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A voxel-wise encoding model for early visual areas decodes mental images of remembered scenes

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ABSTRACT

Recent multi-voxel pattern classification (MVPC) studies have shown that in early visual cortex patterns of brain activity generated during mental imagery are similar to patterns of activity generated during perception. This finding implies that low-level visual features (e.g., space, spatial frequency, and orientation) are encoded during mental imagery. However, the specific hypothesis that low-level visual features are encoded during mental imagery is difficult to directly test using MVPC. The difficulty is especially acute when considering the representation of complex, multi-object scenes that can evoke multiple sources of variation that are distinct from low-level visual features. Therefore, we used a voxel-wise modeling and decoding approach to directly test the hypothesis that low-level visual features are encoded in activity generated during mental imagery of complex scenes. Using fMRI measurements of cortical activity evoked by viewing photographs, we constructed voxel-wise encoding models of tuning to low-level visual features. We also measured activity as subjects imagined previously memorized works of art. We then used the encoding models to determine if putative low-level visual features encoded in this activity could pick out the imagined artwork from among thousands of other randomly selected images. We show that mental images can be accurately identified in this way; moreover, mental image identification accuracy depends upon the degree of tuning to low-level visual features in the voxels selected for decoding. These results directly confirm the hypothesis that low-level visual features are encoded during mental imagery of complex scenes. Our work also points to novel forms of brain–machine interaction: we provide a proof-of-concept demonstration of an internet image search guided by mental imagery.

Introduction

Spend a few moments examining "Betty" (Fig. 1A, second image from left), a famous portrait by the artist Gerhard Richter. With eyes closed generate a mental image of the painting and maintain it for a few seconds. With eyes again open re-examine the painting. Which of its basic features were conserved in your mental image? The position of Betty's head within the center of the frame? The vertical orientation of her torso? The spatial frequencies induced by the strands of her hair, the folds of her sweatshirt, or the floral print along her sleeve?

Low-level visual features such as position, orientation, and spatial frequency are among the fundamental building blocks of visual perception. During perception of an external image these features are encoded in the activity of early visual cortical areas (i.e., V1 and V2), and provide an efficient basis for representing complex natural scenes (Olshausen and Field, 1996). An important and long-standing question in mental imagery research is whether these same low-level visual features contribute to the representation of complex mental images (Pylyshyn, 2002; Kosslyn et al., 2009).

Most of the fMRI research on mental imagery has addressed a closely related but importantly different question, namely: are patterns of activity in early visual cortex generated during mental imagery *similar* to patterns of activity generated during perception? Between 1993 and 2010 at least twenty studies addressed this question by estimating the amplitude of BOLD activity in early visual areas in subjects engaged in mental imagery. At least eight studies reported no significant activity above baseline in early visual cortex during mental imagery (D'Esposito et al., 1997; Ishai et al., 2000; Knauff et al., 2000; Trojano et al., 2000; Wheeler et al., 2000; Formisano et al., 2002; Sack et al., 2002; Daselaar et al., 2010), while at least twelve reported attenuated but significant

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activity (Le Bihan et al., 1993; Sabbah et al., 1995; Goebel et al., 1998; Chen et al., 1998; Klein et al., 2000; O'Craven and Kanwisher, 2000; Ishai et al., 2002; Lambert et al., 2002; Ganis et al., 2004; Handy et al., 2004; Amedi et al., 2005; Cui et al., 2007). Recent evidence suggests that the discrepancy can be explained by differences in experimental factors (Kosslyn and Thompson, 2003) and variation in the vividness of mental imagery across individuals (Cui et al., 2007). Thus, it is safe to conclude that primary visual cortex is weakly but significantly activated by mental imagery.

In recent years at least three studies have used multivoxel pattern classification (MVPC) to measure the similarity between patterns of activity during imagery and perception in early visual cortex (Cichy et al., 2011; Lee et al., 2012; Albers et al., 2013). MVPC is a useful tool for studying mental imagery because it is sensitive to information that is