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Short-term retention of visual information: Evidence in support of feature-based attention as an underlying mechanism

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ABSTRACT

Retention of features in visual short-term memory (VSTM) involves maintenance of sensory traces in early visual cortex. However, the mechanism through which this is accomplished is not known. Here, we formulate specific hypotheses derived from studies on feature-based attention to test the prediction that visual cortex is recruited by attentional mechanisms during VSTM of low-level features. Functional magnetic resonance imaging (fMRI) of human visual areas revealed that neural populations coding for task-irrelevant feature information are suppressed during maintenance of detailed spatial frequency memory representations. The narrow spectral extent of this suppression agrees well with known effects of feature-based attention. Additionally, analyses of effective connectivity during maintenance between retinotopic areas in visual cortex show that the observed highlighting of task-relevant parts of the feature spectrum originates in V4, a visual area strongly connected with higher-level control regions and known to convey top–down influence to earlier visual areas during attentional tasks. In line with this property of V4 during attentional operations, we demonstrate that modulations of earlier visual areas during memory maintenance have behavioral consequences, and that these modulations are a result of influences from V4.

1. Introduction

Recent models of VSTM suggest that the mechanisms underlying the retention of information no longer available as sensory input are the same as the mechanisms supporting sustained attention to online information (Awh and Jonides, 2001; Chun and Johnson, 2011; Gazzaley and Nobre, 2012). Much of the support for these models comes from evidence that VSTM and visual attention recruit common nodes in networks involved in top–down control (Chang et al., 2012; Offen et al., 2010; Sneve et al., 2013). Furthermore, it is well-established that both attention to and maintenance of low-level stimulus features recruits the same areas in visual cortex that are active during sensory processing of the relevant feature (Harrison and Tong, 2009; Martinez-Trujillo and Treue, 2004; Serences and Ester et al., 2009; Sneve et al., 2012). In the present study, we formulate specific hypotheses based on seminal work in feature-based attention and test whether similar modulations of visual cortex take place during VSTM.

Feature-based attention is characterized by the selective enhancement of responses from sensory neurons preferring an attended feature (Maunsell and Treue, 2006). In contrast to spatial attention, which facilitates processing of input to the attended part of the visual field in a non-specific fashion, feature-based attention selectively increases responses in neural subpopulations preferring the attended feature, even when attended and unattended features share the same retinotopic location (Kamitani and Tong, 2005; Liu et al., 2007). A central characteristic of feature-based attention is the relative suppression of irrelevant (i.e., non-attended) information along the same feature spectrum. In visual cortex, such enhancement of attended parts of the feature spectrum, or “feature highlighting”, results from a combination of gain modulation in sensory neurons (Martinez-Trujillo and Treue, 2004), and shifts in individual neurons’ tuning curves towards the attended part of the spectrum (David et al., 2008). Both mechanisms lead to decreased responses in neurons tuned to non-attended feature values in the immediate spectral neighborhood of the attended value. FMRI studies on human subjects have found similar patterns of suppression during feature-based attention: Serences et al (2009) demonstrated that attending to a specific orientation led to reduced blood–oxygen level-dependent (BOLD) responses to neighboring orientations in visual areas V1 and V4. Similarly, Stoppel et al. (2011) showed that responses produced by coherent motion in the motion sensitive visual area V5 (hMT) were reduced when subjects attended to the opposite direction of

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motion. If sustained feature-based attention is the mechanism underlying VSTM maintenance of non-spatial information, we should thus observe decreased activity in the feature spectrum surrounding a maintained feature. Here, we tested this prediction using fMRI of early visual cortex. We instructed participants to remember the spatial frequency (SF) of a sample stimulus to perform a memory discrimination task after a delay interval. During the retention period, a distractor stimulus was presented, and its SF could be identical to the sample, or varied with respect to the sample frequency. Our main hypothesis was that the BOLD responses produced by distractors with SFs in the surrounding areas of the feature spectrum would be reduced, since the neurons selective for distractor SFs should be in a suppressed state in these conditions.

Our second prediction concerned the specific visual regions that are recruited during VSTM for features. During visual attention, top–down signals strengthen representations in visual cortex, particularly through modulation of activity in area V4 (Moore and Armstrong, 2003; Gregoriou et al., 2009; Zhou and Desimone, 2011). These neurophysiological observations have been confirmed in human subjects: one study combined fMRI with concurrent TMS to the putative human frontal eye fields (FEF) and observed BOLD effects in visual areas V1–V4, and this modulation of activity in visual cortex was associated with improved contrast sensitivity, resembling the effects of attention (Ruff et al., 2006). There are no known direct connections between the FEF and primary visual cortex (Stanton et al., 1995), thus the observed influence on sensory processing at this stage must necessarily be conveyed via another area. Area V4 in the macaque is known to have direct and reciprocal connections with V1–V3, as well as with higher-order control areas (Ungerleider et al., 2008). Among early visual areas, V4 activity correlates most strongly with regions outside retinotopic cortex during attentional tasks (Al-Aidroos et al., 2012). Moreover, it has been demonstrated that attentional modulations progress backwards from V4 through the early visual hierarchy (Buffalo et al., 2010), and that the latency of the BOLD-response to attended stimuli occurs significantly later in V1 than in V4 (Bouvier and Engel, 2011). In sum, if V4 is the receiving site of attention-mediated top–down interactions during VSTM, we would expect to find the strongest signatures of feature-based attention at this level in the visual hierarchy. Furthermore, modulations in earlier visual areas should be a result of influences from V4.

Finally, it is well-established that the presentation of a task-irrelevant stimulus during retention intervals in featural VSTM tasks may interfere with memory performance (Pasternak and Greenlee, 2005). The degree of such “memory masking” depends on the specific properties of the distractor stimulus relative to the remembered feature: when maintaining a particular spatial frequency, only distractors that differ from the memoranda along a narrow part of the spatial frequency spectrum lead to interference (Magnussen et al., 1991; Lalonde and Chaudhuri, 2002). The behavioral interference pattern that occurs during memory masking is suggested to be caused by cross-channel interactions between narrowly tuned feature-specific filters in visual cortex (Magnussen, 2000), in effect pulling the maintained information towards parts of the spectrum represented by the distractor (Nemes et al., 2011). Based on the psychophysical finding that memory masking impairs behavior also when interacting stimuli are similar in distal, but not retinotopical size (Bennett and Cortese, 1996), V4 has been suggested as the area where interactions occur, due to its role in calculating size constancy (Magnussen, 2000). Relating this model to the current experiment, we expect to find a correspondence between the strength of the BOLD response produced by the distractor and behavioral performance on the task. If maintaining a specific SF leads to strong suppression of the distractor’s spectral position, this also indicates that the maintained feature is “within reach” of reciprocal disturbing interactions caused by the distractor, that is, the suppressive field produced by sensory processing of the distractor should encompass the spectral position occupied by the maintained feature.

2. Methods

2.1. Participants

Five highly trained subjects (three males) gave written informed consent to participate in this study, which was approved by the Regional Committee for Medical and Health Research Ethics (Southeast Norway). The main experiment comprised 9 fMRI runs per subject (555 fMRI volumes per run). Each subject also participated in three runs of threshold estimation (555 volumes per run), four runs of retinotopic mapping (365 volumes per run), and two runs of region of interest (ROI) localization (325 volumes per run).

2.2. Stimuli

Stimuli were generated and presented using the Psychophysics toolbox (Brainard, 1997) in Matlab (Mathworks, Inc., Natick, MA). For the main experiment, stimuli were sinusoidal grating annuli (inner radius of 1°; Michelson's contrast of .6), presented centrally on a gray screen around a white fixation dot (.1° diameter). Gratings were convolved with a Gaussian kernel, and reached half maximum contrast at a radius 3.3° from center. The transition between the central gray area and the stimulus was smoothed to avoid cues about stimulus SF from sharp edges. A high-resolution image of a grating used in the experiment can be seen in Supplementary Fig. 1.

2.3. Experimental procedure

Each trial started with the appearance of the fixation dot (Fig. 1). Subjects were instructed to fixate on this dot for as long as it was present. After 1.5 s of fixation, the sample was presented for .5 s, and the subject's task was to maintain the precise SF of its grating pattern. The sample SF in a trial was either 2, 3, or 4 cycles per degree (cpd; randomly jittered within the range ±.1 cpd), and the orientation was either 45° or 135° (jittered within a range of ±5°). Phase varied randomly across trials. The changes in orientation, jittering, and phase variations were applied to prevent

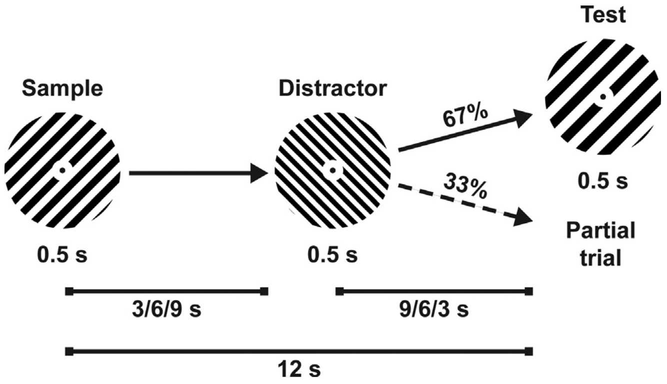

Fig. 1. Participants maintained the spatial frequency of a sample grating when a task-irrelevant distractor stimulus was presented to the same position of the visual field. Following passive viewing of the distractor, a test stimulus was presented in 2/3 of the trials. Participants indicated which stimulus (sample/test) had the highest spatial frequency. The partial trials, and the jittered interstimulus intervals, allowed precise estimation of the BOLD response produced by the distractor.