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Predicting brain activation patterns associated with individual lexical concepts based on five sensory-motor attributes

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ABSTRACT

While major advances have been made in uncovering the neural processes underlying perceptual representations, our grasp of how the brain gives rise to conceptual knowledge remains relatively poor. Recent work has provided strong evidence that concepts rely, at least in part, on the same sensory and motor neural systems through which they were acquired, but it is still unclear whether the neural code for concept representation uses information about sensory-motor features to discriminate between concepts. In the present study, we investigate this question by asking whether an encoding model based on five semantic attributes directly related to sensory-motor experience – sound, color, visual motion, shape, and manipulation – can successfully predict patterns of brain activation elicited by individual lexical concepts. We collected ratings on the relevance of these five attributes to the meaning of 820 words, and used these ratings as predictors in a multiple regression model of the fMRI signal associated with the words in a separate group of participants. The five resulting activation maps were then combined by linear summation to predict the distributed activation pattern elicited by a novel set of 80 test words. The encoding model predicted the activation patterns elicited by the test words significantly better than chance. As expected, prediction was successful for concrete but not for abstract concepts. Comparisons between encoding models based on different combinations of attributes indicate that all five attributes contribute to the representation of concrete concepts. Consistent with embodied theories of semantics, these results show, for the first time, that the distributed activation pattern associated with a concept combines information about different sensory-motor attributes according to their respective relevance. Future research should investigate how additional features of phenomenal experience contribute to the neural representation of conceptual knowledge.

1. Introduction

Brain-based theories of concept representation generally begin with the premise that concepts are learned through a process of generalization or abstraction from individual experiences. Experiences are comprised of identifiable sensory, motor, spatial, temporal, affective, and cognitive components, and the relative contribution of each of these experiential components to concept formation depends on the particular concept being acquired. For example, the concept of "thunder" is learned almost entirely through auditory experiences, whereas the concept of "octopus" has no connection with audition. Concepts for manipulable objects such as "pencil" and "spoon" are learned in part through motor actions performed with those objects, whereas concepts such as "moon" and "giraffe" have very little (if any) basis in motor experience. However, most experiences are inherently multimodal in the sense that they involve simultaneous, covarying information from multiple sensory-motor modalities. Using a pair of scissors, for example, typically involves concurrent sensory-motor experiences related to action planning, proprioceptive and tactile feedback, and the perception of characteristic shape, motion, and sound features. Thus, the concept of "scissors" is likely to include representations of all of these attributes.

Sensory information is processed according to perceptual attributes that can be strictly unimodal (e.g., color) or result from the combination of two or more sensory modalities (e.g., perception of object shape often combines visual and tactile information).

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Embodied or “simulation” theories of concept representation propose that the information abstracted from experience during concept learning is represented to some degree in the same modality-specific and multimodal neural systems through which the learning occurred, and that concept retrieval involves some degree of activation of this sensory-motor information (Damasio, 1989; Barsalou, 2008; Glenberg and Gallese, 2012; Hoenig et al., 2011; Kiefer et al., 2007).

Although embodiment theories have garnered extensive empirical support (for reviews, see Fischer and Zwaan, 2008; Meteyard and Vigliocco, 2008; Binder and Desai, 2011; Kiefer and Pulvermüller, 2012; and Meteyard et al., 2012), most studies have aimed at demonstrating the existence of modality-specific representational systems (e.g., Warrington and Shallice, 1984; McCarthy and Warrington, 1988; Farah and McClelland, 1991), or at implicating a particular modality-specific cortical area in the representation of concrete concepts (e.g., Martin et al., 1996; Chao et al., 1999; Hauk et al., 2004; Aziz-Zadeh et al., 2006; Kiefer et al., 2008; Hsu et al., 2012). One question that remains unanswered is whether the distributed neural representation of a concept combines information originating from various sensory-motor attributes, as predicted by embodiment theories. In the present study, we explore this issue by adopting a novel approach to brain activation data relevant to this question. Instead of searching for localized activations associated with particular semantic attributes, we combine information about five different attributes to predict the activation patterns associated with individual concepts. In other words, we ask whether information about five sensory-motor attributes of lexical concepts is sufficient to predict patterns of brain activation elicited by isolated words. The five attributes selected for study – color, shape, visual motion, sound, and manipulation – are each associated with well-studied brain networks (for a review, see Fernandino et al., 2015). In a prior study, we obtained salience ratings on each of these attributes for a set of 900 English nouns, and showed that these attribute ratings parametrically modulate word-related brain activity in distinct cortical networks containing both unimodal and multimodal nodes (Fernandino et al., 2015). In the present study, attribute-specific activation maps, derived from a set of 820 words (the “modeling set”), were combined into an “encoding model” (Haxby et al., 2014; Naselaris et al., 2011), which was used to predict word-specific, whole-brain activation patterns for the 80 remaining words (the “test set”). The encoding model consisted of a linear combination of the five attribute maps from the training set, weighted by the test word's attribute rating values. The predicted activation patterns were then compared to the observed activation patterns for each test word. Successful prediction of the test word patterns would provide direct evidence that the overall, distributed neural representation of a concrete concept encodes information about the relative relevance of specific aspects of sensory-motor experience, as rated by an independent group of participants.

Another novel aspect of the present study is the focus on group-averaged activation patterns. Studies using multivoxel pattern analysis (MVPA) typically evaluate the performance of the encoding model (or classifier, in the case of pattern classification studies) separately for each participant, to account for individual differences in brain morphology and function-structure mapping, and perform group-level statistical tests on the resulting accuracy scores (e.g., Mitchell et al., 2008; Huth et al., 2012; Haxby et al., 2001). Here, we assess whether similarities in the neural code for concrete concepts across individuals would allow a group-level encoding model to successfully predict the group-averaged activation maps corresponding to different concepts. If prediction is successful, the encoding model can be seen as a first approximation to a subject-independent neural code for concept representation, and the predicted activation maps could be considered as rough neural signatures of the respective concepts.

2. Methods

2.1. Attribute ratings

We focused on five semantic attributes related to sensory-motor experience: sound, color, manipulation, visual motion, and shape. Ratings for these attributes were available for a set of 900 words (see Fernandino et al., 2015, for details). The ratings reflect the salience of each attribute to the meaning of the word on a 7-point Likert scale ranging from “not at all important” to “very important”. The data set included approximately 30 ratings of each attribute for each word. Fig. 1 shows mean ratings for six example words, and Table 1 lists the correlations between the five attribute ratings across all words.

2.2. fMRI data

All analyses were conducted on the data from Fernandino et al. (2015). Data collection procedures from that study are summarized below.

2.2.1. Participants

Forty-four healthy, native speakers of English (16 females; mean age 28.2, range 19–49) with no history of neurological or psychiatric disorders, participated in the study. All were right-handed according to the Edinburgh Handedness Inventory (Oldfield, 1971). Participants were compensated for their participation and gave informed consent in conformity with the protocol approved by the Medical College of Wisconsin Institutional Review Board.

2.2.2. Stimuli

The stimuli consisted of the 900 nouns for which attribute ratings were collected (see Section 2.1. above) and 300 pseudowords. All words were relatively familiar (mean CELEX frequency = 37.4 per million, SD = 118.5), and between 3 and 9 letters in length, with a flat distribution across this length range (i.e., 126–129 words of each length). Six hundred of the words were relatively concrete and 300 were relatively abstract, as determined by either published imageability ratings, which at the time were available for 748 words (Wilson, 1988; Bird et al., 2001; Clark and Paivio, 2004), or consensus judgment of the authors. The pseudowords were generated by a computer program (Medler and Binder, 2005) using constrained trigram statistics (i.e., third-order approximation to English), followed by exclusion of pseudohomophones. Pseudowords were matched to the words on length, orthographic neighborhood density, and bigram and trigram metrics (Table 2).

2.2.3. Task procedure

The stimuli were back-projected in white Courier font on a black background screen that was viewed by the participant through a mirror attached to the head coil. Stimuli subtended an average horizontal visual angle of approximately 2.5°. In addition to the 1200 task trials (900 words, 300 pseudowords), 600 passive fixation events (“+”) were included to act as a baseline and provide jittering for the deconvolution analysis, resulting in a total of 1960 stimulus events distributed across 10 runs. On task trials, the stimulus string was presented for 1000 ms followed by a fixation cross for 1000 ms; on fixation events, the fixation cross appeared for 2000 ms. Thus, each stimulus was followed by a varied fixation interval of 1 s, 3 s, 5 s, etc. The probability distribution of these fixation intervals was an exponentially decaying function with a

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