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Neural representation of object-specific attentional priority

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ABSTRACT

Humans can flexibly select locations, features, or objects in a visual scene for prioritized processing. Although it is relatively straightforward to manipulate location- and feature-based attention, it is difficult to isolate object-based selection. Because objects are always composed of features, studies of object-based selection can often be interpreted as the selection of a combination of locations and features. Here we examined the neural representation of attentional priority in a paradigm that isolated object-based selection. Participants viewed two superimposed gratings that continuously changed their color, orientation, and spatial frequency, such that the gratings traversed the same exact feature values within a trial. Participants were cued at the beginning of each trial to attend to one or the other grating to detect a brief luminance increment, while their brain activity was measured with fMRI. Using multi-voxel pattern analysis, we were able to decode the attended grating in a set of frontoparietal areas, including anterior intraparietal sulcus (IPS), frontal eye field (FEF), and inferior frontal junction (IFJ). Thus, a perceptually varying object can be represented by patterned neural activity in these frontoparietal areas. We suggest that these areas can encode attentional priority for abstract, high-level objects independent of their locations and features.

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Selection of task-relevant information is necessary to guide efficient and adaptive behavior in a complex environment. Attention is the mechanism that can select different aspects of a scene, such as locations, features and objects (Carrasco, 2011; Scolari et al., 2014). Although the neural basis of attention has been extensively studied (Kastner and Ungerleider, 2000; Reynolds and Chelazzi, 2004), a central question remains: how is top-down selection implemented in the brain?

A key assumption of attention theories is that higher-order brain areas maintain attentional priority, akin to a template, that exerts top-down control to guide selection (e.g., Deco and Rolls, 2004; Desimone and Duncan, 1995; Wolfe, 1994). For the control of spatial attention, the neural representation of spatial priority has been strongly linked to spatiotopic neural responses in dorsal frontoparietal areas (Bisley and Goldberg, 2010). Neurophysiological evidence from microstimulation studies suggest that these higher-level topographic representations send top-down control signals to earlier visual areas to implement spatial selection (Ekstrom et al., 2008; Moore and Armstrong, 2003; Moore and Fallah, 2004). For the control of feature-based attention, evidence from human fMRI and monkey neurophysiology has suggested that the dorsal frontoparietal areas can also represent the attended visual feature such as specific color and motion direction (Liu et al., 2011; Liu and Hou, 2013; Mendoza-Halliday et al., 2014). However, real scenes typically contain many objects, and observers often select whole perceptual objects (Scholl, 2001). This raises the question of how attentional priority for perceptual objects is represented in the brain.

One key challenge in studying object-based attention is that objects are always composed of features so it can be difficult to ascertain that selection occurred on the level of whole objects instead of elemental features. For example, in a popular paradigm where participants were instructed to attend to either a face or a house in a superimposed face/house image, the face and house stimuli differ in terms of low level features such as curvature and spatial frequency (Watt, 1998). Thus behavior in these studies can be potentially facilitated by feature-level selection, making it difficult to attribute results to object-based attention.

The goal of the present study is to investigate the neural representation of attentional priority for perceptual objects. Based on previous work showing that the dorsal frontal and parietal areas represent attentional priority for non-spatial features, we hypothesized that these areas can also represent priority for whole perceptual objects. To isolate object-level selection, we employed a compound stimulus composed of two objects that continuously evolved in multiple feature dimensions (Blaser et al., 2000). We then applied both fMRI univariate analysis and multivariate pattern analysis to investigate neural signals that can represent specific attended objects. Because we employed a cueing approach to direct attention, static featural differences associated with the cue could potentially account for classification results. Thus we also ran a control experiment to rule out the contribution of feature-based attention to our results.

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Materials and methods

Participants

Twelve individuals (six females, mean age: 25.5), including the author, participated in the experiment. Participants were recruited from the Michigan State University community (graduate and undergraduate students and the author) and all had normal or corrected-to-normal visual acuity and reported to have normal color vision. Participants were paid at the rate of $20/h for their time. They gave informed consent under the study protocol approved by the Institutional Review Board at Michigan State University. Sample size was determined prior to data collection and was based on comparable studies in the literature on fMRI studies of visual attention. We also conducted a power analysis, using effect size estimated from a previously published study in our lab that used a similar paradigm to decode attentional state (Hou and Liu, 2012). We pooled decoding accuracies from two frontoparietal sites (IPS and FEF) across participants to estimate the effect size. We then used G*Power 3.1.9 (Faul et al., 2007) to estimate the power in detecting a true effect using a two-tailed t-test for significant above-chance classification. This analysis showed that a sample of 12 participants would give a power of 0.82.

Stimulus and display

The visual stimuli consisted of two superimposed Gabor patches ($\sigma = 1.1°$) that varied in their orientation, color, and spatial frequency simultaneously (Fig. 1). The evolution of the features followed fixed, cyclic trajectories in their respective dimensions. On each trial, the Gabors rotated counterclockwise through all possible orientations at a speed of 59°/s; the colors of the Gabors traversed through all hues on a color circle in the CIE L*a*b space ($L = 30$, center: $a = b = 0$, radius $= 80$) at a speed of 59°/s; the spatial frequency of the Gabors varied smoothly in a sinusoidal fashion from 0.5 cycles/deg. to 3 cycles/deg. at a speed of 0.41 cycles/deg./s. Thus, in 6.1 s (the duration of the stimulus movie), the Gabors rotated two full cycles in orientation, traversed one cycle in the color space, and one full period in the sinusoidal modulation of spatial frequency. All features evolved continuously and simultaneously with maximal offset between the two Gabors (opposite angles in color space, orthogonal orientations, opposite phases in the modulation of spatial frequency).

All stimuli were generated using MGL (http://justingardner.net/mgl), a set of custom OpenGL libraries running in Matlab (Mathworks, Natick, MA). Images were projected on a rear-projection screen located in the scanner bore by a Toshiba TDP-TW100U projector outfitted with a custom zoom-lens (Navitar, Rochester, NY). The screen resolution was set to 1024 × 768 and the display was updated at 60 Hz. Participants viewed the screen via an angled mirror attached to the head coil at a viewing distance of 60 cm. Color calibration was performed with a MonacoOPTIX colorimeter (X-rite, Grand Rapids, MI), which generated an ICC profile for a display. We then used routines in Matlab's Image Processing Toolbox to read the ICC profile and calculate a transformation from the CIE L*a*b space to the screen RGB values.

Task and design

Participants tracked one of the Gabor patches on each trial and performed a change detection task. At the beginning of each trial, a number ("1" or "2", 0.4°, white) appeared in the center of the display for 0.5 s. In prior practice sessions (see below), participants had learned to associate "1" with the Gabor that was initially red, horizontal, and high spatial frequency, and to associate "2" with the Gabor that was initially cyan, vertical, and low spatial frequency. The initial image of the two Gabors appeared together with the number cue. We referred to these two Gabors as "Object 1" and "Object 2" in the instruction, and we adopt the same terminology for the rest of this report. During the subsequent 6.1 s, the two objects continuously evolved through the features space as described above, and participants were instructed to track the cued object and monitor for a brief brightening event (0.2 s). On each trial, there was either a brightening of the cued object (target), a brightening of the uncued object (distracter), or no brightening of either object (null). The three trial types (target, distracter, null) were interleaved and equally probable (proportion 1/3 each). The timing of targets and distracters conformed to a uniform distribution in two possible time windows: 1.5–2.5 s or 4.5–5.5 s after trial onset. These time windows were chosen such that the two objects had similar spatial frequency, which made the task challenging. The magnitude of the brightening (luminance increment) was determined for each participant at the beginning of the scanning session with a thresholding procedure (see Practice Sessions below). Participants were instructed to press a button with their right index finger if they detected the target (a brief brightening on the cued object), and withheld response otherwise. They were

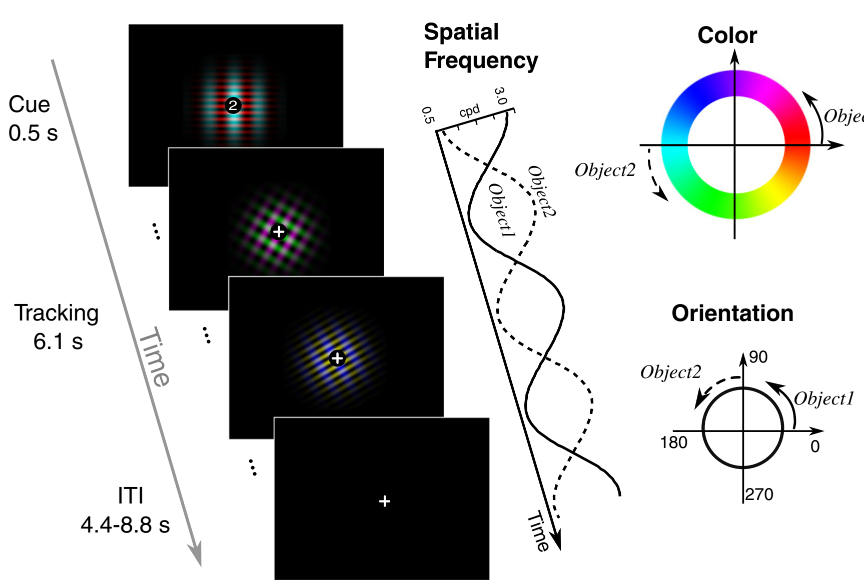

Fig. 1. Schematic of a trial in the main experiment. Two superimposed Gabors continuously changed color, orientation, and spatial frequency. Sample images are shown on the left; the trajectories in feature space are shown on the right (solid and dashed curves represent two objects). Note color and orientation can be conceived as circular dimensions, whereas spatial frequency is a linear dimension. Here a "2" instructs participants to attend to the second object (the initially low frequency, cyan, vertical Gabor).

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