Global effects of feature-based attention in human visual cortex

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The content of visual experience depends on how selective attention is distributed in the visual field. We used functional magnetic resonance imaging (fMRI) in humans to test whether feature-based attention can globally influence visual cortical responses to stimuli outside the attended location. Attention to a stimulus feature (color or direction of motion) increased the response of cortical visual areas to a spatially distant, ignored stimulus that shared the same feature.

Visual attention influences local neuronal responses and psychophysical performance for stimuli at an attended location[1,2]. Another, feature-based mechanism of attention may globally influence responses to stimuli outside the attended location that share features with the attended stimulus[3,4].

Here we asked subjects (without shifting gaze) to attend to one direction of motion (the 'target field') within two overlapping fields of upward and downward moving dots on one side of a central fixation point (**Fig. 1a**). Subjects were asked to ignore a single field of dots moving up or down on the other side. Dots had limited lifetimes (200 ms) to prevent subjects from tracking individual dots.

Subjects did a speed discrimination task at threshold (79% correct, measured by staircase procedure before scanning).
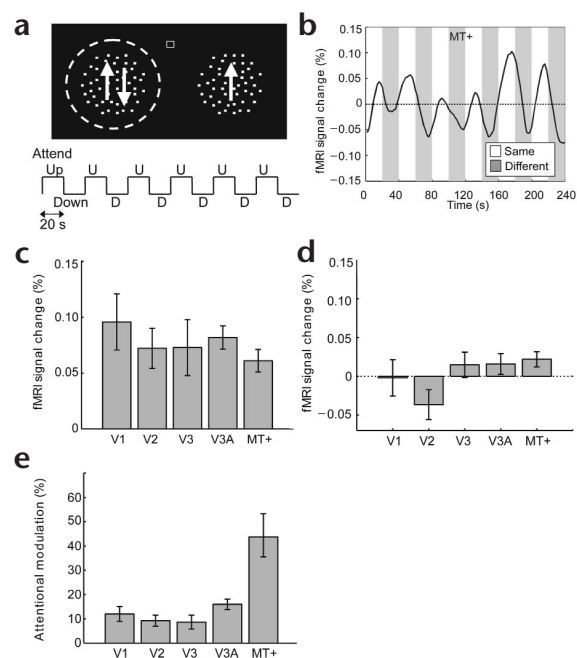
Each of the three fields of dots moved at a baseline speed during one interval and slightly faster during the other interval. Subjects indicated the faster interval in the target field with a key press. A cue (0.5° line at fixation) signaled subjects to shift attention between upward and downward fields every 20 s during the four-minute fMRI scan (**Fig. 1a**). Dots on the ignored side did not change direction. Thus, conditions alternated between 'same' (target field direction matches ignored stimulus) and 'different' (target field in the opposite direction). Before scanning, subjects trained for several hours until performance was stable. During scans, feedback was given during the intertrial interval.

Echo-planar imaging (EPI) was done with a Siemens (Munich, Germany) Vision 1.5-Tesla scanner (4 × 4 × 4 mm voxels, 16 slices, TR = 2 s). We analyzed the blood oxygenation level–dependent (BOLD) response to the ignored stimulus in V1, V2, V3, V3A and MT+, the probable human homologue of the visual motion–responsive macaque areas MT and MST[5]. Visual areas were identified with standard fMRI cortical mapping and flattening techniques[6,7]. We restricted analysis to preselected voxels within each visual area that responded to a reference stimulus presented at the experimental stimulus location. As stimuli were presented in the periphery, responses to the left and right stimuli were separated into different brain hemispheres (with one possible exception for area MT+, below).

All visual areas responded more strongly to the ignored stimulus when it moved in the same direction as the target field (**Fig. 1b**). Response amplitudes to the ignored stimulus were calculated for each visual area (**Fig. 1c**) as the amplitude of the best-fitting sine wave, phase adjusted for a typical hemodynamic delay[8]. Stimulus, eye position (**Supplementary Methods** online), task difficulty and locus of spatial attention did not change, and so this modulation must be due to feature-based attention.

If subjects inadvertently shifted spatial attention to the ignored stimulus in the 'same' condition, that should have impaired task performance[1,9], but it was similar in both conditions (same, 87.6% correct; different, 87.0%, *P* > 0.05). In separate psychophysical trials, performance was impaired
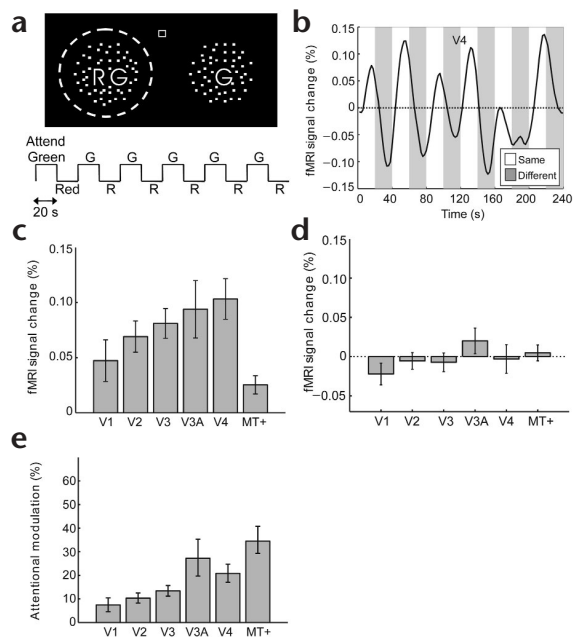

Fig. 1. Feature-based attention to motion. (**a**) Stimuli (not to scale) were circular apertures (radius 5°) of coherently moving random dots in the lower visual field (2.5° below and centered 11° to left and right of fixation, baseline speed 10°/s). Arrow, field of 50 dots moving upward or downward. Dots were white (560 cd/m^2) on a gray background (230 cd/m^2). Dashed circle (not present in the experiment), spatial focus of attention. (**b**) fMRI time series of BOLD response (same versus different) to ignored stimulus for MT+, averaged across three subjects and 24 repetitions per subject. (**c**) Response amplitudes to ignored stimulus. (**d**) Response amplitudes to attended stimulus. (**e**) Attentional response amplitudes as a percentage of stimulus-evoked response. Data in (**c**–**e**) are mean ± s.e.m. During each trial, stimuli were presented for two sequential 1-s intervals separated by a 100-ms interval in which only the fixation point was present. Trials started every 3.3 s. The order of speeds was independently randomized for each field of dots on every trial, and the baseline speed was randomly and independently jittered across trials in all three fields of dots. Scans were counterbalanced for the attended side (left/right), the starting attended direction (up/down) and the direction of motion on the ignored side (up/down). Three subjects with normal visual acuity participated, and all gave written informed consent. These experiments were approved by the Salk Institutional Review Board.

Fig. 2. Feature-based attention to color. (**a**) Stimuli (not to scale) were circular apertures of stationary red and green random dots in the upper visual field (2.5° above, centered 11° to left and right of fixation). R or G, field of 50 red or green dots on gray background. (**b**) fMRI time series in response to ignored stimulus for V4, averaged across three subjects and 24 repetitions per subject. (**c**) Response amplitudes to ignored stimulus. (**d**) Response amplitudes to attended stimulus. (**e**) Attentional response amplitudes as a percentage of stimulus-evoked response. Data in (**c–e**) are mean ± s.e.m.

significantly when subjects were instructed to divide attention across left and right stimuli (**Supplementary Methods** online). Such distribution of attention would decrease fMRI responses to the attended stimulus[10] during the 'same' condition, resulting in negative response amplitudes (different > same), which we did not observe (**Fig. 1d**). Area MT+ showed small but significant (*P* < 0.05) modulation of the response to the attended stimulus by condition (**Fig. 1d**), perhaps because its large receptive fields[11] may have included parts of the visual field responding to the ignored stimulus.

To normalize the effect of attention to the baseline activity of each region in this task, we had our subjects perform a variant of the task, in which the ignored stimulus appeared when subjects attended its matching direction ('same') and disappeared when subjects attended its opposing direction ('off'). We expressed the attentional response as a percentage of the stimulus-evoked response (100 × (same – different)/(same – off); **Fig. 1e**). Thus 0% would indicate no attentional modulation, and 100% would indicate that attention modulated the response to the ignored stimulus as much as removing it.

To determine the generality of this effect, we used color as the attended feature in a second experiment with three subjects with normal visual acuity and color perception. The attended stimulus comprised overlapping fields of stationary red and green dots, and the ignored stimulus was a single field of red or green dots (**Fig. 2a**). We placed stimuli in the upper visual field to include the suspected human homologue of the color-responsive macaque area V4, for which only an upper visual

field representation has been identified[12]. Subjects performed a threshold-increment luminance detection task. Other aspects of the experimental design were unchanged (**Supplementary Methods** online).

The fMRI response to the ignored stimulus was modulated by feature-based attention to color in areas V1, V2, V3, V3A, V4 (**Fig. 2b**) and MT+. Response amplitudes to the ignored stimulus were stronger during the 'same' condition, when its color matched the attended color (**Fig. 2b** and **c**). As in the first experiment, there was no significant difference in task performance between 'same' (89.5%) and 'different' (87.2%, *P* > 0.05) conditions. Additionally, the BOLD response to the attended stimulus did not vary with condition in any area (**Fig. 2d**). As above, we normalized the attentional response amplitudes (**Fig. 2c**) to the response elicited by cycling the ignored stimulus on and off during the task (**Fig. 2e**). In both experiments, attentional modulation in area MT+ was large relative to the stimulus-evoked response, consistent with larger effects of attention at later stages of cortical processing[13].

Our results demonstrate spatially global neuronal modulation due to feature-based attention across multiple early stages of cortical visual processing. Activity modulation by spatial attention occurs in each of these cortical visual areas[14,15]. A feature-based mechanism of attention may thus work in parallel with a spatial mechanism to influence the earliest stages of cortical visual processing. Furthermore, these results are consistent with the proposed feature-similarity gain model[3], whereby feature-based attention modulates the gain of cortical neurons tuned to the attended feature, anywhere in the visual field. The global effect of feature-based attention could be centrally involved in selecting the location of behaviorally relevant stimuli. A feature-based increase in signal strength would be useful for identifying and highlighting relevant peripheral stimuli during visual search, or for identifying parts of the same object by grouping stimuli with common features.

Note: Supplementary information is available on the Nature Neuroscience website.

Competing interests statement

The authors declare that they have no competing financial interests.

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