Distinctive semantic features in the healthy adult brain

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Abstract

The role of semantic features, which are distinctive (e.g., a zebra's stripes) or shared (e.g. has four legs) for accessing a concept, has been studied in detail in early neurodegenerative disease such as semantic dementia (SD). However, potential neural underpinnings of such processing have not been studied in healthy adults. The current study examines neural activation patterns using fMRI while participants completed a feature verification task, in which they identified shared or distinctive semantic features for a set of natural kinds and man-made artifacts. The results showed that the anterior temporal lobe bilaterally is an important area for processing distinctive features, and that this effect is stronger within natural kinds than man-made artifacts. These findings provide converging evidence from healthy adults that is consistent with SD research, and support a model of semantic memory in which patterns of specificity of semantic information can partially explain differences in neural activation between categories.

Keywords Semantic memory · Categorization · fMRI · Semantic features

Retrieving the meaning of a concept (e.g., zebra) requires retrieval of that concept's individual features (e.g., has stripes, has four legs, etc.). These features may be distinctive if they distinguish a concept from other concepts (a zebra has stripes), or they may be shared if they occur across several concepts (a zebra has four legs). Both shared and distinctive features are important to semantic processing: the pattern of shared features across concepts plays an important role in defining category membership (e.g., many mammals have four legs), while distinctive features are necessary to the identification of specific concepts.

Much of the existing literature examining the potential neural underpinnings of shared and distinctive features focuses on neurodegenerative patients. It is common for patients with semantic dementia (SD), Alzheimer's dementia (AD), and herpes simplex encephalitis to lose access to distinctive features earlier in the

course of disease than shared features (Garrard, Lambon Ralph, Patterson, Pratt, & Hodges, 2005; Jefferies, Patterson, & Lambon Ralph, 2008; Laisney et al., 2011; Libon et al., 2013; Moss, Tyler, Durrant-Peatfield, & Bunn, 1998). The most common area of lesion across patients with this deficit is the anterior portion of the temporal lobe (ATL; Hodges, Patterson, Oxbury, & Funnell, 1992; Mummery et al., 2001).

In healthy adults, the ATL has been associated with several forms of highly specific semantic information across modalities: unique social entities (e.g., familiar faces or locations; Gorno-Tempini & Price, 2001; Grabowski et al., 2001; Ross & Olson, 2010; Simmons & Martin, 2009), atypical objects for a category (Rogers, Patterson, Jefferies, & Ralph, 2015; Rogers, Ralph, Hodges, & Patterson, 2004), irregular and low-frequency words (Woollams, 2012), and basic-level naming versus superordinate-level naming (Marques, Mares, Martins, & Martins, 2013; Rogers, Hocking, Mechelli, Patterson, & Price, 2005; Rogers, Ivanou, Patterson, & Hodges, 2006; Tyler et al., 2004; however, see Visser & Lambon Ralph, 2011, for evidence that ATL activation is not limited to basic-level concepts). If the ATL is involved in processing highly specific semantic information, then one might also expect it to play a role in processing the distinctive features of a concept. However, no study has made a direct comparison between shared and distinctive processing within the same concept in healthy adults.

In addition, there has been some debate over the extent to which ATL involvement in semantic processing is bilateral (Lambon Ralph, Pobric, & Jefferies, 2009; Patterson et al.,

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2014). Although SD patients often have bilateral ATL damage, the majority have unilateral left lesions, consistent with the common assumption that the left hemisphere is dominant for language. The social cognition literature has suggested that the right ATL is dominant for visual aspects of social processing, such as detecting famous or familiar faces (Von der Heide et al., 2013), but that only the left ATL plays a role in retrieving unique or specific facts about familiar people (Ross & Olson, 2010). On the other hand, there is evidence that the right ATL plays a role in semantic processing in nonsocial domains as well (Pobric, Lambon Ralph, & Jefferies, 2009; Rice, Lambon Ralph, & Hoffman, 2015a). Behaviorally, Reilly, Machado, and Blumstein (2015) showed in a visual half-field study that distinctive features are accessed more slowly than shared features are when a stimulus is presented to either the left or right visual field, suggesting that both hemispheres play a role in detecting distinctive semantic information. Additionally, distinctive features were particularly slow to be accessed by the right hemisphere, consistent with lateralization models that assume the left hemisphere is dominant over the right for processing fine-grained semantic information (Beeman et al., 1994). It would be valuable to determine whether ATL activation reflects similar lateralization for shared and distinctive features.

One view of semantic processing has proposed that cognitive differences between shared and distinctive features is driven by the structure of categories and the relationships between category members; that is, shared features are more likely to be activated simultaneously within related concepts and form a neural connection often referred to as “correlatedness” (e.g., concepts with two eyes often have a nose and vice versa; Devlin, Gonnerman, Andersen, & Seidenberg, 1998; McRae, Cree, & Westmacott, 1999; Rogers et al., 2004; Taylor, Moss, & Tyler, 2007). Distinctive features, on the other hand, have very low correlatedness with any other features. The pattern of correlatedness is also thought to differ across categories, such that natural kinds, which have a hierarchical taxonomy, tend to have more highly correlated shared features than do man-made artifacts (McRae & Cree, 2002; McRae, De Sa, & Seidenberg, 1997; Moss & Tyler, 2000), and patterns of correlatedness have been included in recent computational models that predict behavioral deficits with high accuracy (Ursino, Cuppini, Cappa, & Catricalá, 2018). Thus, the stimuli in the current study are divided into natural kinds and man-made artifacts in order to investigate whether distinctive feature effects emerge across both domains. Indeed, the ATL may be sensitive to variations in correlatedness across categories, since category-specific deficits arise in SD patients (Lambon Ralph, Lowe, & Rogers, 2007) and damage to the perirhinal cortex (ventral and medial ATL) correlates with the magnitude of patients’ category-specific deficits (Wright, Randall, Clarke, & Tyler, 2015).

Given the symptoms of SD patients and the role of the ATL in accessing unique information in other cognitive domains, it is likely that the ATL’s role in processing conceptual features is to

access semantic features that are uncommon and uncorrelated with other features. If this is the case, the ATL is expected to be recruited more for distinctive features than for shared features. Additionally, if the ATL is sensitive to the pattern of correlatedness between features, then natural kinds should elicit a stronger distinctiveness effect than man-made artifacts.

The ATL is often described as a region of integration or “hub” within a semantic processing network (for review, see Lambon Ralph, Jefferies, Patterson, & Rogers, 2017), and it is structurally and functionally connected with several other language areas (Dronkers, Wilkins, Van Valin, Redfern, & Jaeger, 2004; Jouen et al., 2015; Turken & Dronkers, 2011). Two areas identified as such in the semantic processing literature are the inferior frontal gyrus (IFG) and the angular gyrus (AG). To assess whether these areas also show sensitivity to distinctive versus shared features of concepts, activation patterns were also assessed in these two areas.

The IFG, especially the pars orbitalis, has been implicated in semantic control and selection (Badre et al., 2005; Marques, 2007). The definition of control and selection in the literature has been broad, since there is evidence that the left IFG plays a role in a wide range of relevant tasks, including detection and suppression of semantic competitors (Robinson, Blair, & Cipolotti, 1998; Schnur, Lee, Coslett, Schwartz & Thompson-Schill, 2005), detection of phonological competition (Jefferies & Lambon Ralph, 2006; Rigbi, Blumstein, Mertus, & Worden, 2010), classification and matching along multiple perceptual and semantic dimensions (Thompson-Schill, D’Esposito, Aguirre, & Farah, 1997), selection from among possible verbal labels for an object (Kan & Thompson-Schill, 2004), and selection between multiple meanings of ambiguous words (Bedny, Hulbert, & Thompson-Schill, 2007; Bilenko, Grindrod, & Blumstein, 2009). It is possible that semantic control in the IFG might also distinguish distinctive features from shared features. Wilshire and McCarthy (2002) described a nonfluent aphasic patient who could name pictures in isolation but not when a series of consecutive pictures were presented from the same category, introducing competition from shared features and requiring access to distinctive features. A complementary approach using functional magnetic resonance imaging (fMRI) in healthy adults showed sensitivity to cumulative semantic interference in the IFG, suggesting that the IFG is sensitive to shared semantic features (Canini et al., 2016). On the other hand, Raposo, Mendes, and Marques (2012) found greater activation in the left IFG for concepts with few shared features than for concepts with many shared features, supporting a unique role for the IFG in processing distinctive features.

The AG has also been implicated in a variety of semantic contexts. Its specific role is less well understood than the IFG’s, perhaps because the AG plays a role in many cognitive processes including reading and comprehension, number processing, spatial cognition, theory of mind and social cognition, and has been identified as a cross-modal integrative semantic hub (Bonner,

Peelle, Cook, & Grossman, 2013; Nagel, Schumacher, Goebel, & D'Esposito, 2008; Seghier, 2013). When participants view a list of features of a concept, the left AG is more activated when a highly distinctive feature disagrees with earlier features (e.g., “has an udder” following a list of features about a horse) than when all features are consistent (Peelle, Troiani, & Grossman, 2009). This is interpreted as evidence that the AG is involved in integrating semantic features within a single concept or across concepts, since the AG is also involved in feature similarity-based semantic tasks (Grossman et al., 2002).

The three current regions of interest (ROIs; ATL, IFG, and AG) have also been implicated in typicality effects using fMRI (Santi, Raposo, Frade, & Marques, 2016). Specifically, activation in the ATL and IFG correlated negatively with typicality; that is, highly atypical concepts recruited higher activation. The AG showed the opposite effect. One might expect distinctive features to be an analog to atypical concepts, and shared features to typical concepts. If this is the case, we expect higher activation for distinctive features in the ATL and IFG. Given this evidence and the suggestion above that the AG integrates similar features, one might expect higher activation for shared features in the AG.

In summary, the current experiment aims to investigate the role of three neural areas, the ATL, IFG, and AG, in processing shared and distinctive semantic features in healthy adults. Additionally, the activation patterns for shared and distinctive features in these areas within both natural kinds and man-made artifacts will be examined. If distinctiveness effects are driven by a category-wide pattern of relatedness between shared features, then the difference between shared and distinctive features should be strong in natural kinds, which typically have highly correlated shared features and uncorrelated distinctive features relative to man-made artifacts. On the other hand, if category-level differences exist independent of feature-based relationships, we might expect a main effect of domain that does not interact with feature distinctiveness. Finally, activation patterns in the left and right ATL will be compared to determine whether both hemispheres are involved in the ATL's role in semantic processing.

Method

Participants

Twenty right-handed native English speakers with no history of neurological or hearing disorders volunteered and provided informed consent in compliance with the Brown University Institutional Review Board. Participants were compensated for their time. Three subjects were removed from the analysis for movement greater than 5 mm, and a fourth was unable to complete the experiment. The behavioral and neuroimaging analysis include the data from the remaining 16 participants.

Stimuli

Stimuli were based on the set used by Reilly et al. (2015). There were 192 concept–feature pairs (e.g., zebra/has stripes vs. zebra/has four legs) selected from the feature norms developed by McRae, Hare, Elman, and Ferretti (2005). Ninety-six basic-level concepts were living things (including mammals, birds, insects, reptiles, fruits, and vegetables) and 96 were nonliving (including clothing, musical instruments, tools/weapons, household items, transportation, and buildings). Each concept was paired with one distinctive feature and one shared feature. In addition, 192 false concept–feature pairs were also prepared as fillers, half natural kinds and half man-made artifacts (e.g., musket/found in orchestra). Two lists were created such that each concept appeared with each feature type on one list. Lists were counterbalanced across participants.

Table 1 provides descriptive statistics for the behavioral measures of the stimuli in each condition. Stimuli were balanced between natural kinds and artifacts for frequency (Brysbaert & New, 2009), $F(1, 396) < 1$, $p > 0.1$. Artifacts were marginally more familiar than natural kinds, $F(1, 396) = 2.864$, $p = .091$, consistent with previous studies. Stimuli were also balanced on three feature-based measures: the length of the written feature in characters, the relatedness of the words in each feature–concept pair using latent semantic analysis (LSA; Landauer & Dumais, 1997), and the production frequency of the feature, measured as the number of norming participants who named that feature given the concept (e.g., “has stripes” is listed as a feature of “zebra”) in the McRae et al. (2005) norms. The production frequency measure was included to control for potential differences in the salience and relatedness between each concept–feature pair. In all three of these measures (feature length, LSA similarity, production frequency), there was no main effect of living/nonliving category (all F s < 1), no main effect of feature type (production frequency: $F = 1.4$, other F s < 1), and no interaction between category and feature type (all F s < 1). The *distinctiveness* measure calculated by McRae et al. (2005) was designed to differentiate between the shared and distinctive conditions, $F(1, 380) = 1223$, $p < .0001$. Distinctiveness did not differ between categories, $F(1, 380) < 1$, $p > .1$, nor was there an interaction between category and feature type, $F(1, 380) < 1$, $p > .1$. Finally, the semantic relevance of each feature was calculated, which is a measure that takes into account both the distinctiveness and production frequency (also called “dominance”) of a concept–feature pair (Mechelli, Sartori, Orlandi, & Price, 2006). Indeed, there is evidence that in patients, naming deficits for distinctive features are modulated by those features' relevance (Caticala et al., 2015). Since production frequency was controlled across conditions, semantic relevance is expected to have a similar pattern to the distinctiveness parameter. Indeed, semantic relevance differed between shared and distinctive features, $F(1, 380) = 39$, $p <$

Table 1 Summary of stimulus characteristics

Variable	Natural kinds	Artifacts		
Frequency	13.69 (25.4)	13.27 (12.3)		
Familiarity	5.37 (1.69)	5.68 (1.82)		
	Natural kinds		Artifacts	
	Shared	Distinctive	Shared	Distinctive
LSA similarity	0.141 (0.15)	0.149 (0.17)	0.125 (0.15)	0.136 (0.13)
Feature length	12.60 (3.5)	13.24 (3.5)	13.21 (3.6)	13.26 (3.6)
Production freq.	10.89 (5.5)	9.95 (5.7)	10.90 (4.9)	10.52 (5.5)
Distinctiveness	0.146 (0.11)	0.839 (0.24)	0.176 (0.14)	0.832 (0.24)
Semantic relevance	61.3 (30.2)	86.9 (49.4)	65.3 (31.1)	91.9 (48.7)

Concept-level characteristics (above) and feature-level characteristics (below). Mean (*SD*)

.0003, but there was no difference between natural kinds and man-made artifacts, nor was there an interaction.

Behavioral procedure

A feature verification task was employed in order to measure the latency of access to both types of semantic information (shared and distinctive). Each concept was counterbalanced across participants such that half of the participants read the concept paired with a shared feature, and the other half read it paired with a distinctive feature.

Stimulus presentation and behavioral responses were recorded using the Psychtoolbox in MATLAB (Brainard, 1997; Kleiner et al., 2007). Visual stimuli were projected onto a screen viewed through a mirror attached to the head coil. Responses were made on a button box with the participant's right (dominant) hand.

Figure 1 shows a schematic of a single trial. Following a 250-ms fixation, the concept appeared for 1,000 ms in the center of the screen. Following the concept, the feature was presented for 1,500 ms, and responses were recorded. Participants were asked to press one button with their index finger if the feature was appropriate for the target word (critical trials) or a second button with their second finger if it was not (filler trials). A blank screen followed each trial; intertrial interval (ITI) was jittered at four uniformly distributed intervals between one and four repetition times (TRs) following stimulus presentation (2.5 s, 5 s, 7.5 s, 10 s).

Trials were split into six blocks of 64 trials each; 32 trials in each block were critical stimuli and 32 were fillers. The trials were presented in a different randomized order for each participant. No participant saw the same concept more than once. The entire task lasted about 65 minutes.

Analysis of results

Responses were submitted to a within-subjects 2×2 (Category $\times$ Feature Type) analysis of variance (ANOVA)

using the ez package in R (Lawrence, 2013; R Core Team, 2014). The mean rate of response to nonfiller trials in the 16 subjects in the neuroimaging analysis was 91.0% and the mean accuracy rate on those trials with a response was 91.5%. Results were analyzed for accuracy and reaction times (RTs) for correct responses on the experimental trials. Trials were removed from the RT analysis if response latencies were more than three standard deviations above the mean RTs for each individual subject in each condition (35 trials, or 0.63% of accurate trials).

Imaging procedure

Whole-brain imaging was performed on a Siemens 3T Trim Trio MRI system using a 32-channel head coil. Functional data were acquired continuously using a gradient-echo echo-planer pulse sequence (TR = 2,500 ms, TE = 30 ms; flip angle = 90 degrees; 32 axial slices; matrix = $64 \times 64 \text{ mm}^2$; FoV = 192 mm; 3-mm isotropic voxels; 1,374 total volumes acquired) following a manual shim to reduce whole-brain signal dropout. T1-weighted anatomical images were collected for anatomical visualization with 1-mm isotropic voxels. Head motion was restricted using padding around the head, and subjects were told to try not to move their heads during the scan.

Fig. 1 Procedure of an example trial

Functional imaging data were processed using AFNI (Cox, 1996). Following the removal of extreme signal values using the 3dDespike command in AFNI, each subject's echo-planar imaging (EPI) images were coregistered to their MPRAGE anatomical images, normalized to Talairach space (Talairach & Tournoux, 1988), and corrected for motion using a six-parameter rigid-body transform. The raw fit coefficients for each voxel were then divided by the experiment-wise mean activation of that voxel, resulting in percentage signal change values for each voxel by condition, and smoothed using a 6-mm Gaussian kernel.

Each subject's preprocessed EPI data in each condition were convolved with a canonical hemodynamic response function provided by AFNI (Cox, 1996). Data were then masked using a 14-subject composite mask and submitted to a general linear model regression analysis using the idealized waveforms as regressors. Nuisance regressors included the motion parameters and a regressor for the response reaction time on each trial (to remove effects specific to the act of pressing a button), as well as the first four multinomial trends, as recommended by AFNI. A whole-brain group analysis was performed on the deconvolved single-subject output in a 2×2 (Category $\times$ Feature Type) ANOVA using 3dANOVA3 in AFNI.

A small volume correction was applied to restrict the analysis to areas of the brain that have been associated with language processing, broadly. These areas were selected from a review of language processing (Price, 2012) and included bilateral anterior and posterior cingulate, precentral, postcentral, supplementary motor area, temporal pole, angular gyrus, and superior temporal cortex; and in the left hemisphere only, the inferior frontal, superior frontal, precuneus, inferior parietal, supramarginal, middle temporal, and inferior temporal cortex. The small volume results were corrected for multiple comparisons using the autocorrelation function in AFNI and 3dClustSim with an activation threshold of $p < .001$, and a cluster extent threshold of $p < .05$, unless otherwise stated.

ROIs were anatomically defined using the Talairach–Tournoux atlas, as implemented by AFNI. These included bilateral BA 47, AG, and the ATL. The ATL ROI was defined manually along a diagonal line that ran perpendicular to the temporal lobe. ROIs were fractionized for each participant such that voxels at the edge of the ROI were excluded if less than 20% of the voxel was part of the anatomical subject mask. Center-of-mass coordinates for each fractionized ROI are presented in Table 2.

Percentage signal change was averaged across voxels in each ROI for each condition in each participant, and a within-subjects 2×2 (Category $\times$ Feature Type) ANOVA was performed on the single-subject results using R.

A second model was performed to account for two potential methodological issues. First, RT was included as a regressor of no interest in the model. This allows for an

Table 2 Summary of anatomical regions of interest (ROIs)

ROI	# voxels	X	Y	Z
Left ATL	973	−36	−8	−26
Right ATL	1010	38	−8	−27
Left IFG	332	−35	−23	−10
Right IFG	351	36	−24	−11
Left AG	74	−43	63	34
Right AG	75	46	63	34

Coordinates indicate center of mass in Talairach space

Note. ATL = anterior temporal lobe; IFG = inferior frontal gyrus; AG = angular gyrus

interpretation of the neural results that is independent of potential motor response differences between conditions. Second, the original experimental design did not control for the frequency of individual words across distinctive and shared features. In order to determine whether the results of the previous analyses were not due to frequency differences among the content words of the features, a subset of the data was selected and analyzed controlling for word and production frequency across conditions. In total, there were 164 stimuli used in this analysis (natural kinds: 43 shared, 37 distinctive; artifacts: 39 shared, 45 distinctive). Only this subset of the data was included in the analysis; all other parameters were the same as above.

Finally, the distinctive and shared features included in the McRae et al. (2005) norms were labelled for the type of sensory-motor information they describe. Although the experimental design did not examine these characteristics, it is of interest to see whether the pattern of results varied as a function of these parameters. There were three feature categories that were relatively common across all conditions: Encyclopedic (beaver–lives in dams), functional (apple–used in cider), and visual form and surface (eagle–has wings). A summary of the characteristics of each of these categories across conditions are shown in Table 3. A post hoc ROI analysis explored ATL activation in each condition for each of these feature categories (note that this analysis was similar to the original model without response time as a regressor).

Results

Behavioral results

Table 4 shows the behavioral results. Accuracy results were analyzed for critical trials only (fillers were not included) for the 16 subjects whose neuroimaging data were included in the analysis. A 2×2 (Category $\times$ Feature Type) within-subjects ANOVA revealed no significant main effects of category, $F(1, 15) < 1, p > .1$, or feature type, $F(1, 15) < 1, p > .1$. There was a

Table 3 Summary of most common feature categories in each condition

	Living		Nonliving	
	Distinctive	Shared	Distinctive	Shared
Encyclopedic	34	28	28	20
Function	20	12	28	27
Visual form and surface	20	27	30	30

weak Category $\times$ Feature Type interaction, $F(1, 15) = 3.51$, $p = .08$, showing a larger effect for natural kinds compared to artifacts, with slightly higher accuracy for distinctive features than for shared features.

For reaction times during accurate trials, a 2×2 (Category $\times$ Feature Type) ANOVA showed a marginal main effect of feature type, $F(1, 15) = 3.72$, $p = .054$, such that shared feature responses were faster than distinctive feature responses (see also Reilly et al., 2015). In addition, an interaction emerged, $F(1, 15) = 5.88$, $p = .015$, between category and feature type; the shared feature advantage appears to be driven more strongly by artifacts than by natural kinds.

Neuroimaging results

Table 5 shows the results of the initial whole-brain analysis. Although no clusters survived multiple comparisons correction at an activation threshold of $p < .01$, and cluster extent threshold $p < .05$, one cluster survived correction for multiple comparisons at a threshold of $p < .001$, and cluster extent threshold $p < .05$: The left posterior fusiform gyrus was significantly more activated for living than for nonliving concepts (see Fig. 2; note that this is possible because the cluster size required for significance at an activation threshold of $p < .001$ is smaller than at $p < .01$). No clusters survived correction for the shared versus distinctive contrast, and no additional areas survived the small volume correction using the language processing mask.

A whole-brain and small-volume-corrected analysis was also performed using the subset of the data for which the frequency of the words in the semantic feature were balanced. Only the small-volume-corrected results yielded any significant clusters with an activation threshold of $p < .01$, cluster

corrected at $p < .05$. The small-volume-corrected analysis revealed two left-hemisphere clusters, in the posterior middle temporal gyrus (MTG) and ATL (see Table 6 and Fig. 3).

The ROI analysis investigated the bilateral ATL, IFG, and AG (see Fig. 4). In the ATL, both hemispheres showed an effect of feature type: Distinctive features elicited greater activation than shared features in the left, $F(1, 15) = 10.81$, $p = .005$, and right, $F(1, 15) = 8.34$, $p = .011$. There was no main effect of category nor an interaction between category and feature type. Using a Bonferroni correction for multiple hypothesis tests, only the left ATL survived a correction for the six ROIs.

An ROI analysis in the frequency-corrected and motor-corrected data yielded similar results (see Fig. 5). A main effect of feature distinctiveness emerged in the left ATL, $F(1, 15) = 9.27$, $p = .008$, and right ATL, $F(1, 15) = 9.69$, $p = .007$. There were no main effects of category nor interaction in any ROI. In this analysis, both the left and right ATL survived a Bonferroni multiple-comparisons correction.

A post hoc ROI analysis was performed on the three major subsets of sensory-motor feature categories: encyclopedic, functional, and visual (see Fig. 6). Within the visual features, a main effect of domain (natural kinds vs. artifacts) emerged in both the left, $F(1, 15) = 4.82$, $p = .044$, and right, $F(1, 15) = 5.41$, $p = .034$, ATL ROIs, as well as a marginally significant interaction in the left ATL between domain and feature distinctiveness, $F(1, 15) = 4.82$, $p = .078$. Within functional features, a main effect of feature distinctiveness emerged in both the left, $F(1, 15) = 8.05$, $p = .012$, and right, $F(1, 15) = 5.41$, $p = .034$, ATL, consistent with the omnibus results: Distinctive features were more activated in the bilateral ATL than were shared features. No significant effects emerged in the encyclopedic features, although the general pattern did suggest greater activation for distinctive than for shared features.

Discussion

The goals of this experiment were to investigate the role and lateralization of the ATL in distinctive feature processing, and to explore whether a similar role is present in other regions of interest, namely, the IFG and AG. We address these questions within the context of two different semantic domains, natural kinds and man-made artifacts, whose features are thought to differ in both distinctiveness and sensory-motor distributions. Two hypotheses were supported by the current results. First, consistent with the patient literature, results showed that the ATL is more highly activated during distinctive feature processing than during shared feature processing. Second, this effect emerges primarily for natural kinds and is weaker for man-made artifacts.

Table 4 Behavioral results

Condition	Natural kinds		Artifacts	
	Distinctive	Shared	Distinctive	Shared
Accuracy	0.857 (0.35)	0.827 (0.38)	0.839 (0.37)	0.852 (0.36)
RT (ms)	869 (203)	864 (212)	875 (209)	838 (204)

Proportion of accurate responses and reaction times (RTs). Mean (*SD*)

Table 5 Whole-brain analysis at $p < .001$, corrected

Whole brain ($p < .001$, corrected) Natural kinds > man-made artifacts	Hem	# voxels	X	Y	Z	Peak F
Posterior fusiform	L	32	-23	29	-13	32.9

Behaviorally, the results replicate previous findings (Randall, Moss, Rodd, Greer, & Tyler, 2004; Reilly et al., 2015), such that shared features are accessed faster than are distinctive features (this effect was marginally significant in the current results). Furthermore, an interaction emerged between category and feature type. The effect of feature type on RT is driven by man-made artifacts. The reaction times for all conditions were similar except for the shared features of man-made artifacts, which were faster on average. In order to investigate neural differences between conditions that are not confounded by a speed advantage for shared features of man-made artifacts, we included reaction times as a regressor of no interest in our secondary analysis.

The involvement of the ATL in processing distinctive features is unequivocal. In the initial analysis, only the left ATL ROI survived the correction for multiple comparisons. In the follow-up analysis controlling for a number of parameters that made the stimuli more balanced, the left ATL emerged in the small-volume analysis, and both the left and right ATL survived the Bonferroni-corrected ROI analysis. The pattern of results in the two ROIs is qualitatively very similar across analyses, including the post hoc sensory-motor feature-type analysis. Thus, the current results support a role for the bilateral ATL in semantic processing, such that both hemispheres are recruited more heavily by distinctive features than by shared features. The existence of the Domain $\times$ Distinctiveness interaction in RTs motivates the post hoc secondary analysis that included RT as a regressor, to look for neural effects that are independent of motor responses.

The direction of the ATL effect mirrors the pattern seen in SD patients with ATL pathology. In particular, these patients show deficits in accessing distinctive features. Patient research

is a valuable tool to identifying brain areas where damage impairs cognitive processing, but its findings are difficult to interpret definitively without converging evidence from other methods (Price, Hope, & Seghier, 2017). Deficits for SD patients are often attributed to the ATL, but lesions typically include large portions of the temporal lobe and/or the IFG and orbitofrontal cortex. ROI analysis of fMRI allows for a more anatomically specific and higher-resolution approach to investigating the role of the ATL. Indeed, there is ambiguity as to the specific subregions that should be included in the term “anterior temporal lobe” (Bonner & Price, 2013; Jouen et al., 2015). The temporal pole is the most anterior portion of the temporal lobe, but semantic and visual object recognition effects are often reported in the anterior superior temporal gyrus (STG; Sabsevitz, Mdelier, Seidenberg, & Binder, 2005), the ventral and medial ATL (Binney, Embleton, Jefferies, Parker, & Lambon Ralph, 2010; Peelen & Caramazza, 2012), or the entorhinal/perirhinal cortex (Clarke & Tyler, 2014; Moss, Stamatakis, & Tyler, 2006). In the current analysis, significant effects emerged in the most anterior portion of the temporal pole as well as the ventral ATL between the temporal pole and ITG. The emergence of a ventral area is consistent with the semantic memory literature suggesting that the ventral ATL is important for integrating semantic information across modalities (Rice, Hoffman, & Lambon Ralph, 2015b), in contrast to the perirhinal cortex, which has been purported to play a role in processing distinctive visual information.

The omnibus analyses did not reveal any significant interactions between domain (i.e., natural kind vs. artifacts) and feature distinctiveness, but the difference between shared and distinctive features in the ATL appears to be driven by the features of natural kinds across analyses. This supports the hypothesis raised by computational and patient models that category-specific effects may be an emergent property of the distribution of shared and distinctive features within that category (Devlin et al., 1998; Devlin et al., 2002; Moss et al., 1998). Natural kinds tend to have highly correlated shared features, and their distinctive features tend to be unique to a single concept (e.g., the black-and-white stripes of a zebra). Man-made artifacts, on the other hand, have less rigidly defined overlap, and so distinctive features and category boundaries are more fluid (e.g., the blade of a saw is distinctive for a tool, but not for a household item). Thus, the distinctive features of natural kinds are particularly distinctive relative to other categories, and, as a consequence, appear to

Fig. 2 Results of the whole-brain analysis, contrasting natural kinds > man-made artifacts. Activation is thresholded at $p < .001$, corrected for cluster size at $p < .05$

Table 6 Results of the reduced dataset balanced for feature frequency, using an activation threshold of $p < .01$, corrected at $p < .05$

Small volume ($p < .01$, corrected) Distinctive > shared features	Hem	# voxels	X	Y	Z	Peak F
MTG/STG	L	76	−53	53	9	28.1
ATL	L	71	−35	−11	−28	27.4

Small volume correction was applied to areas broadly associated with language processing in Price (2012)

Note. L = left; MTG = middle temporal gyrus; STG = superior temporal gyrus; ATL = anterior temporal lobe

be more vulnerable to loss early in the disease process. Similarly, the activation patterns of the ATL, particularly in the left hemisphere, show the greatest activation for the distinctive features of living things, comprising the most unique features in the stimulus set.

This line of thinking applies to pattern of sensory-motor features as well. Although the distribution of sensory-motor features was not included in the current experimental design, a post hoc analysis in the ATL examining the three most common sensory-motor feature types (visual, functional, and encyclopedic) revealed that in visual features, the distinctive feature effect was larger in natural kinds than in man-made artifacts. Functional and encyclopedic features, which do not rely heavily on visual information, did not show any trend toward such an interaction between domain and feature distinctiveness. This pattern of results is consistent with the hypothesis that visual features of natural kinds are more distinctive on average than the visual features of man-made artifacts (Taylor et al., 2007; Tyler & Moss, 2001), and may explain some category-specific semantic deficits in SD

patients. This interpretation could also explain the category-specific activation in the current results in the left posterior fusiform gyrus, which was greater for natural kinds than for man-made artifacts. Similar results emerged in a PET study (Rogers et al., 2005) in which the authors suggested that category-specific activation in the posterior fusiform may reflect the degree to which visual features are shared between concepts. This area has been shown to be involved in accessing visual characteristics during semantic processing (Hsu, Schlichting, & Thompson-Schill, 2014; Koustaal et al., 2001; Simons, Koutstaal, Prince, Wagner, & Schacter, 2003).

There is evidence from other linguistic and cognitive domains that the ATL plays a role in processing any “unique” information. For example, the ATL is involved in detecting famous and familiar individual faces and landmarks (Gorno-Tempini & Price, 2001; Grabowski et al., 2001; Olson, McCoy, Klobusicky, & Ross, 2013; Ross & Olson, 2010; Tranel, 2009) or atypical category members (Mayberry, Sage, & Lambon Ralph, 2011; Patterson, Nestor, & Rogers, 2007; Woollams, 2012). The current results support a role for the ATL in processing distinctive semantic information, with a stronger effect for natural kinds, which is consistent with the hypothesis that the ATL plays a domain-general role in processing unique, specific, or fine-grained information.

Results of activation patterns in the other two areas, the IFG and AG, did not survive multiple comparisons correction and so should be interpreted with caution. The IFG showed some sensitivity to feature distinctiveness in both hemispheres, with greater activation for distinctive features than for shared features. We therefore tentatively suggest that the IFG’s role in semantic control extends to accessing uncorrelated distinctive features (Jefferies, 2013; Raposo et al., 2012). The AG findings also did not survive multiple comparisons correction. It has been proposed that the AG is important for integrating semantic information across visual, auditory, and motor inputs, which may be independent of distinctiveness (Binder & Desai, 2011; Bonner et al., 2013), suggesting that the AG plays a role in detecting semantic sensory-motor modality rather than feature specificity. In any case, the current results are agnostic as to its role in detecting distinctive semantic features.

Fig. 3 Results of the subset of data balanced for feature frequency, contrasting distinctive features > shared features. Activation is thresholded at $p < .01$, corrected for cluster size at a small volume corrected $p < .05$

Fig. 4 Percentage of signal change relative to rest in each of the left and right regions of interest. Error bars represent subject-wise standard error. *Note.* ATL = anterior temporal lobe; IFG = inferior frontal gyrus; AG = angular gyrus

Fig. 5 Regions of interest analysis for the subset of data controlling for feature frequency and motor activity. *Note.* ATL = anterior temporal lobe; IFG = inferior frontal gyrus; AG = angular gyrus. Error bars are subjectwise standard error

Inferior to the AG, the posterior MTG (pMTG) showed greater activation for distinctive than shared features in the analysis that controlled for feature frequency. The emergence of this area is unsurprising, given that the specific pMTG region that emerged has been shown to be functionally connected to both the ATL and IFG, and likely plays a role in semantic cognition/selection similar to the IFG (Davey et al., 2016; Jefferies, 2013; Noonan, Jefferies, Visser, & Lambon Ralph, 2013).

In summary, the current results show that in healthy adults, the ATL is more activated for distinctive than for shared features. This is a key finding, as it is the first study to examine the distinctiveness effect in healthy adults. The current results show that in the healthy adult brain, the ATL is sensitive to differences between shared and distinctive semantic features. Furthermore, because shared and distinctive features were used across a common set of concepts (e.g., zebra–stripes; zebra–legs), these effects cannot be attributed to lexical properties such as frequency or category typicality. Results of this study support a model of semantic memory in which the bilateral ATL is sensitive to the level of specificity of semantic information, and this effect is stronger for concepts with unique distinctive features (here, natural kinds). The current results also show that while the ATL is an important area for processing distinctive features, other language areas may be sensitive to this manipulation as well, specifically the left IFG and left posterior MTG.

Fig. 6 Anterior temporal lobe (ATL) region of interest analysis of sensory-motor feature categories. Error bars are subjectwise standard error

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