean functional image intensity over time at each voxel by its standard deviation. We then calculated a group-averaged TSNR map and defined reliable voxels as those with mean TSNR > 40 (Murphy, Bodurka, & Bandettini, 2007). The group-averaged TSNR map indicated adequate reliability of signal in the aMTL region including the PRC (Figure 1). Subsequent group-level analyses included only voxels with group mean TSNR > 40.

Group level random effects analyses were run by entering parameter estimate images from each participant's GLM into one-sample t tests or F contrasts. Results were thresholded at voxel level $p < .01$ uncorrected and cluster level $p < .05$ with FWE correction for multiple comparisons. To explore more completely the a priori predictions that Sharedness would modulate activity in the fusiform gyri and C×D activity in the PRC, we report additional results using a lower cluster size threshold. This is especially critical with respect to the predicted effects of Correlation × Distinctiveness in the PRC, since this region is known to show small changes in BOLD signal (Cohen & Bookheimer, 1994). For this reason, results for Correlation × Distinctiveness are shown both at the standard threshold noted above and at a

Figure 1. TSNR around PRC is sufficient for detection of BOLD activity. Color bar shows group mean TSNR, where a minimum of 40 is needed to detect BOLD activity. Slice positions are reported in MNI coordinates and shown as dotted lines on the axial section.

TSNR

0   40 (threshold)   200

$x = -50$ mm $z = -30$ mm $x = +50$ mm

$y = +10$ mm $y = 0$ mm $y = -10$ mm
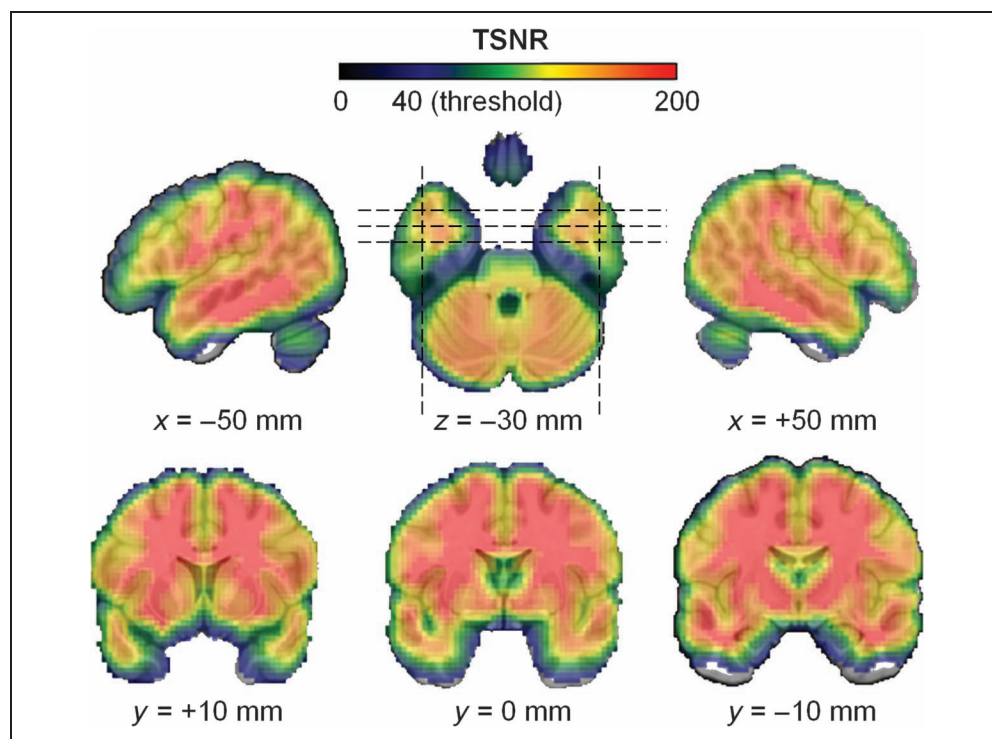
reduced threshold of cluster-level $p < .05$ uncorrected, including only those voxels with low but reliable signal (i.e., intermediate TSNR between 40 and 100). Given our a priori hypothesis that Sharedness would modulate activity within the fusiform gyrus, we examined the effect of Sharedness within the fusiform gyrus without cluster-level thresholding. We defined the extent of the fusiform ROI using the Harvard-Oxford atlas (fsl.fmrib.ox. ac.uk/fsl/fslwiki/Atlases). Voxels were included if the atlas labeled them as "temporal fusiform cortex, posterior

Figure 2. Brain activity associated with picture naming. (top) Contrast of basic level naming versus scrambled images overlaid on the ventral cerebral surface. Activation specific to naming meaningful objects (controlling for verbal output) was found along the anterior to posterior extent of the ventral stream. (bottom) Activity explained by the visual model, where effects were focused in the bilateral occipital poles, with weaker effects extending to the posterior parts of the fusiform and inferior temporal gyri (see text for details). Color bars represent voxel t and F values (degrees of freedom).

Pictures > Scrambled

$z = -18$ mm $z = -9$ mm $z = 0$ mm $z = +9$ mm $z = +18$ mm

0    $t(14)$ 12

Visual model

$z = -18$ mm $z = -9$ mm $z = 0$ mm $z = +9$ mm $z = +18$ mm
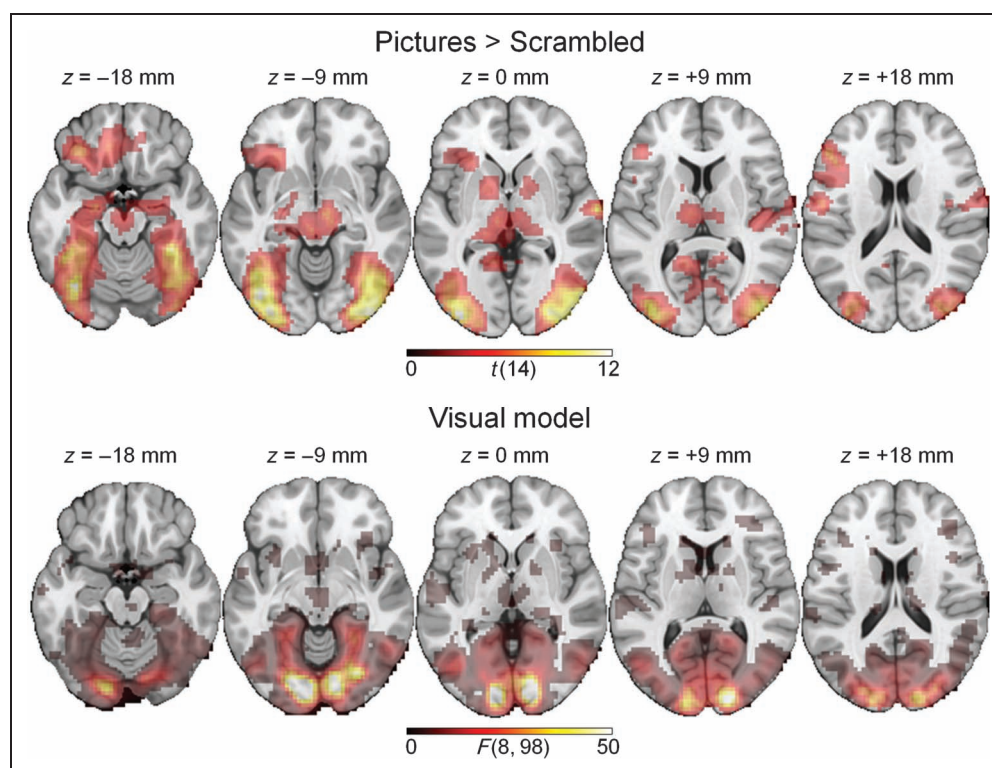
0    $F(8, 98)$ 50

Figure 3. Sharedness of object features modulates BOLD activity within the fusiform gyrus. (top) Objects with relatively more shared features were associated with greater BOLD activity in the bilateral lateral fusiform gyri, regions previously associated with activity for animals (Martin, 2007; Chao et al., 1999), consistent with the greater number of shared features in animals than tools (voxel level threshold $p < .01$, cluster level threshold $p < .05$ FWE). (bottom) The a priori prediction that Sharedness would differentially modulate the medial and lateral fusiform gyri was tested within an anatomically defined fusiform ROI without cluster level thresholding. Objects with more shared features (orange) produce activity in lateral fusiform and those with fewer shared features (blue; corresponding to tools) produce activity in the bilateral medial fusiform gyri. Slice positions are given as MNI coordinates, and color bars represent voxel t values (degrees of freedom).
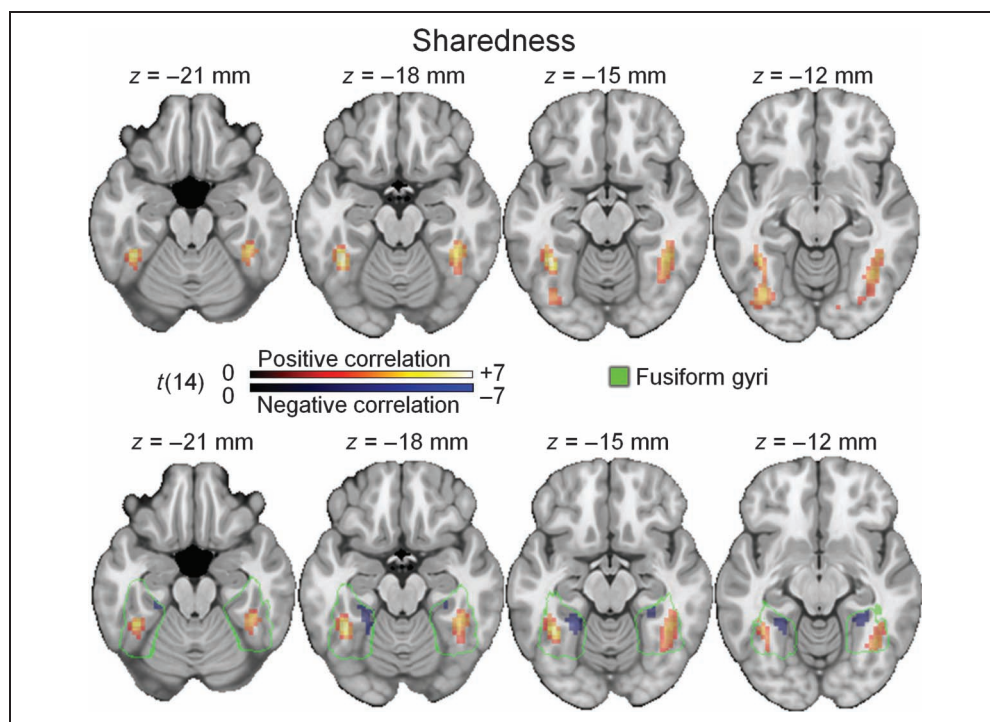
division" or "temporal occipital fusiform cortex" with a probability of >10%.

In follow-up analyses, we determined whether Sharedness generated differential activity in medial and lateral fusiform gyri and whether this tracked category effects in the fusiform (Chao et al., 1999). We defined linear ROIs in each hemisphere as lines of voxels between medial and lateral points in the fusiform gyri in three coronal planes at Montreal Neurological Institute (MNI) $y = -48$, -57, and -66 mm (Figure 4, center column). These planes crossed the anterior, middle, and posterior parts of the category effects reported by Chao et al. (1999). We avoided examining activity in successive sagittal planes (i.e., from medial to lateral along the x axis in MNI space), as this is relatively imprecise and may dilute effects by including nonresponsive voxels. Instead, we defined linear ROIs following the actual anatomy of the fusiform, which is slightly oblique to the x axis in MNI space. Parameter estimates were extracted from successive voxels along the linear ROIs from two additional GLMs, the first based on explicit categories (living and nonliving) and second on the Sharedness variable. As in the main model described above, modulators were orthogonalized serially, with the eight visual parametric modulators entered first. The ninth para-

metric modulator was either category membership ($+1$ for living, -1 for nonliving) or the Sharedness value for each concept. In this way, we examined the differential sensitivity of medial and lateral fusiform gyri to category level information defined either explicitly or using feature statistics in two separate but comparable models.

RESULTS

Picture Naming Performance

Seventy-three percent of responses were scored as correct according to the criteria described in the fMRI Procedure. A further 8% identified the correct concept, but using a verbal label that did not correspond to that in the property norm study (e.g., "loaf" instead of "bread"). Of the remaining 19% of responses scored as incorrect, 4% were no responses, 2% were stutters, and 13% were the incorrect concept (e.g., "lion" instead of "tiger"). This accuracy rate is comparable to those obtained in other studies using large sets of pictures and similar criteria for coding errors (e.g., Taylor et al., 2012; Graves, Grabowski, Mehta, & Gordon, 2007; Alario et al., 2004; Barry, Morrison, & Ellis, 1997; Levelt, Schriefers,

Meyer, Pechman, & Vorberg, 1991). The mean ($\pm SD$) overt basic level naming latency over all correct items was 965 msec (± 77; see Table 1), comparable with previous fMRI studies (e.g., Graves et al., 2007).

Object-related Activity in the Ventral Stream

To identify the neural regions associated with object processing, BOLD activity associated with the correctly named objects was contrasted with the phase-scrambled images (voxel level $p < .001$, cluster level $p < .05$ FWE). We found activity throughout the occipital lobes and bilateral ventral streams through to posterior PRC, extending to right anterior PRC and hippocampus and left amygdala (Figure 2, left), and also in bilateral ventral precentral cortices and left OFC, replicating previous findings (Tyler et al., 2004).

The following analyses focus on the visual and feature statistics variables (see Task Design and Materials). We first correlated BOLD responses with visual features, represented by eight PCA components derived from the Gabor-filtered images. These eight regressors were entered into a one-way ANOVA and tested using an "effects of interest" F contrast. Because this contrast tests for voxels showing a response to any one of the eight visual regressors, we report results using a more conservative voxel level threshold of $p < .05$ FWE with a minimal cluster size threshold of 10 voxels, because correction was applied at the voxel level. Significant main effects were observed in the bilateral occipital poles (Figure 2, right; peak voxels in each hemisphere: MNI 12, -90, -3 mm, $F(8, 98) = 88.3$, and MNI 15, -90, 0 mm, $F(8, 98) = 88.1$), similar to previous results (e.g., Kwong et al., 1992). Outside the occipital lobe, we found weaker activation extending anteriorly along the fusiform and lingual gyri (peak voxels outside occipital lobe: MNI 27, -51, -9 mm, $F(8, 98) = 23.8$ and MNI -24, -48, -9 mm, $F(8, 98) = 21.2$) to the posterior end of the inferior temporal gyrus.

Objects with higher values on the Sharedness variable (i.e., greater degree of feature sharedness) produced

Figure 4. Activity patterns within the fusiform gyrus for the contrast of living versus nonliving objects closely track the correlation with Sharedness, but not the correlation with C×D. Linear ROIs (center column; see Imaging Analyses) traversing the fusiform gyri at $y = -48$ mm (A), -57 mm (B), and -66 mm (C) were used to extract activity values (t values) in successive voxels from left to right. The resulting plots (left and right columns) confirm region-specific similarities in activation between the living versus nonliving contrast (black) and the correlation with Sharedness (solid gray) but not the correlation with C×D (dashed gray). Regions responding preferentially to living things (relative to nonliving things) also respond to concepts with relatively more shared features, and regions responding preferentially to nonliving things (relative to living things) also respond to concepts with relatively fewer shared features. In contrast, these regions are not modulated by the requirement for feature integration (C×D). The fine and course dashed horizontal reference lines indicate t values corresponding to $p < .01$ and .001, respectively.
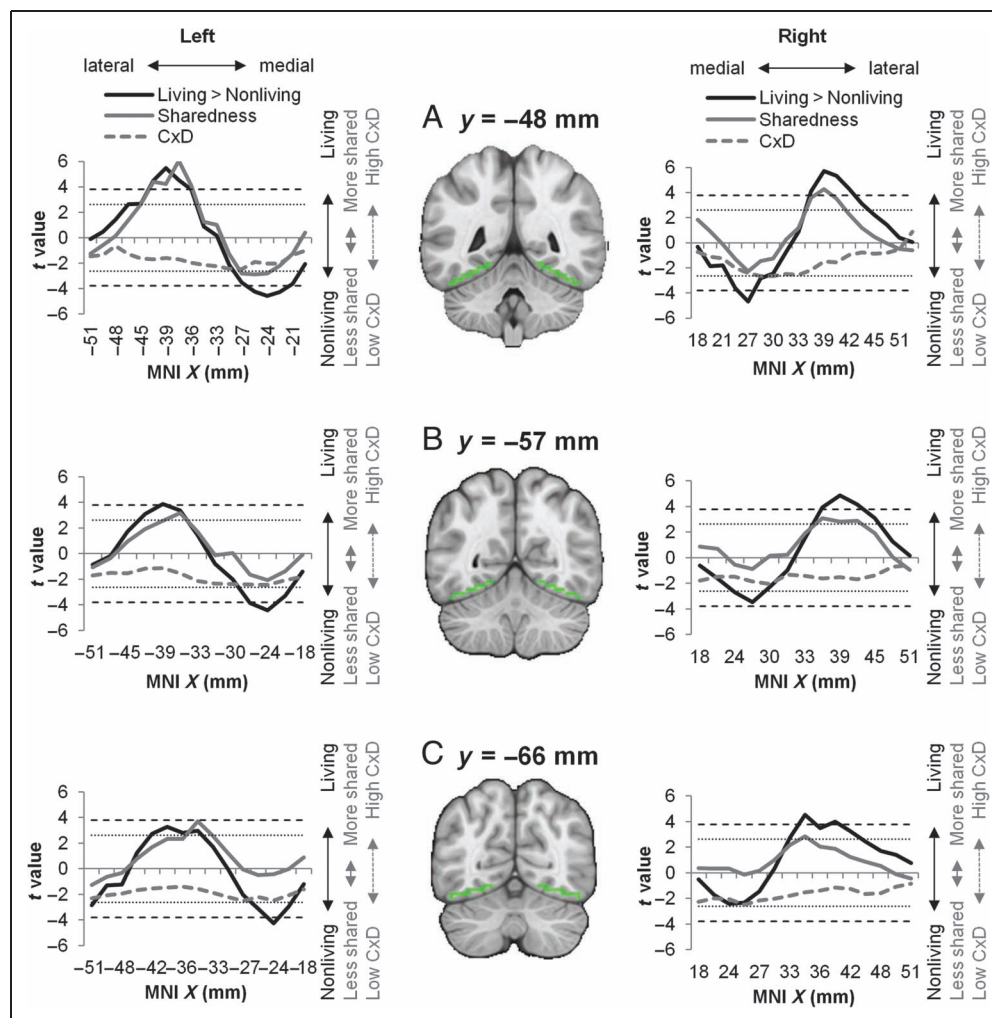
Figure 5. The feature statistic Correlation × Distinctiveness modulates BOLD activity in anteromedial temporal cortex. (top) Objects with lower Correlation × Distinctiveness values—indicating relatively weakly correlated distinctive features requiring more complex feature integration processes for their unique identification—were associated with greater activity in the anteromedial temporal cortex including the left PRC at voxel level $p < .01$, cluster level $p < .05$ FWE. (bottom) At voxel level $p < .01$, uncorrected cluster level $p < .05$ in voxels with intermediate TSNR of 40–100, bilateral PRC activation was seen. To maximize anatomic localizability of the clusters with respect to the PRC (Pruessner et al., 2002), clusters are shown on the average participant brain. Slice positions are reported as MNI coordinates and the color bar represents voxel t values (degrees of freedom).
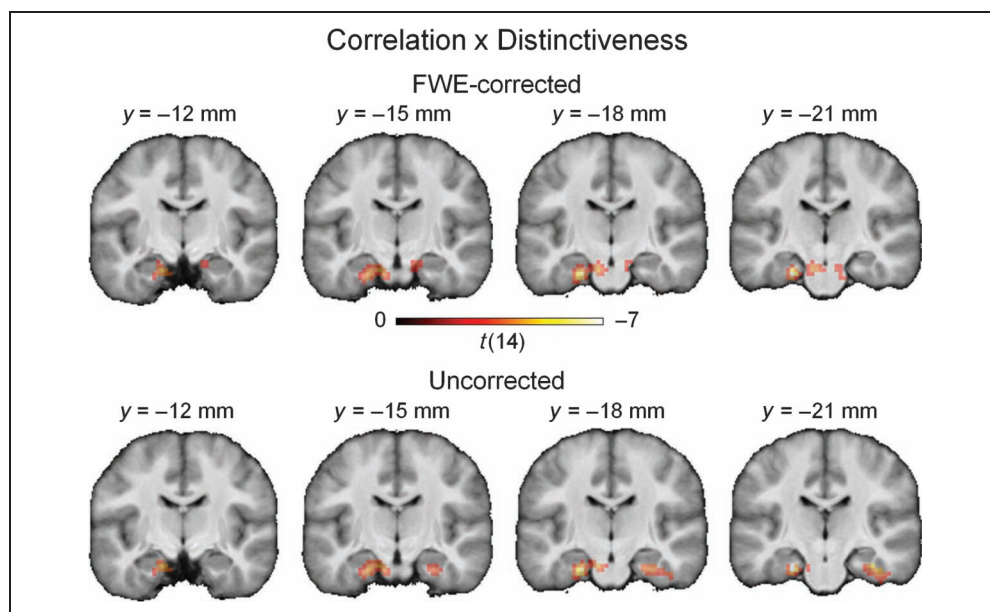
greater activity in bilateral lateral fusiform gyri (Figure 3, top; peak voxels MNI 42, −39, −27 mm, $t(14) = 4.9$ and MNI −39, −48, −18 mm, $t(14) = 4.2$) and posterior occipital and ventral occipitotemporal regions (peak voxel MNI 12, −90, 3 mm, $t(14) = 6.5$). These regions corresponded to those previously reported as showing greater activity to animals than tools (Chao et al., 1999). To further explore these effects, in particular in medial fusiform regions, we examined activity within the fusiform gyrus without cluster-level FWE correction (Figure 3, bottom). At this threshold, we saw the same positive effect of Sharedness in the lateral fusiform, and in addition a negative effect of Sharedness, corresponding to increased activity for objects with lower values of the Sharedness variable (i.e., fewer shared features) in bilateral medial fusiform gyri (peak voxels MNI 30, −45, −9 mm, $t(14) = 3.8$ and MNI −24, −45, −15 mm, $t(14) = 3.6$). This result is consistent with previous reports of greater activity in medial fusiform gyri to tools than animals (Chao et al., 1999).

We then examined anatomical variability of activity within the fusiform gyri along lines of voxels traversing medial to lateral sites (see Imaging Analyses; Figure 4, center column). Medial and lateral fusiform regions showed opposite effects, with lateral regions more active for items with more shared features and medial regions more active for objects with less shared features (Figure 4, gray lines on plots). Lateral voxels at MNI $X = \pm36$–39 mm typically showed the highest positive correlation with Sharedness, whereas medial voxels at MNI $X = \pm24$–

27 mm typically showed the lowest negative correlation. Moreover, the medial to lateral pattern of activity for the Sharedness variable tracked closely with the pattern produced by contrasting the explicit categories "living" and "nonliving" (Figure 4, black lines on plots): The lateral fusiform gyri responded more to living things (which typically have more shared features), whereas the medial fusiform gyri showed the reverse pattern, responding more to nonliving things (which have fewer shared and more distinctive features). To confirm that the living and nonliving objects used in this study differed in their degree of sharedness, we compared the Sharedness values for the living and nonliving objects. Consistent with previous studies, living things had significantly greater feature sharedness (mean Sharedness = .53, $SD = .12$) than nonliving things (mean Sharedness = .40, $SD = .14$; difference between mean living and nonliving; $t(386) = 9.27$, $p < .0001$).

The effects of the Correlation × Distinctiveness variable showed that objects whose distinctive features were relatively more weakly correlated than their shared features (typical of living things) elicited stronger activity in the anteromedial temporal cortex, primarily left perirhinal and entorhinal cortices (Figure 5, left; peak voxel: MNI −24, −21, −27 mm, $t(14) = -6.9$). There were no significant activations associated with relatively more strongly correlated distinctive compared with shared features. We further explored these effects at a reduced threshold (see Imaging Analyses). Whereas the positive contrast remained nonsignificant, the negative contrast

now revealed bilateral PRC activation associated with naming concepts with relatively more weakly correlated distinctive than shared features (see Figure 5, right; peak voxels: $-24, -21, -27, t(14) = -6.9$ and $39, -24, -24, t(14) = -6.0$). Two small clusters were also found in the left medial superior and orbital frontal lobe (peak voxels: MNI $-6, 63, 37$ mm, $t(14) = -5.1$ and MNI $-3, 57, 36$ mm, $t(14) = -4.29$). Because distinctive features must be integrated with a concept's shared features for basic level identification, confusable concepts with relatively weakly correlated distinctive features require more complex feature integration processes supported by the bilateral PRC for their unique identification (Taylor, Devereux, & Tyler, 2011; Tyler & Moss, 2001).

DISCUSSION

In this study, we used a feature-based model of semantics to determine how two key aspects of object semantics—object-specific and category information—are neurally represented and processed. This feature-based approach to object representations in the brain has previously been validated in cognitive studies, which show that feature statistics affect conceptual processing (Taylor et al., 2012; Randall et al., 2004; Pexman et al., 2003; Cree, McRae, & McNorgan, 1999; McRae et al., 1997). The statistics used in these experiments are based on features obtained from large-scale property norming studies (e.g., McRae et al., 2005). Participants in property norm studies are biased to report salient, verbalizable, and distinguishing features (McRae et al., 1997, 2005; Tyler et al., 2000). Although it is assumed that these biases do not interact with concept type or category, this assumption requires experimental validation. Thus, although feature statistics derived from feature norm studies are generally regarded as the "gold standard" for characterizing the semantics of concepts, surpassing semantic feature data obtained using automatic extraction algorithms on large-scale corpora (Devereux, Pilkington, Poibeau, & Korhonen, 2010), the inherent biases in feature norming data represent a potential limitation in any study using these data. Behavioral studies have shown that a variety of feature statistics—including those used here—affect behavioral responses (Taylor et al., 2012; Randall et al., 2004; McRae et al., 1997). For example, Taylor et al. (2012) showed that shared features facilitated category decisions on objects whereas the ease with which distinctive features could be integrated into a concept (as measured by the Correlation × Distinctiveness variable) facilitated object-specific identification, reflecting the functional relevance of different types of information carried by the relationship between different features within a concept.

Consistent with the behavioral studies, in the present experiment, we found that feature statistics, reflecting different aspects of an object's meaning, activated different neural regions. Sharedness—which captures the degree to which a concept's features are shared with other con-

cepts and thus forms the basis of category organization—modulated activity within the fusiform gyri. Moreover, we found greater activation in lateral fusiform gyri for objects with higher Sharedness and greater activation in medial fusiform gyri for objects with lower Sharedness. This profile of lateral to medial activity within each hemisphere closely tracked activity for living and nonliving things, with greater Sharedness showing similar effects as living things and less Sharedness showing similar effects as nonliving things. This correspondence between the effects of Sharedness and living things is consistent with the claim that living things have higher proportions of shared properties than nonliving objects (Randall et al., 2004; Cree & McRae, 2003; Rosch et al., 1976), a pattern replicated in the present set of objects where living things had more shared properties than nonliving things. Feature-based models of semantics claim that category structure (e.g., living, nonliving things) is an emergent property of feature statistics (Vigliocco et al., 2004; Cree & McRae, 2003; Garrard, Lambon Ralph, Hodges, & Patterson, 2001; Tyler & Moss, 2001; Durrant-Peatfield, Tyler, Moss, & Levy, 1997), raising the possibility that features may provide an organizing principle for category structure in the brain. However, this is a difficult hypothesis to test empirically because of the inherent interdependence between Sharedness and category.

In contrast to the effects in the fusiform, feature statistics that differentiate between similar objects and enable object-specific representations were associated with aMTL activity, including in the bilateral PRCs. These results further support the view that the meaning of concrete objects is neurally coded in terms of feature-based representations. Taken together, the present findings suggest a hierarchy of semantic processing in the ventral stream with similar computational properties as has been proposed for the hierarchical model of perceptual object processing developed in nonhuman primates (Taylor et al., 2011; Taylor, Moss, & Tyler, 2007; Tyler et al., 2004). This perceptual model claims that simple visual features are coded in posterior ventral occipital sites, with increasingly more complex feature combinations computed from posterior to anterior regions in ventral temporal cortex (Tanaka, 1996; Ungerleider & Mishkin, 1982). Nonhuman primate IT neurons code for moderately complex features (Tanaka, 1996), whereas PRC, at the endpoint of this hierarchical system, generates feedback signals to bind the relevant information in IT cortex together (pair-coding properties; Higuchi & Miyashita, 1996), thereby coding for the most complex feature combinations necessary to disambiguate highly confusable objects (Murray et al., 2007; Bussey et al., 2002). Critically, nonhuman primate research also demonstrates that the ventral stream codes not only perceptual object properties, but also the meaning of these properties (Hoffman & Logothetis, 2009; Sigala & Logothetis, 2002). Such findings demonstrate that, in contrast to the less flexible, retinotopic coding at the posterior end of the ventral stream, information

represented in the anterior region becomes tuned to meaningful, task-relevant features with experience. Moreover, just as the visual hierarchy is achieved by recurrent activity between posterior and anterior sites within the ventral stream (Hegdé, 2008), so communication between the fusiform and anterior temporal lobe during object processing is underpinned by recurrent activity between these two regions (Clarke, Taylor, & Tyler, 2011).

The finding that the two anatomically distinct regions associated with category selectivity in previous studies—aMTL and fusiform—are sensitive to different aspects of an object's semantic features supports the suggestion that posterior and anterior sites differ in their ability to integrate less or more complex semantic feature conjunctions, respectively. In this study, we found that feature statistics that capture the similarity between objects (shared features) were associated with activity in fusiform regions previously linked to category-specific responses (Martin, 2007). Category responses (e.g., viewing, matching) require simpler feature conjunctions than those needed for fine-grained differentiation between similar objects within a category; these latter involve the most complex feature conjunctions (Moss et al., 2005; Tyler et al., 2004) that are reflected in our second measure of Correlation × Distinctiveness. This measure captures the relative strength of the correlation for distinctive and shared features within an object, and thus the ease with which features can be integrated, thus enabling similar objects to be successfully differentiated from each other. According to property norm data, these are typically living things, especially animals (Taylor et al., 2008, 2012; see also Table 1). The present results show that objects with this statistical profile engage the aMTL, especially the PRC, more than objects whose distinctive features are strongly correlated with its other features and are thus easier to differentiate one from another.

These results are consistent with neuropsychological studies demonstrating that patients with aMTL damage that includes the PRC have particular problems differentiating between highly similar objects, especially animals (Tyler & Moss, 2001). These patients exhibit a very specific kind of category-specific deficit; they have considerable difficulties with the distinctive properties of objects and thus are unable to differentiate similar objects from each other. Thus, they have little difficulty in identifying an object's category but cannot differentiate between members within the same category. Moreover, this problem is much more pronounced for living than non-living things (Moss, Tyler, & Devlin, 2002; Tyler & Moss, 2001; Moss, Tyler, Durrant-Peatfield, & Bunn, 1998). The feature-based model described here can account for this behavioral effect in patients and its association with a specific neural region.

Supporting evidence for a posterior to anterior shift in neural activity in terms of the types of integration computations required comes from studies that manipulate the subject's task and consequently the kind of conceptual representation required (Clarke et al., 2011; Tyler et al., 2004). These task manipulations require participants to process an object at different levels of specificity—as a member of a category or as a specific object (*animal*, *camel*). Naming an object as a member of a category requires simpler feature conjunctions and activity is confined to posterior sites. Making an object-specific response to the same object, which requires the computation of more complex feature conjunctions, also engages aMTL (Barense, Henson, Lee, & Graham, 2010; Moss et al., 2005; Tyler et al., 2004). This is consistent with the notion that both perceptual and conceptual object processing progresses from a coarse- to fine-grained analysis along the ventral stream (Clarke et al., 2013; Taylor et al., 2012; Tyler et al., 2004). The use of a basic level naming task in this study ensured functional activity along the entire ventral stream (Tyler et al., 2004) as well as the integration of distinctive with shared object features required for unique object identification, thus enabling the measurement of the effects of both the relative proportion of shared features and the relative correlational strength of shared and distinctive features.

In conclusion, this study suggests that a conceptual hierarchy, analogous to the perceptual hierarchy, and based on semantic feature statistics which capture statistical regularities of concepts experienced in the world, underpins the recognition of meaningful objects in the ventral temporal cortex. By combining a cognitive model of semantic representations with a neurobiological model of hierarchical processing in the ventral stream, it accounts for variation in neural activity as a function of the semantic structure of individual objects and the relationship between objects, and provides a unifying framework for heretofore unconnected findings of category responses in the fusiform (e.g., Chao et al., 1999) and category effects in anteromedial temporal cortex (Moss et al., 2005).

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