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Dissociating frequency and animacy effects in visual word processing: An fMRI study

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ABSTRACT

In an fMRI investigation of the neural representation of word frequency and animacy, participants read high- and low-frequency words within living and nonliving semantic categories. Both temporal (left fusiform gyrus) and parietal (left supramarginal gyrus) activation patterns differentiated between animal and tool words after controlling for frequency. Activation patterns in a smaller ventral temporal region, a subset of the voxels identified in the animacy contrast, differentiated between high- and low-frequency words after controlling for animacy. Activation patterns in the larger temporal region distinguished between high- and low-frequency words just as well as patterns within the smaller region. However, in analyses by animacy category, frequency effects in these temporal regions were significant only for tool, not for animal, words. Thus, lexical word frequency information and semantic animacy category information are conjointly represented in left fusiform gyrus activation patterns for some, but not all, concrete nouns.

1. Introduction

Research concerning semantic mapping in the human brain is relatively consistent in supporting a distributed conceptual system organized by category- or domain-specific principles; for example, along an animacy dimension for living and nonliving things (e.g., Binder, Desai, Graves, & Conant, 2009; Caramazza & Shelton, 1998; Huth, de Heer, Griffiths, Theunissen, & Gallant, 2016; Kriegeskorte et al., 2008; Mummery, Patterson, Hodges, & Price, 1998). Although there is ample neuroimaging evidence for a distributed system that is both multimodal (visual, auditory, and somatosensory) and involves interactive features such as color or taste (e.g., see Yee, Chrysikou, & Thompson-Schill, 2014 for a review), precisely how various lexicosemantic dimensions are represented and interact is less established. Previous fMRI work with picture stimuli has shown that ventral temporal cortex activation patterns index animacy (e.g., Chao, Haxby, & Martin, 1999) along a gradient (e.g., Connolly et al., 2012; Kriegeskorte et al., 2008), and that animacy is represented separately from other semantic dimensions, such as "predacity" (e.g., Connolly et al., 2016), but comparable work with word stimuli is lacking.

Other lexicosemantic features, such as frequency and concreteness, have also been shown to modulate brain activity during semantic processing (e.g., Chee, Hon, Caplan, Lee, & Goh, 2002; Fiebach, Friederici, Müller, von Cramon, & Hernandez, 2003). Indeed, a neural correlate of the robust behavioral frequency effect, such that high-frequency words and pictures are recognized and responded to more quickly than low-frequency words and pictures (e.g., Coltheart, Rastle, Perry, Langdon, & Ziegler, 2001; Oldfield & Wingfield, 1965; Taft, 1979), has been identified as increased brain activity for low-frequency as compared to high-frequency words and pictures (e.g., Chee et al., 2002; Graves, Grabowski, Mehta, & Gordon, 2007; Liu, Liao, Fang, Chu, & Tan, 2004; Wilson, Isenberg, & Hickok, 2009). This is consistent with interactive word processing models proposing that high-frequency words have a higher resting activation level than low-frequency words (e.g., McClelland & Elman, 1986) and higher "quality" (i.e., more tightly integrated across sublexical and lexicosemantic features) representations (e.g., Perfetti & Hart, 2002).

To our knowledge, no neuroimaging studies of word frequency have directly investigated how the lexicosemantic features of frequency and animacy are represented relative to one another for individual words. Such evidence will advance understanding of how words are meaningfully represented in the human brain, further instantiating and specifying the distributed, interactive, integrated nature of the neural lexicosemantic system (Perfetti & Hart, 2002; Yee et al., 2014). Here,

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we built on the extant fMRI literature on word frequency, reviewed below, by using a well-controlled set of concrete nouns and MVPA (e.g., Norman, Polyn, Detre, & Haxby, 2006) with STATIS (Abdi, Williams, Valentin, & Bennani-Dosse, 2012) to investigate whether processing of lexical word frequency is anatomically distinct from processing of semantic animacy category information.

1.1. Left inferior frontal cortex and word frequency

A number of neuroimaging studies using a lexical decision task have reported word frequency effects in the left prefrontal region, such that low-frequency words elicit more activation than high-frequency words (e.g., Carreiras, Mechelli, & Price, 2006; Carreiras, Riba, Vergara, Hledmann, & Münte, 2009; Chee, Venkatraman, Westphal, & Siong, 2003; Chee, Westphal, Goh, Graham, & Song, 2003; Fiebach, Friederici, Müller, & von Cramon, 2002; Fiebach et al., 2003; Liu et al., 2004; Nakic, Smith, Busis, Vythilingam, & Blair, 2006; Protopapas et al., 2016). However, lexical decision tasks may inflate the role of word frequency in lexical access (e.g., Balota & Chumbley, 1984; Monsell, 1991). Therefore, it is important that a similar pattern of greater activation for low-, as compared to high-, frequency words has also been reported in the left inferior frontal gyrus in studies of silent and overt reading of single words not requiring lexical decision (e.g., Fiez, Balota, Raichle, & Petersen, 1999; Heim, Wehnelt, Grande, Huber, & Amunts, 2013; Kronbichler et al., 2004). For example, in a PET study, Fiez et al. (1999) compared words that were either high- or low-frequency and had either consistent (e.g., *hint*) or inconsistent (e.g., *pint*) spelling-to-sound correspondence. Although associated with word frequency, the authors related the modulation of activation in the inferior frontal gyrus primarily to lexical processing in terms of "orthographic to phonological transformation" (p. 214).

In contrast, Chee et al. (2002) concluded that modulation of activation in inferior frontal gyrus related to word frequency was semantically based; they claimed that "retrieval effort modulates prefrontal activity when deliberate access to semantics is required" (Chee et al., 2002, p. 265). Using fMRI with a semantic judgment task, they presented subjects with word triplets and asked them to decide which of the first two words was either (a) more semantically related or (b) shown in a larger font size in comparison to the third word. The authors reported greater activation in the inferior frontal cortex when subjects were making semantic judgments about low-frequency, as compared to high-frequency, words. However, they also reported that the low-frequency words were longer and had more syllables in comparison to the high-frequency words; these uncontrolled sublexical factors may have influenced the findings.

1.2. Left supramarginal gyrus and word frequency

Although the majority of neuroimaging studies have reported greater activation for low- as compared to high-frequency words, two studies have reported the opposite pattern of activation in the left supramarginal gyrus (Carreiras et al., 2009; Graves, Desai, Humphries, Seidenberg, & Binder, 2010). In an fMRI study with a lexical decision task, Carreiras et al. (2009) found greater activation for high- than low-frequency words in the precuneus/paracentral gyrus region. In another fMRI study in which subjects read 465 monosyllabic words aloud, Graves et al. (2010) reported a similar activation pattern bilaterally in the posterior cingulate, angular gyrus, supramarginal gyrus, and left middle frontal gyrus. This pattern is particularly curious given that frequency effects are thought to reflect the ease with which the meaning of a word is accessed (e.g., Monsell, 1991), and the theoretically higher resting activation levels of high frequency words should make them easier – that is, require fewer processing resources – to access (e.g., McClelland & Elman, 1986). However, given a lack of comparable reports in the literature, activation in the supramarginal gyrus may not typically be modulated by word frequency.

1.3. Left inferior temporal cortex and word frequency

A number of neuroimaging studies have reported that activation in inferior temporal cortex, more specifically, in the left fusiform gyrus, is also modulated by word frequency, with low-frequency words eliciting greater activation than high-frequency words (e.g., Bruno, Zumberge, Manis, Lu, & Goldman, 2008; Chee, Westphal, et al., 2003; Hauk, Davis, & Pulvermüller, 2008; Joubert et al., 2004; Keller, Carpenter, & Just, 2001; Kronbichler et al., 2004). Whereas most of these studies have used noun stimuli exclusively, several have focused on frequency but not controlled for word class or variables such as concreteness or animacy (e.g., Carreiras et al., 2006; Joubert et al., 2004; Liu et al., 2004). This lack of stimulus control may be problematic, as there is fMRI evidence showing that the effects of lexical factors interact generally (e.g., Graves et al., 2010; Yarkoni, Speer, Balota, McAvoy, & Zacks, 2008) and that word class effects interact with word frequency effects more specifically (e.g., Hauk et al., 2008). Tasks in these studies have varied from silent reading (Hauk et al., 2008; Joubert et al., 2004; Kronbichler et al., 2004) to phonological lexical decision, in which participants were asked to decide if silently read stimuli (e.g., *wurld*) sounded like an English word (Bruno et al., 2008), to living/nonliving judgments (Chee, Westphal, et al., 2003). In contrast, studies using a lexical decision task have reported no modulation of left fusiform activation related to word frequency (e.g., Fiebach et al., 2002; Fiebach et al., 2003).

Several studies have reported word frequency effects in the visual word form area (VWFA) specifically, a region within the left fusiform gyrus centered around MNI coordinates −43, −54, −12 (e.g., Bruno et al., 2008; Hauk et al., 2008; Joubert et al., 2004; Kronbichler et al., 2004, see Supplemental Table 1). For example, using nonwords and nouns divided into multiple levels of frequency (controlled for letter length, syllable length, bigram frequency, concreteness, and animacy), Kronbichler et al. (2004) found that the VWFA showed increased activation to nonwords and low-frequency words as compared to middle- and high-frequency words. However, activations within this region are complex: Some meta-analyses have confirmed frequency effects (e.g., Price, 2012), whereas others have not (e.g., Cohen et al., 2002). In a study simultaneously exploring frequency and animacy effects in this area, Chee, Westphal, et al. (2003) investigated memory effects for low- and high-frequency concrete nouns. Subjects made living/nonliving judgments for animal and tool words, and, consistent with prior studies (e.g., Chao et al., 1999), a left fusiform region [−45, −62, −11; see Supplemental Table 2] showed increased activation when making the judgments. In addition, Chee, Westphal, et al. reported increased activation for low- as compared to high-frequency words in the left fusiform gyrus, with a peak 5 mm ventral to the peak for semantic judgments [−45, −62, −6]. However, they did not conduct analyses that directly contrasted the effects of animacy with the effects of word frequency.

Word frequency effects in the VWFA are controversial, as some have argued that VWFA activation reflects a prelexical stage of word processing (e.g., Binder, Medler, Westbury, Liebenthal, & Buchanan, 2006; Dehaene, Cohen, Sigman, & Vinckier, 2005; McCandliss, Cohen, & Dehaene, 2003). Because frequency effects are thought to occur at a lexical stage (e.g., Levelt, Roelofs, & Meyer, 1999), advocates of this view have referred to studies that have shown no modulation of activation in ventral temporal cortex by word frequency (e.g., Fiebach et al., 2002; Fiebach et al., 2003; Protopapas et al., 2016) as evidence of the prelexical nature of processing in the VWFA. Others have countered this prelexical interpretation with evidence indicating that activation in the VWFA is "highly selective for individual real words" (Glezer, Jiang, & Riesenhuber, 2009, p. 199; Glezer, Kim, Rule, Jiang, & Riesenhuber, 2015) – that is, that processing in the VWFA is lexically, rather than prelexically, based; or, perhaps, indexes multiple stages of word processing, including individual word forms (e.g., Hirshorn et al., 2016).

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