Where for what: A meta-analysis for the category-specific activations for living/nonliving concepts in the past two decades

Kimberly D. Derderian (kderderian@scu.edu)
Neuroscience Program, Santa Clara University, 500 El Camino Real, Santa Clara, CA 95053, USA

Xiaojue Zhou (xiaojuez@uci.edu)
Department of Cognitive Sciences, UC Irvine, 2201 Social & Behavioral Sciences Gateway Building, Irvine, CA 92697, USA

Lang Chen (lchen4@scu.edu)
Department of Psychology, Neuroscience Program, Santa Clara Uiversity, 500 El Camino Real, Santa Clara, CA 95053, USA

Abstract

The cortical organization of the semantic network has been studied extensively in neuropsychological and neuroimaging studies. Recent theories have heavily relied on the observation of category-specific activations, i.e., the preferential activations in brain regions for specific semantic categories. With decades of research, a full understanding of the organization has not yet been reached, since little is known about the factors that contribute to the variances in observed activation patterns across numerous neuroimaging studies. In this study, we first reviewed 97 published papers that reported category-specific activations for living or nonliving concepts in the past two decades. Then, using the Activation Likelihood Estimate (ALE) method, we characterized the brain activation associated with living and nonliving concepts, revealing the influences of relevant factors (e.g., neuroimaging mode, task demands, and stimuli modality), and analyzing these findings in relation to theoretical accounts of cortical semantic networks.

Keywords: semantics, category-specific activations, meta-analysis, neuroimaging, domain-specificity

Introduction

Since the first a few cases of category-specific semantic impairment were reported (Warrington, 1975; Warrington & Shallice, 1984), researchers have been trying to understand how the knowledge of the meanings of words and objects is represented in the human brain (Caramazza & Shelton, 1998; Farah & McClelland, 1991; Lambon Ralph, Howard, Nightingale, & Ellis, 1998; McCarthy & Warrington, 1988). With the introduction of neuroimaging techniques, particularly functional Magnetic Resonance Imaging (fMRI) and Positron Emission Tomography (PET), researchers have extended the investigation of cortical semantic network by examining the brain activations for different semantic categories extensively (e.g., Devlin et al., 2002; Gerlach, Law, Gade, & Paulson, 2002; Kellenbach, Brett, & Patterson, 2003; Martin, Haxby, Lalonde, Wiggs, & Ungerleider, 1995). Although existing studies yielded many interesting observations and helped us understand the cortical organizations of semantic knowledge (for reviews, see Chen, Lambon Ralph, & Rogers, 2017; Mahon & Caramazza, 2009, 2011; Martin & Chao, 2001; Tyler & Moss, 2001), findings have been inconsistent due to methodological variances across studies. Thus, their contributions were compromised for adjudicating between different theoretical accounts on cortical semantic networks. Using the ALE meta-analysis (Eickhoff, Bzdok, Laird, Kurth, & Fox, 2012), we aim to provide a comprehensive and quantitative review of previous literature on category-specific activations, focusing on the living/animal vs. nonliving/artifact categories. We further examined important factors that may contribute to the variance of observations in previous studies. This summary will help us gain a complete view of consistent activation patterns for different semantic categories and provide critical implications on existing theories of the neural underpinnings of semantic knowledge.

For decades, there were two dominant theoretical views in the literature. The domain-general view argues that the meanings of all words and objects are acquired through different sensory modalities through learning experience (for recent reviews, see Chen et al., 2017; Farah & McClelland, 1991; Lambon Ralph, Jefferies, Patterson, & Rogers, 2016; McClelland & Rogers, 2003). Established semantic knowledge can be used to make inferences based on observed properties, like you could mentally “feel” the coarse texture when seeing the surface of a tennis ball. The cortical semantic network is thought to support the cross-modal mappings for all semantic domains (Chen et al., 2017). With converging evidence from neuropsychological (Patterson et al., 2006), neuroimaging (Visser, Jefferies, & Lambon Ralph, 2010), and computational modeling (Chen et al., 2017; Rogers & McClelland, 2004) studies, researchers have argued for a unified semantic network in which the anterior temporal lobe (ATL) serves as a hub to represent cross-modal knowledge and motor-sensory cortices support modality-specific representations of words and objects (Lambon Ralph et al., 2016). From this view, the category-specific activations are commonly observed in modality-specific regions because modality-specific properties are systematically different across semantic domains (Leaver & Rauschecker, 2010; Mechelli, Sartori, Orlandi, & Price, 2006; Rogers, Hocking, Mechelli, Patterson, & Price, 2005) and processes of modality-specific properties are constrained by the connectivity patterns of the model (Chen et al., 2017).

The other theoretical account, namely, the domain-specific view, has argued for predisposed brain regions or networks to process different categories of semantic knowledge (Caramazza & Shelton, 1998; Mahon, Anzellotti, Schwarzbach, Zampini, & Caramazza, 2009). From this view, category-specific activations are the natural demonstrations of the specialized functions of different brain regions and networks. Following this argument, studies have showed that even the ATL showed category-specific activations when animate/living kinds were involved (Anzellotti, Mahon, Schwarzbach, & Caramazza, 2011; Simmons, Reddish, Bellgowan, & Martin, 2010). Thus, these studies conclude that the ATL serves as a node in a brain network for animate or social knowledge rather than a domain-general hub. Research on the congenitally blind supports the idea of predisposed brain structures to process and represent domain-specific knowledge (Almeida, Mahon, & Caramazza, 2010; Mahon et al., 2009). This line of research showed that individuals without any visual experience from birth exhibited similar patterns of brain activations to sighted individuals, such as the lateral occipital cortex (LOC) for animals as well as medial fusiform gyrus (mFG) and inferior parietal lobe (IPL) for tools, suggesting that category-specific representations in these regions were experience-independent and brain structures are innately-architected to process knowledge of different domains.

Previous studies have focused on the living/animal vs. nonliving/tool contrast due to their relevance to the theoretical debates. First, this contrast has a long history in neuropsychological studies (Caramazza & Shelton, 1998; Gainotti, 2004; Warrington & Shallice, 1984) and relates to the central debates on the organizations of cortical semantic networks. Second, these two domains have rich representations from multi-sensory modalities, making them ideal cases to test hypotheses from the domain-general view which assumes direct links of the neuroanatomy with the cross-modal and modality-specific representations. Extant literature has converged on a few brain regions about these regions' preferred activation patterns particularly for the nonliving/artifact category, such as the medial posterior fusiform gyrus (pFG; Mahon et al., 2009; Martin & Chao, 2001), IPL (Almeida et al., 2010; Kellenbach et al., 2003), and posterior middle temporal gyrus (pMTG; Chouinard & Goodale, 2010). However, consistent activation patterns for the living/animal category remain elusive for different reasons including learning experience and similarity of the conceptual categories (Chen et al., 2017; Chen & Rogers, 2014; Rogers et al., 2005). Therefore, besides characterizing the consistent activation patterns for the living and nonliving categories, examining the contributing factors of variances in observed brain activations seems to be critical for settling the theoretical debate.

The ALE meta-analysis has been shown to aid in delineating the brain regions involved in semantic processing (Binder, Desai, Graves, & Conant, 2009; Visser et al., 2010). However, the quantitative analysis of literature on category-specific activations has been relatively scarce. To our knowledge, there are two major meta-analysis studies examining category-specific activations using the ALE method so far. The first meta-analysis focused on only 17 studies that used naming tasks to characterize the activation patterns for animals and tools (Chouinard & Goodale, 2010). Across the between-study and within-study comparison, the researchers reported that cuneus, pFG, and LOC were consistently reported for naming animal objects, whereas the left inferior frontal gyrus (IFG) and pMTG were consistently reported for naming tools. Chen et al. (2017) reviewed 49 studies that reported category-specific activations for animals and artifacts across different studies varying in factors such as mode of imaging, task demands, and stimuli modality, revealing the IPL/SPL-pMTG-mFG network for the artifacts with only the lateral FG in the right hemisphere consistently reporting for animals.

However, these two meta-analysis studies presented some limitations. First, the two studies included a relatively small set of studies showing inconsistent results, so a comprehensive summary of the consistent findings remain uncharacterized. Second, these two meta-analyses either included only studies using a specific task (i.e., naming) or included any tasks without differentiation. This difference potentially explains the discrepancies of their findings and further highlights the need to examine the effect of task demands. Third, other factors, such as imaging mode and stimuli modality, were shown to affect the observed brain activations, which is relevant to the theoretical debates, but their effects have not been revealed with previous meta-analysis studies. Therefore, the goal of the current study is two-fold: (a) to characterize the consistent patterns of category-specific activations for living/animal and nonliving/artifact comprehensively with a large set of fMRI studies; and (b) examine how moderators influence observed patterns of category-specific activations. For the moderator analysis, we first examine the effect of imaging mode by focusing on ATL activation in PET studies. As we have shown, the role of ATL is still in debate, since it is hypothesized either as the cross-modal hub for representing concepts of different categories (Rogers & McClelland, 2004) or as a node within a network representing animal or social concepts (Anzellotti et al., 2011; Simmons et al., 2010). However, activation of the ATL has shown to be influenced by the mode of the imaging (Visser et al., 2010). Thus, in order to clarify the role of ATL, we need to review the neuroimaging studies of category-specific activations using PET. Second, we focused on studies with tasks requiring low involvement of semantic knowledge. From the domain-general view, tasks demanding little semantic knowledge are likely to engage the modality-specific representations for the presented stimuli (Rogers et al., 2006), while the domain-specific view does not assume the processing demand would impact the role of predisposed brain regions. Lastly, we aimed to examine studies using nonvisual stimuli to test whether the visual cortex will be involved without visual inputs in healthy participants, since studies supporting the domain-specific view argue that these brain structures are made for processing certain knowledge domains independent of visual experience and inputs.

Method

Literature selection

We followed the standard procedure for the literature search as used in previous studies. We searched in the title, abstract, and keywords of articles published before 2017 in PubMed using the following search words: "category-specific", "living", "nonliving", "animal", "tool", "manmade", and "artifact" in combinations with "fMRI", "PET", "neuroimaging", and "brain". Then, the first and third authors went through the abstracts and filtered irrelevant studies, resulting in 259 articles. Then, all the authors read these papers in detail to filter the articles based on the following exclusion/inclusion criteria: (i) exclude review and meta-analysis articles; (ii) must contain at least one of the following concept categories: living, animates, nonliving, artifact, action concepts; (iii) exclude those studies that ONLY use emotional faces for living/animates category; (iv) must report coordinates in MNI or Talairach Space; (v) only include main effects for these semantic categories based on whole-brain or ROI-based analysis. Thus, a final selection of 97 articles were included for the following ALE meta-analysis.

ALE meta-analysis procedure

We used GingerALE v3.0.2 (Eickhoff et al., 2012) for all the ALE analysis with any coordinates reported in the Talairach space converted into the MNI space. First, we examined the consistent findings for the living and nonliving categories across all fMRI studies (**The primary analysis**), and then we selected a subset of the studies to examine the effects of imaging mode (fMRI vs. PET), task demands on semantics (Low vs. High), and display modality (Visual vs. Nonvisual). We are interested in demonstrating how distinct activation patterns for living and nonliving categories are moderated by these factors (**The moderator analysis**).

The primary analysis The primary analysis characterizes the consistent findings of category-specific activations for living and nonliving concepts with a large dataset. In order to keep the analysis comprehensive and comparable to previous meta-analyses, we selected only the studies using fMRI due to its prevalence (see **Table 1**). Thus, we aimed to use all the fMRI studies to establish a "norm" for the category-specific activations and then examine the activation patterns from studies with important deviations (see **The moderator analysis**). We followed the steps proposed in previous ALE-based meta-analysis studies (Chen et al., 2017; Chouinard & Goodale, 2010). First, we examined the main effects of living and nonliving concepts separately (i.e., concordance of foci showing greater activations for living or nonliving concepts compared to the baseline conditions across different studies). These main effect results are not reported in this paper due to space limits. Next, we combined the ALE maps for living (based on 506 foci from 69 experiments) and nonliving (746 foci from 90 experiments) and tested for brain regions that were activated for both categories (conjunction analysis) or that were activated differently for the two categories (contrast analysis). This analysis characterizes the consistently reported brain activations for living vs. nonliving concepts across a large set of studies for the first time.

The moderator analyses Based on the experimental procedures, each experiment of every study was classified into different moderator categories. The imaging mode classification (fMRI vs. PET) was explicitly reported in studies. We focused on the PET studies to circumscribe the potential signal loss of fMRI studies in the ATL (Visser et al., 2010).

The classification of task demands on semantics was based on the experiment task used in the studies. Picture naming (overt or covert) and category/semantic feature judgement tasks are classified as high semantic demand tasks, whereas passive viewing and perceptual matching (1-back, font judgment, etc.) that required little involvement of the semantic knowledge were classified as low semantic demand tasks. The classification of picture naming as a task of high semantic demand is based on facts that this task has been widely used in testing semantic knowledge in patients (Caramazza & Shelton, 1998; Garrard & Carroll, 2006; Patterson et al., 2006) as well as in neuroimaging studies (Chao, Haxby, & Martin, 1999; for a review, see Chouinard & Goodale, 2010). We focused on the comparison of living and nonliving concepts in the low semantic demand tasks to examine whether task demand modulate the activation pattern. We also examined studies using non-visual stimuli to test whether the modality-specific representations in visual cortex (e.g., pFG) would be involved in tasks with non-visual stimuli. Most of the studies using non-visual modality presented stimuli via auditory modality (e.g., animal sounds).

Table 1: Summary of the number of foci and experiments.

		# of foci	# of experiment
Imaging mode	fMRI	1,252	159
	PET	476	74
Task demands	High	1326	179
	Low	402	54
Modality	Visual	1450	205
	Non-visual	278	28

When examining the effect of each moderator, we sub-selected studies from the focused level of the moderator (e.g., studies using PET), and conducted the main-effect analysis, conjunction analysis, and contrast analysis for the living and nonliving concepts as described in the primary analysis above. Then, we compared the ALE maps qualitatively to reveal the activation patterns that are different from those of the primary analysis (the “norm”). The number of foci and experiments for each level of the moderators are listed in **Table 1**.

Results

The consistent findings for living and nonliving concepts Across all the fMRI studies, the ALE contrast analysis revealed that the lateral pFG on both hemispheres and right posterior superior temporal gyrus (pSTG) were consistently reported for living concepts, whereas the medial pFG on both hemispheres and the left IFG, IPL, and superior parietal lobe (SPL) were consistently reported for the nonliving concepts (see **Figure 1**). The ALE conjunction analysis revealed that most of the overlapping activations for both living and nonliving concepts were in the visual ventral pathways such as in the LOC and pFG.

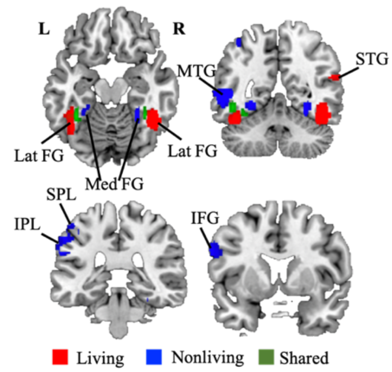

Figure 1. The primary ALE analysis with all fMRI studies.

The effect of imaging mode The ALE analysis studies with PET imaging mode did not reveal any region showing overlapping activation patterns of living and nonliving concepts. The consistent patterns for living were observed in the lateral pFG on both hemispheres, and for nonliving concepts, the only region that was consistently reported was the pMTG (**Figure 2A**). Critically, there was no category-specific activation for living concepts in the ATL.

The effect of task demand on semantics From examining the studies with tasks requiring low level of engagement of semantic knowledge, the ALE contrast analysis revealed the consistent patterns of the medial pFG and MTG for nonliving concepts and the lateral pFG and STG for living concepts. However, the effects for the nonliving in pFG were bilateral, whereas the effect for living concepts in the pFG was only on the right hemisphere (**Figure 2B**). In addition, the conjunction analysis revealed one cluster in the left lateral pFG activated reliably for both living and nonliving concepts.

The effect of display modality Focusing on studies using non-visual stimuli, we primarily focused on the activation patterns in the pFG. The ALE contrast analysis interestingly showed that no consistent activations were found in the ventral visual pathway such as in the pFG. However, the bilateral anterior STG (aSTG) showed reliable activations for the living concepts, and the left pMTG and IPL showed reliable activation for the nonliving concepts.

Discussion

The current study aimed to reveal the consistent patterns of category-specific activations for living and nonliving objects and examine some moderating factors that may alter the observed patterns of activations with important theoretical implications to the cortical organizations of the semantic network. Our primary ALE meta-analysis revealed reliable category-specific activations for living and nonliving concepts across a large set of fMRI studies.

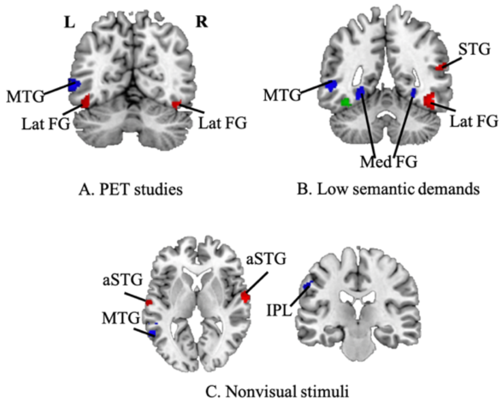

Figure 2. The moderator ALE analysis revealing activation patterns in studies with different imaging mode, task demands and stimuli modality

The occipitotemporal regions showed the most consistent activation patterns across imaging modes and levels of task demands for semantic knowledge. The medial pFG specifically showed reliable activation patterns for nonliving across studies using fMRI, PET, or low semantic demand tasks, but the lateral pFG, especially in the right hemisphere, showed reliable activations for living concepts. In addition, the left pMTG also showed reliable activations for nonliving concepts, and the right pSTG showed reliable activation for living concepts across variations in imaging modes and levels of task demand. The studies using nonvisual stimuli revealed very different patterns of activation for living concepts in the bilateral aSTG, and consistent findings in the pMTG and IPL for the nonliving concepts.

Consistent with the previous meta-analysis and other individual studies (Chen et al., 2017; Chouinard & Goodale, 2010), our meta-analysis further confirmed the role of the pMTG in representing nonliving concepts. It is also the only region that was identified consistently across different studies even with low semantic engagement and nonvisual stimuli. While previous studies have associated the pMTG with representing function properties of tools (Kellenbach et al., 2003), our study further suggests that the activation of function properties for manmade objects are automatic and modality-independent.

Our study supports the functional specialization of lateral and medial pFG for living and nonliving concepts (Mahon & Caramazza, 2009; Martin & Chao, 2001), but our study revealed a few important nuances. First, the activations in the pFG, regardless of the semantic categories, were not consistently observed in studies using nonvisual stimuli. This finding seems to suggest that the nonvisual stimuli may not necessarily engage the visual cortex in healthy subjects. In other words, neither the lateral nor the medial pFG are essential functional modules for processing living or nonliving concepts as suggested by domain-specific views (Mahon et al., 2009), and the activations in the pFG are modality-specific. Second, for studies with low semantic demand, we only observed reliable activation patterns for living concepts in the right hemisphere, which is consistent with the previous meta-analysis (Chen et al., 2017). These results may suggest that for living concepts the involvement of the left lateral pFG requires high semantic demand and some top-down modulation (e.g., from the ATL hub). Third, the overlapping effects of living and nonliving concepts in the pFG was evident bilaterally in our primary analysis and previous meta-analysis studies (Chen et al., 2017), further suggesting that the functional specialization of the lateral and medial pFG was graded rather than discrete (Haxby et al., 2001).

Our study also established new observations and findings regarding semantic task demands and modality-related category specificity. First, for nonliving, the involvement of the frontoparietal regions, such as IFG, SPL, and IPL, may depend on the level of semantic demand. These regions are shown to associate the representations of action plans and function properties for nonliving objects, especially tool concepts (Almeida et al., 2010; Chouinard & Goodale, 2010; Mahon & Caramazza, 2009). Our results suggest that activations in these regions could relate to top-down modulations or spread-activations only when these semantic features were probed from stimuli in the visual or auditory stimuli. Second, the pSTG activations for the living concepts are likely due to studies that examined motion or movement features of animate objects (Grossman & Blake, 2002). Third, the observed bilateral activations in aSTG for living concepts were novel (Leaver & Rauschecker, 2010). This supports the idea that the category-specific activations can be observed in other modality-specific regions due to differences in sensory experience of living and nonliving objects. The sounds from the living objects, particularly animals, could be more complex in acoustic properties (e.g., changes in frequency, amplitude, and duration, etc.) than those of nonliving objects. The aSTG has been associated with speech processing (von Kriegstein, Smith, Patterson, Ives, & Griffiths, 2007), so the preferred activations for living concepts in the aSTG may suggest that the sounds of animals or animate objects are processed in a more speech-like manner.

The results from our meta-analysis have a few important implications for the theories on cortical organizations of the semantic network. First, when examining studies using PET, we did not observe consistent activations in the ATL for living concepts. This evidence does not support some domain-specific views about the ATL being part of the network of processing animal concepts (Anzellotti et al., 2011). However, it also did not reveal overlapping activations for both living and nonliving concepts, seemingly against the domain-general views about the function of ATL (Lambon Ralph et al., 2016). We reason that this finding could result from the literature selection and tasks used in selected studies. Since we only examined studies for category-specific activations, common activations for both categories are likely to be already subtracted out in directional contrasts (e.g., living > nonliving and vice versa). Also, most of the studies did not examine the specific levels of semantic knowledge, but some research has shown that ATL showed stronger involvement when specific features of semantic knowledge are probed (Rogers et al., 2006). Second, our meta-analysis, to our knowledge, showed the consistent category-specific activations for living concepts in the auditory cortex for the first time. This finding supports the domain-general view about the modality-specific representations (Lambon Ralph et al., 2016) and potential functional specializations in modalities other than vision. Third, our meta-analysis characterizes the category-specific activations in the pFG in detail and showed how the observed patterns could be modulated by task demand and modality. These findings are more compatible with the domain-general views which assume that the activation patterns in the pFG may reflect systematic differences between the living/nonliving dichotomy in visual properties (Chen & Rogers, 2014), and the observed category-specific activations in congenitally blind may be due to other reasons such as connectivity constraints for learning cross-mappings of semantic knowledge (Chen et al., 2017).

In conclusion, our meta-analysis provides the first comprehensive and quantitative characterization of category-specific activations for living and nonliving concepts and revealed how these patterns may depend on important experimental factors such as imaging mode, task demand, and stimuli modality. Understanding the effects of these factors furthered our knowledge of cortical organizations of the semantic network, and provide some insights on how the domain-general view may provide a more accurate explanation to category-specific activations observed for the past two decades.

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