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Modality-independent encoding of individual concepts in the left parietal cortex

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ABSTRACT

The organization of semantic information in the brain has been mainly explored through category-based models, on the assumption that categories broadly reflect the organization of conceptual knowledge. However, the analysis of concepts as individual entities, rather than as items belonging to distinct superordinate categories, may represent a significant advancement in the comprehension of how conceptual knowledge is encoded in the human brain.

Here, we studied the individual representation of thirty concrete nouns from six different categories, across different sensory modalities (i.e., auditory and visual) and groups (i.e., sighted and congenitally blind individuals) in a core hub of the semantic network, the left angular gyrus, and in its neighboring regions within the lateral parietal cortex. Four models based on either perceptual or semantic features at different levels of complexity (i.e., low- or high-level) were used to predict fMRI brain activity using representational similarity encoding analysis. When controlling for the superordinate component, high-level models based on semantic and shape information led to significant encoding accuracies in the intraparietal sulcus only. This region is involved in feature binding and combination of concepts across multiple sensory modalities, suggesting its role in high-level representation of conceptual knowledge. Moreover, when the information regarding superordinate categories is retained, a large extent of parietal cortex is engaged. This result indicates the need to control for the coarse-level categorial organization when performing studies on higher-level processes related to the retrieval of semantic information.

1. Introduction

The organization of semantic information in the human brain has been primarily explored through models based on categories. This *domain-specific* approach relies on the assumption, supported by neuropsychological and neuroimaging observations, that the categories of language (e.g., *faces, places, body parts, tools, animals*) broadly reflect the organization of conceptual knowledge in the human brain (Kemmerer, 2016; Mahon and Caramazza, 2009).

However, rather than being limited to differentiate among a small number of broad superordinate categories, a deeper comprehension of conceptual knowledge organization at a neural level should characterize the semantic representation of individual entities (Charest et al., 2014; Clarke and Tyler, 2015; Mahon and Caramazza, 2011). In fact, despite the strong evidence in favor of a categorial organization of conceptual knowledge in the brain (Gainotti, 2010; Pulvermuller, 2013), category-based models are over-simplified and often do not take into account those perceptual and semantic features (e.g., shape, size, function, emotion) involved in the finer-grained discrimination of individual concepts (Clarke and Tyler, 2015; Kemmerer, 2016). Typically, semantic studies limit at controlling those variables within broader and heterogeneous categories, thus restricting the emerging of individual item processing (Baldassi et al., 2013; Bona et al., 2015; Bracci and Op de Beeck, 2016; Ghio et al., 2016; Kaiser et al., 2016; Proklova et al., 2016; Vigliocco et al., 2014; Wang et al., 2016). Furthermore, broader categories are often affected by a high degree of collinearity, as stimuli belonging to highly dissimilar categories according to a sensory-based description (e.g., *faces* and *places*), may also be very dissimilar according to their semantic characterization. Thus, the labeling of certain brain regions might rely either on perceptual or semantic features (Carlson et al., 2014; Fernandino et al., 2016; Jozwik et al., 2016; Khaligh-Razavi and Kriegeskorte, 2014).

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In addition, the transition from lower-level sensory-based representations towards higher-level conceptual representations is still ill defined. For instance, how entities that are similar for one or more perceptual features (e.g., shape: a *tomato* and a *ball*) are represented in the brain as semantically different remains to be understood (Bi et al., 2016; Clarke and Tyler, 2015; Kubilius et al., 2014; Rice et al., 2014; Tyler et al., 2013; Wang et al., 2016, 2015; Watson et al., 2016).

To assess the extent to which the category-based organization relies on sensory information, our group recently adopted a property generation paradigm in sighted and congenitally blind individuals to demonstrate that the representation of semantic categories relies on a modality-independent brain network (Handjaras et al., 2016). Furthermore, the analysis of individual cortical regions showed that only a few of them (i.e., inferior parietal lobule and parahippocampal gyrus) contained distinct representations of items belonging to different semantic categories across presentation modalities (i.e., pictorial, verbal visual and verbal auditory forms or verbal auditory form in congenitally blind individuals) (Handjaras et al., 2016).

In the present study, we intended to describe the representation, across different presentation modalities, of each of the thirty concrete nouns from six different categories, using part of the same dataset of Handjaras and colleagues (2016). Instead of encoding semantic information using a category-based model, here we characterized the representation of the individual entities using a recent method for fMRI data analysis, called representational similarity encoding (Anderson et al., 2016b), to combine representational similarity analysis and model-based encoding. Moreover, the conceptual representation was evaluated by focusing on the entities within each category (e.g., fruits: *apple* vs. *cherry*). This *within-category* encoding is therefore resistant to the effect of category membership and represents an adequate perspective to study how single concepts are processed in the brain. To disentangle the role of perceptual or semantic features and of their complexity (i.e., low- or high-level), we aimed at predicting brain activity using similarity encoding with four models: two semantic models that considered either the complete set of language-based features or a subset of these features related to perceptual properties only (Lenci et al., 2013), and two perceptual models, which provided higher-level descriptions of object shape, or merely focused on low-level visual features (Oliva and Torralba, 2001; van Eede et al., 2006).

We focused the single-item encoding analysis on the angular gyrus and its neighboring regions within the left parietal cortex. The angular region has been solidly associated to a wide gamut of semantic tasks, and its activity during retrieval and processing of concrete nouns or combination of concepts (Binder et al., 2009; Price et al., 2015; Seghier, 2013) makes this region a strong candidate for semantic processing at a finer, single-item level. More importantly, neighboring regions to the angular gyrus within the left lateral parietal cortex have been involved, to a different extent, in semantic processing, thus indicating the need for a more comprehensive characterization of conceptual representations within the parietal lobe (Binder et al., 2009; Jackson et al., 2016; Price, 2012). Therefore, the analyses were performed in a larger map of the left lateral parietal cortex that centered on the angular gyrus, as defined on both anatomical and functional criteria. The definition of different Regions of Interest (ROIs) assessed the different degree of involvement of specific regions in processing of individual concepts, and how such a processing is influenced by sensory modality.

2. Materials and methods

A representational similarity encoding (Anderson et al., 2016b) was applied to data collected in a fMRI experiment, in which sighted and blind participants were instructed to mentally generate properties related to a set of concrete nouns, as described in details in our previous study (Handjaras et al., 2016). In brief, participants were divided in four groups according to the stimulus presentation modality (i.e., pictorial, verbal visual and verbal auditory forms for sighted individuals and verbal auditory form for congenitally blind individuals). Two semantic models were built on the set of concrete nouns and two alternative perceptual models were derived from the pictorial form of the stimuli. Of both semantic and perceptual models, one was a descriptor of high-level features and one relied on lower-level information. The four models were then used to encode the specific brain activity pattern of each concept, in each group of subjects.

2.1. Brief summary of the Handjaras et al. (2016) fMRI protocol and preprocessing

Brain activity was measured in fMRI with a slow event-related paradigm (gradient echo echoplanar images GRE-EPI, GE SIGNA at 3 T, equipped with an 8-channel head coil, TR 2.5 s, FA: 90°, TE 40 ms, FOV = 24 cm, 37 axial slices, voxel size $2 \times 2 \times 4$ mm) in 20 right-handed volunteers during a property generation task after either visual or auditory presentation of thirty concrete nouns of six semantic categories (i.e., vegetables, fruits, mammals, birds, tools, vehicles) (please refer to Supplementary materials for the list of nouns). Two semantic categories (e.g., natural and artificial places) from Handjaras et al. (2016) were excluded here due to a specific limitation of the shape-based perceptual model which required segmented stimuli (e.g., objects). Participants were divided into four groups accordingly to the stimulus presentation format: five sighted individuals were presented with a pictorial form of the forty nouns (M/F: 2/3 mean age ± SD: 29.2 ± 12.8 yrs), five sighted individuals with a verbal visual form (i.e., written Italian words) (M/F: 3/2 mean age ± SD: 36.8 ± 11.9 yrs), five sighted individuals with a verbal auditory form (i.e., spoken Italian words) (M/F: 2/3 mean age ± SD: 37.2 ± 15 yrs) and five congenitally blind with a verbal auditory form (M/F: 2/3 mean age ± SD: 36.4 ± 11.7 yrs). High resolution T1-weighted spoiled gradient recall images were obtained to provide detailed brain anatomy.

During the visual presentation modality, subjects were presented either with images representing the written word (verbal visual form) or color pictures of concrete objects (pictorial form). Stimulus presentation lasted 3 s and was followed by a 7 s-inter stimulus interval (ISI). During the auditory presentation modality, subjects were asked to listen to about 1 s-long words – referring to the same concrete nouns above – followed by 9 s ISI. During each 10 s-long trial, participants were instructed to mentally generate a set of features related to each concrete noun. Each run had two 15 s-long blocks of rest, at its beginning and end, to obtain a measure of baseline activity. The stimuli were presented four times, using, for each repetition, a different image (for pictorial stimuli) or speaker (for auditory stimuli). The presentation order was randomized across repetitions and the stimuli were organized in five runs.

The AFNI software package (Cox, 1996) was used to preprocess functional imaging data. All volumes from the different runs were temporally aligned, corrected for head movement, spatially smoothed (4 mm) and normalized. Subsequently, a multiple regression analysis was performed to obtain *t*-score response patterns of each stimulus, which were included in the subsequent analyses. Each stimulus was modeled using five tent functions which covered the entire interval from its onset up to 10 s, with a time step of 2.5 s. Only the *t*-score response patterns of the fourth tent function (7.5 s after stimulus onset), averaged across the four repetitions, were used as estimates of the BOLD response for each stimulus (Handjaras et al., 2015; Leo et al., 2016). Afterwards, FMRIB's Nonlinear Image Registration tool (FNIRT) was used to register the fMRI volumes to standard space (MNI-152) and to resample the acquisition matrix to a 2 mm iso-voxel (Andersson et al., 2007; Smith et al., 2004).

2.2. Regions of interest

For our measurement of single-item semantic information, we first defined a mask of the left angular gyrus both using the Automated