



Perceptual similarity of visual patterns predicts dynamic neural activation patterns measured with MEG



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ABSTRACT

Perceptual similarity is a cognitive judgment that represents the end-stage of a complex cascade of hierarchical processing throughout visual cortex. Previous studies have shown a correspondence between the similarity of coarse-scale fMRI activation patterns and the perceived similarity of visual stimuli, suggesting that visual objects that appear similar also share similar underlying patterns of neural activation. Here we explore the temporal relationship between the human brain's time-varying representation of visual patterns and behavioral judgments of perceptual similarity. The visual stimuli were abstract patterns constructed from identical perceptual units (oriented Gabor patches) so that each pattern had a unique global form or perceptual 'Gestalt'. The visual stimuli were decodable from evoked neural activation patterns measured with magnetoencephalography (MEG), however, stimuli differed in the similarity of their neural representation as estimated by differences in decodability. Early after stimulus onset (from 50 ms), a model based on retinotopic organization predicted the representational similarity of the visual stimuli. Following the peak correlation between the retinotopic model and neural data at 80 ms, the neural representations quickly evolved so that retinotopy no longer provided a sufficient account of the brain's time-varying representation of the stimuli. Overall the strongest predictor of the brain's representation was a model based on human judgments of perceptual similarity, which reached the limits of the maximum correlation with the neural data defined by the 'noise ceiling'. Our results show that large-scale brain activation patterns contain a neural signature for the perceptual Gestalt of composite visual features, and demonstrate a strong correspondence between perception and complex patterns of brain activity.

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Introduction

Judgments of perceptual similarity require integrating information across a complex hierarchical network of brain regions. An early idea of how perceptual similarity might be conceived at the neural level is as a product of representational distance (Shepard, 1964; Torgerson, 1965). Specifically, visual objects that appear similar are assumed to share similar underlying neural representations. One of the first demonstrations of this idea with fMRI showed that different object categories (such as faces, houses, chairs) that share image-based attributes also share a similar underlying neural structure (O'Toole et al., 2005). Similarity in stimulus structure and in brain activation patterns for object categories were both defined by a classification analysis on the principal components derived from either the stimulus set or the patterns of fMRI activation; and categories that were more confusable with image-based

classification were also more confusable in their brain activation patterns.

Building on this mapping between stimulus similarity and neural representation, several studies have observed a correlation between behavioral similarity judgments for objects and their corresponding neural representations. Rotshtein et al. (2005) used morphs between famous faces within an fMRI adaptation paradigm and found that different brain regions associated with face processing were responsive to the physical features of faces (inferior occipital gyrus) versus the perceived identity of faces (right fusiform gyrus). Several studies have used rich image sets (such as objects from multiple categories) and shown that stimuli that are rated more similar by human observers also share more similar patterns of fMRI activation (Edelman et al. 1998; Hiramatsu et al. 2011, Mur et al. 2013; Connolly et al. 2012). These results suggest that objects that appear more similar have more similar brain representations; however, since these studies have focused on object recognition, they have used stimuli in which perceptual similarity is unavoidably conflated with conceptual similarity. Other studies have emphasized the role of image statistics, and used

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naturalistic stimuli varying on both semantic and visual dimensions (Hiramatsu et al., 2011), in which the mapping between different feature dimensions and perceptual similarity is complex. Consequently, in these experiments it is not possible to separate out the effects of perceptual similarity from other forms of similarity among the stimulus classes.

A notable exception is a series of studies examining fMRI activation patterns for novel shapes and objects in the object-selective lateral occipital complex (LOC). In an early demonstration, Kourtzi and Kanwisher (2001) found that following adaptation, the BOLD response in LOC for stimuli with the same shape was reduced compared to that for different shapes, even when the local contours of the 'same shape' condition were changed through manipulations in stereoscopic depth and occlusion. This suggests that stimuli with similar perceived shape have more similar activation patterns in LOC, irrespective of differences in local contours. Similarly, Haushofer et al. (2008) reported that fMRI activation patterns in the anterior LOC (pFs) for novel two-dimensional shapes that varied parametrically in aspect ratio and skew correlated with the results of a same-different task with human observers; shapes that were more confusable have more similar activation patterns. Conversely, activation patterns in the posterior LOC (LO) correlated more with the physical parameters of the stimuli (i.e., the absolute magnitude of difference in aspect ratio and skew, rather than perceived shape similarity). Op de Beeck, Torfs and Wagemans (2008) reported a significant correlation between the similarity of fMRI activation patterns in LOC and ratings of perceived shape similarity for novel categories of objects defined by their shaded three-dimensional shape. In contrast to Haushofer et al. (2008), Op de Beeck et al. (2008) observed the correlation with perceptual similarity across LOC, which the authors attribute to differences between the studies in both the stimuli and the similarity task.

In sum, there is substantial evidence that the similarity of coarse-scale fMRI activation patterns can be related to the perceived similarity of visual objects of varying complexity (e.g. Op de Beeck et al., 2008; Haushofer et al., 2008; Edelman et al. 1998; Hiramatsu et al. 2011, Mur et al. 2013; Connolly et al. 2012). The aims of the present study are to build on this work by examining the extent to which perceptual similarity is accessible in dynamic large-scale brain activation patterns measured with MEG, and to probe the structure of the underlying neural representation by comparing the temporal performance of several models. In order to separate perceptual similarity from other forms (e.g. conceptual or semantic), we use a set of abstract visual patterns as stimuli (see description below) and compare the performance of models of early visual processing and stimulus properties to a model of perceptual similarity. Most studies examining representational geometry have used fMRI (e.g. Clarke and Tyler, 2014; Edelman et al., 1998; Hiramatsu et al. 2011; Mur et al., 2013), and focused on the transformation of the representational space across spatial networks of brain regions. Compared to other neuroimaging methods, fMRI has limited temporal resolution, and consequently the temporal evolution of the mapping between behaviorally relevant features and the structure of neural representations has remained largely unexplored. To complement previous fMRI results, our focus here is on the temporal (rather than spatial) evolution of the neural representational geometry in response to visual patterns.

In order to investigate the information content of the brain's time-varying representation of the stimuli, we employed representational similarity analysis (RSA; Kriegeskorte and Kievit, 2013) to test several candidate models of the representational structure, including a model of perceptual similarity. RSA is a model-testing approach for studying brain activation patterns, which builds on traditional brain 'decoding' methods (e.g. multivariate pattern analysis) to facilitate conclusions about the content of decodable information (Kriegeskorte and Kievit, 2013). The intuition behind RSA is that differences in the decodability of stimuli can be interpreted as a proxy for neural representational similarity. Stimuli that are more difficult to decode from each other

are assumed to have more similar underlying neural representations. If a model successfully predicts the representational distance between stimuli, it provides evidence that the source of representational information in the model is present in the neural population code. An additional strength of applying RSA to MEG data is that the fine-scale temporal resolution of the neuromagnetic signal reveals the emergence of representational geometry over time, providing a more complete characterization of the model's performance.

In order to systematically decouple perceived similarity from both semantics and lower-level visual features, we used an abstract stimulus set of visual patterns constructed from arrangements of Gabor patches. These stimuli will drive the response of neurons in early visual cortex, and make straightforward predictions for a range of models that can be used to characterize the evoked cortical response to the stimuli. The stimulus set varied along three dimensions: the number of elements, the local orientation of each Gabor patch, and the degree of orientation coherence among the elements. Critically, although the stimuli are constructed from identical elements, each stimulus has a unique global form or perceptual 'Gestalt' (Fig. 1A). The advantage of this stimulus set is that models of early visual processing and stimulus features can easily be constructed for comparison with a higher-level perceptual RDM based on the unique global form produced by the different arrangements of Gabors. We compare a perceptual similarity model derived from ratings of the stimuli made by human observers to several models¹ based on the neural processing of low-level visual features: (1) a model based on differences in retinotopic stimulation between the stimuli, (2) a V1-like model based on HMAX (Riesenhuber and Poggio, 1999; Serre and Riesenhuber 2004; Hubel and Wiesel, 1965), (3) a model of local orientation differences between the stimuli, and (4) a model which predicts decodability based on inter-stimulus differences in the radial bias (e.g. Schall et al., 1986; Sasaki et al., 2006).

Materials and methods

Participants

Twenty volunteers (8 male, 12 female) with an average age of 21.6 years participated in the experiment and received financial reimbursement. Informed written consent was obtained from each volunteer prior to the experiment, and all experimental procedures received approval from the institutional ethics committee at the University of Maryland.

Stimuli

Visual stimuli were arrays of Gabor patches (sine wave convolved with a 2D Gaussian window) in a log polar arrangement (inner radius: 1°, outer radius: 8°) with four rings and twelve spokes (Fig. 1A). The size of the elements was log scaled based on their position relative to central fixation to account for cortical magnification in early visual cortex. The 26 visual stimuli were designed in 13 complementary pairs to facilitate pairwise multivariate pattern classification as a foundation for RSA. Nine stimulus pairs were *orientation* complements constructed from 48 individual Gabors (Fig. 1A, sets 1–4). In each pair, elements at corresponding spatial locations were rotated 90°. These patterns were thus maximally different in terms of orientation disparity, but equivalent in terms of coarse scale retinal stimulation. The remaining four pairs were *retinal* complements, constructed from 24 individual Gabors (Fig. 1A, set 5). For these pairs, elements present in one pattern were absent in the corresponding spatial location of its complement. Four

¹ We use the broad definition of 'model' implied by the Representational Similarity Analysis framework, as any potential explanation for the variance in the similarity of the brain representations observed for the visual stimuli – hypotheses which may be based on e.g. computational models, behavioral ratings, or straightforward predictions based on shared stimulus features.

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