NeuroImage 155 (2017) 437–449

Contents lists available at ScienceDirect

NeuroImage

journal homepage: www.elsevier.com/locate/neuroimage

Task alters category representations in prefrontal but not high-level visual cortex

Lior Bugatus[a,*], Kevin S. Weiner[a], Kalanit Grill-Spector[a,b]

[a] Department of Psychology, Stanford University, Stanford, CA, 94305, USA
[b] Stanford Neuroscience Institute, Stanford University, Stanford, CA 94305, USA

A R T I C L E I N F O

Keywords:
Object processing
Attention
Working memory
Categorization
Prefrontal cortex
Occipito-temporal cortex

A B S T R A C T

A central question in neuroscience is how cognitive tasks affect category representations across the human brain. Regions in lateral occipito-temporal cortex (LOTC), ventral temporal cortex (VTC), and ventro-lateral prefrontal cortex (VLFPC) constitute the extended "what" pathway, which is considered instrumental for visual category processing. However, it is unknown (1) whether distributed responses across LOTC, VTC, and VLPFC explicitly represent category, task, or some combination of both, and (2) in what way representations across these subdivisions of the extended 'what' pathway may differ. To fill these gaps in knowledge, we scanned 12 participants using fMRI to test the effect of category and task on distributed responses across LOTC, VTC, and VLPFC. Results reveal that task and category modulate responses in both high-level visual regions, as well as prefrontal cortex. However, we found fundamentally different types of representations across the brain. Distributed responses in high-level visual regions are more strongly driven by category than task, and exhibit task-independent category representations. In contrast, distributed responses in prefrontal cortex are more strongly driven by task than category, and contain task-dependent category representations. Together, these findings of differential representations across the brain support a new idea that LOTC and VTC maintain stable category representations allowing efficient processing of visual information, while prefrontal cortex contains flexible representations in which category information may emerge only when relevant to the task.

Introduction

The human ventral stream, also referred to as the "what" pathway, extends from occipital cortex to high-level visual regions in lateral occipito-temporal cortex (LOTC) and ventral temporal cortex (VTC), and is involved in object recognition and categorization (Goodale and Milner, 1992; Grill-Spector and Weiner, 2014; Mishkin and Ungerleider, 1982). LOTC and VTC have both clustered (Cohen et al., 2000; Downing et al., 2001; Epstein and Kanwisher, 1998; Kanwisher, 1997) and distributed representations of object categories (Grill-Spector and Weiner, 2014; Haxby et al., 2001), which are organizational features believed to contribute to the speed of categorization (Thorpe et al., 1996). Further, a large body of research has documented that distributed responses across LOTC and VTC contain linearly separable category representations (Cox and Savoy, 2003; Grill-Spector and Weiner, 2014; Jacques et al., 2016; Kravitz et al., 2011; Kriegeskorte et al., 2008; Sayres and Grill-Spector, 2008; Spiridon and Kanwisher, 2002; Walther et al., 2009; Weiner and Grill-Spector, 2010). Linear separability is computationally advantageous because it enables combinatorial coding of distributed responses resulting in representations of tens of thousands of categories (Haxby et al., 2001, 2011), as well as rapid and efficient readout of category information (DiCarlo and Cox, 2007; Grill-Spector and Weiner, 2014).

The "what" pathway is thought to extend from VTC to ventro-lateral prefrontal cortex (VLPFC) for two reasons. First, VTC is anatomically connected to VLPFC via white matter connections such as the uncinate fasciculus (Catani et al., 2002; De Schotten et al., 2012; Gerbella et al., 2010; Schmahmann and Pandya, 2006; Ungerleider et al., 1989). Second, VLPFC is sensitive to the content of visual stimuli, rather than the location of visual stimuli, particularly under selective attention (Baldauf and Desimone, 2014; Çukur et al., 2013; Harel et al., 2014; Peelen et al., 2009; Rushworth et al., 2005) and working memory tasks (Courtney et al., 1997; Goldman-Rakic, 1996; Muller et al., 2002; Volle et al., 2008; Demb et al., 1995). Additional evidence suggests that "what" responses related to stimulus attributes emerge in VLPFC only when they are task-relevant (Asaad et al., 2000; Johnston and Everling, 2006; Lee and Baker, 2016; McKee et al., 2014; Miller and Cohen, 2000; Waskom et al., 2014). Thus, while VLPFC is considered part of

* Corresponding author at: Department of Psychology, Stanford University Stanford, CA 94305, USA.
E-mail address: liorbu@stanford.edu (L. Bugatus).

http://dx.doi.org/10.1016/j.neuroimage.2017.03.062
Received 1 March 2017; Accepted 30 March 2017
Available online 04 April 2017
1053-8119/

the extended "what" pathway (Kravitz et al., 2013; Romanski, 2012; Wilson et al., 1993), VLPFC neural responses likely do not represent visual attributes alone (Rigotti et al., 2013; Romanski, 2004).

Since a key computational goal of the ventral "what" pathway is categorization (Haxby et al., 2001; Kiani et al., 2007; Kriegeskorte et al., 2008; Grill-Spector and Weiner 2014), it is natural to ask whether VLPFC responses also contain category representations. Previous studies provide some evidence for visual category representations in VLPFC. Indeed, both electrophysiology experiments in macaques and fMRI measurements in humans observed face-selective responses (Scalaidhe et al. 1997; Tsao et al., 2008; Chan, 2013), as well as representation of categorical boundaries between pairs of stimuli (Freedman et al., 2001; Miller et al., 2002; Jiang et al., 2007; Meyer et al., 2011). For example, Jiang et al. (2007) showed that human VLPFC responses are sensitive to categorical boundaries, rather than physical differences among exemplars of the category. However, the nature of distributed responses in VLPFC has not been extensively investigated. Thus, it remains unknown if distributed responses in VLPFC contain category representations for multiple categories, and if these representations are robust and linearly separable as found in high-level visual cortex.

Notably, research in both human and non-human primates suggests that category-selective responses in VLPFC may be task-dependent (Jiang et al., 2007; McKee et al., 2014; Rigotti et al., 2013; Romanski, 2004). For example, McKee et al. (2014) reported that category-selective responses in VLPFC were observed only when category distinctions were task-relevant, but not during passive viewing. Additionally, researchers have observed that selective attention to categories alters distributed responses in VLPFC (Çukur et al., 2013; Peleen et al., 2009). However, prior studies differ on how task and attention affect category-selective responses in high-level visual cortex. While some studies report task independent category-selective responses (McKee et al. 2014, Jiang et al. 2007), other studies indicate that selective attention can alter distributed responses in high-level visual cortex (Çukur et al., 2013; Peleen et al., 2009). Thus, it remains unresolved whether task effects are equivalent or different from the effects of selective attention, and if these effects are region-specific or common across the extended "what" pathway.

Given these unresolved issues, we asked: (1) Do distributed responses across LOTC, VTC, and VLPFC explicitly represent category, task, or some combination of both? (2) Do category representations differ across cortical regions constituting the extended "what" pathway? (3) Are category representations similarly affected by task and selective attention?

To address these questions, we measured distributed responses in LOTC, VTC, and VLPFC while participants viewed images from five object categories and performed three types of cognitive tasks: oddball (OB), working memory (WM), and selective attention (SA, Fig. 1). We chose these tasks as they (1) have been widely used in studies of high-level visual cortex and VLPFC, (2) vary in the cognitive operations required, and (3) vary in the relevancy of the stimulus to the task. We first investigated how task and visual category affect amplitudes of distributed responses across the extended "what" pathway. We then examined how task and selective attention affect distributed category-selective representations. Critically, for each of these analyses, we examined whether effects were uniform or differential across LOTC, VTC, and VLPFC.

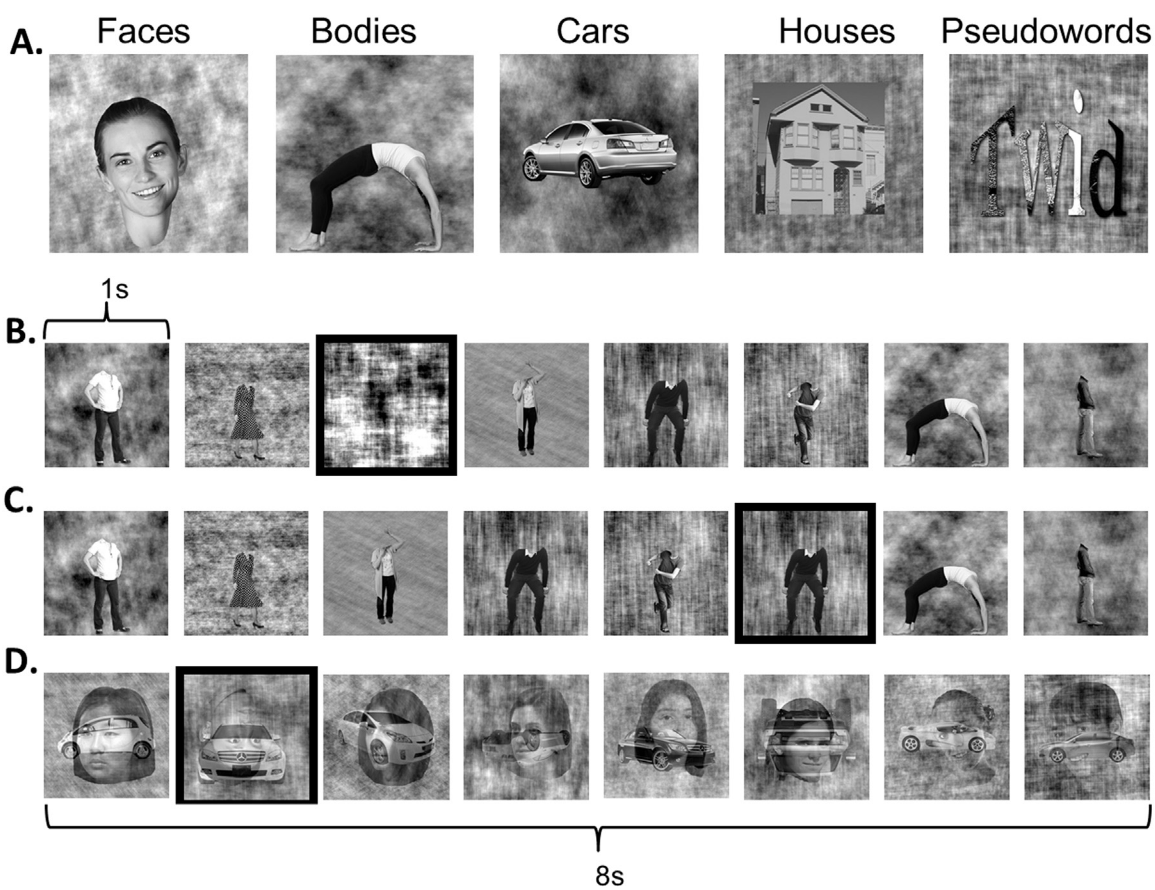

Fig. 1. Experimental design. (A) Example images from each category used in the experiment. This base set of images was used for all experiments. Superimposed stimuli from these images were generated for the selective attention (SA) task, see Fig. 1D. (B)–(D) Example stimuli for a block for each task in the experiment. Block lengths were equated for the number and duration of stimuli. (B) Oddball (OB): subjects indicated via a button when a phase-scrambled image appeared. (C) Working memory (WM): subjects indicated when a stimulus repeated after an intervening stimulus. (D) Selective Attention (SA): subjects viewed superimposed stimuli of two categories (in this example faces and cars) and were asked to attend to one category (as indicated by the cue preceding each block). Subjects indicated when a stimulus of the attended category was presented upside down.