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AVERAGE ACTIVITY, BUT NOT VARIABILITY, IS THE DOMINANT FACTOR IN THE REPRESENTATION OF OBJECT CATEGORIES IN THE BRAIN

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Abstract—To categorize the perceived objects, brain utilizes a broad set of its resources and encoding strategies. Yet, it remains elusive how the category information is encoded in the brain. While many classical studies have sought the category information in the across-trial-averaged activity of neurons/neural populations, several recent studies have observed category information also in the within-trial correlated variability of activities between neural populations (i.e. dependent variability). Moreover, other studies have observed that independent variability of activity, which is the variability of the measured neural activity without any influence from correlated variability with other neurons/populations, could also be modulated for improved categorization. However, it was unknown how important each of the three factors (i.e. average activity, dependent and independent variability of activities) was in category encoding. Therefore, we designed an EEG experiment in which human subjects viewed a set of object exemplars from four categories. Using a computational model, we evaluated the contribution of each factor separately in category encoding. Results showed that the average activity played a significant role while the independent variability, although effective, contributed moderately to the category encoding. The inter-channel dependent variability showed an ignorable effect on the encoding. We also investigated the role of those factors in the encoding of variations which showed similar effects. These results imply that the brain, rather than variability, seems to use the average activity to convey information on the category of the perceived objects.

Key words: object category encoding, signal variability, EEG, computational model, representational analysis.

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INTRODUCTION

When humans perceive objects, neural representations form highly distributed and dynamical patterns of activity across several regions of the brain (Ishai et al., 1999; Cox and Savoy, 2003). In addition to the large body of literature which reported dominant roles for the lateral occipital and ventral temporal cortices in category encoding (Grill-Spector et al., 2001; Reisenhuber and Poggio, 2002; Grill-Spector and Weiner, 2014), there is evidence suggesting contributions from the frontal and prefrontal cortices to the encoding of categories (Freedman et al., 2001; Jiang et al., 2007; Goddard et al., 2016). While several studies have found clusters of category-specific neurons (such as for faces, body parts, etc.) on the temporal cortex (Freiwald and Tsao, 2010; Orlov et al., 2010; Connolly et al., 2012), many others argued for distributed and overlapping category maps in the same area (Edelman et al., 1998; Haxby et al., 2001; Grill-Spector and Kanwisher, 2001; Grill-Spector and Weiner, 2014). What has remained mostly unanswered by the mentioned studies is whether the separate neural populations (i.e. in the same or different areas) encode category information independently or in cooperation with each other. Indeed, despite much improvements in the methods of population-level representational analysis (Kriegeskorte et al., 2008a; Kaneshiro et al., 2015), it has not yet been investigated whether the distinct category-related regions of the brain provide category information in independent activities (which are finally stacked up to form population codes) or whether extra category-related information would appear by considering the correlation of activities between those regions.

A large set of studies have shown a significant role for the inter-neuron and inter-area correlated trial-to-trial variability of activities (i.e. known as noise correlation) in visual perception (Cohen and Maunsell, 2009; Zenon and Krauzlis, 2012; Ruff and Cohen, 2016) and decision-making (Shadlen et al., 1996; Nienborg et al., 2012). Other findings have shown that the trial-to-trial variability of activities (i.e. known as Fano factor) was modulated to improve the visual perception (Churchland et al., 2010; Herrero et al., 2013). It was revealed by Cohen and Maunsell (2009), that dependent (or correlated) trial-to-trial variability of activities between neurons contributed more dominantly to stimulus perception in an attention-deployed task compared to independent variability of activities (i.e. which is the variability measured by Fano factor from which the effect of correlated variability is removed) for each neuron. Thus, these studies revealed a significant role for dependent and independent variability in the encoding of categories in the brain. However, as these experiments investigated the trial-to-trial variability of activities, they remain silent on the role of within-trial variability of activities on the neural encoding.

Generally, activities of individual neurons, voxels and EEG channels are averaged within trials and treated independently from other sources (i.e. neurons, voxels or EEG channels) in the current population representational analyses to obtain information on the perceived stimuli (Kiani et al., 2007; Kriegeskorte et al., 2008b; Kaneshiro et al., 2015). This averaging overlooks several time-dependent dimensions of neural processing which have been shown to play roles in the encoding of information. Theoretical studies have shown that gamma-band synchronization (Engel et al., 1991), millisecond precision spike trains (Abeles, 1991; Oram et al., 1999) and the order of response latencies (Van Rullen et al., 1998; Thorpe et al., 2001) can also provide suitable representational brain spaces for information. Moreover, experimental studies have shown that the temporal patterns of activity convey information regarding the edge co-occurrences (Eckhorn et al., 1988), orientations in primary visual cortex (Celebrini et al., 1993) and light intensity in the retina (Gollisch and Meister, 2008). For the object category representation, an EEG study has shown the involvement of temporal phase encoding at work (Behroozi et al., 2015). Another study has shown that the within-trial correlation of activities between regions of the temporal cortex played a prominent role in object category representation (Majima et al., 2014).

Motivated by these latter studies on the importance of within-trial variability, we asked which component of the recorded activity carried the highest amount of information regarding categories within the time course of trials: is it the average activity of the region, each region's independent variability of activity or the variability of activities which are correlated between distinct regions? It should be noted that, by variability we mean the changes of signal amplitude within the time course of trials which is totally different from the classical definitions of noise correlation and Fano factor which measure the trial-to-trial variability of neural activities (Abbot and Dayan, 1999; Churchland et al., 2010).

To answer this question, we designed a whole-brain EEG recording paradigm to measure the object-evoked activity from human subjects. EEG allowed us to record high-resolution temporal signals from different brain regions simultaneously, which was generally difficult to obtain from fMRI or single-cell recording. We provided a method to quantitatively compare the contribution of the within-trial average activity, independent variability as well as the dependent variability of different brain regions in conveying category-related information. Accordingly, a modified version of a previously developed computational model (Shadlen et al., 1996) was used to generate artificial trials whose statistics closely matched those measured in the experiment. The model received three input parameters, namely the mean of activity, the variance and the correlation of activities, which were extracted from category representations. The mean activity represented the within-trial sample mean of the activities recorded in individual electrodes evoked by each stimulus. While the within-trial variance of the activity showed the accumulation of independent variability and dependent variability of individual electrodes, the within-trial correlations between (all possible) pairs of electrodes were measures of in-phase synchronization between every pair of electrodes (Majima et al., 2014). By neutralizing an individual parameter at a time, the model allowed us to investigate the contribution of each parameter independently from the other two parameters in the representational enhancement. To measure the category separability in the brain and the model representational spaces, we defined a separability index which provided several key advantages to the common decoding schemes which were previously used to extract information regarding the object categories (Majima et al., 2014; Kaneshiro et al., 2015; Goddard et al., 2016), object variations (Isik et al., 2014; Hong et al., 2016) in both invasive (Majima et al., 2014; Hong et al., 2016) and non-invasive (Kaneshiro et al., 2015; Goddard et al., 2016) recording experiments.

Results showed that the mean activity of individual brain areas contributed more significantly to category representation compared to the independent variability of individual brain areas and the correlated variability between different brain areas.

EXPERIMENTAL PROCEDURES

Stimulus set

Since our goal was to investigate the representations of objects in the brain, we needed realistic forms of objects under everyday variations, rather than the effects of background, color or other category-unrelated parameters which could interfere with the brain representations of the target objects (Martinovic et al., 2008). Therefore, an object image set was generated in which 16 object exemplars were put in four object categories, namely animal, car, face and plane (Fig. 1A).

To generate the image set we downloaded free 3D object models from (http://tf3dm.com/) and rendered them under different variation conditions (Fig. 1B) using Blender software (https://www.blender.org/). Since the variations were integral parts of object encoding which accompany the object representations even at the highest levels of the visual streams (Hong et al., 2016), we had to include them into the generation of the image set to fully activate the object-related mechanisms of the brain for an inclusive representational analysis. Therefore, the variations were applied in four dimensions including the light source direction, pose, size and position each of which in three conditions. The variation conditions were chosen so as to expose the dynamics of object representations in different visual areas such as the occipital, occipito-temporal and parietal cortices as they have shown the highest contributions to object representations (Kaneshiro et al., 2015). To generate the