

RESEARCH ARTICLE | *Sensory Processing*

Characterizing the effects of feature salience and top-down attention in the early visual system

Sonia Poltoratski,¹ Sam Ling,² Devin McCormack,¹ and Frank Tong¹

¹Vanderbilt Vision Research Center, Psychology Department, Vanderbilt University, Nashville, Tennessee; and ²Department of Psychological & Brain Sciences, Center for Computational Neuroscience and Neural Technology, Boston University, Boston, Massachusetts

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Poltoratski S, Ling S, McCormack D, Tong F. Characterizing the effects of feature salience and top-down attention in the early visual system. *J Neurophysiol* 118: 564–573, 2017. First published April 5, 2017; doi:10.1152/jn.00924.2016.—The visual system employs a sophisticated balance of attentional mechanisms: salient stimuli are prioritized for visual processing, yet observers can also ignore such stimuli when their goals require directing attention elsewhere. A powerful determinant of visual salience is local feature contrast: if a local region differs from its immediate surround along one or more feature dimensions, it will appear more salient. We used high-resolution functional MRI (fMRI) at 7T to characterize the modulatory effects of bottom-up salience and top-down voluntary attention within multiple sites along the early visual pathway, including visual areas V1–V4 and the lateral geniculate nucleus (LGN). Observers viewed arrays of spatially distributed gratings, where one of the gratings immediately to the left or right of fixation differed from all other items in orientation or motion direction, making it salient. To investigate the effects of directed attention, observers were cued to attend to the grating to the left or right of fixation, which was either salient or nonsalient. Results revealed reliable additive effects of top-down attention and stimulus-driven salience throughout visual areas V1–hV4. In comparison, the LGN exhibited significant attentional enhancement but was not reliably modulated by orientation- or motion-defined salience. Our findings indicate that top-down effects of spatial attention can influence visual processing at the earliest possible site along the visual pathway, including the LGN, whereas the processing of orientation- and motion-driven salience primarily involves feature-selective interactions that take place in early cortical visual areas.

NEW & NOTEWORTHY While spatial attention allows for specific, goal-driven enhancement of stimuli, salient items outside of the current focus of attention must also be prioritized. We used 7T fMRI to compare salience and spatial attentional enhancement along the early visual hierarchy. We report additive effects of attention and bottom-up salience in early visual areas, suggesting that salience enhancement is not contingent on the observer's attentional state.

fMRI; lateral geniculate nucleus; primary visual cortex; salience; visual attention

AT ANY GIVEN MOMENT, our visual system is presented with far more information than it can process, yet we seldom feel that our visual experience is incomplete or degraded. This reflects a sophisticated balance of attentional mechanisms: the observer

can willfully guide attention toward a task-relevant item but is also predisposed to notice salient stimuli that appear outside of the current focus of attention. Our ability to navigate the dynamic visual environment critically depends on this interplay of top-down guidance of spatial attention and bottom-up processing of visually salient information.

The visual salience of an item or portion of the visual field describes the degree to which it can “grab” attention; this subjective percept is strongly influenced by the local feature differences that occur within the visual scene. Behavioral studies have demonstrated that local differences in color, orientation, size, motion, or other basic features can be rapidly detected in visual search tasks (Nothdurft 1993). Accordingly, computational models of visual salience have underscored the importance of an initial computation of local feature differences, although models differ on whether feature-selective interactions at early stages of visual processing sufficiently compute a salience map (Koene and Zhaoping 2007; Li 2002; Zhang et al. 2012) or whether a summation of various feature-contrast maps occurs at a higher stage of the visual pathway (Itti and Koch 2001). These models can predict where people are more likely to look when viewing natural scenes (Itti and Koch 2001), although cognitive goals and top-down factors can also exert powerful influence (Henderson 2003).

Neurophysiological studies have found that early visual areas are strongly modulated by local feature contrast. The response of a V1 neuron, for example, is suppressed when a presented stimulus extends beyond the neuron's receptive field and into the surround; this suppression is orientation-tuned such that greater suppression occurs when the orientation of the surround matches that of the center than when the center and surround orientations are orthogonal (Blakemore and Tobin 1972; Cavanaugh et al. 2002a; Nelson and Frost 1978). This form of feature-tuned surround suppression has been shown to emerge for a variety of visual features (Allman et al. 1985; Blakemore and Tobin 1972; Li and Li 1994; DeAngelis et al. 1994; Jones et al. 2001; Kapadia et al. 1995; Zipser et al. 1996). Multiple mechanisms likely contribute to feature-tuned surround suppression, including shorter range interactions arising from horizontal connections between feature-selective neurons within V1 as well as more distal interactions that rely on feedback from higher extrastriate areas (Angelucci and Bressloff 2006; Bair et al. 2003; Cavanaugh et al. 2002b; Gilbert and

Address for reprint requests and other correspondence: S. Poltoratski, Dept. of Psychology, Vanderbilt University, 422 Wilson Hall, 111 21st Ave. South, Nashville, TN 37240 (e-mail: sonia.poltoratski@vanderbilt.edu).

Wiesel 1979; Lamme 1995). The computation of local feature contrast can be explained in terms of greater mutual inhibition, or divisive normalization (Carandini and Heeger 2011), among neurons that share similar feature preferences. Thus a local region that differs in feature content from its immediate surround should evoke a stronger visual response due to a release from feature-tuned surround suppression.

Human neuroimaging studies have investigated the effects of orientation-selective surround suppression and orientation-defined salience, using both simple and more complex displays. Studies employing large target stimuli with immediately abutting surrounds have reported powerful effects of surround suppression (Zenger-Landolt and Heeger 2003) as well as a more modest feature-selective component of surround suppression (McDonald et al. 2009). Other studies have tested for effects of orientation-defined salience using more complex displays of multiple spatially separated gratings or lines, akin to the displays commonly used in behavioral investigations of attention and visual search (e.g., Nothdurft 1993). Results from these neuroimaging studies have been mixed: some studies find that a salient, uniquely oriented item evokes stronger responses in V1 (Schallmo et al. 2016; Zhang et al. 2012), whereas others find no reliable differences in early visual areas (Beck and Kastner 2005; Bogler et al. 2013) or more complex interactions that depend on top-down spatial attention (Flevaris and Murray 2015; Hopf et al. 2004). Our understanding of visual salience and its neural bases relies critically on testing with multi-item displays, which inform much of our knowledge of the mechanisms of attention and visual search. One factor to consider is that feature-tuned suppression may be more difficult to detect with widely separated items, because surround suppression effects in V1 are known to decrease as a function of retinotopic distance (Adesnik et al. 2012; Bair et al. 2003; Shushruth et al. 2013). Another consideration is that some prior studies have employed more complex visual tasks, raising the possibility that visual attention may interact with the processing of salient visual information.

Prioritization of visual stimuli is determined not only by stimulus-driven factors but also by voluntary selective attention, by which one can enhance the processing of stimuli corresponding to his or her specific goals and needs. Whereas frontal and parietal networks have been implicated in the control of attention (see for reviews Corbetta and Shulman 2002; Kastner and Ungerleider 2000; Silver and Kastner 2009; Squire et al. 2013), considerable work has shown that attention strongly modulates responses in early cortical visual areas, and even the lateral geniculate nucleus (LGN; Brefczynski and DeYoe 1999; Gandhi et al. 1999; Ling et al. 2015; O'Connor et al. 2002; Schneider and Kastner 2009).

Our goal in this functional MRI (fMRI) study was to determine how directed spatial attention and feature-defined salience modulate responses at early stages of visual processing. One possibility is that once an item is attended, its salience does not provide any further enhancement. Alternatively, it could be that the effects of top-down attention and feature-based salience are simply summed to determine the overall prioritization of a stimulus in the visual field. We also sought to determine the earliest stages at which salience and top-down attention would lead to reliable modulations of visual activity. Recent work from our laboratory has demonstrated orientation-selective responses in the human LGN as well as modulatory

effects of attention (Ling et al. 2015). Neurophysiological studies in animals suggest the presence of coarse selectivity in LGN (Cheong et al. 2013; Smith et al. 1990; Suematsu et al. 2012; Xu et al. 2002), arising primarily from elongation of the RF (Leventhal and Schall 1983). Moreover, there is some evidence to suggest that orientation-tuned surround suppression emerges within cat LGN (Jones et al. 2000; Naito et al. 2007). Therefore, it seemed possible that the LGN might be sensitive to orientation-defined salience. However, feature-selective interactions among spatially distributed items require either long-range connections between feature-tuned neurons or feedback from higher visual regions (Nassi et al. 2013; Nurminen and Angelucci 2014); these effects may be restricted to cortical visual areas, which have larger receptive fields and effective surrounds.

We used high-resolution fMRI at 7 Tesla to quantify the effects of top-down spatial attention and feature-defined salience at multiple levels of the visual pathway, including areas V1 through hV4 and the LGN. Observers viewed multi-item displays that contained a single salient grating with a unique orientation or motion direction, and were cued to attend to either the salient or a nonsalient grating that was located immediately to the left or right of central fixation. The spatial separation of these elements emphasized longer range feature-tuned contextual interactions. By testing both orientation- and motion-defined salience, we could evaluate the generality of the effects of feature-defined salience, since most previous research has focused exclusively on orientation processing (Bogler et al. 2013; Flevaris and Murray 2015; Hopf et al. 2004; McDonald et al. 2009; Schallmo et al. 2016; Zhang et al. 2012; but see also Harrison et al. 2007).

MATERIALS AND METHODS

Participants. Six healthy adults (ages 22–31 yr, 1 woman) participated in *experiment 1*, and six (ages 22–33 yr, 3 women) participated in *experiment 2*. Three subjects participated in both experiments. All participants had normal or corrected-to-normal vision and were compensated for their role. All aspects of the study were approved by the Vanderbilt University Institutional Review Board.

Stimuli and task: experiment 1. Our experimental displays, illustrated in Fig. 1A, were created using MATLAB and the Psychophysics Toolbox (Brainard 1997; Pelli 1997). Displays consisted of a 3×4 array of Gabor gratings presented at 100% Michelson contrast, 1.5 cycles/deg, and Gaussian envelope $\sigma = 0.4^\circ$. The stimuli measured 3.8° center to center. If one considers the effectively visible portions of the Gabor to span 5 standard deviations in width, where the contrast at the edge would dip to 4%, then each Gabor grating can be considered to have an effective width of 1° with a gap of 1.8° between the Gabors.

In each block, all gratings except for one appeared with a common orientation, either vertical or horizontal; the other, salient, grating had an orthogonal orientation. The salient grating appeared at one of two possible target locations, immediately to the left or right of the fixation point (0.5° in diameter with a central dot of 0.175°); we refer to these as the left and right “target locations” for our region of interest (ROI) analyses. All patches flickered on/off in 200-ms intervals (i.e., 2.5 Hz), with the spatial phase of the Gabors randomized on each presentation.

In each experimental block, the participant was shown a cue at fixation and instructed to covertly attend to one of the target gratings while keeping the eyes focused on the central fixation point. The attentional cue consisted of a pair of dots (0.1°) that appeared to the left and right of fixation. One of these dots was black, and the other

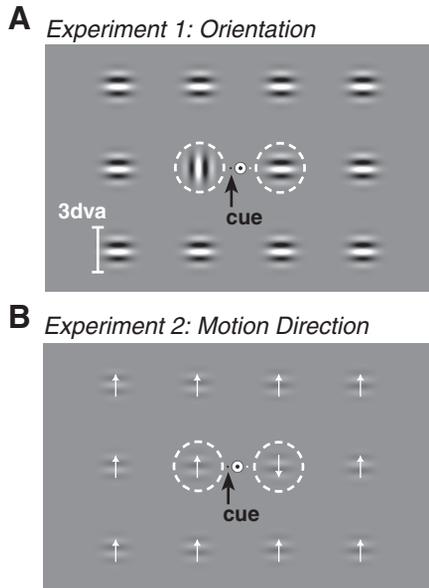


Fig. 1. Annotated sample displays for both experiments. Feature-contrast salience is defined by orientation in *A* and by drifting motion direction in *B* (indicated by arrows, which were not present during the experiment). Dashed circles (likewise not present during the experiments) indicate the 2 locations at which the salient patch could appear and to which spatial attention could be directed. Although the task-relevant contrast decrement occurred at both of these locations, the observer was instructed to only perform the detection task on 1 patch, as indicated throughout each block by a small cue. In these examples, if the participant is cued to attend to the black cue (as labeled), in *A*, the left patch is attended/salient, whereas the right patch is unattended/nonsalient; in *B*, the left patch is attended/salient, and the right patch is unattended/salient. Gabor patch edges were Gaussian blurred and also spatially separated by a gap of 0.8° , yielding an effective spatial separation of $\sim 1.8^\circ$. dva, Degrees of visual angle.

white; each participant was told to attend to the side marked by one of these two colors throughout the experiment. The spatially balanced design of this fixation cue ensured equivalent stimulus-driven activity in each hemifield and avoided potential effects of exogenous cuing, which could occur with a single lateralized cue (Jehee et al. 2011, 2012). The attended cue color was counterbalanced across participants.

Participants were asked to perform an attentionally engaging contrast-decrement detection task on the cued stimulus. We chose this task to direct covert spatial attention to the cued grating, and to minimize the potential influences of feature-based attention. In previous work, we have shown that the performance of an attentional task on the orientation of a grating leads to a strong enhancement of orientation-selective responses in V1–V4, whereas tasks that require attending to the contrast of a grating do not (Jehee et al. 2011). Contrast decrements occurred at independent intervals at each of the two target locations throughout the experimental block, but participants were instructed to respond to decrements only at the cued location via a button box. The decrement occurred 8 times per 16-s block at randomly determined intervals, lasting for the full 200-ms duration of that “on” interval with a minimum 800-ms time difference between targets.

Stimuli and task: experiment 2. The stimulus parameters were similar to those of *experiment 1*, except for two key differences: motion direction, rather than orientation, was used to define salience, and the drifting Gabor patches were continuously presented at 30% contrast (see Fig. 1*B*). All of the patches were oriented horizontally and phase-randomized, and the gratings drifted either upward or downward at a speed of 5 deg/s (temporal frequency 7.5 Hz) within a stationary window. The salient patch moved in the opposite direction relative to the motion of all other Gabor gratings in the array. We

chose upward-downward motion directions to minimize the likelihood of inducing involuntary optokinetic nystagmus (OKN; Honrubia et al. 1968) and to further ensure that if a small eye movement was occasionally induced, it would not be directed toward either of the lateralized target gratings. Participants were asked to perform an attentionally engaging contrast-decrement detection task on the cued stimulus. The contrast decrement lasted for 400 ms and occurred on 20% of these implicit 400-ms intervals within each 16-s stimulus block.

In a separate behavioral eye-tracking session, we confirmed that our participants could maintain stable fixation while viewing these arrays of moving gratings. Participants performed the same experimental task on displays that matched the stimuli and timing (16-s blocks) of the fMRI experiment. Overall, our subjects kept their eyes fixed well within the 0.5° fixation dot. Horizontal eye movement deviations (reported as the standard deviation from the true fixation position) ranged from 0.07° to 0.33° across the 6 participants (median 0.15°); vertical deviations ranged from 0.11° to 0.48° (median 0.23°).

Experimental design and procedure. Apart from differences in the stimuli, the design of both experiments was identical. There were three experimental factors that consisted of 1) location of the salient grating (left or right of fixation), 2) location to be spatially attended (left or right grating), and 3) the context feature (horizontal or vertical orientation in *experiment 1*, upward or downward motion in *experiment 2*). This $2 \times 2 \times 2$ factorial design led to 8 experimental conditions, which were presented in a randomized order within each run. Each experimental run followed a 16-s block design (272s duration), with each of the 8 experimental conditions occurring once, interleaved with 16-s fixation-rest periods that also occurred at the beginning and end of each run. A fixation circle remained present throughout the experimental run; the spatial attention cue appeared 1 s before the onset of each stimulus block, informing participants to direct their attention toward the left or right grating. Participants were informed of their performance accuracy at the end of each run, and the magnitude of the contrast decrement was adjusted between runs so that the detection hit rate for each subject fell in a range from ~ 70 to 90% ; across subjects, the magnitude of the contrast decrement ranged from 25% to 40% of the original contrast value.

Behavioral performance. In *experiment 1*, performance at the contrast detection task led to a mean hit rate across individual subjects of 76.4% (SD 12.1%). Contrast decrements applied to the salient target in the display were detected with 77.4% accuracy, whereas those applied to nonsalient targets yielded 75.4% correct performance. There was no significant difference in performance for salient and nonsalient targets across the group [$t(5) = 0.81$, $P = 0.45$]. In *experiment 2*, subjects averaged 83.4% hit rate (SD 7.1%), 83.7% correct on salient targets, and 82.5% correct on nonsalient targets; again, there was no reliable difference in performance for the salient and nonsalient targets [$t(5) = 0.59$, $P = 0.58$]. Our task, which requires contrast discrimination using suprathreshold contrast changes, was designed to manipulate the locus of spatial attention rather than to assess sensitivity to contrast, which has been shown to be enhanced at salient locations (e.g., Joo et al. 2012; Kapadia et al. 1995). These behavioral results suggest that participants were able to attend selectively to the nonsalient grating location when it was the target and were not distracted by the presence of the salient grating.

fMRI data acquisition. Data were acquired using a Philips Achieva 7T MRI scanner at the Vanderbilt University Institute of Imaging Science, with a 32-channel head coil equipped for SENSE imaging. The functional scans employed single-shot gradient-echo echo planar imaging to measure blood oxygen level dependent (BOLD) activity and were aligned approximately parallel to the anterior commissure-posterior commissure line to best capture the LGN and occipital pole. Subjects were scanned using either 1.5-mm isotropic voxel resolution in 20 slices (6 subjects in *experiment 1*, 4 in *experiment 2*) or a $2\text{-mm} \times 1.875\text{-mm} \times 1.875\text{-mm}$ voxel resolution in 36 slices (2 subjects in *experiment 2*). The 1.5-mm thickness scans used the

following parameters: repetition time (TR) 2 s, echo time (TE) 26 ms, flip angle 75°, field of view (FOV) 192 mm, with no gap. The 2-mm scans used identical parameters, except that the FOV was 210 mm. Twelve to 16 runs of functional data and 2–3 localizer runs were collected for each subject. The spatial extent of our slice prescription allowed us to monitor BOLD activity in the LGN and areas V1, V2, V3, and hV4. Area V3A often appeared outside of this slice prescription and therefore was not included in this study.

Functional ROI definition. Cortical visual areas V1–hV4 were demarcated using standard retinotopy procedures, with the use of data acquired from separate scan sessions at 3T (Engel et al. 1997; Wandell et al. 2007). We used a typical phase-encoded design in which subjects fixated while they viewed flickering checkerboards consisting of rotating wedges to map polar angle and expanding rings to map eccentricity. Retinotopy data was acquired using a Philips 3T Intera Achieva MRI scanner equipped with an eight-channel coil. Subjects were scanned using 3-mm isotropic resolution (TR 2 s, TE 35 ms, flip angle 80°, 28 slices, 192 × 192 FOV). Boundaries between retinotopic areas V1–hV4 were delineated by hand, by identifying reversals in the phase of the polar angle map measurements; the resulting ROIs were aligned to the functional space of the current experiment using FSL and FreeSurfer software.

In the experimental scan session, we ran two to three runs of a visual localizer to identify the target ROIs corresponding to the spatial extent of the left and right gratings. This involved presenting flickering checkerboards at full contrast within a Gaussian contrast envelope at each of the two target locations, with alternating 16-s cycles of left or right stimulation, as well as a 16-s fixation period at the beginning and end of each run. Individual checks were 0.75° in width and contrast-reversed at a rate of 5 Hz. Subjects did not perform a task during localizer runs and were instructed to keep their eyes on a central fixation point. Cortical ROIs were selected from the conjunction of retinotopy and a statistical map of the left vs. right contrast of our functional localizer. We report results from the 100 most functionally selective voxels as defined by the *t*-statistic map in each lateralized ROI in early visual areas.

The lateral geniculate nucleus was defined functionally from the same localizer contrast, using a *t*-value threshold of no less than 2.8; thresholds for each subject were selected to yield distinct, continuous clusters of voxels such that left and right hemisphere nuclei were generally aligned dorsally and were maximally lateralized, so as to avoid the inclusion of the pulvinar region. Because the LGN cannot be localized anatomically from T1- or T2-weighted images, we cannot be fully sure that our ROIs do not include other portions of the thalamus. However, the LGN is more readily activated by visual stimulation than other subcortical regions, and there is evidence to suggest that functional localizers that rely on passive viewing, as ours did, do not activate pulvinar activity as strongly as the LGN (Kastner et al. 2004).

In sessions using a 1.5-mm isotropic voxel size, the bilateral LGN ROI consisted of an average of 72.9 voxels (SD 16.8); in the two participants who were tested using a larger voxel size of 2 mm × 1.875 mm × 1.875 mm, the LGN ROI encompassed an average of 42.5 voxels.

fMRI analysis: preprocessing. Data were preprocessed using FSL and FreeSurfer tools (documented and freely available for download at <http://surfer.nmr.mgh.harvard.edu>), beginning with 3-D motion correction and linear trend removal, followed by a high-pass filter cutoff of 60 s. Functional images were registered to a reconstructed anatomical space for each subject; this registration was first automated in FSL and then checked and corrected by hand. This allowed the alignment of the current fMRI data to the retinotopy data, which were collected in a separate session. The functional localizer was spatially smoothed using a 1-mm Gaussian kernel; no spatial smoothing was done for the experimental runs. Further analyses were conducted using a custom MATLAB processing stream. For each ROI-based analysis, data were masked using the labels defined from the retinotopy and functional localizer, which corresponded to the left and right

target grating locations in each visual area. Each voxel's intensities were normalized by the mean of the time series, converting to mean percent signal change within each run. Outliers were defined as time points for which the voxel's response measured more than three times its standard deviation from its mean and were Winsorized (Hastings et al. 1947). This condition-blind preprocessing step minimizes the impact of rare spikes in MR intensity while preserving the temporal structure of the responses in each voxel. Only a small fraction of a percentage of data points in the current experiments were marked as outliers (0.26–0.41% across experiments and ROIs). Furthermore, voxels that left the volume at any time point due to head motion were excluded from that run's analysis. Additionally, we found that during one session in *experiment 1*, a combination of slice placement and head motion caused some regions to intermittently clip the edge of the volume. For this subject, we excluded two runs from the analysis of bilateral V2 and right hV4, based on dropout of visually selective responses that was restricted to these ROIs.

fMRI analysis: mean BOLD. To calculate the average mean BOLD response for each experimental condition, we first converted the MR time series of each voxel from signal intensity units to units of percent signal change. Next, we calculated the average BOLD amplitude for each block, after shifting the response period by 2 TRs to account for hemodynamic lag. To account for baseline differences preceding each condition's onset, the average of the 2 TRs immediately preceding each block was subtracted from its mean. For every stimulus block, we obtained a measure of the mean BOLD response in each ROI, and further calculated the overall BOLD response across all blocks for each experimental condition.

Conditions were defined relative to lateralized ROI responses such that, for example, a block in which the left target patch was salient was labeled "salient" in the right hemisphere and "nonsalient" in the left hemisphere; data were pooled in this way across the left and right hemisphere ROIs. We also combined data across specific feature values (e.g., when the salient target was vertical vs. horizontal in *experiment 1*), which were not pertinent to our hypotheses. In each bilateral region, we performed a 2 × 2 repeated-measures ANOVA to characterize the effects of salience and spatial attention, as well as their interaction.

RESULTS

fMRI: experiment 1. In this experiment, orientation was used to define one salient target location in an array of gratings while the participant spatially attended to the salient target or to a nonsalient target in the contralateral hemifield (see Fig. 1A). We compared fMRI responses in early visual areas evoked by the salient grating and by the contralateral nonsalient grating across attended and unattended conditions, pooling the data across the left and right ROIs.

The time course of mean BOLD responses in the LGN and areas V1–hV4 are shown in Fig. 2B, *top*, and the mean response amplitudes observed in each block are plotted in Fig. 2B, *bottom*. Figure 2A shows the modulatory effects of both attention and salience as average difference in BOLD response. Spatial attention led to positive increases in the BOLD response throughout the visual pathway, in both subcortical and cortical ROIs. We observed reliable effects of top-down attentional modulation in all individual cortical visual areas [V1: $F(1,5) = 7.59$, $P < 0.041$; V2: $F(1,5) = 8.08$, $P < 0.037$; V3: $F(1,5) = 23.7$, $P < 0.005$; hV4: $F(1,5) = 19.2$, $P < 0.008$]. This effect was likewise present in the LGN [$F(1,5) = 9.11$, $P < 0.030$], consistent with previous fMRI reports that the human LGN can be reliably modulated by spatial attention (Ling et al. 2015; O'Connor et al. 2002; Schneider and Kastner 2009).

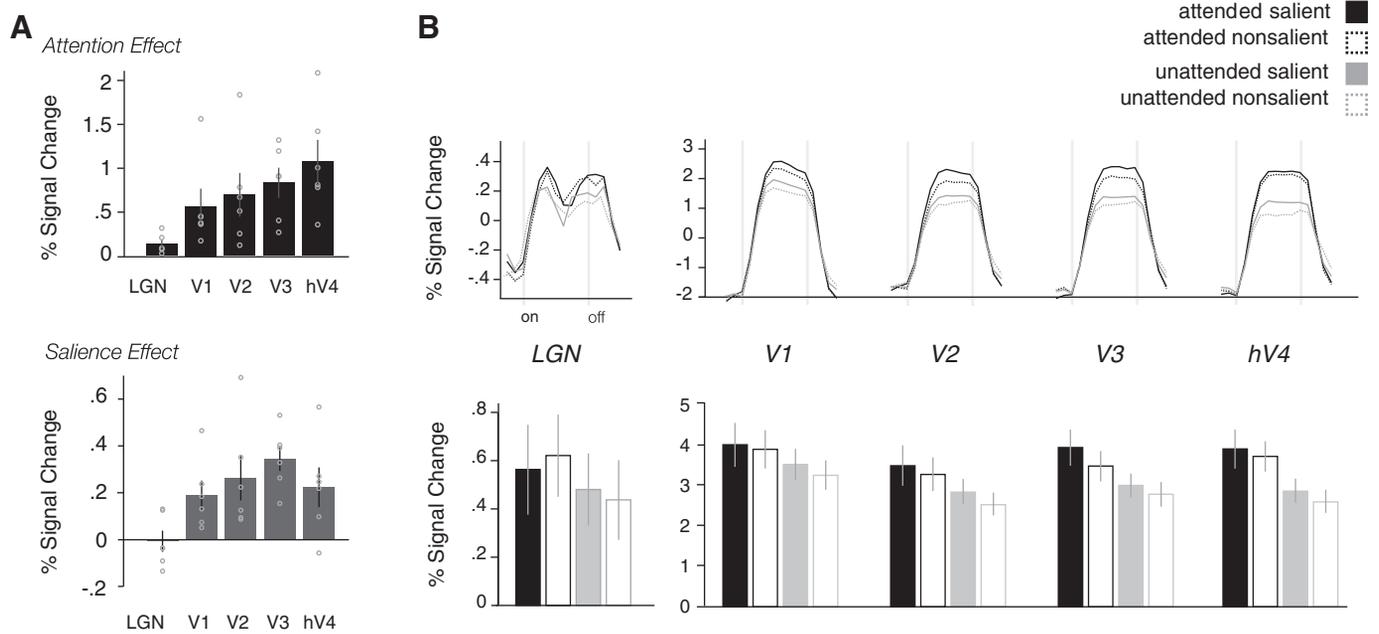


Fig. 2. Results of *experiment 1* for the 4 salience and attention conditions. *A*: magnitude of the attention and salience effects across ROIs, computed as the difference in percent signal change. Circles show the effect in individual subjects, and error bars depict SE (across subjects). In the LGN, only attention significantly modulated BOLD responses; neither the main effect of salience nor the interaction effect were significant. A significant effect of salience first emerged in V1 and is evident in each cortical ROI. Attention also modulated BOLD responses in V1 through hV4, but the 2 effects did not reliably interact in any region. *B, top*: mean ROI time courses time-locked to the beginning of each experimental block, which lasted 8 TRs and is demarcated by dotted lines. *Bottom*, the same data averaged across the block, offset to account for hemodynamic lag, and normalized by subtracting the mean response of the 2 TRs immediately preceding the block. Error bars on block averages depict SE in the mean BOLD response across subjects.

In contrast, we found that the effect of salience was evident only in the visual cortex. No reliable difference between salient and nonsalient items was observed in the LGN [$F(1,5) = 0.028$, $P = 0.87$]. Early visual cortical areas, however, exhibited clear and reliable effects of salience, with higher mean BOLD responses to the salient grating than to the nonsalient grating that matched the orientation of the surrounding context [V1: $F(1,5) = 9.47$, $P < 0.003$; V2: $F(1,5) = 8.53$, $P < 0.034$; V3: $F(1,5) = 42.8$, $P < 0.002$; hV4: $F(1,5) = 7.35$, $P < 0.043$].

Interestingly, the main effects of salience and spatial attention did not significantly interact in any of our measured ROIs [V1: $F(1,5) = 1.83$, $P = 0.24$; V2: $F(1,5) = 0.14$, $P = 0.73$; V3: $F(1,5) = 2.34$, $P = 0.19$; hV4: $F(1,5) = 0.12$, $P = 0.74$]. That is, the enhancement of salient items is not contingent on the observer's attentional state or goals. The LGN, which did not show a significant main effect of salience but was reliably modulated by attention, likewise showed no interaction effect [$F(1,5) = 1.07$, $P = 0.35$].

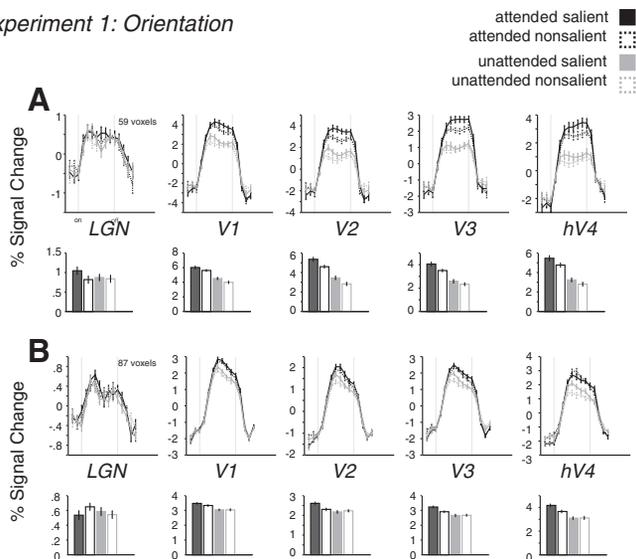
As shown in Fig. 2A, comparison of the magnitude of these effects across cortical visual areas reveals a significant difference between regions [ANOVA, $F(3,15) = 5.74$, $P < 0.009$], suggesting a trend of increasing attention modulation along the visual hierarchy [F -test, $t(2) = 9.00$, $P < 0.013$]. There appeared to be no difference in the magnitude of salience modulation across visual areas V1 through V4 [$F(3,15) = 1.68$, $P = 0.21$]. Including the LGN in this comparison, however, did yield significant differences across ROIs [$F(4,29) = 7.8$, $P < 8.0 \times 10^{-4}$]. Specifically, the salience modulation of the LGN was not significantly different from zero [$t(5) = 0.16$, $P = 0.87$] and was significantly weaker than the salience effect observed in V1 [$t(5) = 4.7$, $P < 0.0054$].

We performed a Bayes factor analysis to estimate the likelihood that the results from the LGN could have arisen from a null effect of salience. We calculated the JZS Bayes factor (Rouder et al. 2009), applying a scale factor of 1 for the prior on effect size for the alternative hypothesis, and obtained a value of 3.44 in favor of the null hypothesis. It has been suggested that odds factors greater >3 should be considered as evidence in favor of a hypothesis (Jeffreys 1961); thus the LGN data are not strongly conclusive but do tend to favor the null hypothesis.

To further test for the possible presence of an interaction effect between salience and spatial attention, we performed an ANOVA on the data of individual subjects, using the fMRI response amplitudes observed on individual fMRI blocks for each participant (Fig. 6). Consistent with our group analysis results, we observed statistically significant main effects of salience and top-down attention in early visual areas for the majority of individual subjects. However, the interaction between salience and attention did not reach statistical significance in any ROI for any subject. To illustrate the quality of data collected, as well as the differences between measurements of the LGN and of cortex, representative single-subject data from this experiment are shown in Fig. 3, A and B.

All preceding analyses were performed on the mean activations of the functional ROIs; in the cortex, these were selected from individual retinotopic regions and defined as the 100 most selective voxels in each hemisphere on the basis of independent localizer runs. We assessed whether this ROI size criteria had a meaningful effect on the pattern of our results by calculating the magnitude of attentional and salience-based modulation for a wide range of ROI sizes. Figure 4 plots the magnitude of attention- and salience-based enhancement as a

Experiment 1: Orientation



Experiment 2: Motion

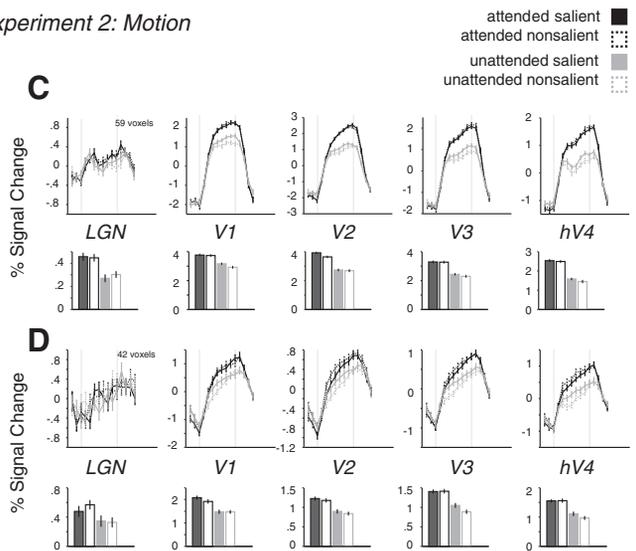


Fig. 3. Examples of average fMRI time courses from representative subjects in *experiment 1* (A and B) and *experiment 2* (C and D). Error bars depict \pm SE for each experimental condition, and each of the 4 panels shows data from a different individual. As expected, there is some variability between subjects; fMRI responses in the LGN are also more variable than those in early visual areas, partly because of the LGN's smaller size and the presence of greater physiological noise in midbrain structures.

function of the number of voxels selected from each ROI. As can be seen, these effects are broadly consistent across a wide range of ROI sizes.

The results of *experiment 1* suggest that effects of orientation-defined salience emerge in the primary visual cortex, with a similar degree of enhancement observed in higher extrastriate visual areas. Although orientation-specific responses have recently been demonstrated in the human LGN (Ling et al. 2015), we found no evidence of enhanced responses to orientation-defined salience at this subcortical site. However, we did find that spatial attention reliably modulates responses in the LGN, in agreement with previous fMRI studies (Ling et al. 2015; O'Connor et al. 2002). The finding that effects of visual salience and top-down attention emerged at different levels of the visual pathway provides support for the proposal that these

mechanisms operate independently and are functionally distinct. Consistent with this proposal, the modulatory influences of spatial attention and orientation-defined salience appeared to be separable and additive in early visual areas of interest.

fMRI: experiment 2. Do the effects of orientation-based salience generalize to other feature domains? Most studies that find salience enhancement in early visual areas have focused on orientation as the defining feature (Joo et al. 2012; Li 2002; Schallmo et al. 2016; Zhang et al. 2012); however, direction-selective contextual interactions in V1 have been reported for spatially separated moving stimuli (Harrison et al. 2007). In *experiment 2*, we were motivated to test whether motion-defined salience would also yield similar effects of top-down attention and stimulus-driven salience across the visual hierarchy. In this experiment, one Gabor grating drifted in a direction opposite to that of all other gratings in the display and was deemed salient. Meanwhile, observers performed an attentionally demanding task on either the salient item or on a nonsalient item, as illustrated in Fig. 1B.

As can be seen in Fig. 5, mean BOLD responses were consistently greater for attended than unattended items. A repeated-measures ANOVA indicated that this modulatory effect of attention was statistically significant in all ROIs, including the lateral geniculate nucleus [LGN: $F(1,5) = 27.5$, $P < 0.004$; V1: $F(1,5) = 47.9$, $P < 9.7 \times 10^{-4}$; V2: $F(1,5) = 44.0$, $P < 0.0013$; V3: $F(1,5) = 37.6$, $P < 0.002$; hV4: $F(1,5) = 96.6$, $P < 1.9 \times 10^{-4}$]. Whereas absolute BOLD amplitudes in the LGN were variable across subjects, as evidenced by the size of the error bars in Fig. 5B (which correspond to \pm SE across the 6 subjects), the within-subject effect of attention was statistically reliable in the LGN. Moreover, the effect of attention appeared highly consistent in both LGN and visual cortex, with every participant showing attentional modulations in the predicted direction. This is illustrated in Fig. 5A, which depicts individual subjects' effect amplitudes as gray circles overlaid on the mean effect across ROIs; representative individual subject data for *experiment 2* are shown in Fig. 3, C and D.

In the visual cortex, we again observed significant modulation by salience: nonsalient gratings that drifted in the same direction as the contextual gratings elicited weaker mean BOLD responses than did items that drifted in the opposite direction. Significant enhancement of salient items was observed in each of the cortical ROIs, beginning in V1 [$F(1,5) = 33.7$, $P < 0.003$] and persisting through V2–hV4 [V2: $F(1,5) = 10.0$, $P < 0.026$; V3: $F(1,5) = 42.5$, $P < 0.002$; hV4: $F(1,5) = 18.1$, $P < 0.009$]. However, this motion-defined salience did not significantly modulate activity in the LGN [$F(1,5) = 0.14$, $P = 0.72$].

Critically, the enhancements of BOLD activity elicited by attention and salience did not appear to interact in this experiment. ANOVA indicated that salience and attention conditions did not lead to a significant interaction effect in any of the cortical ROIs [V1: $F(1,5) = 0.015$, $P = 0.91$; V2: $F(1,5) = 4.4$, $P = 0.09$; V3: $F(1,5) = 0.083$, $P = 0.78$; hV4: $F(1,5) = 0.62$, $P = 0.47$], nor in the LGN [$F(1,5) = 1.90$, $P = 0.23$]. Thus the degree of enhancement observed for salient items appeared comparable under conditions of attention and inattention.

Figure 5A shows the modulatory effects of spatial attention and of salience in *experiment 2* for each ROI. Similar to the

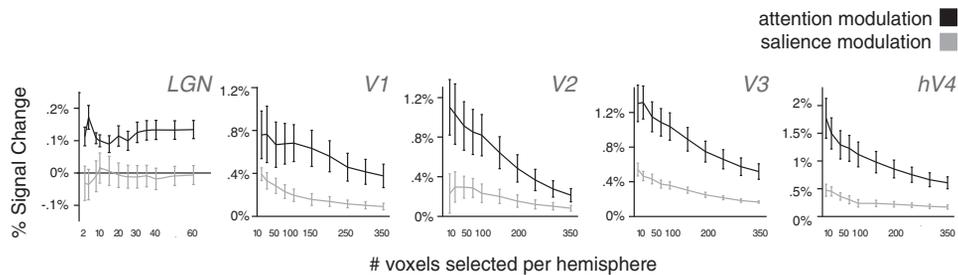


Fig. 4. Magnitude of attention and salience effects plotted as a function of ROI size. We calculated the difference in BOLD response for attended minus unattended conditions and salient minus nonsalient conditions for a wide range of ROI sizes, ranging from 2 to 60 maximum voxels per hemisphere in the LGN and from 10 to 350 voxels per hemisphere in individual cortical visual areas. Error bars indicate SE across subjects. Our findings of positive salience and attention effects in each cortical ROI are highly consistent across a wide range of ROI sizes.

results of the first experiment, we see a trend toward increasing attentional modulation as one ascends from V1 to V4 [ANOVA, $F(3,15) = 4.26$, $P = 0.023$; F -test, $t(2) = 7.19$, $P < 0.019$]. Salience modulations appear similar in magnitude across areas V1–hV4, and no reliable difference was found among these cortical ROIs [$F(3,15) = 0.38$, $P = 0.77$]. A difference emerged across brain areas when data from the LGN were included in the ANOVA [$F(4,29) = 7.46$, $P < 9.0 \times 10^{-4}$], and paired comparisons indicated that salience modulation was significantly weaker in the LGN than in V1 [$t(5) = 4.88$, $P < 0.0046$]. As in the previous experiment, salience modulation in the LGN did not significantly differ from zero [$t(5) = 0.38$, $P = 0.72$]. In this case, a Bayes factor analysis indicated a value of 3.25, in moderate favor of the null hypothesis. We again note the difficulty in interpreting a null effect in the LGN: small effect sizes, when present, are difficult to detect, and the increased physiological noise when measuring subcortical activity can impede the reliability of fMRI measures. However, the magnitude of salience modulation appears clustered around zero for the majority (5/6) of our individual subjects (Fig. 5A), in contrast with individual effects of attention in the LGN or of salience in cortex.

Overall, the two experiments yielded very similar patterns of results, demonstrating that both orientation- and motion-defined salience lead to common effects of enhancement in the early visual cortex. These effects did not significantly interact in any region of interest, neither in the group analysis nor in analysis results for any individual subject (Fig. 6), suggesting that stimulus-driven salience and top-down attention provide independent sources of modulatory influence at early stages of the visual system.

DISCUSSION

In two experiments, we used high-field fMRI to characterize the effects of top-down attention and feature-defined salience at multiple levels of the visual hierarchy. We found that orientation- and motion-defined salience consistently enhanced responses to stimuli in areas V1 through hV4, implying a common mechanism for detecting local feature differences across spatially disparate stimuli. These feature-tuned contextual interactions are critical for the computation of the local salience of a region, as predicted by modeling work (Itti and Koch 2001; Li 2002). Additionally, we found that directed spatial attention enhanced responses in all regions of interest, including the LGN; our findings add to a growing number of studies indicating that activity in the LGN can be altered by top-down attentional goals (Ling et al. 2015; McAlonan et al. 2008; O'Connor et al. 2002; Schneider and Kastner 2009). In contrast, we did not find evidence that LGN activity is reliably modulated by feature-defined salience. Although one must be cautious about the interpretation of null effects, the absence of a statistically reliable effect of salience in the LGN is consistent with the proposal that long-range feature-selective interactions depend on cortical mechanisms (Bair et al. 2003; Nassi et al. 2013; Shushruth et al. 2009, 2013). Our results support the proposal that at the earliest stages of visual processing, salience is distinct from mechanisms of top-down attention.

Consistent with this view, we found that the effects of salience did not lead to significant interactions with the effects of attention in any of our regions of interest. Our findings suggest that the effects of top-down attention and bottom-up salience are summed in a simple additive manner such that

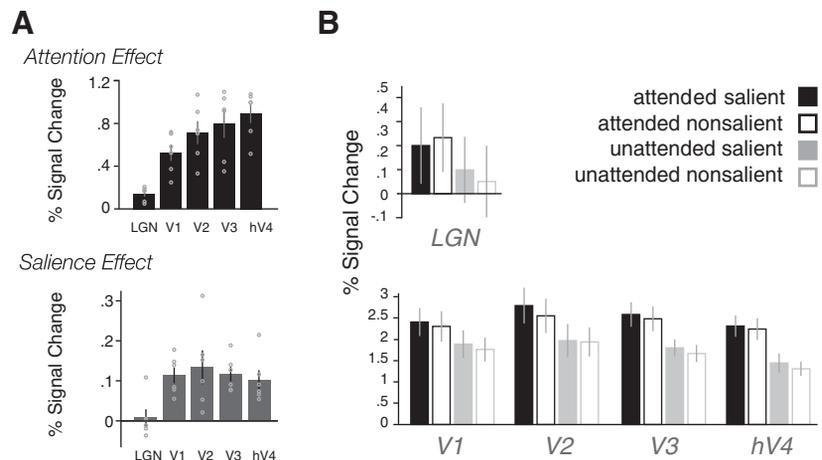


Fig. 5. Mean BOLD amplitudes in *experiment 2*, in which salience was defined by the direction of drifting motion of Gabor patches. *A*: attention and salience effects (% signal change difference) across ROIs, with circles plotting individual subjects' results and error bars showing SE across subjects. *B*: results in each condition averaged across the stimulus block and normalized by a prestimulus window for each condition. The pattern of results follows that of *experiment 1*: attentional enhancement is evident in each ROI, including the LGN, whereas salience modulated only cortical mean BOLD responses. In every region studied, the effects of attention and salience did not significantly interact.

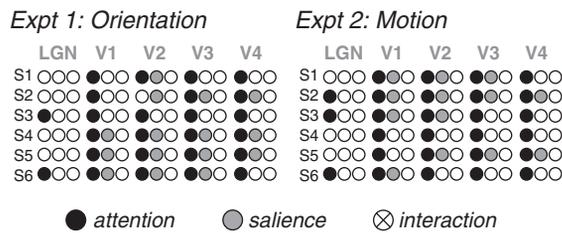


Fig. 6. Individual subject ANOVA results for *experiment 1* (Expt 1; left) and *experiment 2* (Expt 2; right). Each experimental session was analyzed independently, with experimental run as the repeated measure. Filled circles indicate significant effects of attention (black), salience (gray), or their interaction (cross) at $P < 0.05$ level. Subject labels (S1–S6) are arbitrary and unmatched between the 2 experiments. Although many subjects exhibited significant main effects of attention and salience, the interaction of these 2 factors was not significant in any ROI in any subject.

both mechanisms distinctly inform the prioritization of items within a visual scene. These results concur with a recent fMRI study by Schallmo et al. (2016), although it should be noted that more complex interactions between bottom-up mechanisms and top-down attention may occur if attention is allowed to spread to other neighboring items. For example, feature-based attention may counteract the influence of feature-tuned suppression with certain stimulus configurations and tasks. Flevaris and Murray (2015) found that an attended target grating evoked greater responses when flanked by orthogonally oriented gratings than when the target and flankers were iso-oriented. When participants attended to one of the flanking gratings, however, attention appeared to spread to the target if the gratings shared a common orientation. This reported interaction presumably emerged due to the spatial spreading of feature-based attention (Saenz et al. 2002). In the present study, attention was cued to shift between target locations in separate hemifields, thereby minimizing the spread of attention between the lateralized target regions. Under these conditions, we observed separate additive effects of top-down attention and salience at each of the target locations. We should note, however, that the limited range of contrast levels in the current experiments may bias us toward finding additive effects if the neural response function is saturated (Carrasco 2006).

Our results support the view that processing of feature-defined salience in V1 relies on horizontal interactions within the region (Adesnik et al. 2012; Stettler et al. 2002) as well as more long-range effects of feedback from higher extrastriate areas to V1 (Angelucci and Bressloff 2006; Bair et al. 2003; Nassi et al. 2013). Such feature-selective interactions are believed to underlie a variety of early contextual effects (Stettler et al. 2002), including tilt repulsion (Dragoi et al. 2001; Jin et al. 2005), collinear enhancement (Kapadia et al. 1995), and figure-ground processing (Lamme 1995); the current experiments considered how these early visual interactions may function over spatially disparate elements in a scene, which is critical toward building a behaviorally relevant representation of salience. Of course, further processing of salience occurs in higher level extrastriate and parietal regions as the observer orients his or her attention during visual search (Melloni et al. 2012), integrates many features in a naturalistic environment (Bogler et al. 2011), shifts attention (Kincade et al. 2005), or plans eye movements (Fecteau and Munoz 2006; Gottlieb et al. 1998; Mazer and Gallant 2003). The current work informs the wider study of salience by investigating the early cortical

stages involved in these processes and by demonstrating that the representation of this information is unaffected by the observer's attentional focus.

Our results in the LGN suggest that feature-selective surround effects in this region are either negligible or too weak to be reliably detected in the current paradigm, which relied on spatially separated gratings to manipulate salience. Existing neurophysiological work is consistent with these views. Studies of the LGN in cats and monkeys have demonstrated size-tuned responses to gratings due to strong suppression from the immediate surround, which likely arises from mechanisms originating from the retina (Alitto and Usrey 2008) as well as effects of cortical feedback (Jones et al. 2012). Although some orientation bias has been reported in LGN neurons in several species (e.g., cat: Suematsu et al. 2012; owl monkey: Xu et al. 2002; Cheong et al. 2013; and macaque: Smith et al. 1990), positive effects of feature-tuned suppression in this structure have been predominantly reported in the cat (Cudeiro and Sillito 1996; Jones et al. 2000; Naito et al. 2007). Given the known anatomical differences between cat and primate LGN, our null effect could reflect a lack of feature-tuned surround suppression in the region. It is also possible that feature-tuned suppression in the LGN may operate at a more local spatial scale than our Gabor array displays were designed to probe (Angelucci and Bressloff 2006), as suggested by our group's positive report of modulatory effects of orientation masking in this structure (Ling et al. 2015). Alternatively, it may be that particular elements of our experimental design precluded us from detecting modulatory effects: we were limited in testing only one contrast level in each experiment and in using a constant spatial frequency (1.5 cycles/deg) throughout the study.

These findings contribute to a broader understanding of how surround suppression functions toward a behaviorally relevant representation of the visual scene. The effects of surround suppression have been shown to fall off with distance; however, modulations in apparent contrast of a central stimulus can be detected even with spatial separation of several degrees between the center and surround (Cannon and Fullenkamp 1991; Petrov and McKee 2006). Although the generalization of surround suppression to natural image or movie inputs has posed a challenge in vision research, recent work has suggested that the suppression may be gated by the degree of redundancy in a natural image (Coen-Cagli et al. 2015). Homogeneity in a natural image was found to elicit stronger suppression, which may act to reduce redundancy in visual input and code natural input more efficiently (Vinje and Gallant 2000). fMRI studies of perceptual grouping report effects of global configuration, consistent with this view of redundancy reduction (Joo et al. 2012). Given the visual system's adaptive nature, sensitivity to the statistics of natural input may provide a bridge from fundamental mechanisms of suppression and contextual interactions to behaviorally relevant representations of salience in the environment (Coen-Cagli et al. 2012; Kayser et al. 2004), especially as these mechanisms function across different spatial scales (Nurminen and Angelucci 2014). By representing the influences of visual salience and top-down attention at the earliest stages of cortical visual processing, the visual system is able to achieve a balance between automatic prioritization of local regions throughout the visual field and voluntary guidance based on current goals and tasks.

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DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the authors.

AUTHOR CONTRIBUTIONS

S.P., S.L., and F.T. conceived and designed research; S.P. and D.M. performed experiments; S.P. analyzed data; S.P., S.L., D.M., and F.T. interpreted results of experiments; S.P. prepared figures; S.P., S.L., and F.T. drafted manuscript; S.P., S.L., D.M., and F.T. edited and revised manuscript; S.P., S.L., D.M., and F.T. approved final version of manuscript.

REFERENCES

- Adesnik H, Bruns W, Taniguchi H, Huang ZJ, Scanziani M. A neural circuit for spatial summation in visual cortex. *Nature* 490: 226–231, 2012. doi:10.1038/nature11526.
- Allitto HJ, Urey WM. Origin and dynamics of extraclassical suppression in the lateral geniculate nucleus of the macaque monkey. *Neuron* 57: 135–146, 2008. doi:10.1016/j.neuron.2007.11.019.
- Allman J, Miezin F, McGuinness E. Stimulus specific responses from beyond the classical receptive field: neurophysiological mechanisms for local-global comparisons in visual neurons. *Annu Rev Neurosci* 8: 407–430, 1985. doi:10.1146/annurev.ne.08.030185.002203.
- Angelucci A, Bressloff P. Contribution of feedforward, lateral and feedback connections to the classical receptive field center and extra-classical receptive field surround of primate V1 neurons. *Prog Brain Res* 154: 93–120, 2006. doi:10.1016/S0079-6123(06)54005-1.
- Bair W, Cavanaugh JR, Movshon JA. Time course and time-distance relationships for surround suppression in macaque V1 neurons. *J Neurosci* 23: 7690–7701, 2003.
- Beck D, Kastner S. Stimulus context modulates competition in human extrastriate cortex. *Nat Neurosci* 8: 1110–1116, 2005. doi:10.1038/nm1501.
- Blakemore C, Tobin EA. Lateral inhibition between orientation detectors in the cat's visual cortex. *Exp Brain Res* 15: 439–440, 1972. doi:10.1007/BF00234129.
- Bogler C, Bode S, Haynes JD. Decoding successive computational stages of saliency processing. *Curr Biol* 21: 1667–1671, 2011. doi:10.1016/j.cub.2011.08.039.
- Bogler C, Bode S, Haynes JD. Orientation pop-out processing in human visual cortex. *Neuroimage* 81: 73–80, 2013. doi:10.1016/j.neuroimage.2013.05.040.
- Brainard DH. The Psychophysics Toolbox. *Spat Vis* 10: 433–436, 1997. doi:10.1163/156856897X00357.
- Brefczynski JA, DeYoe EA. A physiological correlate of the 'spotlight' of visual attention. *Nat Neurosci* 2: 370–374, 1999. doi:10.1038/7280.
- Cannon MW, Fullenkamp SC. Spatial interactions in apparent contrast: inhibitory effects among grating patterns of different spatial frequencies, spatial positions and orientations. *Vision Res* 31: 1985–1998, 1991. doi:10.1016/0042-6989(91)90193-9.
- Carandini M, Heeger DJ. Normalization as a canonical neural computation. *Nat Rev Neurosci* 13: 51–62, 2011.
- Carrasco M. Covert attention increases contrast sensitivity: psychophysical, neurophysiological and neuroimaging studies. In: *Visual Perception: Fundamentals of Vision: Low and Mid-Level Processes in Perception* (Progress in Brain Research), edited by Martinez-Conde S, Macknik SL, Martinez LM, Alonso JM, and Tse PU. Amsterdam: Elsevier Science, 2006, vol. 154A, p. 33–70.
- Cavanaugh JR, Bair W, Movshon JA. Nature and interaction of signals from the receptive field center and surround in macaque V1 neurons. *J Neurophysiol* 88: 2530–2546, 2002a. doi:10.1152/jn.00692.2001.
- Cavanaugh JR, Bair W, Movshon JA. Selectivity and spatial distribution of signals from the receptive field surround in macaque V1 neurons. *J Neurophysiol* 88: 2547–2556, 2002b. doi:10.1152/jn.00693.2001.
- Cheong SK, Tailby C, Solomon SG, Martin PR. Cortical-like receptive fields in the lateral geniculate nucleus of marmoset monkeys. *J Neurosci* 33: 6864–6876, 2013. doi:10.1523/JNEUROSCI.5208-12.2013.
- Coen-Cagli R, Dayan P, Schwartz O. Cortical surround interactions and perceptual salience via natural scene statistics. *PLOS Comput Biol* 8: e1002405, 2012. doi:10.1371/journal.pcbi.1002405.
- Coen-Cagli R, Kohn A, Schwartz O. Flexible gating of contextual influences in natural vision. *Nat Neurosci* 18: 1648–1655, 2015. doi:10.1038/nn.4128.
- Corbetta M, Shulman GL. Control of goal-directed and stimulus-driven attention in the brain. *Nat Rev Neurosci* 3: 201–215, 2002. doi:10.1038/nrn755.
- Cudeiro J, Sillito AM. Spatial frequency tuning of orientation-discontinuity-sensitive corticofugal feedback to the cat lateral geniculate nucleus. *J Physiol* 490: 481–492, 1996. doi:10.1113/jphysiol.1996.sp021159.
- DeAngelis GC, Freeman RD, Ohzawa I. Length and width tuning of neurons in the cat's primary visual cortex. *J Neurophysiol* 71: 347–374, 1994.
- Dragoi V, Rivadulla C, Sur M. Foci of orientation plasticity in visual cortex. *Nature* 411: 80–86, 2001. doi:10.1038/35075070.
- Engel SA, Glover GH, Wandell BA. Retinotopic organization in human visual cortex and the spatial precision of functional MRI. *Cereb Cortex* 7: 181–192, 1997. doi:10.1093/cercor/7.2.181.
- Fecteau JH, Munoz DP. Saliency, relevance, and firing: a priority map for target selection. *Trends Cogn Sci* 10: 382–390, 2006. doi:10.1016/j.tics.2006.06.011.
- Flevaris AV, Murray SO. Attention determines contextual enhancement versus suppression in human primary visual cortex. *J Neurosci* 35: 12273–12280, 2015. doi:10.1523/JNEUROSCI.1409-15.2015.
- Gandhi SP, Heeger DJ, Boynton GM. Spatial attention affects brain activity in human primary visual cortex. *Proc Natl Acad Sci USA* 96: 3314–3319, 1999. doi:10.1073/pnas.96.6.3314.
- Gilbert CD, Wiesel TN. Morphology and intracortical projections of functionally characterized neurones in the cat visual cortex. *Nature* 280: 120–125, 1979. doi:10.1038/280120a0.
- Gottlieb JP, Kusunoki M, Goldberg ME. The representation of visual salience in monkey parietal cortex. *Nature* 391: 481–484, 1998. doi:10.1038/35135.
- Harrison LM, Stephan KE, Rees G, Friston KJ. Extra-classical receptive field effects measured in striate cortex with fMRI. *Neuroimage* 34: 1199–1208, 2007. doi:10.1016/j.neuroimage.2006.10.017.
- Hastings C Jr, Mosteller F, Tukey JW, Winsor CP. Low moments for small samples: a comparative study of order statistics. *Ann Math Stat* 18: 413–426, 1947. doi:10.1214/aoms/1177730388.
- Henderson JM. Human gaze control during real-world scene perception. *Trends Cogn Sci* 7: 498–504, 2003. doi:10.1016/j.tics.2003.09.006.
- Honrubia V, Downey WL, Mitchell DP, Ward PH. Experimental studies on optokinetic nystagmus. II. Normal humans. *Acta Otolaryngol* 65: 441–448, 1968. doi:10.3109/00016486809120986.
- Hopf J-M, Noesselt T, Tempelmann C, Braun J, Schoenfeld MA, Heinze H-J. Popout modulates focal attention in the primary visual cortex. *Neuroimage* 22: 574–582, 2004. doi:10.1016/j.neuroimage.2004.01.031.
- Itti L, Koch C. Computational modelling of visual attention. *Nat Rev Neurosci* 2: 194–203, 2001a. doi:10.1038/35058500.
- Jeffreys SH. *The Theory of Probability* (3rd ed.). Oxford: Oxford University Press, 1961.
- Jehee JF, Brady DK, Tong F. Attention improves encoding of task-relevant features in the human visual cortex. *J Neurosci* 31: 8210–8219, 2011. doi:10.1523/JNEUROSCI.6153-09.2011.
- Jehee JF, Ling S, Swisher JD, van Bergen RS, Tong F. Perceptual learning selectively refines orientation representations in early visual cortex. *J Neurosci* 32: 16747–16753, 2012. doi:10.1523/JNEUROSCI.6112-11.2012.
- Jin DZ, Dragoi V, Sur M, Seung HS. Tilt aftereffect and adaptation-induced changes in orientation tuning in visual cortex. *J Neurophysiol* 94: 4038–4050, 2005. doi:10.1152/jn.00571.2004.
- Jones HE, Andolina IM, Ahmed B, Shipp SD, Clements JTC, Grieve KL, Cudeiro J, Salt TE, Sillito AM. Differential feedback modulation of center and surround mechanisms in parvocellular cells in the visual thalamus. *J Neurosci* 32: 15946–15951, 2012. doi:10.1523/JNEUROSCI.0831-12.2012.
- Jones HE, Andolina IM, Oakely NM, Murphy PC, Sillito AM. Spatial summation in lateral geniculate nucleus and visual cortex. *Exp Brain Res* 135: 279–284, 2000. doi:10.1007/s002210000574.
- Jones HE, Grieve KL, Wang W, Sillito AM. Surround suppression in primate V1. *J Neurophysiol* 86: 2011–2028, 2001.
- Joo SJ, Boynton GM, Murray SO. Long-range, pattern-dependent contextual effects in early human visual cortex. *Curr Biol* 22: 781–786, 2012. doi:10.1016/j.cub.2012.02.067.
- Kapadia MK, Ito M, Gilbert CD, Westheimer G. Improvement in visual sensitivity by changes in local context: parallel studies in human observers

- and in V1 of alert monkeys. *Neuron* 15: 843–856, 1995. doi:10.1016/0896-6273(95)90175-2.
- Kastner S, O'Connor DH, Fukui MM, Fehd HM, Herwig U, Pinsk MA.** Functional imaging of the human lateral geniculate nucleus and pulvinar. *J Neurophysiol* 91: 438–448, 2004. doi:10.1152/jn.00553.2003.
- Kastner S, Ungerleider LG.** Mechanisms of visual attention in the human cortex. *Annu Rev Neurosci* 23: 315–341, 2000. doi:10.1146/annurev.neuro.23.1.315.
- Kaysers C, Körding KP, König P.** Processing of complex stimuli and natural scenes in the visual cortex. *Curr Opin Neurobiol* 14: 468–473, 2004. doi:10.1016/j.conb.2004.06.002.
- Kincade JM, Abrams RA, Astafiev SV, Shulman GL, Corbetta M.** An event-related functional magnetic resonance imaging study of voluntary and stimulus-driven orienting of attention. *J Neurosci* 25: 4593–4604, 2005. doi:10.1523/JNEUROSCI.0236-05.2005.
- Koene AR, Zhaoping L.** Feature-specific interactions in salience from combined feature contrasts: evidence for a bottom-up saliency map in V1. *J Vis* 7: 6.1–6.14, 2007. doi:10.1167/7.7.6.
- Lamme VA.** The neurophysiology of figure-ground segregation in primary visual cortex. *J Neurosci* 15: 1605–1615, 1995.
- Leventhal AG, Schall JD.** Structural basis of orientation sensitivity of cat retinal ganglion cells. *J Comp Neurol* 220: 465–475, 1983. doi:10.1002/cne.902200408.
- Li CY, Li W.** Extensive integration field beyond the classical receptive field of cat's striate cortical neurons—classification and tuning properties. *Vision Res* 34: 2337–2355, 1994. doi:10.1016/0042-6989(94)90280-1.
- Li Z.** A saliency map in primary visual cortex. *Trends Cogn Sci* 6: 9–16, 2002. doi:10.1016/S1364-6613(00)01817-9.
- Ling S, Pratte MS, Tong F.** Attention alters orientation processing in the human lateral geniculate nucleus. *Nat Neurosci* 18: 496–498, 2015. doi:10.1038/nn.3967.
- Mazer JA, Gallant JL.** Goal-related activity in V4 during free viewing visual search. Evidence for a ventral stream visual salience map. *Neuron* 40: 1241–1250, 2003. doi:10.1016/S0896-6273(03)00764-5.
- McAlonan K, Cavanaugh J, Wurtz RH.** Guarding the gateway to cortex with attention in visual thalamus. *Nature* 456: 391–394, 2008. doi:10.1038/nature07382.
- McDonald JS, Seymour KJ, Schira MM, Spehar B, Clifford CW.** Orientation-specific contextual modulation of the fMRI BOLD response to luminance and chromatic gratings in human visual cortex. *Vision Res* 49: 1397–1405, 2009. doi:10.1016/j.visres.2008.12.014.
- Melloni L, van Leeuwen S, Alink A, Müller NG.** Interaction between bottom-up saliency and top-down control: how saliency maps are created in the human brain. *Cereb Cortex* 22: 2943–2952, 2012. doi:10.1093/cercor/bhr384.
- Naito T, Sadakane O, Okamoto M, Sato H.** Orientation tuning of surround suppression in lateral geniculate nucleus and primary visual cortex of cat. *Neuroscience* 149: 962–975, 2007. doi:10.1016/j.neuroscience.2007.08.001.
- Nassi JJ, Lomber SG, Born RT.** Corticocortical feedback contributes to surround suppression in V1 of the alert primate. *J Neurosci* 33: 8504–8517, 2013. doi:10.1523/JNEUROSCI.5124-12.2013.
- Nelson JL, Frost BJ.** Orientation-selective inhibition from beyond the classic visual receptive field. *Brain Res* 139: 359–365, 1978. doi:10.1016/0006-8993(78)90937-X.
- Nothdurft HC.** The role of features in preattentive vision: comparison of orientation, motion and color cues. *Vision Res* 33: 1937–1958, 1993. doi:10.1016/0042-6989(93)90020-W.
- Nurminen L, Angelucci A.** Multiple components of surround modulation in primary visual cortex: multiple neural circuits with multiple functions? *Vision Res* 104: 47–56, 2014. doi:10.1016/j.visres.2014.08.018.
- O'Connor DH, Fukui MM, Pinsk MA, Kastner S.** Attention modulates responses in the human lateral geniculate nucleus. *Nat Neurosci* 5: 1203–1209, 2002. doi:10.1038/nn957.
- Pelli DG.** The VideoToolbox software for visual psychophysics: transforming numbers into movies. *Spat Vis* 10: 437–442, 1997. doi:10.1163/156856897X00366.
- Petrov Y, McKee SP.** The effect of spatial configuration on surround suppression of contrast sensitivity. *J Vis* 6: 224–238, 2006. doi:10.1167/6.3.4.
- Rouder JN, Speckman PL, Sun D, Morey RD, Iverson G.** Bayesian *t* tests for accepting and rejecting the null hypothesis. *Psychon Bull Rev* 16: 225–237, 2009. doi:10.3758/PBR.16.2.225.
- Saenz M, Buracas GT, Boynton GM.** Global effects of feature-based attention in human visual cortex. *Nat Neurosci* 5: 631–632, 2002. doi:10.1038/nn876.
- Schallmo MP, Grant AN, Burton PC, Olman CA.** The effects of orientation and attention during surround suppression of small image features: a 7 Tesla fMRI study. *J Vis* 16: 19, 2016. doi:10.1167/16.10.19.
- Schneider KA, Kastner S.** Effects of sustained spatial attention in the human lateral geniculate nucleus and superior colliculus. *J Neurosci* 29: 1784–1795, 2009. doi:10.1523/JNEUROSCI.4452-08.2009.
- Shushruth S, Ichida JM, Levitt JB, Angelucci A.** Comparison of spatial summation properties of neurons in macaque V1 and V2. *J Neurophysiol* 102: 2069–2083, 2009. doi:10.1152/jn.00512.2009.
- Shushruth S, Nurminen L, Bijanzadeh M, Ichida JM, Vanni S, Angelucci A.** Different orientation tuning of near- and far-surround suppression in macaque primary visual cortex mirrors their tuning in human perception. *J Neurosci* 33: 106–119, 2013. doi:10.1523/JNEUROSCI.2518-12.2013.
- Silver MA, Kastner S.** Topographic maps in human frontal and parietal cortex. *Trends Cogn Sci* 13: 488–495, 2009. doi:10.1016/j.tics.2009.08.005.
- Smith EL 3rd, Chino YM, Ridder WH 3rd, Kitagawa K, Langston A.** Orientation bias of neurons in the lateral geniculate nucleus of macaque monkeys. *Vis Neurosci* 5: 525–545, 1990. doi:10.1017/S095252380000699.
- Squire RF, Noudoost B, Schafer RJ, Moore T.** Prefrontal contributions to visual selective attention. *Annu Rev Neurosci* 36: 451–466, 2013. doi:10.1146/annurev-neuro-062111-150439.
- Stettler DD, Das A, Bennett J, Gilbert CD.** Lateral connectivity and contextual interactions in macaque primary visual cortex. *Neuron* 36: 739–750, 2002. doi:10.1016/S0896-6273(02)01029-2.
- Suematsu N, Naito T, Sato H.** Relationship between orientation sensitivity and spatiotemporal receptive field structures of neurons in the cat lateral geniculate nucleus. *Neural Netw* 35: 10–20, 2012. doi:10.1016/j.neunet.2012.06.008.
- Vinje WE, Gallant JL.** Sparse coding and decorrelation in primary visual cortex during natural vision. *Science* 287: 1273–1276, 2000. doi:10.1126/science.287.5456.1273.
- Wandell BA, Dumoulin SO, Brewer AA.** Visual field maps in human cortex. *Neuron* 56: 366–383, 2007. doi:10.1016/j.neuron.2007.10.012.
- Xu X, Ichida J, Shostak Y, Bonds AB, Casagrande VA.** Are primate lateral geniculate nucleus (LGN) cells really sensitive to orientation or direction? *Vis Neurosci* 19: 97–108, 2002. doi:10.1017/S0952523802191097.
- Zenger-Landolt B, Heeger DJ.** Response suppression in v1 agrees with psychophysics of surround masking. *J Neurosci* 23: 6884–6893, 2003.
- Zhang X, Zhaoping L, Zhou T, Fang F.** Neural activities in v1 create a bottom-up saliency map. *Neuron* 73: 183–192, 2012. doi:10.1016/j.neuron.2011.10.035.
- Zipser K, Lamme VA, Schiller PH.** Contextual modulation in primary visual cortex. *J Neurosci* 16: 7376–7389, 1996.