Spatial attention enhances object coding in local and distributed representations of the lateral occipital complex

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ABSTRACT

The modulation of neural activity in visual cortex is thought to be a key mechanism of visual attention. The investigation of attentional modulation in high-level visual areas, however, is hampered by the lack of clear tuning or contrast response functions. In the present functional magnetic resonance imaging study we therefore systematically assessed how small voxel-wise biases in object preference across hundreds of voxels in the lateral occipital complex were affected when attention was directed to objects. We found that the strength of attentional modulation depended on a voxel's object preference in the absence of attention, a pattern indicative of an amplificatory mechanism. Our results show that such attentional modulation effectively increased the mutual information between voxel responses and object identity. Further, these local modulatory effects led to improved information-based object readout at the level of multi-voxel activation patterns and to an increased reproducibility of these patterns across repeated presentations. We conclude that attentional modulation enhances object coding in local and distributed object representations of the lateral occipital complex.

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Introduction

Attention is a cognitive process that enables us to focus on certain aspects of the environment for the benefit of improved performance (Bashinski and Bacharach, 1980; Cameron et al., 2002; Carrasco et al., 2000; Hawkins et al., 1990). One way in which attention has been found to impact neural processing is through an amplification of neural responses to attended spatial locations, objects, or features (for review, see Treue, 2003). In the visual domain, attentional amplification has been found throughout the visual processing hierarchy, from the earliest stage of visual neural processing in the lateral geniculate nucleus (O'Connor et al., 2002), primary visual cortex (Gandhi et al., 1999; Martínez et al., 1999; Somers et al., 1999), up to high-level visual cortices (Murray and Wojciulik, 2004; O'Craven et al., 1999; Serences et al., 2004) and the frontal lobes (Gitelman et al., 1999). However, the nature of attentional modulation remains a topic of debate. A number of studies have reported that attention leads to a multiplicative scaling of neuronal responses (Di Russo et al., 2001; McAdams and Maunsell, 1999; Treue

and Martínez Trujillo, 1999; Treue and Maunsell, 1999), which results in an increase of a neuron's signal to noise ratio. In contrast, other studies reported results that violated the predictions of the multiplication hypothesis, by showing that spatial attention leads to increased neural responses in visual areas in the absence of any visual stimulation (Kastner et al., 1999; Luck et al., 1997; Ress et al., 2000; Silver et al., 2007). According to these studies, attentional modulation involves an unspecific baseline shift of activity.

A common approach to investigate the effects of visual attention is the recording of neural responses across a range of a stimulus parameter (e.g., orientation or motion direction) both in the presence and absence of attention. In this way, previous studies have examined the attentional modulation of single-neuron (McAdams and Maunsell, 1999; Motter, 1993; Treue and Martínez Trujillo, 1999) or voxel (Saproo and Serences, 2010, 2014) tuning profiles. However, a complicating factor for the investigation of attentional modulation in high-level object-coding areas like the human lateral occipital complex (LOC) is the lack of analogous neuronal tuning functions. Similarly, the analysis of contrast response functions – a technique that has been used to study the nature of attentional modulation for low-level visual stimuli (Reynolds et al., 2000; Williford and Maunsell, 2006) – is problematic, because object-related neuronal responses become increasingly invariant to contrast along the visual hierarchy (Avidan et al., 2002; Rolls and

Baylis, 1986) and this invariance may itself depend on attention (Murray and He, 2006). In the present work we therefore used a different approach by exploiting the fact that the LOC represents objects in a distributed fashion across ensembles of neural populations (Haxby et al., 2001; Rice et al., 2014). At the spatial resolution of fMRI this distributed code is expressed in a differential preference of voxels for a given stimulus, likely representing the cumulative stimulus preference of neurons within these voxels. Thus, if attention causes an amplification of neural activity as opposed to a mere baseline shift, these preferences should be augmented with attention, and as a consequence single- and multi-voxel responses should become more informative about the stimuli encoded in these voxels.

In the present study we presented human participants with objects under conditions of spatial attention and inattention in a functional magnetic resonance imaging (fMRI) experiment. We had two aims. First, we sought to probe the nature of attentional modulation of visual object responses in the LOC as described above, by examining whether attentional modulation increased with a voxel's preference for a given object in the absence of attention, or whether the modulation was independent of object preference. In a second step we investigated whether these local modulatory effects of attention resulted in a more informative and reliable object code. To this end we used a mutual information metric (Saproo and Serences, 2010; Serences et al., 2009) to assess whether single-voxel responses became more informative about object identity with attention. At the multi-voxel pattern level we examined how these local changes affected the quality of object representations through pattern similarity and classification-based analyses.

Materials and methods

Disclosure

A previous article (Guggenmos et al., 2015) was based on the same fMRI dataset, but pursued a different research question and orthogonal analyses.

Participants

Eighteen healthy participants (11 female, mean age ± SEM, 23.4 ± 0.8 years) took part in the experiment for payment after giving written informed consent. The study was conducted according to the declaration of Helsinki, and approved by the local ethics committee.
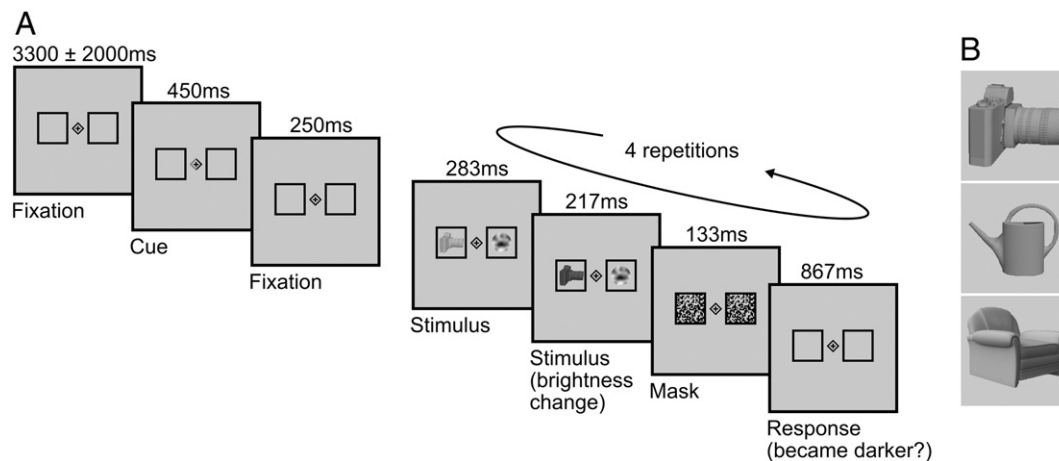
Experimental design

Our key experimental manipulation was to direct participants' spatial attention to either an object (attended condition) or a noise stimulus (unattended condition). Overall the experimental design comprised the factors attention (attended, unattended) as a factor of interest, as well as object (camera, watering can, chair), configuration (intact, split) and side of presentation (left, right) as factors of no interest. Configuration was manipulated by minimally scrambling (half-splitting) the objects, but note that the analyses in this article were based on intact objects only. Within each of 8 experimental runs, an object appeared in 4 trials in each attention condition (in 2 trials per side of presentation). The order of presentation was randomized across the 48 trials of each run.

Experimental procedures

In each trial (Fig. 1A), participants viewed a stimulus display that contained an object and a noise stimulus on either side of a central fixation cross. Spatial attention was manipulated by means of a brightness discrimination task that was performed either on the object (attended condition) or the contralateral noise stimulus (unattended condition). A trial (Fig. 1A) started with a blank fixation screen for 3300 ms ± 2000 ms, after which one half of a central black fixation diamond turned red, indicating the side to which attention should be directed. Following this cue and a short fixed interval (250 ms), four repetitions of the stimulus–response phase appeared. Each stimulus–response phase lasted 1500 ms and comprised the presentation of the stimulus screen (500 ms), a pattern mask (133 ms) and a response screen (867 ms). The object appeared on one side of the fixation cross (offset 3.84° of visual angle) and a noise stimulus at the same offset on the other side of the stimulus screen. All visual stimuli subtended 3.81 by 3.81° of visual angle. A brightness change occurred 283 ms after stimulus onset simultaneously on both the object and the noise stimulus, such that they became independently and randomly either darker or lighter. Participants were instructed to press a button on the response box when the stimulus on the cued side became darker. Responses were counted as valid within a time window of 1000 ms after stimulus offset. In each repetition of the stimulus–response phase, the same object was shown at the same position. The noise stimulus, while also presented at the same position, was randomly generated for each repetition.

To independently identify object-responsive regions of the lateral occipital complex (LOC) in each participant (Malach et al., 1995), we

Fig. 1. Experimental procedures and stimuli. A. In each trial a cue indicated the side to which attention should be directed. Subsequently, four repetitions of the stimulus–response phase appeared, during each of which participants had to detect a decrease in brightness of either the object (attended condition) or the noise stimulus (unattended condition). B. The stimulus set consisted of three objects in an intact and half-split configuration.