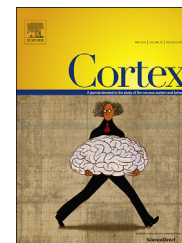


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Role of features and categories in the organization of object knowledge: Evidence from adaptation fMRI



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ABSTRACT

There are two general views regarding the organization of object knowledge. The feature-based view assumes that object knowledge is grounded in a widely distributed neural network in terms of sensory/function features (e.g., Warrington & Shallice, 1984), while the category-based view assumes in addition that object knowledge is organized by taxonomic and thematic categories (e.g., Schwartz et al., 2011). Using a functional magnetic resonance imaging (fMRI) adaptation paradigm, we compared predictions from the feature- and category-based views by examining the neural substrates recruited as subjects read word pairs that were identical, taxonomically related, thematically related or unrelated while controlling for the function features involved across the two categories. We improved upon previous study designs and employed an fMRI adaptation task, obtaining results overall consistent with both the category-based and feature-based views. Consistent with the category-based view, we observed for both hypothesized regions of interest (ROI) and exploratory (whole-brain analyses) reduced activity in the left anterior temporal lobe (ATL) for taxonomically related versus unrelated word pairs, and for the exploratory analysis only, reduced activity in the right ATL. In addition, the exploratory analyses revealed reduced activity in the left temporo-parietal junction (TPJ) for thematically related versus unrelated word pairs. Consistent with the feature-based view, we found in the exploratory analyses that activity reduced in the bilateral precentral gyri (i.e., function regions) including part of premotor cortex as the function relatedness ratings increased. However, we did not find a relationship between adaptation effects in the bilateral ATLS and left TPJ and corresponding ratings of taxonomic/thematic relationships suggesting that the adaptation effects may potentially not reflect aspects of taxonomy that have been traditionally assumed. Together, our findings indicate that both feature and category information are important for the organization of object knowledge although the exact nature of those organization principles is an important question for future research.

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How we organize the knowledge associated with objects is a fundamental question in cognition. It is commonly assumed that object knowledge is grounded in a widely distributed neural network involving the sensory, motor, and supramodal cortical systems (e.g., Allport, 1985; Barsalou, 1999, 2008; Warrington & Shallice, 1984). For example, our knowledge of “dog” is represented by various attributes, such as visual (e.g., four leg and a tail), motor, and sound (e.g., bark) features that are represented in the corresponding brain regions for processing visual form, perception of motor, and sound information. An alternative view of object knowledge organization assumes that besides features, object knowledge is also organized by taxonomic and thematic categories, two parallel and complementary semantic systems (e.g., Mirman & Graziano, 2012; Schwartz et al., 2011). For instance, we can group dogs, fish and snakes as animals (i.e., taxonomic category) even though they have very different features. Additionally, our knowledge also includes links between concepts that play complementary roles in the same scenes or events, referred to as thematic categories (e.g., “The mouse ate the cheese”). This organization suggests that our brain contains semantic hubs to support generalizations across concepts that have similar conceptual relations but very different feature profiles. In this view, the bilateral anterior temporal lobes (ATLs) serve as a semantic hub to represent taxonomic categories and bind all modality-specific regions (see Patterson, Nestor, & Rogers, 2007 for a review) whereas the left temporo-parietal junction (TPJ) serves as another semantic hub representing thematic categories (Mirman & Graziano, 2012; Schwartz et al., 2011). The purpose of our study is to investigate the degree to which object knowledge is organized by taxonomic/thematic categories or modality-specific features (e.g., visual and function features) using a functional magnetic resonance imaging (fMRI) adaptation approach.

1. Evidence for the feature-based view

There is both neuroimaging and neuropsychological evidence in support of the feature-based view that taxonomic categories are represented via various features. Although each object concept is represented by features in terms of the feature-based view, the critical features for taxonomic categories vary. For example, living things (e.g., animals) rely more on perceptual features whereas non-living things (e.g., tools) rely more on motor/function features (e.g., Barsalou, 1999, 2008; Warrington & Shallice, 1984). Consistent with the feature view, feature norms in adults (Cree & McRae, 2003; McRae, Cree, Seidenberg, & McNorgan, 2005) demonstrate that natural kinds such as animals are mainly defined by perceptual/visual attributes, while artifacts such as tools are mostly characterized by functional/motor features. Additionally, in object identification and naming tasks, words and/or pictures referring to tools activated both left premotor cortex and left posterior middle temporal gyrus (pMTG) which are found to be involved in action observation and execution (for a review see Noppeney, 2008; but see Bruffaerts et al., 2013; Devereux, Clarke, Marouchos, & Tyler, 2013; Fairhall & Caramazza, 2013). Animal concepts activated bilateral ventral temporal cortices (i.e., fusiform) which are responsible

for processing color and form (see reviews, Martin, 2001, 2007; Thompson-Schill, 2003). Moreover, the feature-based view predicts that patients with a selective impairment for a specific taxonomic category (e.g., living things) should show problems with a particular feature (e.g., visual feature) critical for defining that taxonomic category. For example, patients with impaired knowledge of living things (e.g., fruit) have poor performance on the visual property judgments (e.g., *Is a banana yellow?*) (e.g., Crutch & Warrington, 2003; Borgo & Shallice, 2001, 2003 but see Capitani, Laiacona, Mahon, & Caramazza, 2003 and Mahon & Caramazza, 2009 for counter-arguments to this evidence). In sum, in this feature-based view, taxonomic categories are primarily represented via the contribution of different features.

The feature-based view generates clear predictions for the neural substrates underpinning not only taxonomic categories but also thematic categories. Although thematically related concepts usually do not share visual features (e.g., *cheese* and *mouse*), they often share motor/function or spatial features (e.g., *The mouse ate the cheese*). Hence, the feature-based view predicts that if taxonomic and thematic categories involve similar features (e.g., function features, e.g., *cutting*) for taxonomically (e.g., *saw-axe*) and thematically related concepts (e.g., *saw-wood*), both should activate the same brain regions (e.g., premotor, pMTG) for processing these features (e.g., *cutting*). However, to our knowledge, no one has yet explored the neural substrates of taxonomic and thematic categories while controlling for the features involved across the two categories.

2. Evidence for the category-based view

In contrast, the category-based view assumes that there are distinct brain regions representing taxonomic and thematic categories, specifically the bilateral ATLs for taxonomic categories and left TPJ for thematic categories (Mirman & Graziano, 2012; Schwartz et al., 2011). Patients with focal atrophy of the bilateral ATLs typically show a progressive loss of semantic knowledge, especially taxonomic knowledge. Patients with severe bilateral ATL atrophy use more general category labels (e.g., animal) to classify or name objects (e.g., robin) compared to patients with less severe atrophy who use basic level (e.g., bird) and specific names (e.g., robin) (e.g., Rogers & Patterson, 2007; Hodges, Graham, & Patterson, 1995; see Patterson et al., 2007 for a review; but see Wheatley, Weisberg, Beauchamp, & Martin, 2005). Converging evidence for the role of the bilateral ATLs in object knowledge also comes from functional neuroimaging studies of neurologically intact participants. Bilateral ATL activation was observed in fMRI and positron emission tomography (PET) studies when subjects completed a categorization task where three words (e.g., taxi, boat, bicycle) from a single taxonomic category (e.g., vehicle) were presented and subjects decided if the fourth word (e.g., “plane” or “spoon”) was also in the same category (e.g., Devlin et al., 2000; Visser, Embleton, Jefferies, & Lambon Ralph, 2009). Anzellotti, Mahon, Schwarzbach, and Caramazza (2011) found ATL activation for tools in a category verification task (i.e., is it a tool?) using fMRI. Rogers et al. (2006) observed ATL activation for animal and vehicle

categories compared to baseline using PET. Further evidence of the necessity of the bilateral ATLs for taxonomic category representation comes from three repetitive transcranial magnetic stimulation (rTMS) studies where healthy participants showed slower semantic processing for both living and non-living categories (e.g., synonym judgment, picture naming) when rTMS was applied to the bilateral ATLs (Lambon Ralph, Pobric, & Jefferies, 2009; Pobric, Jefferies, & Lambon Ralph, 2007, 2010). In summary, there is also neuropsychological, TMS, and functional neuroimaging evidence to suggest that the representation of objects includes organization by taxonomic category, representations subserved by the bilateral ATLs.

In contrast to the evidence for the neuroanatomical substrates for taxonomic categories, thematic categories are much less studied from a neuroanatomical perspective. Schwartz et al. (2011) examined the relationship between brain lesions in 86 stroke patients and picture naming errors on the Philadelphia Naming Task (Roach, Schwartz, Martin, Grewal, & Brecher, 1996) using voxel-based lesion-symptom mapping (Bates et al., 2003). Lesions in the left TPJ were associated with producing thematic errors (e.g., name an *apple* picture as *worm*) whereas lesions in the left ATL were associated with producing taxonomic errors (e.g., name an *apple* picture as *pear*). In another study using eye tracking methodology (Mirman & Graziano, 2012), patients with damage to the left TPJ showed less fixations on thematically related pictures compared to healthy controls in a spoken word comprehension task. Consistent with Schwartz et al. (2011) and Mirman and Graziano (2012), two fMRI studies show more activity in the left TPJ for thematic categories compared to taxonomic categories in comprehension and production tasks (Kalénine et al., 2009; de Zubicaray, Hansen, & McMahon, 2013). Thus, there is neuropsychological and neuroimaging evidence to suggest that objects are organized by thematic category and these representations are subserved by the left TPJ.

3. Methodological confounds with previous fMRI studies

Although several fMRI studies compared the neural substrates between taxonomic and thematic categories (Kalénine et al., 2009; Sachs, Weis, Krings, Huber, & Kircher, 2008; Sachs et al., 2011; Sass, Sachs, Krach, & Kircher, 2009), there are multiple methodological issues which cloud clear interpretation of the results. First, in a picture-matching task, participants selected which of two pictures was related to a target picture, where the relationship was either taxonomic or thematic (Kalénine et al., 2009). Greater activation was observed for taxonomically related pictures in bilateral visual areas (cuneus, BA 18) and greater activation for thematically related pictures in a bilateral temporo-parietal network including inferior parietal lobes (BA 39/40) and pMTG (BA 21/22). Left pMTG is considered a key region for action and tool knowledge (e.g., Beauchamp & Martin, 2007; Martin & Chao, 2001; Noppeney, 2008). The authors argued that these results reflect the different features inherent in the two categories, namely in general, more visual features associated with taxonomic categories and more functional features associated

with thematic categories. However, due to the fact that this study did not match the visual similarity or complexity for the pictures used in the taxonomically and thematically related conditions, the greater activity in the cuneus might not purely reflect the difference between the two categories, but instead reflect early visual processing associated with contrast and luminance (e.g., Vanni, Tanskanen, Seppä, & Uutela, Hari, 2001). Likewise, without controlling for function/motor features involved in the stimuli used for the two categories, the greater activation in the bilateral pMTG might not purely reflect the difference between the two categories, but instead reflect stimuli differences, for example, more motor/function features involved in the stimuli used for the thematically related condition compared to the different stimuli used in the taxonomically related condition. Thus, the first goal of our study is to examine the neural substrates underlying taxonomic and thematic categories while simultaneously controlling for the types of sensory/function features potentially subserving these representations.

The second methodological confound with recent fMRI studies of taxonomic/thematic relations (Sachs et al., 2011; Sass et al., 2009) is that the semantic priming paradigm chosen (a lexical decision task) may not fully activate the features associated with taxonomic and thematic categories. In these studies, subjects performed a lexical decision task on target words that were taxonomically, thematically related or unrelated to the prime words, and in both studies taxonomic and thematic categories recruited similar brain regions. However, previous behavioral studies suggest that the lexical decision task may not fully activate all the features involved in the word pairs (Pecher, Zeelenberg, & Raaijmakers, 1998) or engage deep semantic processing (Becker, Moscovitch, Behrmann, & Joordens, 1997; Joordens & Becker, 1997). For example, perceptually related prime words (e.g., *coin*) did not facilitate lexical decision for target words (e.g., *pizza*) but did so after subjects made judgments about the perceptual properties of the words' referents (Pecher et al., 1998). Pecher et al. argued that the lexical decision task did not fully activate all the features associated with the word pairs, but the perceptual judgment prior to this task boosted the activation of perceptual features, resulting in the perceptual priming effect. Furthermore, smaller or non-significant priming effects in the lexical decision task were reported in comparison to the semantic decision task (e.g., decide whether the object is a living or non-living thing) (Becker et al., 1997; Joordens & Becker, 1997). Hence, this may explain why Sass et al. (2009) and Sachs et al. (2011) did not find the activity in the brain regions that are responsible for feature processing for either taxonomic or thematic word pairs.

4. Current study

The purpose of this study was to distinguish between the feature-based (e.g., Allport, 1985; Barsalou, 1999, 2008; Warrington & Shallice, 1984) versus category-based (e.g., Mirman & Graziano, 2011, 2012; Schwartz et al., 2011) views of the organization of our object knowledge. We examined the neural substrates underpinning taxonomic and thematic categories with similar function features involved across the

two categories using an fMRI adaptation paradigm. The assumption underlying the fMRI adaptation paradigm is that repeated presentation of the same visual or verbal stimulus produces BOLD signal change in brain regions that process that stimulus, because of firing-rate adaption, enhanced neural synchronization, or rapid stimulus-response learning (see recent reviews, [Gotts, Chow, & Martin, 2012](#); [Segaert, Weber, de Lange, Petersson, & Hagoort, 2013](#)). In order to obtain a measure of neurally perceived difference, the adaptation paradigm can be employed while varying the level of stimulus similarity (e.g., [Fang, Murray, Kersten, & He, 2005](#); [Kourtzi & Kanwisher, 2001](#); [Wheatley et al., 2005](#); [Yee, Drucker, & Thompson-Schill, 2010](#)): the greater the similarity, the greater the expected adaptation (but see [Doehrmann, Weigelt, Altmann, Kaiser, & Naumer, 2010](#); [Sachs et al., 2011](#)). For example, in [Wheatley et al. \(2005\)](#), participants read word pairs silently which were either identical (e.g., *cucumber–cucumber*), taxonomically related (e.g., *fox–pig*), or unrelated (e.g., *hat–gun*). The greatest activity in left ventral temporal cortex, a region for processing of visual features associated with objects, was observed for unrelated word pairs, less for the taxonomically related pairs, the least for the identical pairs. Similarly, in [Yee et al. \(2010\)](#), subjects were presented with word pairs that were identical (e.g., *drill–drill*), similar in shape and function (e.g., *pencil–pen*), similar in either shape (e.g., *marble–grape*) or function (e.g., *flashlight–lantern*), or unrelated (e.g., *saucer–needle*). The degree of function similarity was correlated with the BOLD signal changes in four left hemisphere regions (i.e., premotor cortex, intraparietal sulcus, medial temporal lobe and pMTG). However, some studies have shown that sometimes BOLD signal increased (instead of decreased) for stimuli repetition and importantly the repetition enhancement correlated with behavioral improvement (e.g., response time) (e.g., [Salimpoor, Chang, & Menon, 2010](#); [Thoma & Henson, 2011](#)). For example, [Salimpoor et al. \(2010\)](#) compared the response times and BOLD signal changes during novel versus repeated presentation of three-operand mathematical equations. The BOLD signal in the hippocampus and the posteromedial cortex increased during repeated versus novel presentation of the equations, where the response time differences were directly correlated with the increased BOLD signal change. Because of the sensitivity to similarity, the fMRI adaptation paradigm is a natural fit for examining the neural correlates underpinning taxonomic and thematic categories to provide evidence to distinguish between feature-based versus category-based theories of object organization.

In this study, we adapted the fMRI paradigm used in [Yee et al. \(2010\)](#). Subjects read word pairs that were identical, taxonomically related, thematically related or unrelated. Critically, all the word pairs in the taxonomically and thematically related conditions involve similar function features (i.e., the purpose of use), because the feature-based view predicts that if taxonomic and thematic categories are categories by virtue of the function features they share, signal changes in function regions (i.e., left pMTG, left premotor cortex; [Canessa et al., 2008](#); [Yee et al., 2010](#)) should be observed for taxonomically/thematically related versus unrelated word pairs regardless of the taxonomic/thematic categories involved. Although the two categories both involve

similar function features, the functional relationships in the two categories are distinct from one another due to the inherent nature of the categories. For example, two objects (e.g., saw-axe) which share a similar function (e.g., cutting) are likely to be in the same taxonomic category (e.g., tools). However, two thematically related objects (e.g., saw-wood) are not likely to share function (e.g., cutting) in the same way, but instead are related in a different way with regards to function, as a saw is used to cut wood. Therefore, in order to balance for the function features involved in the two categories, we took these two function relationships into account. Specifically, using subject ratings for all taxonomically and thematically related word pairs, we measured function in two ways. First, based on a definition of function feature as the purpose of use (e.g., [Canessa et al., 2008](#); [Moss, Ostrin, Tyler, & Marslen-Wilson, 1995](#); [Yee, Huffstetler, & Thompson-Schill, 2011](#)) we measured function similarity according to how similar the functions are for two objects [i.e., the purpose of use, e.g., saw and axe are used for cutting; a similar definition used in [Yee et al. \(2010\)](#) and [Canessa et al. \(2008\)](#)]. Second, we measured function similarity according to how likely the purpose of use for one of the two objects is to perform action on the other one (function relatedness, e.g., a saw is used to cut wood; a similar definition used in [Moss et al. 1995](#)). Therefore, the function similarity and relatedness scores reflect the function features involved in both taxonomic and thematic categories.

With regards to comparisons between conditions, the feature-based view predicts that there should be BOLD signal differences between the taxonomically related versus unrelated conditions and between thematically related versus unrelated conditions but there should be no interaction between the two in the function regions (premotor cortex and pMTG) for both subject and item analyses. In contrast, the category-based view predicts that a) bilateral ATLs should show significant BOLD signal difference between taxonomically related versus unrelated conditions but no difference between thematically related versus unrelated conditions; and b) left TPJ should show significant BOLD signal difference between thematically related versus unrelated conditions but no difference between taxonomically related versus unrelated conditions. Additionally, because the feature-based and category-based accounts are not necessarily mutually exclusive (e.g., [Patterson et al., 2007](#)), it is possible that we could observe adaptations between the related versus unrelated conditions in not only the function related brain regions (i.e., left pMTG, left premotor cortex) but also the category specific regions (i.e., ATL and TPJ).

To assess the degree to which brain activity is related to more fine-grained assessments of function (similarity and relatedness) and categorical (taxonomic and thematic) relationships, we correlated brain activity with subject ratings of these relationships across stimuli. We measured taxonomic and thematic ratings on a 7-point scale according to what extent these two words are members of the same category (i.e., taxonomic rating) and what extent these two words co-occur in a situation or scene (i.e., thematic rating) (similar definitions used in [Mirman & Graziano, 2011](#)). According to the feature-based view, the degree of signal change in the function regions should correlate with function ratings for word

Table 1 – Mean relatedness ratings (scale 1–7) assessing function similarity (how similar the functions are for two objects), function relatedness (how likely the purpose of use for one of the two objects is to perform action on the other one), taxonomic relationship (to what extent two objects are members of the same category), and thematic relationship (to what extent two objects co-occur in a situation or scene) for word pairs across taxonomic, thematic, and unrelated conditions (M = mean, SD = standard deviation).

Condition	Function similarity		Function relatedness		Taxonomic		Thematic	
	M	SD	M	SD	M	SD	M	SD
Thematically related	2.3	.7	5.7	.9	3.3	.9	5.8	1.0
Thematically unrelated	1.4	.2	1.8	.7	1.3	.3	1.8	.7
Taxonomically related	4.9	.7	2.4	1.0	5.6	.8	4.9	.9
Taxonomically unrelated	1.5	.5	1.5	.4	1.4	.5	1.6	.7

pairs independent of their taxonomic or thematic relationship. In contrast, the category-based view predicts that the degree of signal change in bilateral ATLS should correlate with the degree of taxonomic relatedness whereas the degree of adaptation in left TPJ should correlate with the degree of thematic relatedness.

In summary, our study has the potential to help us understand the degree to which there are brain regions responsible for higher order generalization (e.g., taxonomic and thematic categories; [Mirman & Graziano, 2011, 2012](#); [Schwartz et al., 2011](#)) and whether categories are more likely represented via features in neurally dedicated substrates (e.g., [Allport, 1985](#); [Barsalou, 1999, 2008](#); [Warrington & Shallice, 1984](#)). By improving upon previous study designs and employing the fMRI adaptation task, this study clarifies the role of semantic categories and features in the organization of object knowledge in healthy participants.

5. Proposed experiment

5.1. Methods

5.1.1. Participants

In order to have enough power to distinguish between the category-based and feature-based theories, we recruited 20 right-handed and native English speakers from Rice University to achieve a power estimate of .90 (alpha = .05) (G^* power 3, [Faul, Erdfelder, Lang, & Buchner, 2007](#)). We calculated the power estimate based on effect sizes obtained from [Kalénine et al. \(2009\)](#) and [de Zubicaray et al. \(2013\)](#).¹ Specifically, for Kalénine et al., we calculated two effect sizes using the average beta contrast weights across a collection of voxels in the left TPJ (i.e., inferior parietal lobe, Tailarach coordinates –56, –45, 34; Cohen's $d = 1.26$; estimated power = .91 with 9 subjects) and in left middle temporal gyrus (Tailarach coordinates –50, –63, 13, Cohen's $d = 1.63$; estimated power = .94 with 7 subjects) which Kalénine et al. found to be significantly more active across 16 subjects when comparing thematic versus taxonomic conditions (see Kalénine et al., [Table 1](#), p. 1157). For [de Zubicaray et al. \(2013\)](#), we calculated two effect sizes using the average beta contrast weights in the left TPJ (i.e., angular gyrus, Tailarach coordinates –48, –65, 36; Cohen's $d = 2.06$; estimated power = .92 with 5 subjects) and in left middle

temporal gyrus (Tailarach coordinates –56, –9, 15, Cohen's $d = 1.03$; estimated power = .92 with 13 subjects), two regions of interests (ROIs) where there was significantly greater activity in thematic versus taxonomic conditions across 20 subjects (see [de Zubicaray et al., 2013, Fig. 4](#), p. 139). Subjects were safety-screened, given informed consent, and reimbursed in accordance with the Rice University Institutional Review Board for the Protection of Human Subjects. Subjects completed screening forms to ensure no history of neurological or psychiatric illness and no current use of medication affecting the central nervous system. Data from participants with excessive head movement during image acquisition, defined as motion exceeding 2 mm within a single imaging run were excluded. Given that there was no accuracy measurement in our behavioral task (see below) we used response consistency as a criterion for excluding subjects who did not successfully attend to the task. After subjects completed the experiment in the scanner, they re-did the experiment outside of the scanner, repeating the same stimuli. We calculated the percentage of stimuli with the same responses across repetitions for each subject and excluded a subject if his mean deviated from the group mean by more than three standard deviations. The same group of subjects performed the four rating tasks (i.e., taxonomic, thematic, function similarity, function relatedness) in the following week after the fMRI experiment. If any of the four ratings followed a clear pattern (e.g., using the same rating for all word pairs), if possible we asked the subject to redo that specific rating task or alternatively, removed the data from the correlation analysis.

5.1.2. Materials

There were 38 target words (e.g., *saw*), each paired with a taxonomically related (e.g., *axe*) and a thematically related (e.g., *wood*) word, resulting in 114 stimuli words (see Appendix A). The two related conditions also shared similar function features. Specifically, based on a definition of function feature as the purpose of use (e.g., [Canessa et al., 2008](#); [Moss et al., 1995](#); [Yee et al., 2011](#)), the function feature overlap for taxonomically related word pairs (e.g., *saw – axe*) referred to whether the two objects share the same purpose of use (e.g., *cutting*) and for thematically related word pairs (e.g., *saw – wood*) whether the purpose of use for one of the two objects is to perform an action on the other object (e.g., *a saw is to cut wood*). Following the instructions used in [Yee et al. \(2010, 2011\)](#) and [Moss et al. \(1995\)](#), we collected ratings from 20 subjects for all related and unrelated word pairs on a 1–7 scale for function similarity: “rate the following pairs of objects according to

¹ We thank Solène Kalénine and Greig de Zubicaray for providing information for the effect size calculations.

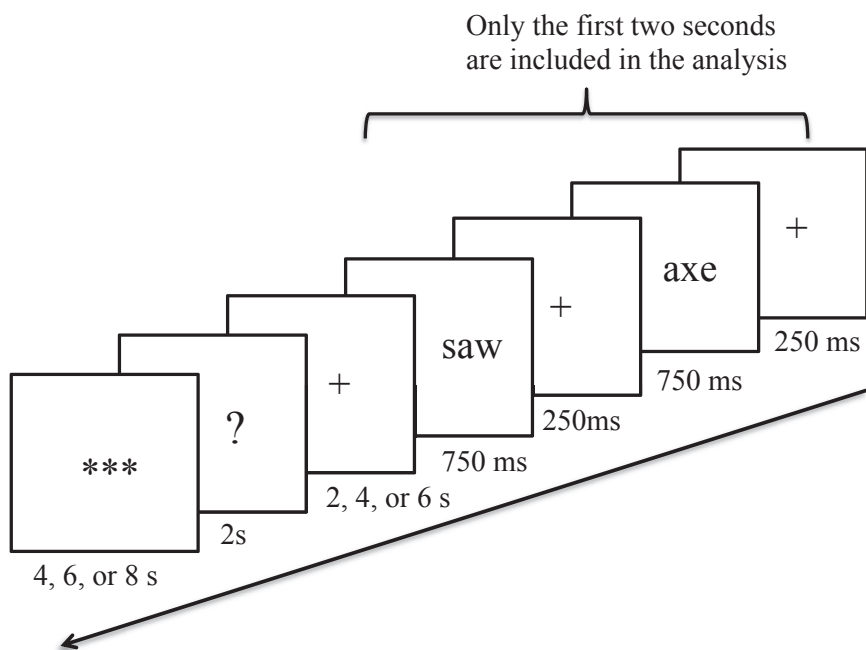
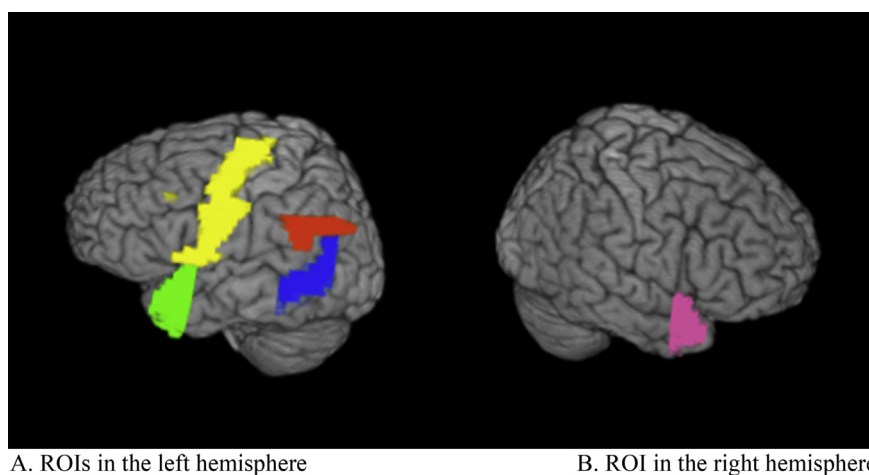


Fig. 1 – An example trial structure with question phrase. For those trials without a question phrase, the trial proceeds from the target (e.g., “saw”) directly to fixation (i.e., “*”). Critical task-related activity was modeled for the first two seconds of the trial (i.e., during the word pair presentation).**



A. ROIs in the left hemisphere

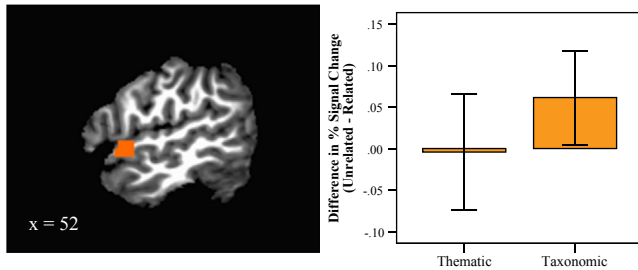
B. ROI in the right hemisphere

Fig. 2 – Anatomical ROIs defined in the Talairach atlas. In the left hemisphere (Panel A), the green ROI is the ATL (anterior to $y = 3$ in the left temporal lobe); the red ROI is the TPJ which combines angular and supramarginal gyri; the blue ROI is the pMTG (the region between $y = -40$ and $y = -69$ in the left MTG); and the yellow ROI is the premotor cortex (BA 6). In the right hemisphere (Panel B), the pink ROI is the ATL (anterior to $y = 5$ in the right temporal lobe). Abbreviations: ROI = Region of interest; ATL = anterior temporal lobe; TPJ = temporo-parietal junction; pMTG = posterior middle temporal gyrus.

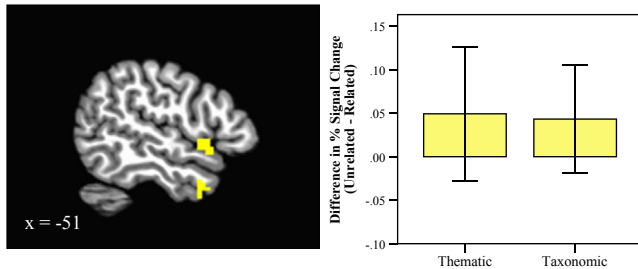
how similar their functions are (i.e., the purpose of use)”, and collected ratings from another 20 subjects to assess function relatedness: “rate the following pairs of objects according to how likely the purpose of use for one of the two objects is to perform action on the other one”. As expected, the taxonomically related word pairs had higher function similarity ratings compared to the thematically related pairs [t_1 (19) = 6.84, $p < .001$; t_2 (74) = 16.79, $p < .001$], and the thematically related word pairs had higher function relatedness

ratings compared to the taxonomically related word pairs [t_1 (19) = 13.53, $p < .001$; t_2 (74) = 14.58, $p < .001$] (see Table 1). Additionally, following Mirman and Graziano (2011), we collected taxonomic and thematic ratings from another 40 subjects for each related word pair (20 in taxonomic ratings and 20 in thematic ratings). For the taxonomic ratings, subjects were asked to “decide to what extent these two things are members of the same category”. In the thematic rating session, subjects were asked to “decide to what extent these

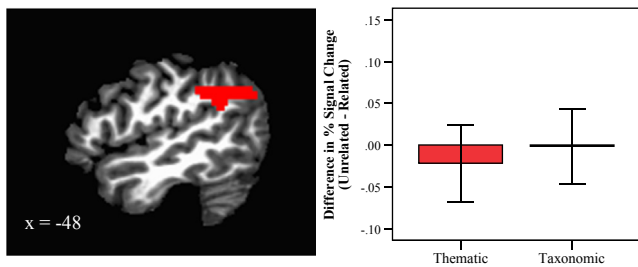
A. Anatomical-functional left ATL ROI



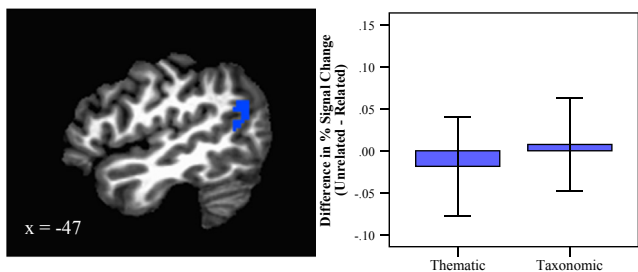
B. Anatomical-functional right ATL ROI



C. Anatomical-functional left TPJ ROI



D. Anatomical-functional left pMTG ROI



E. Anatomical-functional left premotor ROI

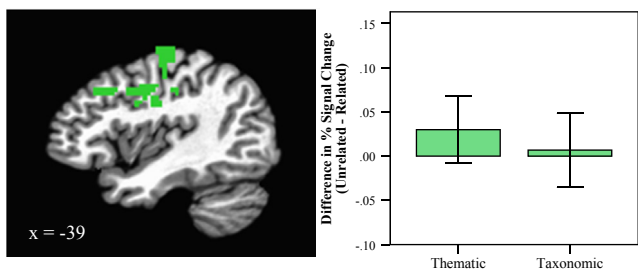


Fig. 3 – Anatomical-functional ROIs (on the left) with the corresponding percent signal change differences (on the right) for word pairs in the thematic and taxonomic categories (the adaptation effects). Error bars indicate 95%

two things co-occur in a situation or scene.” The results showed that the taxonomically related word pairs had higher taxonomic ratings compared to the thematically related word pairs [t_1 (19) = 7.59, $p < .001$; t_2 (74) = 11.11, $p < .001$] whereas the thematically related word pairs had higher thematic ratings compared to taxonomically related pairs [t_1 (19) = 4.00, $p < .001$; t_2 (74) = 4.03, $p < .001$] (see Table 1). Word pairs were matched for associative strength (Nelson, McEvoy, & Schreiber, 1998) across the taxonomically and thematically related conditions ($t < 1$).

5.1.3. Design

The design was a semantic category (thematic, taxonomic) by relatedness (related, unrelated) full factorial design, yielding four conditions. However, in order to ensure that the quality of the fMRI data was sufficiently good to obtain meaningful results, we also included a word-target repetition (i.e., identical) condition and its corresponding unrelated condition (see below). We expected adaptation in the left inferotemporal cortex (visual word form area or VWFA) following previous results (e.g., Cohen, Jobert, Bihan, & Dehaene, 2004; McDonald et al., 2010; for a review, see Cohen & Dehaene, 2004). The experiment consisted of six conditions as follows. All six conditions shared the same target words.

- Thematically related*: 38 words (e.g., wood) were thematically related to their corresponding target words (e.g., saw).
- Thematically unrelated*: the same 38 words from the thematically related condition were regrouped to form this unrelated condition.
- Taxonomically related*: another 38 words (e.g., axe) were taxonomically related to the target words (e.g., saw).
- Taxonomically unrelated*: the same 38 words from the taxonomically related condition were regrouped to form this unrelated condition.
- Identical*: the same 38 target words were repeated in this condition.
- Unrelated*: the same 38 target words were regrouped to form this unrelated condition.

5.1.4. Data acquisition

The MRI scanning was performed on a 3T Siemens Trio MRI scanner at the Human Neuroimaging Laboratory at Baylor College of Medicine, Houston, TX. The structural images were collected at the beginning of each scanning session, consisting of 176 1 mm slices. T2 weighted BOLD data was then collected in the echo planar imaging (EPI) sequence with an echo time of 31 msec, a repetition time of 2000 msec, and a 90° flip angle. Thirty-eight 3 mm axial slices were collected per volume, covering the entire brain for most participants, where care was taken to cover specific ROI (i.e., ATL, premotor cortex, middle temporal lobes, and TPJ). The voxel size was 3*3 mm. The field of view was 220*220 mm, and the acquisition matrix

confidence intervals (within-subject). Sagittal Talairach coordinates are in the lower left-corner. Abbreviations: ROI = Region of interest; ATL = anterior temporal lobe; TPJ = temporo-parietal junction; pMTG = posterior middle temporal gyrus.

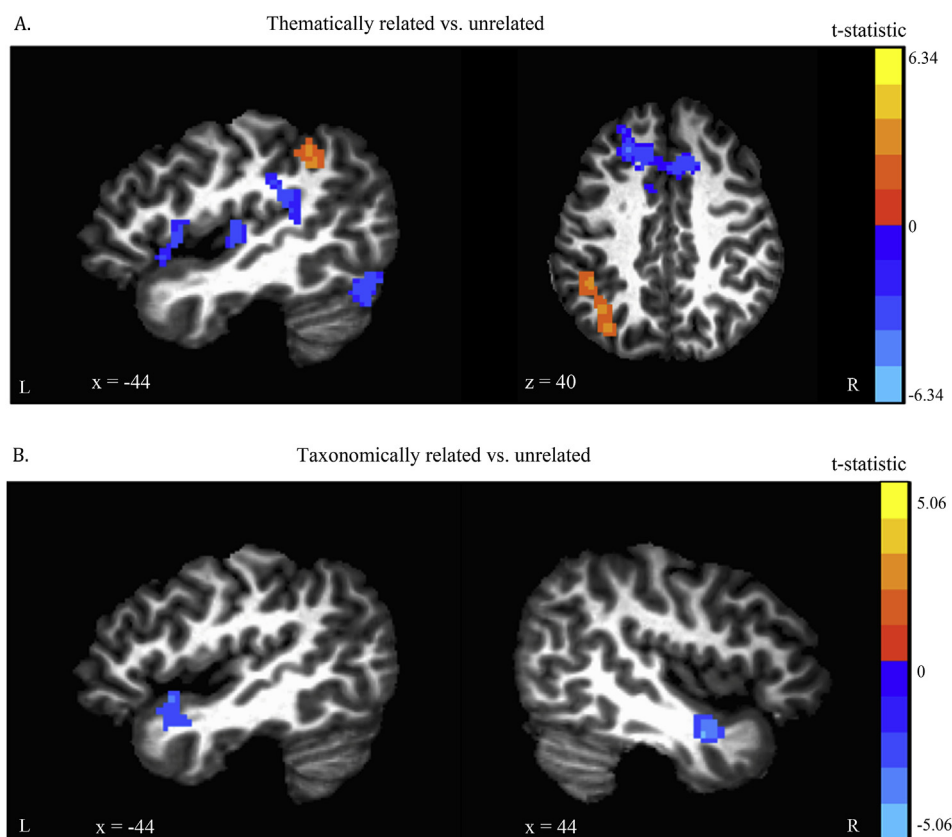


Fig. 4 – Representative peak activation differences in cerebral regions showing significant changes in BOLD activity for thematically related compared to unrelated word pairs (Panel A) and taxonomically related compared to unrelated word pairs (Panel B) in the subject-wise whole brain analysis (corrected threshold: $p < .05$; minimum cluster size: 187). Talairach coordinates are at the bottom. Scale bars show t-values for statistical contrasts. Negative values represent more activity for taxonomically/thematically unrelated word pairs in comparison to related word pairs. Positive values represent more activity for taxonomically/thematically related word pairs compared to unrelated word pairs. Abbreviations: L = left; R = right.

was 74×74 , resulting in a 3×3 mm in-plane resolution. A 32-channel send-receive head coil was used for all functional and structural scanning runs to minimize EPI distortions in the ATLs. Functional data was collected in 6 runs of about 6 min each. Each run began with a fixation for 6 sec to allow for steady state magnetization. E-prime was used to present stimuli and collect response times.

5.1.5. Procedure

Stimuli was displayed on Intel-based computers using E-Prime software. We first acquired participants' T1-weighted images. Pseudo-randomized rapid-event related fMRI paradigms were used, with stimulus presentation time-locked to each scanner repetition time (TR). Within each 2 sec TR, a fixation appeared for 250 msec first and then participants saw one word from the pair for 750 msec via a mirror centered above the participant's eyes. After a 250 msec fixation, the second word was presented in the center of the screen for 750 msec. Each word pair was seen one time, in pseudo-random order in the scanner such that no condition was seen more than three times in a row. In each run, there were 38 experimental word pairs and a filler word pair presented at

the beginning of each run. The participants were asked to pay attention to the meaning of each word. In order to ensure that subjects engaged in deep semantic processing for each word pair, we asked subjects to make a decision about which object they encounter more frequently in their daily life when they see a question mark after randomly selected word pair presentations. In order to eliminate the impact of the question on word presentation, we did not present the question for all word pairs, but instead we presented the question for eight word pairs randomly distributed across each run (2 in each condition per run, excluding the identical and the corresponding unrelated conditions) resulting in 12 questions per condition for taxonomically related/unrelated and thematically related/unrelated conditions across all runs (for a similar task see Harvey & Burgund, 2012; see Fig. 1). In addition, we used longer jittered delays (4, 6, or 8 sec) between the question and next word pair. When no question was presented, we introduced a jittered delay (4, 6, or 8 sec) between two word pair presentations. Participants responded to the familiarity question as quickly and accurately as possible. They pressed the left button if they encountered the first object more often or the right button if they encountered the second object more

often. The question remained on the screen for 2 sec regardless of the participant's response.

Participants had ten practice trials outside of the scanner before the experiment. After subjects completed the experiment in the scanner, they re-did the experiment outside of the scanner (identical presentation format except without jitter delays), repeating the same stimuli, in order to measure response consistency to the familiarity questions, as a control for participants staying on task. The entire fMRI experiment (inside and outside the scanner) lasted about an hour for each subject. The same group of subjects performed the four rating tasks (i.e., taxonomic, thematic, function similarity, function relatedness) in the following week after the fMRI experiment.

5.1.6. Imaging data analysis

We adopted two analysis strategies, correlation and condition comparisons (whole-brain and functional anatomical ROI) for three reasons. First, correlation may be a more sensitive measure, as it does not average BOLD signal across items (see [Yee et al., 2010](#)). Second, it also can clarify the role of features in the condition comparisons. As we discussed above, the functional relationships in taxonomic and thematic categories are similar but distinct from one another due to the inherent nature of the categories. Therefore, for example, even if we observe activity differences in the bilateral ATLs between taxonomically related versus unrelated conditions, this could be due to either taxonomic category or the specific function features involved in taxonomic categories. However, the correlation analyses have the potential to clarify this type of confound. For example, by conducting correlation analyses between taxonomic ratings and BOLD signal in the bilateral ATLs, if the BOLD signal in the ATLs significantly correlates with the taxonomic ratings but not with the functional similarity ratings, then we can conclude that consistent with the category-based view, the bilateral ATLs are more likely to reflect a hub for taxonomic categories. For similar reasons, we also used this logic for the other hypothesized ROI comparisons. Third, both analyses can provide converging evidence in support of the theoretical predictions. For example, if in the bilateral ATLs we found a significant difference in BOLD signal for the taxonomic versus unrelated condition, but we did not find correlations in the ATLs between BOLD signal and the taxonomic ratings, we would need to conclude the following: Although there is a relationship between ATL activity and the processing of taxonomic versus unrelated objects, because the activity is unrelated to a fine-grained measure of taxonomic relationships (i.e., the ratings adopted from [Mirman & Graziano, 2011](#)), ATL activation may potentially not reflect aspects of taxonomy that have been traditionally assumed (i.e., by ourselves and others, e.g., [Mirman & Graziano, 2011](#); [Kalénine et al., 2009](#); [Crutch & Warrington, 2005, 2010](#)). Lastly, with regards to the condition comparison analysis, we conducted both hypothesized ROI and exploratory whole-brain analyses to ensure that we did not miss any potentially important but unexpected brain regions which show adaptation between related (i.e., taxonomically/thematically related, identical) versus unrelated conditions.

5.1.6.1. PREPROCESSING. Given that there are susceptibility issues associated with the signal quality of bilateral ATLs,

following the method used in [Anzellotti et al. \(2011\)](#) and [Simmons, Reddish, Bellgowan, and Martin \(2009\)](#), we calculated temporal signal-to-noise ratio maps (TSNR, the ratio of the average signal intensity to the signal standard deviation) to ensure that the quality of the signal in the whole brain, particularly in bilateral ATLs was good enough to detect a BOLD signal. Simulations indicate that a TSNR of 20 is the minimum to reliably detect effects between conditions in fMRI data ([Binder et al., 2011](#); [Coutanche & Thompson-Schill, 2014](#); [Peelen & Caramazza, 2012](#)).

The imaging data were analyzed using the AFNI software package ([Cox, 1996](#)). We followed a script generated by the AFNI program `afni_proc.py` to run the preprocessing for each participant. First, the AFNI program `3dTshift` was used to perform a slice time correction. Second, the individual subject anatomical images were transformed to the Colin N27 template (TT_N27) using `@auto_tlrc`. Third, EPI volumes were registered to the volume acquired in closest temporal proximity to the T1-weighted anatomical scan (the first volume of the first EPI scan) using the AFNI program `3dvolreg` with the cubic polynomial interpolation option. Fourth, an 8-mm full-width half maximum (FWHM) Gaussian blur was then applied using AFNI's `3dmerge` program. Fifth, the data was then scaled in order to calculate the percentage signal change. Sixth, the data was submitted to a general linear model using AFNI's `3dDeconvolve` program covariates. Covariates of interest were convolved with a standard hemodynamic response function (HRF). The final voxel size after preprocessing stayed the same (i.e., 3*3 mm).

We analyzed the data using both subjects and items as random effects in the first and second level analyses following [Bedny, McGill and Thompson-Schill, \(2008\)](#) and [Yee et al. \(2010\)](#). In the first-level individual subject analysis, we performed both subject- and item-wise analyses in the deconvolution analysis. For the subject-wise random effects analysis, a first-level analysis was performed by modeling BOLD signal for each subject as a function of condition, on each trial. Covariates were created for each event type including: word pair presentation (i.e., taxonomically related and unrelated, thematically related and unrelated word pairs, identical and unrelated word pairs) and the familiarity probe. The individual subject analysis produced a beta value map for each condition at each voxel collapsed across items within each condition for each subject (for more details see [Bedny et al., 2008](#)). Similarly, for the item-wise random effect analysis, individual subject first-level models were created using a general linear model with each of the 228 word pairs (38 items by 6 conditions) entered as a covariate of interest ([Bedny et al., 2008](#)). This yielded 228 beta maps (38 targets in each condition) per subject, which were averaged across subjects to obtain a single beta map per item.

For the second-level analysis (i.e., group analysis), we discarded the familiarity probe condition, and only analyzed the word pair presentations. We then conducted the second-level subject- and item-wise, exploratory whole-brain and hypothesized ROI analyses using the beta values generated from the first-level models following the general procedures in [Bedny et al. \(2008\)](#) and [Dodell-Feder, Koster-Hale, Bedny, and Saxe \(2011\)](#). An effect was considered significant only when it was significant for both the subject and item analyses. If one

was significant and the other not at a $p < .05$, the effect was considered marginally significant, as is the accepted standard in these types of analyses.

5.1.6.2. DEFINING THE FUNCTIONAL-ANATOMICAL ROI. As we have *a priori* hypotheses concerning specific neuroanatomical regions associated with taxonomic and thematic relationships and function features, we used functional-anatomical ROI (see Fig. 2). First, five anatomical ROIs were delimited using the Talairach atlas (TT atlas). The left BA 6 was defined as left premotor cortex. The left pMTG was defined as the region between $y = -40$ and $y = -69$ in the left MTG following Simmon, Reddish, Bellgowan, and Martin (2009). We defined the regions involved in processing thematic categories following results in Schwartz et al. (2011) and Kalénine et al. (2009). Left angular and supramarginal gyri were combined to form the ROI for the left TPJ. Given that there was no clear definition for the ATLS in the TT atlas, we followed the method described in Insausti et al. (1998) to define the ATL bilaterally as all areas in the temporal lobes anterior to the limen insula (Left $y = 3$; Right $y = 5$ in the TT atlas). Second, within these anatomical ROI boundaries, functional ROIs were defined by the voxels in which activity during the presentation of the word pair differed from baseline (ITI) using the data from the first level subject-wise analysis. We evaluated the statistical significance of activation clusters based on their size, applying a threshold of $p < .05$ corrected for multiple comparisons at the voxel-wise level in each ROI by using the AFNI program 3dClustSim (see Yee et al., 2010 for a similar method). The cluster sizes calculated via 3dClustSim vary depending on the total number of voxels in each ROI. Thus, the minimum cluster sizes were 18 voxels for left premotor cortex, 13 voxels for left pMTG, 13 voxels for left TPJ, 14 voxels for left ATL, and 12 voxels for right ATL. If any of the ROIs did not show the BOLD signal difference in the contrast between task and fixation, we would not include that particular ROI in further analysis.

5.1.6.3. ROI ANALYSES

5.1.6.3.1. SUBJECT-WISE AND ITEM-WISE CONDITION COMPARISONS.

For the second-level within-subject random-effects analysis, the BOLD signal across all voxels within each functional-anatomical ROI was averaged for each subject. To determine whether there was adaptation in these regions, we compared the averaged BOLD signals in the taxonomically related to unrelated conditions and the thematically related versus unrelated conditions using two sample t-tests treating subjects as a random variable. For the second-level within-item random-effects analysis, the BOLD signal across all voxels within each functional-anatomical ROI was averaged for each item. To determine whether there was adaptation in these regions, we did the same comparisons as in the within-item analysis but treating items as the random variable instead. An effect was considered significant only when it is significant at a $p < .05$ level for both the within-subject and within-item analyses.

5.1.6.3.2. CORRELATION ANALYSIS. To determine whether activity in the functional-anatomical ROIs correlated with the degree of function relatedness and/or taxonomic/thematic relatedness (i.e., shows adaptation), we performed several

correlations. Specifically, in each functional-anatomical ROI we correlated the BOLD signal from each item when presented in the taxonomic, thematic, and associated unrelated conditions with its corresponding ratings (i.e., the taxonomic, thematic, and two functional ratings) across subjects.

5.1.6.4. EXPLORATORY WHOLE-BRAIN ANALYSIS. In addition to the ROI analyses, we conducted an exploratory, unrestricted whole-brain analysis to identify activity in regions which showed adaptation between related (i.e., taxonomically/thematically related, identical) versus unrelated conditions and correlation between the ratings for each word pair in all four taxonomic and thematic conditions and voxel wise BOLD activity.

Specifically, a second-level within-subject random effects analysis was performed on the beta maps generated from the first-level models for all six conditions. We computed condition differences (taxonomically related versus unrelated; thematically related versus unrelated; identical versus unrelated) via t-tests at each voxel, treating subjects as a random variable. The exploratory whole-brain contrasts were corrected for multiple comparisons at $p < .05$ using the AFNI program 3dClustSim. In the within-item random-effects analysis, the same second-level random effects analysis was conducted treating items as a random variable, following the same subsequent procedures as in the within-subject analysis. An effect was considered significant only when it was significant at a $p < .05$ level for both the within-subject and within-item analyses.

Following Yee et al. (2010), we also conducted item-based correlation analyses between ratings and BOLD signal for each word pair collapsing all subjects in the four taxonomic and thematic conditions in each voxel. The item-based correlational analysis was corrected for multiple comparisons at $p < .05$ using the AFNI program 3dClustSim.

6. Results

To access table of raw data go to: <http://dx.doi.org/10.17632/bNWvGpFvhF.1>. We tested 23 subjects (Age: 20 years + 1.5; Female: 11) and discarded three from further analysis due to head motion exceeding 2 mm within a single imaging run. Response consistency to the probe question (“which object do you encounter more frequently in your daily life?”) averaged across all subjects was 86% and none of the subjects' mean response consistencies deviated from the group mean by more than three standard deviations. In the results reported below, an effect was considered significant only when it was significant at a $p < .05$ level for both the within-subject and within-item analyses. Otherwise we report results as marginally significant if they were significant only by subject or by item analysis. See Table 2 for a summary of the result patterns consistent and inconsistent with the feature- and category-based views, as well as for the VWFA.

6.1. TSNR in bilateral temporal lobes

In order to verify that we obtained good signal from the bilateral ATLS, we calculated TSNR for the bilateral ATLS and

the whole brain. TSNR values were high for both ATL regions (left ATL mean = 145.2; right ATL mean = 160.6) as well as for the whole brain (average = 173.5). TSNR values in the bilateral ATLs far exceeded the threshold of 20, the minimum to reliably detect effects between conditions in fMRI data (Binder et al., 2011; Coutanche & Thompson-Schill, 2014; Peelen & Caramazza, 2012).

6.2. ROI analyses

6.2.1. Subject-wise and item-wise condition comparisons

Partially consistent with the category-based view (Mirman & Graziano, 2011, 2012; Schwartz et al., 2011), in the left ATL ROI there was marginally less activity in the taxonomically related versus unrelated conditions [$t_1(19) = 2.26, p = .04; t_2(37) = 1.83, p = .07$; Cohen's $d = .54$; see Fig. 3]. We found no other significant results in the ROI analyses.²

6.2.2. Correlation analyses

For each functional-anatomical ROI (i.e., bilateral ATLs, left pMTG, left TPJ, and left premotor cortex) we correlated the BOLD signal from each item (averaged across subjects) with the item's corresponding ratings (i.e., the taxonomic, thematic, functional similarity and functional relatedness ratings) when presented in a) the taxonomically related and unrelated conditions and b) thematically related and unrelated conditions resulting in 20 correlation analyses (i.e., four ratings by five ROIs). We found no significant results.³

6.3. Exploratory whole-brain analysis

6.3.1. Subject-wise and item-wise condition comparisons

We computed condition differences (taxonomically related vs unrelated; thematically related vs unrelated; identical vs unrelated) via t -tests at each voxel, treating either subjects or items as a random variable. The whole-brain contrasts were corrected for multiple comparisons at $p < .05$ using the AFNI

² Specifically, in line with the category-based view there was no significant difference in the left ATL ROI between the thematically related versus unrelated conditions (t 's < 1). However, in contrast to the prediction of the category-based view, there was no significant difference in the left TPJ between thematically related and unrelated conditions (t 's < 1). We found no ROI comparison results consistent with the feature-based view (e.g., Allport, 1985; Barsalou, 1999, 2008; Warrington & Shallice, 1984). Specifically, we observed no significant difference between taxonomically related and unrelated conditions and between the thematically related and unrelated conditions in the two function regions (i.e., left premotor cortex, left pMTG; p 's $> .10$).

³ Specifically, in contrast to the predictions of the category-based view (Mirman & Graziano, 2011, 2012; Schwartz et al., 2011), there were no significant correlations between activity in the bilateral ATLs and the taxonomic ratings (r 's $< .10, p$'s $> .25$) and no significant correlation between the activity in the left TPJ and the thematic ratings ($r = .002, p = .98$). In contrast to the predictions of the feature-based view (e.g., Allport, 1985; Barsalou, 1999, 2008; Warrington & Shallice, 1984), there were no significant correlations between activity in the two function regions (i.e., left premotor cortex and left pMTG) and the two function ratings (function similarity and function relatedness; r 's $< .10, p$'s $> .25$). Other correlations were also not significant (r 's $< .10, p$'s $> .20$).

program 3dClustSim, resulting in a minimum cluster size of 187 voxels (voxel-wise $p = .04$).

The exploratory whole-brain analysis supports the hypothesized ROI analysis but also reveals additional regions of activation consistent with the category-based view (Mirman & Graziano, 2011, 2012; Schwartz et al., 2011). There was marginally less activity in both the left and right ATLs for the taxonomically related versus unrelated conditions. In addition, the left supramarginal gyrus (a part of the left TPJ) revealed marginally greater activity in the thematically related versus unrelated condition. We performed a post-hoc analysis to reveal whether the significant regions identified in the whole-brain analysis were consistent with the predicted ROIs by overlapping the voxels identified in the anatomical-functional ROIs (i.e., voxels that were significantly more active in the language vs baseline tasks) with the significant voxels in the whole-brain analysis (see Post-hoc analysis Section for these results). For results related to the *a priori* predicted ROIs see Fig. 4 and for results including those outside of the *a priori* predicted ROIs see Table 3.

In order to ensure that the quality of the fMRI data was sufficiently good to obtain meaningful results in the exploratory whole-brain analyses, we included a word-target repetition (i.e., identical) condition and its corresponding unrelated condition and predicted reduced activity in the VWFA for the identical versus unrelated conditions. In contrast to this prediction, the identical versus unrelated comparison did not show a significant difference in the VWFA and instead revealed significantly greater activity in bilateral inferior parietal lobes, left superior temporal gyrus, and right inferior frontal gyrus. Given that the identical word pairs comprised less than 10% of the entire experiment, these word pairs likely attracted attention from subjects, resulting in activation of the attention network which elsewhere is found to include the bilateral inferior parietal lobes and right inferior frontal gyrus (e.g., Downar, Crawley, Mikulis, & Davis, 2001). Regarding the absence of the adaptation in the VWFA, this may be a result of the high repetition of target words in our experimental design. Specifically, the words used in the identical and unrelated conditions were repeated eight times across all conditions, as the same words were used as target words for the other four conditions (i.e., taxonomically related and unrelated conditions and thematically related and unrelated conditions). The high repetition may have rendered the identical condition adaptation in the VWFA difficult to detect (resulting in a Type II error). Most previous studies did not repeat their word stimuli more than once when investigating adaptation in the VWFA for word repetition (e.g., Cohen et al., 2004; Dehaene et al., 2010; McDonald et al., 2010). Therefore, we conducted a more sensitive analysis using the VWFA as an ROI and report the results as part of the post-hoc analyses.

6.3.2. Correlation analyses

For the item-based correlational analyses at the exploratory whole-brain level, we used Amplitude Modulated (AM) regression (<http://afni.nimh.nih.gov/pub/dist/doc/misc/Decon/AMregression.pdf>) to detect the voxels whose activity linearly changed with each of the four ratings respectively (i.e., taxonomic, thematic, function similarity, and function

Table 2 – Results are summarized as consistent (in green) or inconsistent (in red) with predictions from the feature-based (Feature) and the category-based (Category) views as well as the visual word form area (VWFA; for the identical vs unrelated comparison). Predictions consistent with the null hypothesis are not labeled. Planned statistical comparisons include: Taxonomically related (Taxo.rel) versus unrelated, Thematically related (Them.rel) versus unrelated, Identical versus unrelated, correlations between BOLD signal across all item pairs and a pairs' ratings for degree of taxonomic, thematic, functional similarity, and function relatedness relationship. With regards to the feature-based and category-based views, hypothesized regions of interest include the left and right anterior temporal lobes (ATLs), left temporal parietal junction (TPJ), left posterior middle temporal gyrus (pMTG) and left premotor cortex. Regarding condition comparisons, the feature-based view predicts that there should be significant BOLD signal differences in left pMTG and premotor cortex between thematically/taxonomically related word pairs and unrelated word pairs. The category-based view predicts that a) the bilateral ATLs should show significant BOLD signal differences between taxonomically related versus unrelated conditions but no differences between thematically related versus unrelated conditions; and b) the left TPJ should show a significant BOLD signal difference between thematically related versus unrelated conditions but no difference between taxonomically related versus unrelated conditions. For the identical versus unrelated comparison, we predicted that the visual word form area (VWFA) should show a BOLD signal difference. Regarding correlations, the feature-based view predicts that the degree of signal change in the function regions (i.e., left pMTG and premotor cortex) should correlate with function ratings (i.e., function similarity and function relatedness) for word pairs independent of their taxonomic or thematic relationship. In contrast, the category-based view predicts that the degree of signal change in the bilateral ATLs should correlate with the degree of taxonomic relatedness whereas the degree of adaptation in the left TPJ should correlate with the degree of thematic relatedness. Because no results were significant by both subject and item analyses, results are labeled significant when significant by subject only and when significant in either the hypothesized ROI, exploratory whole-brain, or both analyses. Results significant for the exploratory whole-brain analysis only are marked with an '*' and significant for the hypothesized ROI analysis only are marked with a '±'. For non-significant results in the hypothesized ROI analyses, we report Bayes factors (Dienes, 2014) in parentheses. n.s. = non-significant.

Statistical comparisons	Regions of interest				
	Left ATL	Right ATL	Left TPJ	Left pMTG	Left premotor
Condition contrasts					
Taxo.rel versus Unrelated	Category	Category*	n.s., B's < .3	Feature (n.s., B's < .3)	Feature (n.s., B's < .3)
Them.rel versus Unrelated	n.s., B's < .3	n.s., B's < .62	Category* (n.s. B's < .36)	Feature (n.s., B's < .3)	Feature (n.s., B's < .5)
Identical versus Unrelated	VWFA (Left inferior temporal cortex)±				
Rating Correlations					
Taxonomic	Category (n.s., B's < .3)	Category (n.s., B's < .3)	n.s., B's < .3	n.s., B's < .3	n.s., B's < .3
Thematic	n.s., B's < .3	n.s., B's < .63	Category (n.s., B's < .3)	n.s., B's < .3	n.s., B's < .3
Function similarity	Feature (n.s., B's < .3)	Feature* (n.s., B's < .3)	n.s., B's < .3	Feature (n.s., B's < .3)	Feature (n.s., B's < .3)
Function relatedness	Feature (n.s., B's < .3)	Feature (n.s., B's < .6)	n.s., B's < .3	Feature (n.s., B's < .3)	Feature* (n.s., B's < .3)

*Significant in the exploratory whole-brain analysis only.
± Significant in the hypothesized ROI analysis only.

relatedness). Correcting for multiple comparisons (a threshold of $p < .05$) required 187 voxels as the minimum cluster size.

Overall, correlation whole-brain analyses were partially consistent with predictions from the feature-based view (e.g., Allport, 1985; Barsalou, 1999, 2008; Warrington & Shallice, 1984). Activity in the bilateral precentral gyri including part of premotor cortex significantly decreased as function relatedness ratings increased. However, there was no significant correlation between activity in the bilateral precentral gyri and the function similarity ratings. Instead, we found that the activity in the right temporal pole was negatively correlated with the function similarity ratings. Inconsistent with the category-based view, we found no significant correlations between activity and the taxonomic and thematic relatedness ratings in bilateral ATLs and left TPJ. For all significant correlations including those outside of the *a priori* predicted ROIs see Table 4.

6.4. Post-hoc analyses

6.4.1. Visual word form area ROI analysis

We hypothesized that the lack of an adaptation effect in the VWFA was due to the high repetition of words across the experiment (i.e., the words used in the identical and unrelated conditions were repeated eight times across all conditions). To achieve more specificity (and potentially avoid a Type II error) we conducted an ROI analysis of the VWFA to examine whether there was a significant difference between the identical and unrelated conditions. We used VWFA MNI coordinates from Dehaene et al. (2010; $-40, -50, -14$) to define the VWFA ROI (a sphere with an 8-mm radius; Talairach coordinates: $-40, -49, -9$). We conducted subject and item analyses (following Results Section 2.1) to compare the percent signal change in the identical versus unrelated conditions. There was marginally less activity in the identical versus unrelated condition [t_1 (19) = 2.36, $p = .03$; t_2 (37) = 1.82, $p = .08$; Cohen's $d = .23$],

Table 3 – Cerebral regions significantly activated during thematic, taxonomic, and word repetition processing contrasts in the whole-brain analyses by subject (Table 3a) and by item (Table 3b). For each cluster, the region showing the maximum t value is listed. The Talairach coordinates (x, y, z) for the peak voxels are indicated.

a. Whole-brain subject-wise analysis.							
Contrast	Area	BA	No. voxels	x	y	z	T or F
Them_r < Them_ur	L cingulate gyrus		1855	-16	4	26	6.34
	L insula	13	454	-31	-24	11	5.84
	L lingual gyrus*	18	526	-11	-74	-4	4.14
	L medial frontal gyrus	6	548	-19	29	34	4.84
	R culmen		716	24	-34	-26	4.24
Them_r > Them_ur	R medial frontal gyrus	32	369	21	39	36	4.3
	L supramarginal gyrus	40	203	-39	-49	36	3.19
Taxo_r < Taxo_ur	L fusiform gyrus	37	240	-34	-37	-7	3.29
	L superior temporal gyrus	38	387	-39	10	-11	3.63
Semantic context × relatedness ^a		38	118	-39	11	-9	3.96
	R middle temporal gyrus	21	222	54	4	-11	4.14
	R parahippocampal gyrus*	34	396	19	-11	-16	3.96
	R culmen*		471	9	-41	-19	18.25
	Ident > Ident_ur	L superior temporal gyrus*	38	325	-54	19	-29
	L supramarginal gyrus	40	1059	-56	-44	31	6.94
	R inferior frontal gyrus*	10	741	-49	49	1	4.79
	R inferior frontal gyrus	44	1151	51	9	21	4.94
	R inferior parietal lobe*	40	945	64	-39	36	3.66
	R medial frontal gyrus*	10	188	6	64	-6	3.76
b. Whole-brain item-wise analysis.							
Contrast	Area	BA	No. voxels	x	y	z	T
Them_r < Them_ur	L superior frontal gyrus	9	2140	-19	56	39	4.29
	L lingual gyrus*	18	448	-21	-79	1	4.03
	L cerebellum		225	-9	-49	-26	3.68
Taxo_r < Taxo_ur	R parahippocampal gyrus*	34	231	19	-4	-16	4.55
	R cingulate gyrus	32	193	16	29	26	3.63
Semantic context × relatedness ^a	R culmen*		287	6	-41	-16	13.25
	L lingual gyrus	19	198	-31	-66	-1	11.46
Ident > Ident_ur	L inferior parietal lobe	40	2930	-51	-44	44	6.19
	L superior temporal gyrus*	38	273	-49	31	-24	3.77
	R inferior frontal gyrus*	9	1853	54	6	24	5.01
	R inferior parietal lobe*	40	1611	64	-31	41	5.74
	R medial frontal gyrus*	10	327	9	64	-6	4.97
	R middle temporal gyrus	37	447	56	-46	-6	4.27
	R superior frontal gyrus	8	626	16	44	44	3.81

* Significant by both subject and item analyses.
 Abbreviations: L = left hemisphere; R = right hemisphere; Them_r = thematically related; Them_ur = thematically unrelated; Ident = identical; Ident_ur = unrelated; BA = Brodmann area; No. voxels = number of voxels in the cluster.
^a Semantic context × relatedness = Semantic Context (taxonomic/thematic) and Relatedness (related/unrelated) Interaction.

suggesting that the quality of the fMRI data was sufficiently good to obtain meaningful results in the analyses by subject, but not by item in the planned ROI analyses. To calculate the power for the item VWFA ROI analysis, we did a post-hoc power analysis using G*Power 3 (Faul et al., 2007). Power was .37 for the VWFA ROI item analysis, suggesting that we did not have sufficient power to detect significant signal changes in the ROI item analyses. We discuss this further in the Summary section.

6.4.2. Semantic context (taxonomic/thematic) and relatedness (related/unrelated) interactions

In order to further investigate whether the bilateral ATLS and left TPJ specifically responded to taxonomic and thematic relationships respectively, we carried out semantic context (taxonomic and thematic) and relatedness (related and unrelated) interactions in both the hypothesized ROI and

exploratory whole-brain analyses. In the hypothesized ROI analyses, there were no significant interactions between semantic context and relatedness in either ATL region [Left: $F_1(1, 19) = 2.04, p = .17, MSE = .01, B_1 < .03; F_2 < 1, B_2 < .03$; Right: $F_1 < 1; B_1 < .03$] or left TPJ ($F_1 < 1; B_1 < .03$).⁴ To calculate the power for the ROI interaction analysis, we did a post-hoc power analysis using G*Power 3 (Faul et al., 2007). Power was extremely low for the ROI interaction analysis (left ATL: .26; right ATL: .05; left TPJ: .09) suggesting that we did not have sufficient power to detect significant signal changes in the interaction analyses. Similarly, in the whole-brain analysis for

⁴ B value reported here represents the Bayes factor, which estimates the strength of evidence for null results where values less than .3 indicate substantial evidence for the null over the alternative hypothesis (cf. Dienes, 2014).

Table 4 – Cerebral regions significantly negatively correlated with ratings of taxonomic, thematic, function similarity, and function relatedness respectively in the whole-brain item-wise analysis.

Rating	Area	BA	No. voxels	x	y	z	T
Taxonomic	L insula	13	427	−41	4	16	−4.6
	R insula	13	304	44	6	14	−3.64
Thematic	L middle frontal gyrus	11	614	−41	39	−14	−4.25
	L precentral gyrus	4	228	19	26	51	−3.67
	L superior frontal gyrus	6	188	−11	26	56	−4.19
	R superior temporal gyrus	22	189	64	−36	14	−4.41
Function similarity	L medial frontal gyrus	9	312	−4	56	41	−3.51
	R temporal pole	38	197	61	1	−24	−4.24
Function relatedness	L precentral gyrus	4	228	−19	−26	51	−3.67
	L thalamus		278	−26	−31	11	−5.02
	R fusiform gyrus	35	287	31	−26	−16	−4.08
	R precentral gyrus	4	297	29	−26	65	−4.38

For each cluster, the region showing the maximum t value is listed. The Talairach coordinates (x, y, z) for the peak voxels are indicated. Abbreviations: L = left hemisphere; R = right hemisphere.

the hypothesized bilateral ATLS and left TPJ, there were no significant interactions between semantic context and relatedness. The only significant interaction was observed in right culmen. For results including those outside of the *a priori* predicted ROIs see Table 3.

6.4.3. Comparison between hypothesized anatomical-functional ROI loci and exploratory whole-brain analyses results loci

We performed a post-hoc analysis to reveal whether the significant regions identified in the exploratory whole-brain analysis were consistent with the hypothesized ROIs by overlapping the voxels identified in the anatomical-functional ROIs (i.e., voxels that were significantly more active in the language vs baseline tasks) with the significant voxels in the whole-brain analysis. We found large overlaps between the predicted functional-anatomical ROIs in the left ATL and left TPJ and significant voxels identified in the whole-brain analysis within the left ATL and left TPJ. There was overlap between the predicted anatomical-functional ROIs in the right ATL and significant voxels identified in the whole-brain analysis within the right ATL (see Fig. 5).

7. Summary

Before summarizing the results with regards to the predictions for the feature- and category-based views, we discuss the overall issue of power to detect significance both in the item and interaction analyses. First, any significant results were significant only in the subject but not the item analyses and the post-hoc tests of the interaction between semantic context (i.e., taxonomic and thematic) and relatedness (i.e., related and unrelated) were not significant. We are the first to report statistical comparisons in neural activity between taxonomic and thematic categories (and subsequent interactions) using a conservative criterion of significance routinely adopted in behavioral studies, i.e., significance by both subject and item analyses. Significant subject and item analyses demonstrate generalizability of effects across both subjects and items (cf. Bedny et al., 2008). To our knowledge,

all previous fMRI studies testing the neural mechanisms of taxonomic and thematic categories only reported condition comparison results by subject and did not report item and interaction analyses (i.e., Kalénine et al., 2009; Sachs et al., 2008, 2011; Sass et al., 2009; de Zubicaray et al., 2013). As a result, although we were able to determine from previously published studies (i.e., Kalénine et al., 2009; de Zubicaray et al., 2013) *a priori* subject sample size to achieve power of at least .90 for the condition comparisons (i.e., taxonomically related vs unrelated; thematically related vs unrelated), the lack of previous item and interaction analyses precluded us from calculating the appropriate sample size for items and subjects to achieve sufficient power. The post-hoc power analyses revealed that we likely did not have enough power with only 38 items to detect significant signal changes in the ROI item analyses. Similarly, we did not have enough power with 20 subjects to detect significant signal changes in the interaction analyses. Future research should use larger item and subject sample sizes to achieve sufficient power. Because we did not have enough power to detect significant signal change in the item and interaction analyses, we restrict subsequent discussion of results to the subject analyses only.

We summarize significant findings by comparing similarities and differences between the hypothesized ROI vs exploratory whole-brain analyses results. With regards to the category-based view of concept organization (Mirman & Graziano, 2011, 2012; Schwartz et al., 2011) both ROI and whole-brain analyses were mostly consistent, where inconsistencies between the ROI and whole-brain analyses may have been a result of a lack of anatomical specificity in the anatomical ROIs we chose. Specifically, in support of the category-based view, the ROI and whole-brain analyses both revealed marginally significant left ATL activation differences for the taxonomic vs unrelated comparisons⁵ with overlap

⁵ The exploratory whole-brain condition comparison alone revealed marginally reduced activity in the right ATL for the taxonomically related versus unrelated condition and a significant correlation between the right ATL and function similarity ratings. We likely did not find these effects for the ROI analysis because there was little overlap between the whole-brain analysis and the anatomical-functional ROI of the right ATL (see Fig. 5).

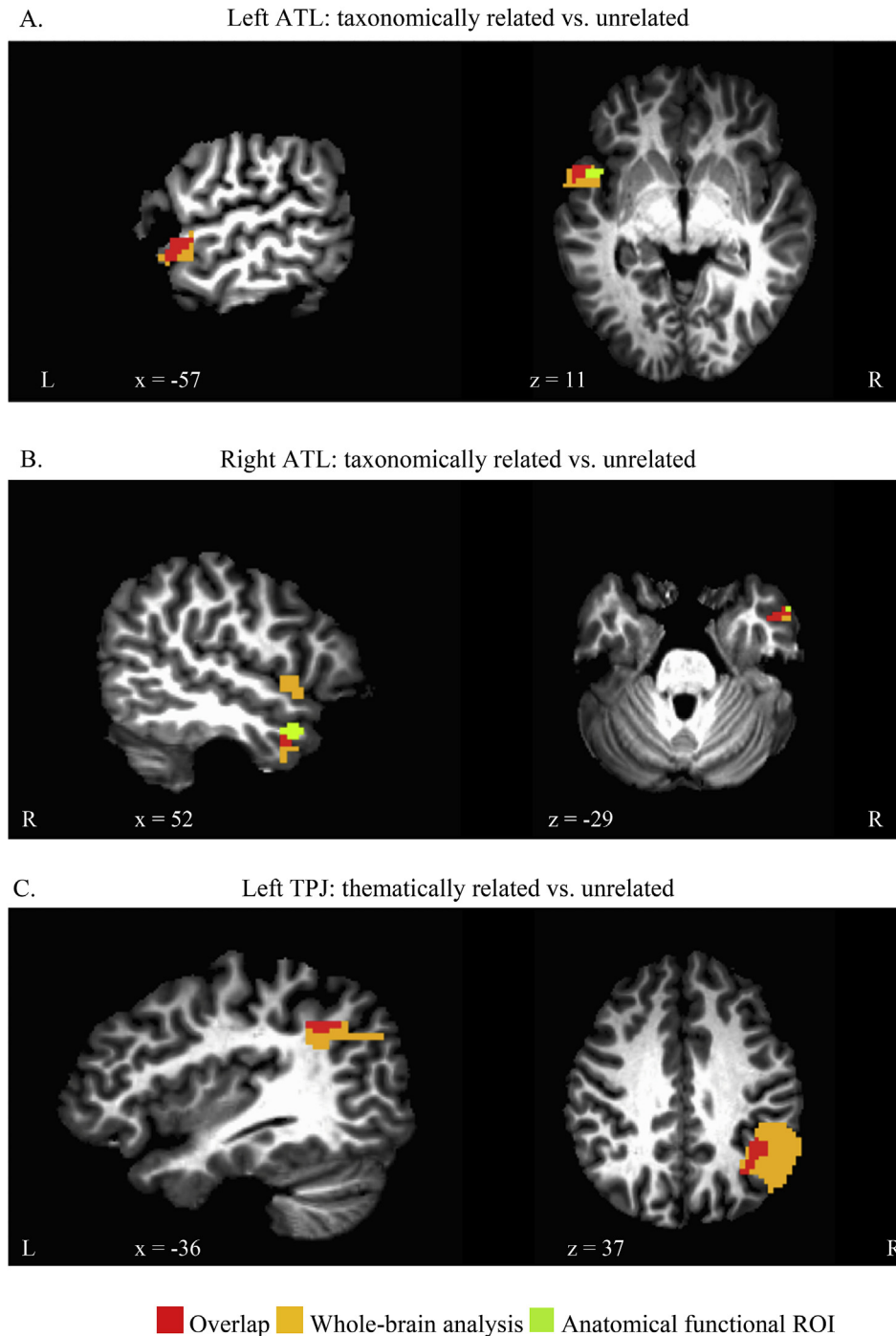


Fig. 5 – Comparisons between anatomical-functional ROI locations and spatially proximal results from the whole-brain analyses. Talairach coordinates are in the lower left. Abbreviations: ROI = region of interest; L = left; R = right; ATL = anterior temporal lobe; TPJ = temporo-parietal junction.

between areas of significant activation across both analyses (see Fig. 5). In the whole-brain analysis, there was greater activity in the left supramarginal gyrus (a part of the left TPJ) and the left inferior parietal lobe for the thematically related versus unrelated condition, but the left inferior parietal lobe was not included in the TPJ ROI (which only included the left supramarginal and angular gyri). This discrepancy may be

explained by the fact that the region which showed significant activity in the whole-brain analysis was adjacent to but more superior compared to the TPJ ROI. In support of the feature-based view (e.g., Barsalou, 1999, 2008; Warrington & Shallice, 1984), in the whole-brain correlation analyses there was reduced activity in the bilateral precentral gyri including part of the premotor cortex as the function relatedness ratings

increased, but not in the ROI analysis. Here too this discrepancy may be explained by a lack of ROI anatomical specificity, where the region which showed the significant correlation with function ratings in the whole-brain analysis was adjacent but more anterior compared to the left premotor anatomical ROI. Taken together, our findings suggest that both feature and category information are important for the organization of object knowledge (e.g., [Patterson et al. 2007](#)).

8. General discussion

In order to investigate the role of features and semantic categories in organizing object knowledge, we employed an fMRI adaptation paradigm. We examined the neural substrates underpinning taxonomic (e.g., saw-axe) and thematic categories (e.g., saw-wood) with similar function features (e.g., cutting). Subjects viewed word pairs, and performed attention catch-trials on 10% of total trials (subjects decided which of the two objects in the word pair they encountered more frequently in their daily life). To assess the function features shared in a word pair, subjects rated word pairs from two different perspectives: how likely two objects shared similar function (function similarity) and how likely one object performed an action on the other object (function relatedness). Subjects also rated word pairs on the degree to which words were taxonomically and thematically related. Consistent with the category-based view ([Mirman & Graziano, 2012](#); [Schwartz et al., 2011](#); for a review, see [Patterson et al., 2007](#)), when subjects viewed taxonomically related versus unrelated word pairs, for both the hypothesized ROI and exploratory whole-brain analyses we observed adaptation (i.e., reduced activity) in the left ATL and for the whole-brain analysis, in the right ATL. Also consistent, in the whole-brain analysis when subjects viewed thematically related word pairs, we observed adaptation in the left supramarginal gyrus (part of the TPJ) hypothesized to support thematic categories ([Mirman & Graziano, 2012](#); [Schwartz et al., 2011](#)). Consistent with the feature-based view (e.g., [Allport, 1985](#); [Barsalou, 1999, 2008](#); [Warrington & Shallice, 1984](#)), the exploratory whole-brain correlation analysis revealed that activity decreased in the bilateral precentral gyri including part of the premotor cortex with increasing function relatedness ratings. However, we did not find a relationship between adaptation effects in the bilateral ATLs and left TPJ with corresponding ratings of taxonomic/thematic relationships suggesting that the adaptation effects may potentially not reflect aspects of taxonomy that have been traditionally assumed. Together, our findings indicate that both feature and category information are important for the organization of object knowledge although the exact nature of those organization principles is an important question (e.g., [Patterson et al., 2007](#)).

Our study is novel in three aspects. First, we present the first fMRI study to our knowledge in healthy subjects which provides converging evidence with neuropsychological ([Schwartz et al., 2011](#)) and MEG evidence ([Lewis, Poeppel, & Murphy, 2015](#)) demonstrating specific relationships between taxonomic categories and the ATLs and between thematic categories and the left TPJ. Second, in order to clarify the feature confound present in previous studies (e.g., that

categories differed not only in categorical relationship, but also the types of features inherent to the category, e.g., [Kalénine et al., 2009](#)), we directly compared brain activity for taxonomic and thematic categories while controlling for the function features involved in the two categories. However, as we will discuss below, although this was a better attempt than previous, it was not entirely successful. Lastly, in order to better understand the role of brain regions in representing features and categories (i.e., bilateral ATLs, left TPJ, left pMTG, and premotor cortex) we investigated correlations between brain activity and four ratings assessing feature and category similarity. Below, we first consider the findings which suggest a role for features in organizing object knowledge and then discuss the results supporting the role of semantic categories.

8.1. Neural substrates underlying features

To test the feature-based view of object knowledge organization (e.g., [Allport, 1985](#); [Barsalou, 1999, 2008](#); [Warrington & Shallice, 1984](#)) which assumes that objects (e.g., dog) are represented by various features in visual (e.g., black, four legs and a tail), action (e.g., jump), function (e.g., a key is to open a door) and auditory (e.g., bark) modalities located in the sensory/motor brain regions, we selected word pairs based on the function features they shared. We selected word pairs sharing function features related to purpose of use (referred to as function similarity) for taxonomic categories (e.g., saw-axe) and word-pairs sharing function features associated with how likely the purpose of use for one of the two objects is to perform action on the other one (referred to as function relatedness) for thematic categories (e.g., saw-wood). The feature-based view predicts that when subjects understand two features related words in a sequence a) there should be adaptation in corresponding “feature” brain regions and b) the activity in these regions should correlate with the degree to which subjects rated the words as similar in function similarity and function relatedness. Although we did not find adaptation in predicted “feature” brain regions (i.e., left pMTG and premotor cortex) for related (by function feature) versus unrelated word pairs, brain activity correlated with ratings of word pair function relatedness in bilateral premotor cortex and ratings of function similarity in the right ATL. We hypothesize that the diverging correlation results between the function similarity and function relatedness ratings were due to how the different rating instructions emphasized different features, i.e., one focusing on function (function similarity), the other on action (function relatedness).

We used two different rating instructions to best capture the function features shared between word-pairs. First, to measure function similarity (e.g., the “cutting” feature shared by saw-axe), we used the following instruction: “rate the following pairs of objects according to how similar their functions are”. To measure function relatedness (e.g., the “cutting” feature shared by saw-wood), we employed a different instruction: “rate the following pairs of objects according to how likely the purpose of use for one of the two objects is to perform action on the other one”. The wording differences between instructions for the two function ratings likely resulted in measuring similar, but different features, as reflected in the pattern of results.

The result that different regions responded to the ratings (i.e., precentral gyri for functional relatedness and right ATL for function similarity) is a pattern partially consistent with recent neuropsychological and neuroimaging evidence (e.g., Buxbaum & Saffran, 2002; Canessa et al., 2008; Spatt, Bak, Bozeat, Patterson, & Hodges, 2002). This evidence suggests that low-level object feature knowledge (e.g., action, shape) is represented only in sensory/motor brain regions (e.g., precentral gyri, premotor cortex, inferior temporal cortex) whereas high-level abstract object feature knowledge (e.g., function, location) is represented not only in sensory/motor brain regions but also in the bilateral ATLs that are considered as a hub binding all the information from sensory/motor brain regions (e.g., Canessa et al., 2008; Peelen & Caramazza, 2012). For example, patients with brain damage as a result of stroke show a double dissociation when accessing function and action feature knowledge (e.g., Buxbaum & Saffran, 2002; Spatt et al., 2002). When selecting objects sharing the same manner of manipulation (i.e., an action feature) (e.g., typewriter and piano), patients with frontoparietal lesions (including precentral gyri) made more errors compared to patients with anterior inferotemporal lesions. Interestingly, the same two groups of patients showed the opposite pattern when selecting objects sharing the same function (e.g., broom and vacuum). These results were replicated by later neuroimaging studies with healthy participants (e.g., Kellenbach, Hovius, & Patterson, 2005; Canessa et al., 2008). Taken together, the correlation results in the present study and evidence elsewhere suggest that action features are represented in the motor/action regions (e.g., precentral gyri) and function features are represented in the bilateral ATLs (e.g., Canessa et al., 2008). Therefore, the correlation results in our study are partially consistent with the feature-based view that feature information, grounded in the sensory/motor brain regions, is a critical principle for organizing object knowledge.

8.2. Neural substrates underlying categories

To test the category-based view which assumes that the bilateral ATLs represent taxonomic categories and the left TPJ represents thematic categories (Mirman & Graziano, 2012; Schwartz et al., 2011), we manipulated taxonomic (e.g., saw-axe) and thematic category (e.g., saw-wood) relationships for different word-pairs. The category-based view predicts that a) when using adaptation fMRI, the bilateral ATLs should show adaptation (reduced or greater activity) for taxonomically related versus unrelated word pairs; b) the left TPJ should show adaptation for thematically related versus unrelated word pairs; and c) adaptation in the bilateral ATLs and left TPJ should correlate with the degree the word pairs are taxonomically or thematically related respectively. Consistent with the first two predictions, there was reduced activity in the bilateral ATLs during the presentation of taxonomically related versus unrelated word pairs and greater activity in the left TPJ during the presentation of the thematically related versus unrelated word pairs. However, inconsistent with the third prediction, we did not observe that the adaptation in the bilateral ATLs or left TPJ changed (decreased or increased) with the degree the word pairs were taxonomically or thematically related, as explicitly judged by subjects. The absence of correlations between

activity in the categorical regions (i.e., bilateral ATLs and left TPJ) and their respective categorical ratings (i.e., taxonomic and thematic) does not necessarily suggest that the bilateral ATLs and TPJ do not represent category information (see Lewis, Poeppel, & Murphy, 2015). It is possible that the bilateral ATLs and the left TPJ differentially respond to some aspect of similarity for taxonomic and thematic categories respectively, but the exact nature of this similarity was not assessed by the explicit subject ratings.

We designed our taxonomic category ratings to measure how likely items share the same superordinate category (e.g., animal), for example, “dog” and “cat” are more likely to be members of the same category versus “dog” and “ant”. However, the bilateral ATL adaptation for taxonomically related versus unrelated word pairs may have been the result of other similarities not measured by the ratings. Neuropsychological evidence suggests that the bilateral ATLs carry basic-level and subordinate information of a taxonomic category, not only general superordinate information (e.g., Crutch & Warrington, 2008; Humphreys & Forde, 2005; Lambon Ralph, Sage, Jones, & Mayberry, 2010). Evidence from semantic dementia suggests that severe ATL atrophy results in the loss of subordinate or basic category knowledge but superordinate category knowledge remains relatively preserved (Crutch & Warrington, 2008; Humphreys & Forde, 2005; Rogers & Patterson, 2007). For example, patients with severe bilateral or left ATL atrophy recognized a Chihuahua picture as an animal but they could not identify it as a dog or cat whereas patients with less severe atrophy used more specific category labels like dog or Chihuahua to name the picture (e.g., Rogers & Patterson, 2007). In line with the neuropsychological evidence, a PET study (Rogers et al., 2006) showed that the left ATL showed greater activity when subjects made a category decision at the subordinate (e.g., robin) level compared to the basic (e.g., bird) and superordinate (e.g., animal) levels. These findings suggest that the bilateral ATLs store basic and subordinate level information for taxonomic categories (see a similar argument in Rogers et al., 2006). In addition, the bilateral ATLs may also be relevant for the typicality of a taxonomic category. For example, when judging whether an object belongs to a specific category (e.g., cat), patients with more severe bilateral ATL atrophy were more likely to incorrectly reject an atypical category exemplar (e.g., a hairless cat) (Lambon Ralph et al., 2010). Critically, in our study, the taxonomic ratings may have tapped superordinate category information (e.g., animal) instead of more specific information (basic and subordinate) or exemplar typicality information subserved by the ATL, thus providing a possible explanation for why bilateral ATL activity was not related to the degree word pairs were taxonomically related.

Similarly, although the left TPJ responded to words that were thematically related (as seen in the exploratory whole-brain analysis), the degree to which subjects rated word pairs as thematically related was unrelated to the change in activity. Here too, the ratings may not have captured the similarity critical to the thematic relationship. We designed the thematic ratings to measure the co-occurrence of two objects in a familiar scene. However, there are complex relations involved across thematic categories where many can be considered as co-occurrence (see Anderson, Murphy, & Poesio, 2014; Estes, Golonka, & Jones, 2011). For example, the

word pair *saw* and *wood* includes a function/action relationship (e.g., cut) and a spatial relationship (e.g., on). How the TPJ represents different types of thematic relations remains unclear. Lewis, Poeppel, and Murphy (2015) observed that subjective relatedness ratings (i.e., two words can be considered as related if they are the same general kind of thing (velcro and zipper) or if they are related to one another (pants and zipper)) correlated with activity in the left TPJ for both thematically related and taxonomically related word pairs. In a recent eye tracking study (Mirman & Graziano, 2012), when selecting a picture corresponding to a target word from a picture array consisting of a target picture, a thematically related picture and two unrelated pictures, patients with left TPJ lesions made fewer eye fixations toward the thematically related picture compared to healthy controls (Mirman & Graziano, 2012). This result suggests that if the left TPJ is damaged, people do not recognize the thematic relationship between two objects (e.g., dog and bone). If true, then patients with left TPJ lesions should produce fewer thematic errors when naming pictures. However, two neuropsychological studies showed that patients with left TPJ lesions were more likely to produce thematic errors in picture naming (Jefferies & Lambon Ralph, 2006; Schwartz et al., 2011). Therefore, although our results are consistent with the neuropsychological evidence suggesting a relationship between the left TPJ and thematic categories, the mechanism underlying the left TPJ for representing thematic categories is not clear.

Although the present study to date is the best attempt to our knowledge to control for the function features involved across taxonomic and thematic categories, we need to interpret with caution exactly what aspect of similarity between these word pairs was responsible for the activity patterns. Because we used different instructions for the two function feature ratings, the word pairs in the two categories may have differed not only in terms of category (taxonomic vs thematic) but also in terms of features (i.e., more function features associated with the taxonomic category vs more action features associated with the thematic category). Although neuropsychological studies (e.g., Lambon Ralph et al., 2010; Rogers & Patterson, 2007; see Patterson et al., 2007 for a review) clearly demonstrate a relationship between taxonomic category information and the bilateral ATLs, the bilateral ATLs may also represent specific features (e.g., function, location) associated with certain exemplars independent of their category membership (e.g., Canessa et al., 2008; Peelen & Caramazza, 2012). With regards to the relationship between left TPJ and feature/thematic category information, our results and two previous neuropsychological studies (Jefferies & Lambon Ralph, 2006; Schwartz et al., 2011), suggest that the left TPJ represents thematic category information, although defining the information which constitutes a thematic relationship needs to be empirically explored. The picture that emerges is that the bilateral ATLs likely support knowledge about both taxonomic categories and features whereas the left TPJ likely supports thematic category information. This leaves open questions concerning the nature of the knowledge that distinguishes brain regions which subservise both categorical and feature knowledge from sensory/motor brain regions specific to features (like the bilateral precentral gyri).

8.3. Conclusion

The present adaptation fMRI study in healthy subjects demonstrates that both feature and category information associated with an object are important for organizing object knowledge. Consistent with the category-based view, the bilateral ATLs were sensitive to word pairs sharing taxonomic category membership while the left TPJ was sensitive to word pairs sharing thematic category membership. Consistent with the feature-based view, activity in the precentral gyri correlated with the degree that objects shared features related to action. However, we did not observe significant relationships between activity in the bilateral ATLs and the TPJ and the degree to which word pairs were judged as sharing the same taxonomic and thematic categories, potentially due to the specificity of the rating instructions (e.g., the lack of emphasis on basic/subordinate level categorical information and object typicality). Instead, we observed a correlation between the activity in the right ATL and the degree of function similarity between two objects, suggesting that at least the right ATL carries specific feature information. Future research should further identify the aspects of taxonomic and thematic relationships that are similar across members of a given category in order to better understand how the bilateral ATLs and left TPJ differentially support taxonomic and thematic categories.

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Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.cortex.2016.01.006>.

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