Angular gyrus responses show joint statistical dependence with brain regions selective for different categories

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Abstract

Category-selectivity is a fundamental principle of organization of perceptual brain regions. Human occipitotemporal cortex is subdivided into areas that respond preferentially to faces, bodies, artifacts, and scenes. However, observers need to combine information about objects from different categories to form a coherent understanding of the world. How is this multi-category information encoded in the brain? Studying the multivariate interactions between brain regions with fMRI and artificial neural networks, we found that the angular gyrus shows joint statistical dependence with multiple category-selective regions. Additional analyses revealed a cortical map of areas that encode information across different subsets of categories, indicating that multi-category information is not encoded in a single stage at a centralized location, but in multiple distinct brain regions.

Keywords: fMRI, multi-category information, multivariate statistical dependence, neural networks, angular gyrus

Introduction

Many tasks require integrating information about entities from different categories. Mechanisms that integrate information about people and artifacts are already at work in early stages of development: infants are more willing to help individuals who intended to give them a desirable toy over those who did not (Dunfield & Kuhlmeier, 2010), and children observing repeated interactions between a person and an inanimate object infer that the person has feelings of ownership towards that object (Cleroux & Friedman, 2020). However, visual information about animate and inanimate entities is processed by separate, specialized brain regions: using functional magnetic resonance imaging (fMRI), researchers have identified regions responding selectively to faces, bodies, artifacts and scenes (Hecaen & Angelergues, 1962; Sergent, Ohta, & MacDonald, 1992; Kanwisher, McDermott, & Chun, 1997; Epstein & Kanwisher, 1998; Downing, Jiang, Shuman, & Kanwisher, 2001; Martin & Chao, 2001). Investigating directly how the brain integrates information across different object categories is challenging. However, if a brain region integrates information across multiple categories, we would expect it to also show joint statistical dependence with multiple category-selective regions (note that the latter does not guarantee the former). In this study, we aim to identify brain regions that show joint statistical dependence with multiple category-selective regions.

Previous work studied joint statistical dependence with regions encoding information about shape and color (Coutanche & Thompson-Schill, 2015). A recent study implicated the angular gyrus in the joint representation of facial expressions and locations (Lanzoni et al., 2020).

Here, we expand on this previous work, investigating joint dependence across multiple object categories (faces, bodies, artifacts and scenes). Analyzing fMRI responses to complex stimuli (Hanke et al., 2016) with multivariate pattern dependence (Anzellotti, Caramazza, & Saxe, 2017; Anzellotti & Coutanche, 2018) based on artificial neural networks (Fang, Poskanzer, & Anzellotti, 2021; Poskanzer, Fang, Aglinskas, & Anzellotti, 2021), we identify brain regions showing joint statistical dependence with multiple category-selective regions ("multi-category dependence"). We find evidence for multi-category dependence across all four categories in the angular gyrus (AG), as well as a cortical map of areas showing joint dependence with different subsets of categories.

Methods and Results

Data, preprocessing, regions of interest

We analyzed fMRI data from 14 participants watching the 2h movie stimulus 'Forrest Gump' (from the publicly available *studyforrest* dataset: (Hanke et al., 2016)). Using the category localizer provided with the dataset, in each individual participant we identified: face-selective ROIs (occipital face area - OFA, fusiform face area - FFA, face-selective posterior superior temporal sulcus - face STS), body-selective ROIs (extrastriate body area - EBA, fusiform body area - FBA, body-selective posterior superior temporal sulcus - body STS), artifact-selective ROIs (medial fusiform gyrus - mFus, middle temporal gyrus - MTG), and scene-selective ROIs (transverse occipital sulcus - TOS, parahippocampal place area - PPA, retrosplenial cortex - RSC). Each category-selective ROI contains 80 voxels with the highest t-values for the contrast between the preferred category and the other categories, with the restriction that they fall within a 9mm radius from the peak.

MVPN: Multivariate pattern dependence network

Most research on the interactions between brain regions focuses on the mean response within each region, but important information encoded in multivariate patterns could be lost by spatial averaging. Multivariate pattern dependence (MVPD) leverages multivariate patterns, achieving greater sensitivity than univariate methods (Anzellotti et al., 2017). In this study we used a recent, improved version of MVPD, based on artificial neural networks: MVPN (details in (Fang et al., 2021)). The networks received multivariate patterns of response in one or more sets of category-selective ROIs as inputs, and were trained with a leave-one-run-out procedure to predict the patterns of response in the gray matter. The voxel-wise proportion of variance explained between the predictor regions and each voxel in gray matter was calculated as a measurement of the multivariate statistical dependence.

Multi-category dependence

To better understand multi-category dependence, we aimed to find brain regions where the responses are predicted significantly better by MVPN whose inputs including all category-selective ROIs, than just the ROIs for the one single best-predicting category in isolation. Such regions reflect unique contributions from multiple category-selective ROIs to the overall statistical dependence. We developed a three-step "combined-minus-max" analysis: (1) we used MVPN to calculate the variance explained in each gray matter voxel with each of the four category-selective ROIs (face, body, artifact and scene) individually ("single MVPN"); (2) we calculated the variance explained using all four category-selective ROIs jointly as inputs ("combined MVPN"); (3) we calculated for each voxel the difference in variance explained ΔvarExpl between the combined MVPN on hand, and of the single MVPN of the best-predicting category on the other hand.

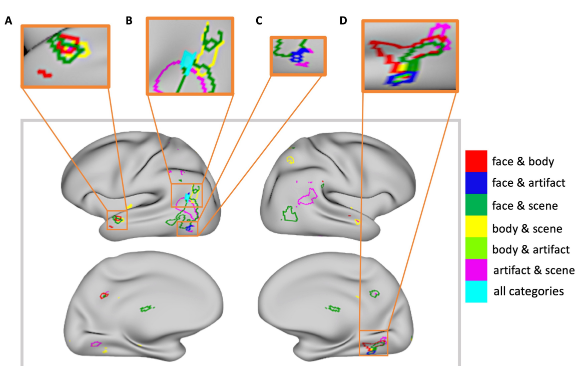

Figure 1: **Multi-category dependence.** AG region showing multi-category dependence across all categories ($p<0.05$ FWE corrected) in aqua, areas showing dependence for category pairs ($p<0.05$ FWE corrected) shown as outlines.

To establish the robustness of results across network architectures, we computed ΔvarExpl with three architectures: one-layer feedforward network (**1Layer**), five-layer feedforward network (**5Layer**), and five-layer feedforward network with dense connections (**5Layer Dense**). For each network, we used a group-level analysis to identify voxels in which ΔvarExpl was greater than zero ($p < 0.05$ corrected with SnPM). We also performed a control analysis with randomly selected non-overlapping V1 voxels as ROIs, to rule out the possibility that positive values of ΔvarExpl might be driven by the larger number of input voxels in the combined model.

We found that in a region within left AG (Fig.1B, peak MNI: -57, -69, 21), ΔvarExpl was significantly greater than zero for all MVPN architectures tested, while the control anaysis did not show significant effects. AG has been previously found to integrate information across multiple sensory modalities (Bonnici, Richter, Yazar, & Simons, 2016), our results indicate that it also encodes information across multiple object categories.

Further, we investigated brain regions that encode responses from specific subsets of categories, finding that left AG region is surrounded by areas jointly encoding information between scenes and each of the other three categories separately. A region in dorsal ATL showed multi-category dependence for face-body, face-scene, and body-scene (Fig.1A). Multi-category dependence was also observed in the left MTG (Fig.1C) and in ventral occipitotemporal cortex (Fig.1D).

Discussion

Using MVPN, we identified multi-category dependence in the left AG, as well as a cortical map of neighboring regions encoding pairwise-category information. AG is a multimodal integration area implicated in a variety of cognitive processes - semantic and episodic memory, bottom-up attention, and combinatorial semantics. Our results directly demonstrate the statistical dependence of AG responses on multiple category-selective ROIs during movie watching. The cortical map around AG is characterized by regions encoding scene-selective responses with responses selective for one other category – AG might integrate objects and their scene contexts to represent complex situations and events, in line with the hypothesis that AG might contribute to event representation and might serve as a temporary buffer that integrates spatiotemporal information (Humphreys, Ralph, & Simons, 2021).

Besides AG, we observed multi-category dependence in other regions. Multi-category dependence does not occur at a single centralized location, but at multiple cortical sites, that might implement distinct mechanisms that contribute to different tasks. More work is needed to investigate what kind of computations occur within these sites, and to determine whether they use information about objects from different categories to generate representations of their relationships and interactions.

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