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Research Report

Category expectation modulates baseline and stimulus-evoked activity in human inferotemporal cortex

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ABSTRACT

Expectation of locations and low-level features increases activity in extrastriate visual areas even in the absence of a stimulus, but it is unclear whether or how expectation of higher-level stimulus properties affects visual responses. Here, we used event-related functional magnetic resonance imaging (fMRI) to test whether category expectation affects baseline and stimulus-evoked activity in higher-level, category-selective inferotemporal (IT) visual areas. Word cues indicating an image category (FACE or HOUSE) were followed by a delay, then a briefly presented image of a face or a house. On most trials, the cue correctly predicted the upcoming stimulus. Baseline activity in regions within the fusiform face area (FFA) and parahippocampal place area (PPA) was modulated such that activity was higher during expectation of the preferred (e.g., FACE for FFA) vs. non-preferred category. Stimulus-evoked responses reflected an initial bias (higher overall activity) followed by increased selectivity (greater difference between activity to a preferred vs. non-preferred stimulus) after expectation of the preferred vs. non-preferred category. Consistent with the putative role of a frontoparietal network in top-down modulation of activity in sensory cortex, expectation-related activity in several frontal and parietal areas correlated with the magnitude of baseline shifts in the FFA and PPA across subjects. Furthermore, expectation-related activity in lateral prefrontal cortex also correlated with the magnitude of expectation-based increases in stimulus selectivity in IT areas. These findings demonstrate that category expectation influences both baseline and stimulus-evoked activity in category-selective inferotemporal visual areas, and that these modulations may be driven by a frontoparietal attentional control network.

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1. Introduction

The ability to anticipate some aspect of a stimulus can provide an advantage for subsequent visual processing of that stimulus. For instance, stimuli appearing within anticipated locations are processed more efficiently (Posner et al., 1980; Yeshurun and Carrasco, 1999), and similarly, attention to, or expectation of, other low-level features (e.g., color, direction of motion) leads to facilitated processing of stimuli containing those features (e.g., Ball and Sekuler, 1981; Corbetta et al., 1990; Saenz et al., 2002). Moreover, violations of expectation regarding simple stimulus attributes such as spatial location

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or low-level features can also incur perceptual *costs* in the form of increased reaction times for detection or discrimination (Posner et al., 1980).

In the real world, however, our expectations range from simple estimates of the potential locations of upcoming events, higher-level predictions related to the types of objects or scenes we will encounter, and even expectations regarding the identity of objects or individuals we will come into contact with. Recent studies have shown that the efficiency of perceptual processing of complex visual stimuli (e.g., faces, scenes) can be influenced by expectation of their category (Puri and Wojciulik, 2008) or identity (Faulkner et al., 2002; Puri and Wojciulik, 2008), leading to benefits for discrimination after valid expectation, and costs after invalid expectation. Thus, expectation of higher-level attributes (e.g. category) of complex stimuli can also enhance and/or interfere with perception.

What are the neural bases for expectation-based facilitation and interference? Results from studies of spatial and feature attention in monkeys and humans suggest that this may occur through modulation of pre-stimulus activity in relevant cortical regions after an attentional cue (baseline shifts), as well as attention-dependent changes in stimulus-evoked responses. Baseline shifts in visual cortex have been observed following cues to locations or low-level stimulus features (e.g., color, direction of motion) (Chawla et al., 1999; Fannon et al., 2008; Giesbrecht et al., 2003, 2006; Haenny et al., 1988; Hopf and Mangun, 2000; Hopfinger et al., 2000; Kastner et al., 1999; Luck et al., 1997; Luks and Simpson, 2004; Ress et al., 2000; Reynolds et al., 1999), and attention to particular locations or features is typically associated with increased firing rate or population response to an effective stimulus when it appears in that location and/or contains the expected feature (Anllo-Vento and Hillyard, 1996; Gandhi et al., 1999; McAdams and Maunsell, 2000; Moran and Desimone, 1985; O'Craven et al., 1997; Saenz et al., 2002; Spitzer et al., 1988; Treue and Martinez-Trujillo, 1999).

At the level of more complex stimuli, however, it is less clear how anticipatory attention affects related cortical activity. Although it has been demonstrated that attention to objects or object categories can modulate responses in monkey and human object processing areas during stimulus presentation (Chelazzi et al., 1998, 1993; Corbetta et al., 2005; Murray and Wojciulik, 2004; O'Craven et al., 1999; Serences et al., 2004; Wojciulik et al., 1998; Yi et al., 2006), the few studies that have investigated expectation-related, stimulus-independent baseline shifts in human object processing areas have been inconclusive (e.g., Corbetta et al., 2005). Moreover, the influence of pre-stimulus expectation on subsequent stimulus-evoked activity in human category-selective visual cortex has never been explored in the absence of competing stimuli; previous studies have not distinguished between effects induced by expectation per se and modulation due to selective attention to a subset of stimuli present in a display. Available evidence regarding cortical mechanisms of selective attention and how competitive interactions between stimulus representations arise, whether consistent with the predominant neural gain model (e.g., McAdams and Maunsell, 1999; Treue and Martinez-Trujillo, 1999) or (less commonly) demonstrating changes in tuning at the individual neuron level (Haenny et al., 1988; Spitzer et al., 1988), suggests at least two ways in which expectation of a particular stimulus or category of stimuli could influence activity in neural populations selectively involved in processing that stimulus when it appears (Desimone and Duncan, 1995; Duncan, 1998).

First, expectation of a region's preferred stimulus may result in increased activity to *any* stimulus, reflecting an overall *bias* in neural populations selectively involved in processing the expected stimulus. Second, expectation of a particular stimulus could have the effect of increasing *selectivity* of population responses in relevant regions. That is, a greater *difference* between activity to a preferred vs. non-preferred stimulus after expectation of the preferred vs. non-preferred category could reflect enhancement/suppression of differentially tuned subpopulations within a region, regardless of the population's overall preference for a particular category, consistent with previous findings at the feature and early object-processing levels (Martinez-Trujillo and Treue, 2004; Murray and Wojciulik, 2004) and evidence for distributed representation of object categories in human inferotemporal cortex (Haxby et al., 2001; Ishai et al., 1999). Thus, effects of category expectation on stimulus-evoked activity in a category-selective region could include an overall bias (increased response to any stimulus), a relative increase in selectivity for the preferred stimulus, or a combination of both.

To distinguish between these possibilities, we used event-related functional magnetic resonance imaging (fMRI) to examine effects of category expectation on baseline and stimulus-evoked activity in extrastriate regions thought to be selectively involved in processing particular categories of complex objects, specifically, faces (fusiform face area [FFA]: Kanwisher et al., 1997; Puce et al., 1995) and scenes (parahippocampal place area [PPA]: Aguirre et al., 1998; Epstein and Kanwisher, 1998). During scanning, participants were cued on each trial to expect an image belonging to one of two object categories (faces and houses). After several seconds of expectation, on most trials an image from the expected category would appear; however, occasionally, an image from the other category would be presented instead (Fig. 1). This design enabled us to assess effects of category expectation on baseline activity in the FFA and PPA as well as to characterize stimulus-evoked activity as a function of both expectation and stimulus category. Additionally, we explored the relationship between activity in frontal and parietal regions and our observed effects of expectation in FFA and PPA, as effects of attention on baseline and stimulus-evoked activity in sensory cortex are generally considered to be driven by top-down signals generated in frontal and parietal cortex (Corbetta and Shulman, 2002; Kastner and Ungerleider, 2000; Miller and Cohen, 2001).

2. Results

2.1. *Behavior*

Reaction times (RTs) and accuracy (percent correct) for the behavioral task were recorded during the scanning runs in order to identify trials on which participants were not engaged in the task. Trials with incorrect responses were excluded