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

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Q14 *Jingyi Geng and Tatiana T. Schnur* *

Department of Psychology, Rice University, Houston, TX, USA

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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 an 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 in the bilateral precentral gyri (i.e., function regions) including part of premotor cortex reduced 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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* *Corresponding author*. Department of Psychology, Rice University, Houston, TX 77005, USA. Q1
E-mail address: ttschnur@rice.edu (T.T. Schnur).

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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 Q2 Q3 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 et al., 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, Q4 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. Q5 Q6

The feature-based view generates clear predictions for the Q7 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 feature (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; Hoges, 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

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