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Report

Long-Range, Pattern-Dependent Contextual Effects in Early Human Visual Cortex

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Summary

The standard view of neurons in early visual cortex is that they behave like localized feature detectors [1–7]. Here we demonstrate that processing in early visual areas goes beyond feature detection by showing that neural responses are greater when a feature deviates from its context compared to when it does not deviate from its context. Using psychophysics, fMRI, and electroencephalography methodologies, we measured neural responses to an oriented Gabor ("target") embedded in various visual patterns as defined by the relative orientation of flanking stimuli. We first show using psychophysical contrast adaptation and fMRI that a target that differs from its context results in more neural activity compared to a target that is contained within an alternating sequence, suggesting that neurons in early visual cortex are sensitive to large-scale orientation patterns. Next, we use event-related potentials to show that orientation deviations affect the earliest sensory components of the target response. Finally, we use forced-choice classification of "noise" stimuli to show that we are more likely to "see" orientations that deviate from the context. Our results suggest that early visual cortex is sensitive to global patterns in images in a way that is markedly different from the predictions of standard models of cortical visual processing.

Results

In separate experiments, we measured neural responses using psychophysical contrast adaptation, human fMRI, and event-related potentials (ERPs) to an oriented Gabor stimulus ("target") embedded in various visual patterns as defined by the relative orientation of flanking stimuli. Specifically, we varied whether a central target deviated from its context by changing the orientation of distant gratings while leaving the immediately neighboring flankers unchanged. For example, we hypothesized that the neural response to a vertically oriented target grating would be greater when it deviated from the orientation of its flankers (horizontal flankers, HHVHH) compared to when it was grouped into an alternating sequence of orientations (VHVHV). Keeping the local orientation configuration around the target the same across conditions (e.g., HVH) eliminates effects of simple spatial summation [8–10].

Contrast Adaptation: Deviations from the Context Result in More Adaptation

Our first experiment used psychophysical contrast adaptation to infer the magnitude of the neural response in early visual cortex to the target stimulus [11–13]. To quantify adaptation strength, we calculated the ratio of each observer's contrast detection threshold for a target before and after adaptation. Our assumption is that more adaptation—as indexed by an increase in postadaptation detection thresholds—reflects stronger neural activity in response to the adapting stimulus [11, 14–21] (see also Figure S1A available online). Observers were initially adapted to a stimulus for 30 s before performing a two-interval forced choice detection task. A 5 s top-up adaptation period was inserted between trials to maintain stable adaptation (see Figure S1B and Supplemental Experimental Procedures for detail).

Using a vertically oriented target (V), we found more adaptation with orthogonal, horizontally oriented local flankers (HVH, "orthogonal" condition) compared to vertically oriented local flankers (VVV, three-element "same" condition) [paired two-tailed t test, $t(6) = 6.15$, $p < 0.001$; Figure 1A]. In an additional experiment, we found that the horizontal and vertical flankers alone (no stimulus in the target position) did not produce any adaptation, indicating that differences in adaptation observed between the same and orthogonal condition were due to differences in the orientation relationship between the target and flankers and not due to differences in the flankers themselves (Figure S1A). Larger adaptation to a target with orthogonally oriented flankers is consistent with electrophysiology studies showing larger neural responses in V1 to a stimulus when it is surrounded by orthogonal as compared to iso-oriented stimuli [9, 22, 23]. One possible interpretation of this result is that neurons respond more strongly to stimuli that deviate from the context. However, because this condition also manipulates the local orientation arrangement of the target and flankers, this result in isolation can also be explained through local orientation-selective spatial summation or normalization [8–10].

We then added distant flankers to the original three-element stimuli to create five-element stimuli. This allowed us to manipulate whether the target deviated from the context without changing the local (the target and its immediate neighbors) feature arrangement. Adding distant vertical flankers to the three-element "same" condition, generating a five-element same condition (VVVVV), did not change the amount of adaptation [$t(6) = 1.23$, $p = 0.26$], demonstrating that additional vertical flankers do not necessarily alter responses to the target. Importantly, we observed a significant difference in our critical condition: adaptation to the three-element orthogonal condition (HVH) was significantly reduced when distant vertical flankers were added, producing a five-element "alternating" condition (VHVHV) [$t(6) = 4.25$, $p = 0.005$], presumably because the target does not deviate from—and is grouped into—the alternating pattern induced by the flankers. As a further test, we directly compared the amount of adaptation between the alternating VHVHV condition and the orthogonal HHVHH condition. Consistent with our hypothesis, the amount of adaptation was significantly less in the alternating condition (see Figure S1C).

We observed the same results for horizontally (Figure 1B) and obliquely (Figure 1C) oriented targets. In all cases, the three-element orthogonal condition resulted in more

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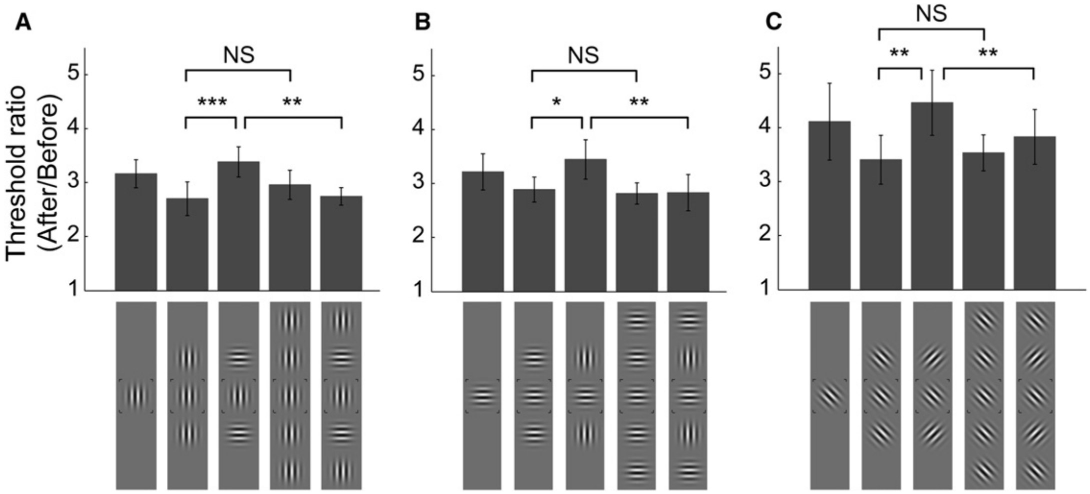

Figure 1. Adaptation Experiment

Threshold ratio—calculated as the contrast threshold after adaptation divided by the contrast threshold before adaptation—of each target orientation in five conditions. The threshold ratio of the vertical target, the horizontal target, and the oblique target is shown in (A), (B), and (C), respectively. *p < 0.05; **p < 0.01; ***p < 0.001; NS, not significant. Error bars are the SEM across observers. See also Figure S1.

adaptation than the three-element same condition [t(6) = 2.80, p = 0.03 for horizontal target; t(6) = 3.95, p < 0.01 for oblique target]. Also in all cases, the three-element same condition did not differ from the five-element same condition [t(6) = 0.70, p = 0.51 for horizontal target; t(6) = 0.46, p = 0.66 for oblique target]. Critically, in all cases, adding distant flankers to the three-element orthogonal condition to create a five-element alternating sequence significantly reduced the amount of adaptation [t(6) = 4.09, p < 0.01 for horizontal target; t(6) = 3.76, p < 0.01 for oblique target]. Overall, these results indicate that distant flankers that make the target part of an alternating sequence reduce neural responses in early human visual cortex.

fMRI: Deviations from the Context Result in Larger Responses

Given these initial behavioral results using adaptation, our expectation was that the fMRI response to the target within early visual cortex would show a similar dependence on whether the target was grouped into or deviated from the pattern of orientations induced by the contextual elements. We measured the fMRI signal in early visual cortex (areas V1, V2, and V3) in response to the target under similar orientation configurations. The patterns were simultaneously presented in both the left and right visual field and positioned so that the targets were in the upper visual quadrants.

Localizer scans of Gaussian windowed counterphase-flickering checkerboards were used to isolate the cortical region in each visual area that represents the target position. These localizer scans contained three conditions: target position, flanker-1 positions, and flanker-2 positions (Figure S2A) intermixed with blank screen fixation in a block design. Target regions of interest (ROIs) were defined as those regions with a larger fMRI response to the target position than the flanker-1 position (see Figure S2B for the spatial specificity of the target ROI).

We then measured the fMRI response in the target ROI to three different five-element stimulus conditions: target matching all flankers ("same" [VVVVV or HH**H**HH]), target orthogonal to all flankers ("orthogonal" [VVHVV or HH**V**HH]), and target part of an alternating sequence ("alternating" [VHVHV or HV**H**VH]). Importantly, the local configuration between the target and the flankers is the same in the orthogonal and alternating conditions (V**H**V or H**V**H)—only the orientation of the distant flankers varies. Conditions were presented in a block design that switched between the three stimulus conditions (same, orthogonal, and alternating; Figure 2A) intermixed with blank-screen fixation periods. Vertical and horizontal targets were presented in separate scans. The flankers were continuously present and flickered in square-wave counterphase at 0.5 Hz to remove unwanted perceptual fading effects. Targets were flashed on (250 ms) and off (250 ms) repeatedly during the block to drive neural responses. To maintain an equivalent attentional state across all conditions, participants performed a demanding central fixation task that required detecting brief luminance changes in the fixation mark (see Supplemental Experimental Procedures for performance data).

There was no main effect or interaction between horizontal and vertical target conditions, so their responses are averaged. In all three visual areas, there was a significantly larger response for the orthogonal (HH**V**HH or VV**H**VV) than the same condition [HH**H**HH or VVVVV, paired two-tailed t tests: V1, t(5) = 2.75, p = 0.04; V2, t(5) = 3.41, p = 0.02; V3, t(5) = 5.37, p = 0.003; Figure 2B]. In the critical comparison we saw, as expected, a greater response to the target in the orthogonal condition (VVHVV or HH**V**HH) than for the alternating condition (VHVHV or HV**H**VH) in both V2 [t(5) = 2.87, p = 0.035] and V3 [t(5) = 3.80, p = 0.01]. In V1, the reduction in response was similar but did not reach statistical significance [t(5) = 2.29, p = 0.07]. A further analysis confirmed that the effects were confined to the target ROI (Figures S2C and S2D). Overall, our results show that the fMRI response across early visual cortex is affected not only by the specific local orientation relationship between the target and immediately adjacent flankers but also by whether or not the target is part of an alternating sequence.

Event-Related Potentials: Deviations from the Context Affect Early Components

Our assumption is that the pattern-related effects we have observed are the result of a dynamic feedback process

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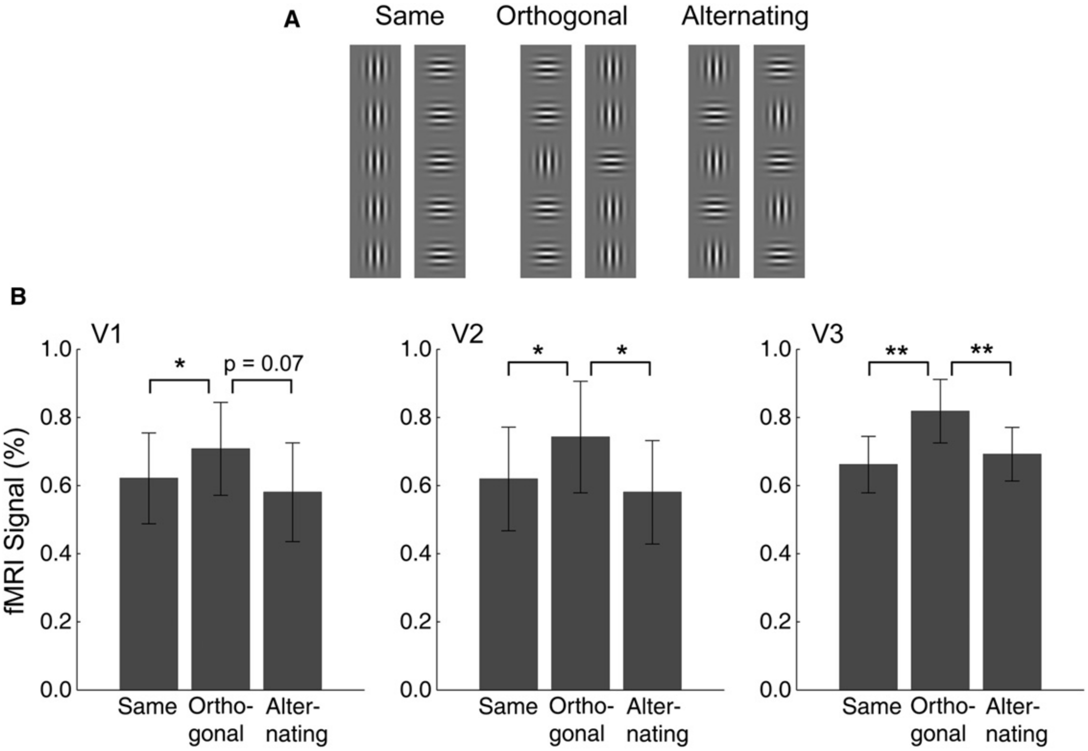

Figure 2. fMRI Experiment

(A) The stimulus conditions used in the main fMRI experiment.

(B) Percent signal change from blank fixation in the target region of interest for each of the three stimulus conditions in V1, V2, and V3. $*p < 0.05$; $**p < 0.01$. Error bars are the SEM across observers.

See also Figure S2.

between early visual areas with small receptive fields representing the individual components of the stimuli and higher visual areas with large receptive fields encompassing the entire pattern. If our pattern-related effects are indeed due to such a feedback process, then we can make predictions about their expected time course, and specifically how these effects will depend upon the relative timing of flanker and target onset. In particular, our prediction is that if the flankers precede the onset of the target by a sufficient length of time, the putative feedback process is likely to be in place and stabilized before the onset of the target. Consequently, the differential response between alternating and same conditions as compared to the orthogonal conditions should appear early in the neural response to the target.

To test this prediction, we performed an ERP experiment using similar stimulus configurations as our previous experiments. The flankers were presented first to ensure that the hypothesized feedback processes induced by the flankers could be in place at the time of target processing (see Supplemental Experimental Procedures). The first prominent ERP component that was observed in response to the target was a positive deflection that peaked at approximately 150 ms (P1). Previous research has suggested that the P1 originates from early extrastriate visual areas [24, 25]. The C1 component—which is believed to originate in V1 [24, 25]—was not observed in our data. The scalp distribution of the P1 was confined to the occipital pole (see Figure S3). To characterize the magnitude of the P1, we averaged signals from the six electrodes around the occipital pole (Oz, O1, O2, POz, PO3, and PO4). We calculated the magnitude of the P1 as the average amplitude between 130 ms and 170 ms. A repeated-measures analysis of variance showed no significant effect of orientation [$F(1,13) = 1.23$, $p = 0.29$] or interaction [$F(2,26) = 0.49$, $p = 0.62$], so the data from the two target orientations were collapsed for further analysis. Figure 3 shows the average waveforms and P1 amplitudes for each flanker conditions. There was a significant effect of flanker conditions [$F(2,26) = 9.46$, $p < 0.001$], and planned contrasts showed that the P1 amplitude was greater for the orthogonal condition compared to same [$F(1,13) = 15.08$, $p = 0.002$] and alternating conditions [$F(1,13) = 9.11$, $p = 0.01$]. These results indicate that when the flankers precede the presentation of the target, the initial feedforward processing of the target is affected by whether the target is grouped into or deviates from the contextual elements.

Classifying Noise Images: Biased Responses toward Deviations from the Context

Across three separate methodologies (psychophysics, fMRI, and ERP), we observed larger neural responses to the target when it deviated from the context. An important question is whether this neural modulation has direct perceptual consequences. We hypothesized that when asked to report whether a noise target containing no specific orientation information was horizontal or vertical, observers would be more likely to "see" the orientation that deviates from the context. In other words, we expected that the influence of the flankers would result in orientation-specific modulation of the noise stimulus

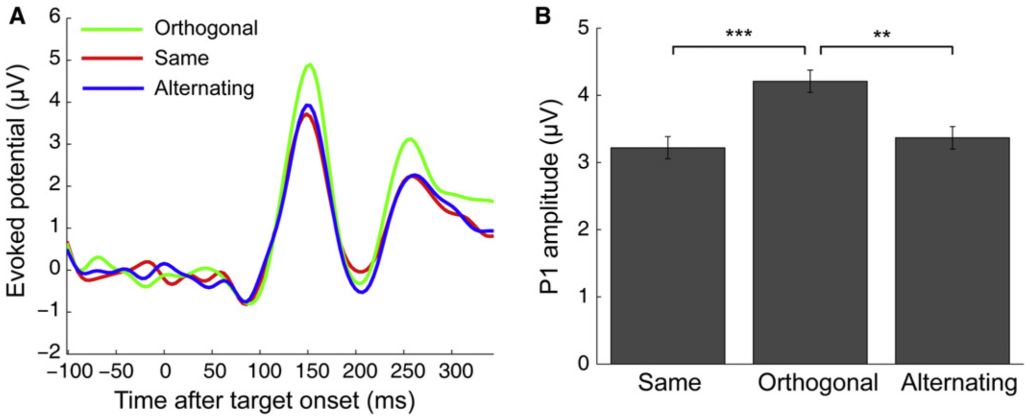

Figure 3. ERP Experiment

(A) The averaged ERP waveforms across observers for the three stimulus conditions: same (red), orthogonal (green), and alternating (blue). The ERPs were the averaged evoked potentials of the six electrodes (Oz, O1, O2, POz, PO3, and PO4).

(B) The P1 amplitudes for three stimulus conditions. The P1 amplitudes of each electrode were measured by averaging the amplitude within the temporal window of 130–170 ms after the target onset. P1 amplitudes of each electrode were then averaged and used for the statistical analysis. **p = 0.01; ***p < 0.01. Error bars are the SEM across observers.

See also Figure S3.

to bias perception away from orientations contained in the contextual elements. Such results would be consistent with a model that subtracts or inhibits context-matching orientations in the noise target [26].

Observers were asked to classify briefly presented targets as either horizontal or vertical. There were three target conditions: noise-only (30% luminance contrast), noise + 8% contrast orientated Gabor (either horizontally or vertically oriented), and noise + 24% contrast oriented Gabor (Figure 4A). Responses to the noise-only conditions were our primary interest—the noise + 8% and noise + 24% trials were used to maintain observer motivation and to assess individual performance in the task (see Figure S4 for performance data). A noise target (N) could be displayed within one of five flanker conditions: “single” (no flankers), “vertical” (VVNVV), “horizontal” (HHNHH), and “alternating” (VHNHV and HVNVH). The single, noise-only condition was used to measure any baseline bias toward vertical or horizontal responses. On trials containing flankers, the flankers appeared first, followed by a random interstimulus interval selected from a random distribution of 1–2 s, and then the target was displayed for 150 ms along with the flankers. The flankers were presented first to ensure that the hypothesized feedback processes induced by the flankers could be in place at the time of the perceptual judgment. We quantified each observer’s response bias toward “vertical” responses by subtracting the proportion of vertical responses for the single condition from vertical responses in each flanker condition: a positive value indicates that the presence of flanking stimuli biased observers toward more “vertical” responses.

We found that the orientation of flanking stimuli significantly biased the perceived orientation of noise stimuli. We saw a response bias toward “horizontal” in the vertical (VVNVV) condition [one-sample two-tailed t tests, mean = −9.96%, t(11) = 4.24, p = 0.0014; Figure 4B] and a bias toward “vertical” in the horizontal (HHNHH) condition [mean = 6.25%, t(11) = 3.37, p = 0.0062]. This indicates that a noise stimulus is “seen” to be biased toward the orientation orthogonal to the flanking stimulus. In addition, even though the local configurations were equivalent, changing the distant flankers eliminated the response bias [t(11) = 1.29, p = 0.22 in HVNVH condition and t(11) = 0.10, p = 0.34 in VHNHV condition]. Pairwise comparisons also confirmed the effect of distant flankers [t(11) = 2.37, p = 0.04, VVNVV versus HVNVH; t(11) = 2.50, p = 0.03, HHNHH versus VHNHV] on the perceptual decision of the central noise image within global patterns. Overall, our results show that perceptions of the target are biased toward orientations that deviate from the surrounding context.

Discussion

The standard model of information processing in early visual cortex is that neurons behave like localized, linear, bandpass filters that are optimized to detect specific features in restricted regions of an image [1–7]. However, inconsistent with the standard model, it is well known that responses of V1 neurons to a stimulus inside the classical receptive field (CRF) can be modulated by stimuli presented outside the CRF [27–30]. These findings have led to revisions of the standard model that include various forms of divisive normalization from neighboring neurons [31–33], and, to a first approximation, these revised models can account for a wide variety of contextual surround effects [8–10]. Importantly, normalization models still act like localized feature detectors but offer a mechanism for nonlinear gain control.

However, the view that neurons in early visual cortex are localized feature detectors has been challenged in recent years [34, 35], and recent studies have pointed to a potential role of early visual areas in processing high-level, “global” attributes of an image. For example, it has been suggested that early visual areas may be modulated by processes such as perceptual pop-out [22, 23, 36, 37], figure-ground segmentation [38, 39], and contour integration [40–43]. However, many of the apparently complex contextual effects seen in early visual areas can be accounted for through simple, local spatial summation and normalization processes [8]. In addition, many of the studies that have examined global, perceptually based explanations for surround effects have confounded changes

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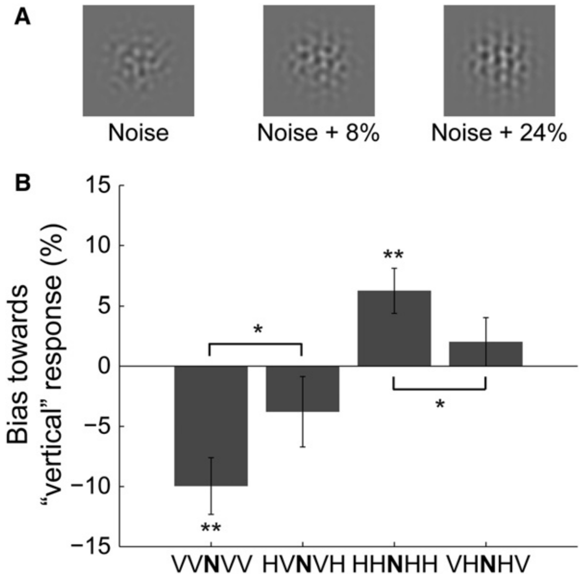

Figure 4. Noise Classification Experiment

(A) The left image shows an example of the noise-only image. The middle and right images show examples of the combination of noise + orientation images (8% and 24%, respectively). Only examples of the addition of vertical orientation are shown.

(B) The y axis represents the response bias toward "vertical" orientation to noise-only images with different flanker configurations as compared to the single condition (noise-only without flankers). The x axis represents context conditions: V, vertical orientation; H, horizontal orientation; N, the noise image. *$p < 0.05$; **$p < 0.01$. Error bars are the SEM across observers.

See also Figure S4.

in local stimulation in V1 and perception. For example, studies that have examined perceptual pop-out [22, 23, 36, 37] have changed the orientation relationship between a target and immediately adjacent flankers. Similarly, contour integration has been investigated by varying the distance between a target and collinear flankers [41, 42]. In both instances, it is not possible to determine whether modulations of neural activity are due to changes in the stimulus configuration affecting low-level summation and normalization processes [8, 9] or are due to changes in global attributes of the image, or both.

Our stimuli eliminated the confound between the local stimulus arrangement and global attributes of an image. The addition of the second flankers allowed us to maintain the same local stimulus arrangement (target plus immediately adjacent flankers) while changing whether the target was grouped with or deviated from the orientation pattern of the flankers. Our results from different methodologies—psychophysics, fMRI, and ERP—clearly show that the neural response to the target is affected by global attributes of the image: when the target could be grouped with the flankers, neural responses were smaller compared to when it deviated from the flankers. We consider this to be a global process because to recognize whether the central target belongs to or deviates from the flankers necessarily means that its orientation relationship to all other features in the image is analyzed. This is a novel finding that appears to contradict standard models of visual processing that emphasize the role of early visual areas in localized feature detection [1–7].

Revisions of the standard model designed to account for nonlinear neural activity in V1 can explain some types of contextual effects such as surround suppression. Although many of these models are not orientation specific, there do exist versions of the standard model that have been proposed to account for orientation-specific surround effects between a target and immediately adjacent flankers [8, 9]. Our results are inconsistent with these models (and any natural variant of them). Suppose a model is constructed—based purely on local mechanisms between the receptive field and immediately adjacent surround—that predicts larger responses when flankers are orthogonal (i.e., larger response to the target in a VHV configuration than a HHH configuration). This model would necessarily predict a further enhancement of the central target when distant flankers are added that are orthogonal to the first flankers (HVHVH) because the second distant flankers would enhance the response to the first flankers (because they are orthogonal), which would in turn further enhance the response to the target. Instead, we show that the response to the target is reduced in a HVHVH configuration. Our results show that in addition to the known local normalization processes in early visual cortex, there is also an additional global pattern-based process that is sensitive to orientation patterns across a large spatial scale.

Experimental Procedures

All experiments were carried out in accordance with the regulations of the Institutional Review Board of the University of Washington. See Supplemental Experimental Procedures for details.

Supplemental Information

Supplemental Information includes four figures and Supplemental Experimental Procedures and can be found with this article online at doi:10.1016/j.cub.2012.02.067.

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