

# Contextual effects in human visual cortex depend on surface structure

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**Joo SJ, Murray SO.** Contextual effects in human visual cortex depend on surface structure. *J Neurophysiol* 111: 1783–1791, 2014. First published February 12, 2014; doi:10.1152/jn.00671.2013.—Neural responses in early visual cortex depend on stimulus context. One of the most well-established context-dependent effects is orientation-specific surround suppression: the neural response to a stimulus inside the receptive field of a neuron (“target”) is suppressed when it is surrounded by iso-oriented compared with orthogonal stimuli (“flankers”). Despite the importance of orientation-specific surround suppression in potentially mediating a number of important perceptual effects, including saliency, contour integration, and orientation discrimination, the underlying neural mechanisms remain unknown. The suppressive signal could be inherited from precortical areas as early as the retina and thalamus, arise from local circuits through horizontal connections, or be fed back from higher visual cortex. Here, we show, using two different methodologies, measurements of scalp-recorded event-related potentials (ERPs) and behavioral contrast adaptation aftereffects in humans, that orientation-specific surround suppression is dependent on the surface structure in an image. When the target and flankers can be grouped on the same surface (independent of their distance), orientation-specific surround suppression occurs. When the target and flankers are on different surfaces (independent of their distance), orientation-specific surround suppression does not occur. Our results demonstrate a surprising role of high-level, global processes such as grouping in determining when contextual effects occur in early visual cortex.

contextual modulation; contrast adaptation; early visual cortex; ERP; grouping

IT IS WELL-ESTABLISHED THAT there can be neural suppression in early visual cortex measured at the individual neuron level (Allman et al. 1985; Blakemore and Tobin 1972; Cavanaugh et al. 2002; DeAngelis et al. 1994; Maffei and Fiorentini 1976; Sillito et al. 1995), by human fMRI (Joo et al. 2012; Zenger-Landolt and Heeger 2003), and by human event-related potential (ERP; Haynes et al. 2003; Joo et al. 2012) when surrounding stimuli (“flankers”) match the center (“target”) orientation: orientation-specific surround suppression. Despite the importance of orientation-specific surround suppression in potentially mediating a number of important perceptual effects, including saliency (Kastner et al. 1997; Knierim and Van Essen 1992; Zipser et al. 1996), contour integration (Dobbins et al. 1987; Kapadia et al. 1995), and orientation discrimination (Mareschal et al. 2001), the underlying neural mechanisms remain unknown. For example, the suppressive signal could be inherited from precortical areas as early as the retina (Solomon et al. 2006) and thalamus (Alitto and Usrey 2008), arise from V1 local

circuits through horizontal connections (Adesnik et al. 2012; Kapadia et al. 2000), or be fed back from higher visual cortex (Angelucci et al. 2002; Bair et al. 2003).

However, a number of recent psychophysical findings have shown that high-level perceptual grouping can influence basic visual detection and discrimination performance in stimulus configurations that resemble those used in orientation-specific surround suppression experiments (Huang et al. 2012; Joo et al. 2012; Manassi et al. 2012; Mareschal et al. 2001; Sayim et al. 2008). Thus we hypothesized that perceptual grouping would influence orientation-specific surround suppression such that it would occur only when the target and flankers were grouped into a single array. For example, we predicted that stimulus manipulations that isolated the target from the flankers, such as increasing the spatial separation or making the target and flankers appear to be on different surfaces, would eliminate orientation-specific surround suppression. On the other hand, manipulations that grouped the target and flankers into a single array, such as decreasing the spatial separation or making the target and flankers appear to be on the same surface, would promote orientation-specific surround suppression.

Here, we used two different experimental methodologies, behavioral contrast adaptation aftereffect and ERP measurements, to test our grouping hypothesis. We measured the response to a target in stimulus configurations that manipulated distance (near and far) and surface placement (target and flankers on the same vs. different surface). Our results demonstrate that orientation-specific surround suppression in early visual cortex occurs under stimulus conditions that promote grouping of the target and flankers into a single array of elements.

## MATERIALS AND METHODS

### Observers

**Experiment 1 (behavioral contrast adaptation experiments).** All observers had normal or corrected-to-normal vision, and all gave informed, written consent approved by the University of Texas at Austin Institutional Review Board. Five observers, including the first author, voluntarily participated.

**Experiment 2 (ERP experiments).** All observers had normal or corrected-to-normal vision, and all gave informed, written consent approved by the University of Washington Institutional Review Board. Eighteen observers, including the first author, participated in *experiment 2A*. A total of 48 observers participated in *experiments 2B, 2C, and 2D* (16 per experiment). All observers were assigned to only 1 experiment. Except for the first author, all were naïve observers who volunteered for either course credit or monetary compensation (\$20/h).

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### Stimuli and Procedure: Experiment 1

The stimuli were generated using MATLAB Psychtoolbox (Brainard 1997; Pelli 1997) on a Mac Pro computer and displayed on a 17-in. Sony OLED monitor (PVM-1741, 60-Hz refresh rate with a resolution of 1080p and flicker-free mode on). The monitor was linearized using a standard gamma correction procedure. Ten-bit luminance steps were generated using the native ten-bit mode supported by the graphics card (ATI Radeon HD 4870) and Psychtoolbox driver. The viewing distance was 68 cm.

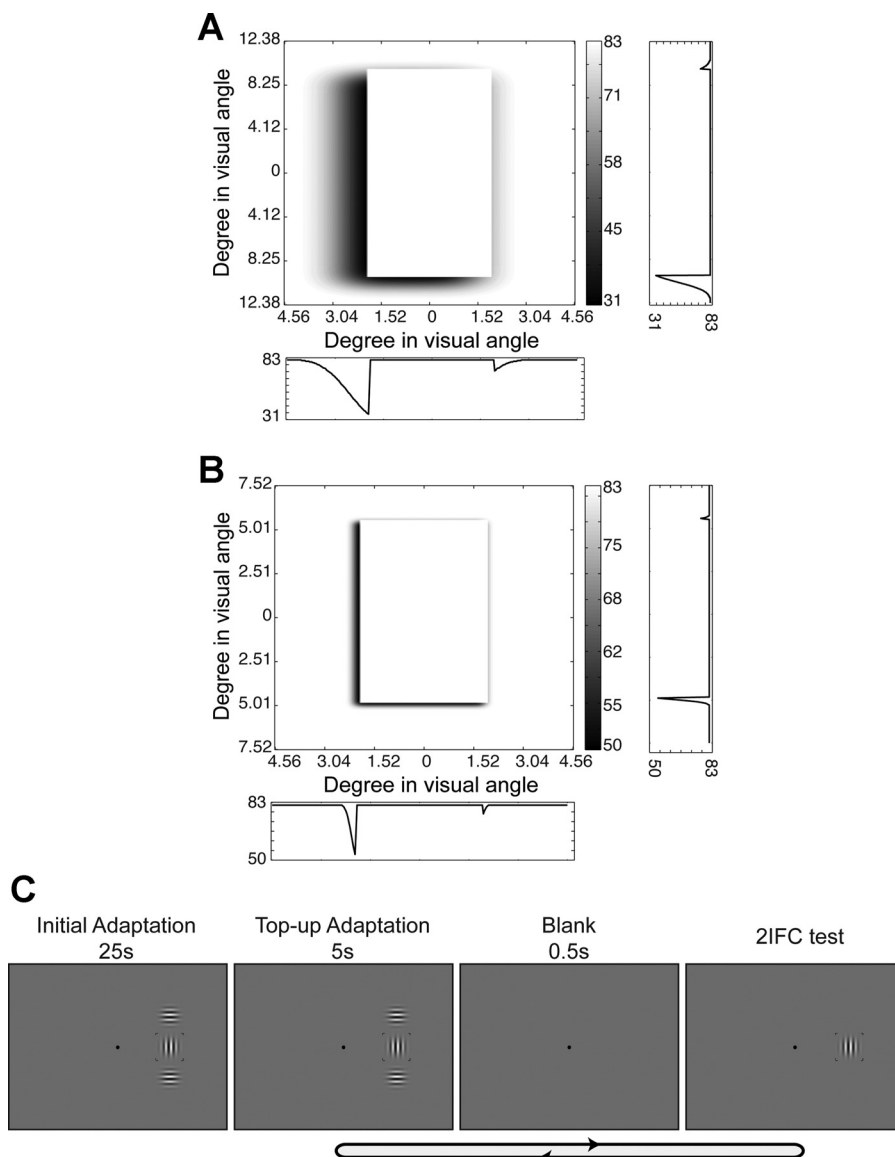
The Gabor patches had an SD of  $0.72^\circ$  and a spatial frequency of two cycles per degree and were 30% contrast. The surface patches were generated using the “drop shadow” function (mode: overlay, opacity: 75%, blur: 0.18 cm) in Adobe Illustrator CS3 (Adobe Systems). We manipulated x- and y-offset parameters in the drop shadow function to minimize the spatial overlap between the target and the shadow in *experiments 1D* and *2D*. Figure 1, *A* and *B*, shows cross-sectional luminance profiles of these stimuli. A fixation point ( $0.48^\circ$  in diameter) was displayed at the center of the display. The target is displaced by  $6^\circ$  horizontally from the fixation point.

Four stimulus configurations were used: 1) in *experiment 1A* (near, no-surface configuration), the flankers were positioned so that the center-center distance of the target and flankers was  $3^\circ$ ; 2) in *experiment 1B* (far, no-surface configuration), the flankers were positioned

so that the center-center distance was  $6^\circ$ ; 3) in *experiment 1C* (far, same-surface configuration), the target and flankers were separated by  $6^\circ$  and appeared on the same rendered surface; and 4) in *experiment 1D* (near, different-surface configuration), the target and flankers were separated by  $3^\circ$  and rendered on different surfaces. In this condition, we adjusted the shadow position and size to prevent overlap between the shadow edge and the target.

To measure the contrast detection threshold for a target, three randomly interleaved, independent QUEST (Watson and Pelli 1983) staircases were used. The detection task was a two-interval, forced-choice (2IFC) task where observers indicated which interval had the target. Each interval (200 ms) was indicated by a high-pitched tone, and there was a gray blank (300 ms) between intervals. Auditory feedback was given for an incorrect response. Each observer participated in 8 sessions (4 experiments  $\times$  2 repetitions). We measured the amount of adaptation with a vertical target orientation embedded in either horizontal-orientation (orthogonal condition) or vertical-orientation (same condition) flankers. At the beginning of each session, each observer's contrast detection threshold of the target was measured using the same 2IFC tasks to define the baseline. A session consisted of two adaptation blocks (same and orthogonal condition),

Fig. 1. The luminance profile of surface stimuli and the procedure of *experiment 1*. *A*: the surface stimuli used in *experiments 1C* and *2C*. *B*: the surface stimuli used in *experiments 1D* and *2D*. *X*- and *y*-axes represent the distance in visual angle from the center of the stimuli. The *insets* represent horizontal and vertical cross-sectional luminance profiles at the center of the stimuli. The gradient bars represent the grayscale luminance values (candelas per square meter) and correspond to the values of *y*-axis in *insets*. *C*: the procedure used in the behavioral contrast adaptation experiments. The “orthogonal” condition is shown. Observers initially adapted to the adapting pattern for 30 s before the 1st trial. A top-up adaptation period was inserted between the trials to maintain the adaptation state. A 0.5-s blank period was inserted between the adaptation period and the trial. During this blank period, the fixation point changed its luminance from black to white to cue the start of the trial. 2IFC test, 2-interval, forced-choice test.



and the order of blocks was counterbalanced across sessions per observer. A 5-min break was inserted between blocks to prevent any carryover effect from the previous block. There were 60 trials (20 trials per staircase) in a block. The last contrast values of 6 staircases (2 repetitions  $\times$  3 staircases) were averaged to estimate an observer's contrast detection threshold for 82% performance. If a staircase did not converge ( $>1$  SD from the mean of the 6 data points), the staircase was discarded. This excluded 10 data points from a total possible of 240 data points across observers.

Adapting stimuli consisted of a target and flankers. Observers were initially adapted for 30 s followed by the first 2IFC task trial. A 5-s top-up adaptation period was inserted between subsequent trials to maintain stable adaptation (Fig. 1C). Stimuli were counterphase-flickered at 2 Hz. A 500-ms gray blank was inserted before each trial began. During this blank period, a black line was displayed next to the fixation point to indicate the beginning of a trial. The target location was always marked during both the adaptation and task periods to remove effects of location uncertainty on the detection task (Petrov et al. 2006). To equate the attentional state across conditions, observers performed a contrast decrement task on the fixation mark during adaptation periods (Bi et al. 2009). The contrast decrement (10%) was displayed for 150 ms, and the onset of the contrast decrement was selected randomly from a uniform distribution between 1 and 1.5 s. To quantify the amount of adaptation, we defined the threshold ratio between detection threshold before and after adaptation.

#### Stimuli and Procedure: Experiment 2

We used the same stimulus parameters and configurations as in *experiment 1* except for the following: 1) the fixation point was placed

3° below from the center of the display; and 2) the target stimuli were displayed in the upper quadrant of both visual fields 3° horizontally and 3° vertically from the fixation point. The center-to-center distance between the stimuli comprising a pattern was 3° in *experiment 2A* (the near, no-surface configuration) and *experiment 2D* (the near, different-surface configuration) and 6° in *experiment 2B* (the far, no-surface configuration) and *experiment 2C* (the far, same-surface configuration). The stimuli were generated and controlled by Presentation (Neurobehavioral Systems) on a personal computer, and they were displayed on a 21-in. cathode-ray tube (CRT) monitor (60-Hz refresh rate). The viewing distance was  $\sim 70$  cm.

Target orientation could be either vertical or horizontal orientation. There were three flanker conditions (single, same, and orthogonal). The flanker orientation varied according to the target orientation (Fig. 2A). The flanker orientation matched the target orientation in the same condition but was orthogonal to the target orientation in the orthogonal condition. A thin circle (0.2°) that matched the size and contrast of Gabor stimuli was displayed in the flanker positions in the single condition to equate the stimulus timing.

Figure 2B shows an example trial. On a given trial, flankers (or flankers and cast shadow in *experiments 2C* and *2D*) appeared before the onset of the target. After a random duration chosen from a uniform distribution between 1 and 2 s, targets were briefly flashed for 100 ms. After the target offset, the flankers remained in the display for 500 ms. The intertrial interval was 3 s. Observers were asked to maintain fixation and to limit eye blinks to the intertrial interval.

One experimental block consisted of 12 trials (2 target orientation conditions  $\times$  3 flanker conditions  $\times$  2 repetitions). The order of trials was randomized within a block. Observers finished 22–51 blocks (264–612 trials). Observers initiated each block after a 5-s break by

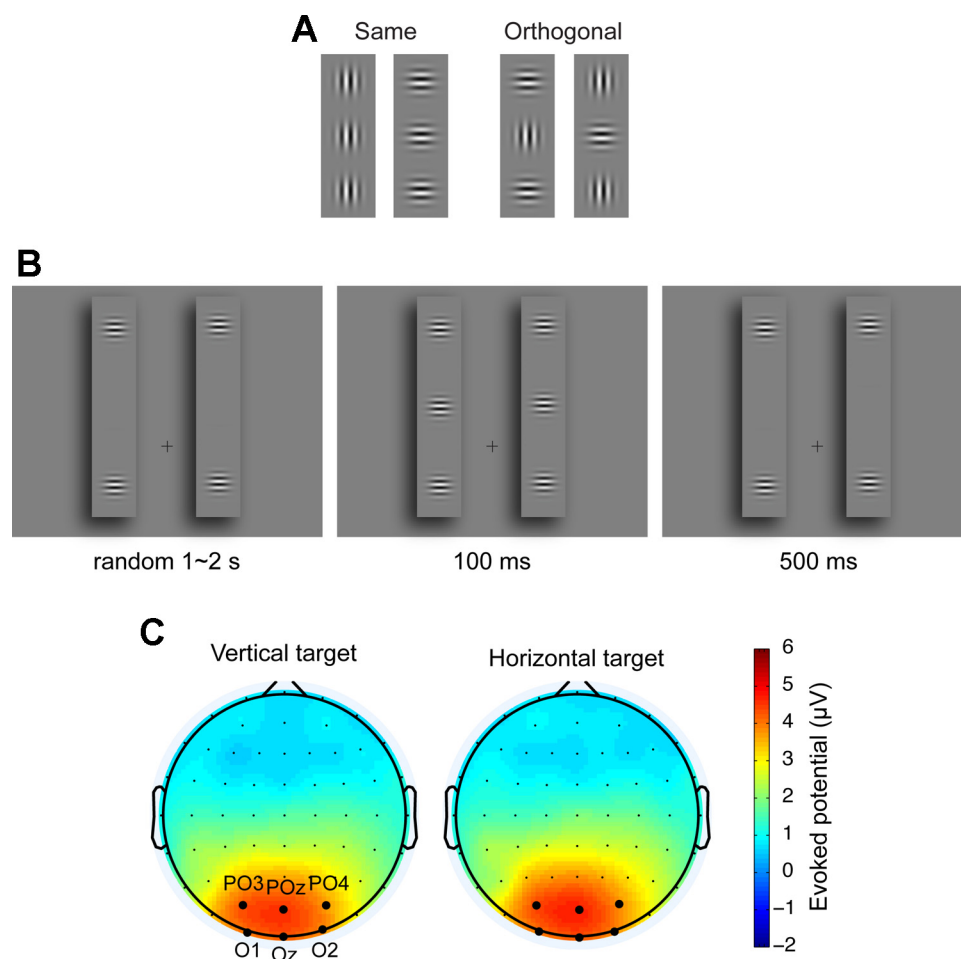


Fig. 2. The general experimental conditions and event-related potential (ERP) experimental procedure. A: the stimulus configuration consisted of 3 Gabor stimuli: a central target with 2 flankers (1 above and 1 below the target). The target orientation could be either vertical or horizontal. Flanker orientation matched the target orientation in the same condition (left) or was orthogonal to the target orientation in the orthogonal condition (right). B: on a given trial, flankers (or flankers and cast shadow in *experiments 2C* and *2D*) appeared before target onset. After a random duration between 1 and 2 s, the target was briefly flashed (100 ms). After target offset, flankers (or flankers and cast shadow) remained in the display for 500 ms to ensure that flanker offset did not contaminate the evoked potential to target onset. C: scalp topographical maps of the evoked potential at 150 ms after target onset referenced to the average of the left and right mastoids for the vertical (left) and horizontal (right) target collapsed across flanker conditions in *experiment 1*. The color bar represents voltage (microvolts). Each dot represents the 64 electrode recording sites. We averaged the waveforms across 6 occipital recording sites depicted by thicker dots to define the ERP signal.



pressing a designated key on the button box. The 1st block served as practice.

### EEG Recording and Data Analysis

EEG waveforms were recorded using BioSemi active Ag-AgCl electrodes from 64 sites. The signals were referenced to the left mastoid during online acquisition and rereferenced to the average of right and left mastoids offline. Vertical electrooculography (EOG) was measured using an electrode placed below the left eye, and horizontal EOG was measured using an electrode placed at the outer canthus of the right eye. The signals were digitized at a sampling rate of 256 Hz.

EEG epochs started 100 ms before the target onset and lasted 400 ms after the target onset. Each waveform was baseline-corrected to the average voltage of the interval  $-100$  to  $0$  ms before the target onset and low-pass filtered at 40 Hz to remove high-frequency noise. Trials with waveforms that had a  $>50$ - $\mu$ V peak-to-peak vertical and that exceeded  $\pm 50$   $\mu$ V on other electrodes were excluded as these were trials deemed to be contaminated with eye blinks or other sources of noise. Data from five observers (*experiment 2A*) and one observer (*experiments 2B, 2C, and 2D*) were discarded due to excessive artifact rejection ( $>50\%$ ). The resulting waveforms were averaged across conditions individually for statistical analyses and then averaged across observers for figures.

P1 amplitude on six electrodes (Oz, O1, O2, POz, PO3, and PO4) was measured by averaging the ERP amplitudes during the time window of 130–170 ms. These electrodes were centered over the maximum of the P1 component (150 ms after target onset) as determined through visual inspection of the scalp topography (Fig. 2C). These individual amplitudes were averaged across six electrodes to represent P1 amplitude. We conducted a repeated-measures ANOVA for the statistical analysis. The data from the single condition was not included in the analysis because the response to the single condition (interaction between an oriented target and circles) was categorically different from the other conditions (interaction between an oriented target and oriented flankers). The single condition was only used to assess any difference between vertical and horizontal targets in the absence of oriented flankers and in the presence of the cast shadows.

## RESULTS

### Experiment 1: Behavioral Contrast Adaptation Experiments

We measured the amount of behavioral contrast adaptation to a vertical target Gabor with horizontal (orthogonal) flankers and vertical (same-orientation) flankers. Psychophysical contrast adaptation aftereffects can be used to infer the magnitude of the neural response in early visual cortex to the target stimulus (Blakemore and Campbell 1969; Bradley et al. 1988; Movshon and Lennie 1979). To quantify adaptation strength, we calculated the ratio of each observer's contrast detection threshold for a target before and after adaptation. The assumption is that more adaptation, as indexed by an increase in postadaptation detection thresholds, reflects stronger neural activity in response to the adapting stimulus (Blake et al. 2006; Blakemore and Campbell 1969; Carandini et al. 1998; Dragoi et al. 2000; Engel 2005; Fang et al. 2005; Kohn and Movshon 2003; Larsson et al. 2006; Priebe et al. 2002). To equate attentional state across conditions, subjects performed a demanding luminance decrement task at fixation. The mean performance on the fixation task was  $90 \pm 7\%$ , and there were no significant performance differences across conditions.

We found adaptation aftereffects suggesting orientation-specific surround suppression only with stimulus configura-

tions that promoted grouping of the target and flankers into a single array (Fig. 3, A–D). First, in *experiment 1A*, we confirmed that the amount of adaptation was modulated by the orientation of nearby ( $3^\circ$  separation) flankers. Specifically, the vertical target surrounded by nearby ( $3^\circ$  separation) vertical flankers resulted in a smaller threshold ratio compared with nearby horizontal flankers (Fig. 3A;  $t_4 = 3.78$ ,  $P = 0.02$ ). This smaller threshold ratio in the same condition compared with the orthogonal condition is consistent with less neural activity to the target and a signature of orientation-specific surround suppression.

After establishing orientation-specific surround suppression using our adaptation protocol, we tested our grouping hypothesis. First, in *experiment 1B*, we simply increased the distance between the target and flankers by doubling the center-to-center distance ( $6^\circ$ ; Fig. 3B) used in *experiment 1A*. Perceptually, with the increased distance, the stimulus now appeared to be three isolated Gabor patches rather than a single array of three Gabor patches following the well-known Gestalt principle of proximity. Thus, because the target and flankers were no longer grouped into a single array, we predicted that orientation-specific surround suppression would be eliminated. Consistent with this prediction, the basic orientation-specific surround suppression effect was not present with distant ( $6^\circ$  separation) flankers (Fig. 3B;  $t_4 = 0.06$ ,  $P = 0.96$ ). However, this finding that increasing the distance between the target and flankers eliminates orientation-specific surround suppression is consistent with a number of potential explanations, ranging from local normalization models (Cavanaugh et al. 2002; Shapley 2004) to our high-level, grouping hypothesis.

To distinguish between these alternatives, in *experiment 2C* we used the distant-flanker configuration of *experiment 2B* but made the target and flankers appear to be grouped on a common surface that was distinct from the background. This was done by adding a small cast shadow in the region around the stimuli to create a surface that appeared to be at a closer depth plane than the background (Fig. 3C). Any model of orientation-specific surround suppression that emphasized local orientation interactions between the target and flankers would again predict no orientation-specific surround suppression, as in *experiment 1B*. However, based on our grouping hypothesis, we expected to observe orientation-specific surround suppression because the target and flankers were now grouped on a common surface separate from the background. Consistent with the grouping hypothesis, when the distant-flanker configuration was displayed on a cast-shadow surface, orientation-specific surround suppression was restored: the threshold ratio was smaller in the same condition compared with the orthogonal condition (Fig. 3C;  $t_4 = 3.40$ ,  $P = 0.03$ ).

If surface representations are indeed important for determining when orientation-specific surround suppression effects occur, we predicted that moving the target and flankers to different surfaces would eliminate orientation-specific surround suppression even with spatial parameters that would otherwise result in strong orientation-specific surround suppression. In *experiment 1D*, we used the same spatial parameters of *experiment 1A*, where we observed strong orientation-specific surround suppression but moved the flankers to different surfaces than the target (Fig. 3D). Although the flankers were displayed in the near proximity of the target, orientation-specific surround suppression was eliminated: there was no

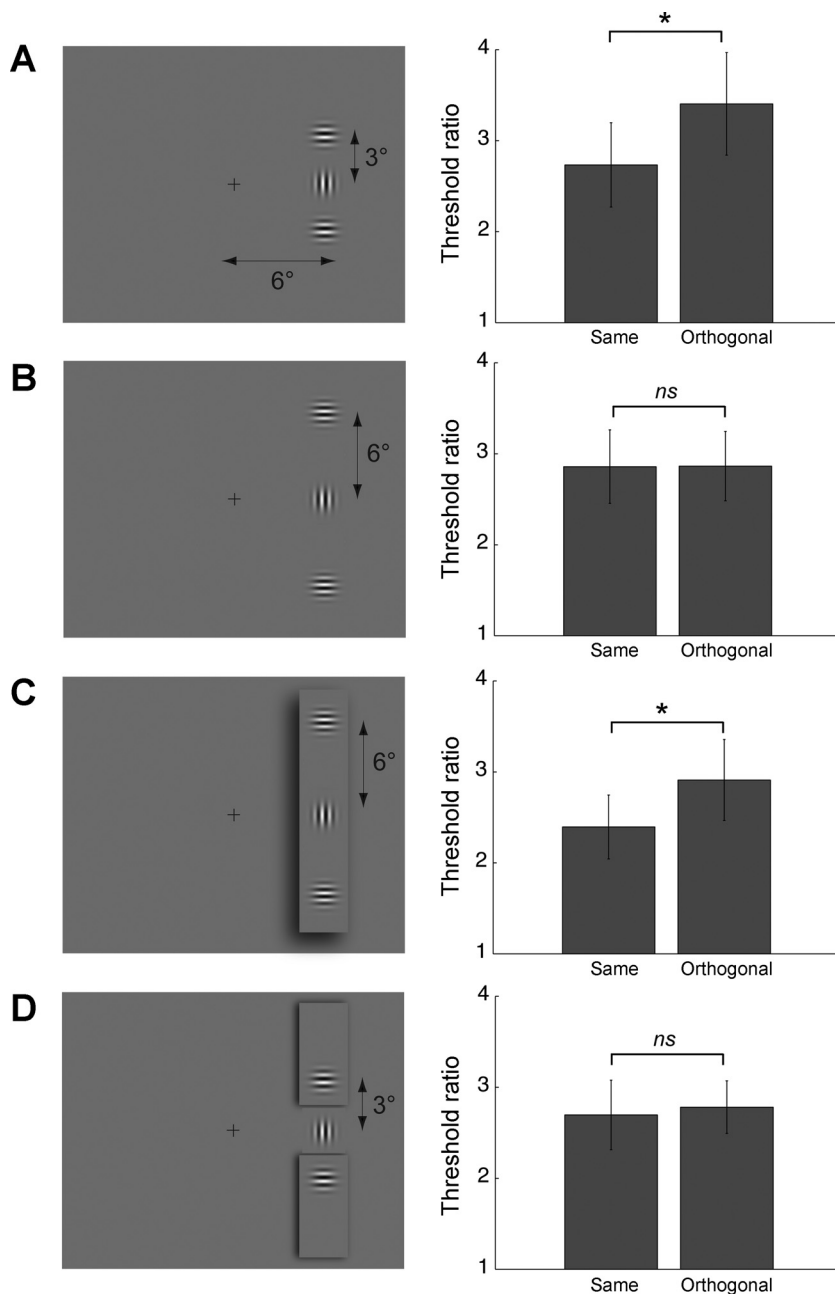


Fig. 3. Stimulus configurations and the threshold ratio in each stimulus configuration in *experiment 1*. *A*: near flankers. The center-to-center distance between the target and flankers was 3°, and the target was displaced by 6° horizontally from the fixation point. *B*: far flankers. The center-to-center distance between the target and flankers was 6°. *C*: far flankers on the same surface as the target. The center-to-center distance between the target and flankers was 6°. *D*: near flankers on a different surface from the target. The center-to-center distance between the target and flankers was 3°. \* $P < 0.05$ ; ns, not significant. Error bars represent SE across observers.

difference in the amount of adaptation between the same and orthogonal condition (Fig. 3D;  $t_4 = 0.40$ ,  $P = 0.71$ ).

These findings suggest that low-level, long-term contrast adaptation can be modulated by high-level image structure while attention was controlled. In the next series of experiments, we used an ERP technique to measure the visual evoked potential (VEP) to the onset of the target to characterize the time course of the orientation-specific surround suppression in early visual cortex. To generalize more our findings, we used two target orientations (vertical and horizontal).

#### Experiment 2: ERP Experiments

We measured the ERP response to an oriented Gabor (target) with flankers above and below the target. Critically, to ensure that the flanker (and cast shadow) onset and offset did not contaminate the evoked potential to the target, flankers (and

cast shadows) were displayed before target onset and remained in the display until after target offset (Fig. 2B and MATERIALS AND METHODS). The target was briefly flashed for 100 ms. The duration between flanker onset and target onset was randomized between 1 and 2 s. This duration was long enough such that the visually evoked potentials to the flankers diminished to baseline levels before target onset, thus ensuring that we measured the ERP response to only the target stimulus. The target could be either vertically or horizontally oriented and be displayed with flankers that matched the target orientation (same condition; Fig. 2A, left) or flankers that were orthogonally oriented compared with the target (orthogonal condition; Fig. 2A, right).

In *experiment 2A*, we established the basic orientation-specific surround suppression effect in the ERP response using stimulus configurations where the target was surrounded by

nearby flankers (Fig. 4A; target-flanker distance =  $3^\circ$ ). We used the amplitude of the earliest component of our data (P1; 150 ms after target onset) to index neural activity in early visual cortex (Clark et al. 2004; Joo et al. 2012). The amplitude of the P1 was defined by averaging ERP amplitudes during the time window between 130 and 170 ms after target onset on six occipital electrodes (Oz, O1, O2, POz, PO3, and PO4). These electrodes were centered over the maximum of the ERP am-

plitudes at 150 ms after target onset as determined through visual inspection of the scalp topography (Fig. 2C).

A repeated-measures ANOVA revealed that there was no significant effect of target orientation ( $F_{1,12} = 0.016$ ,  $P = 0.901$ ) or interaction between target orientation and flanker condition ( $F_{1,12} = 0.002$ ,  $P = 0.964$ ). We found a similar pattern of results, no significant effect of target orientation or interaction, across all of our ERP experiments. However, P1

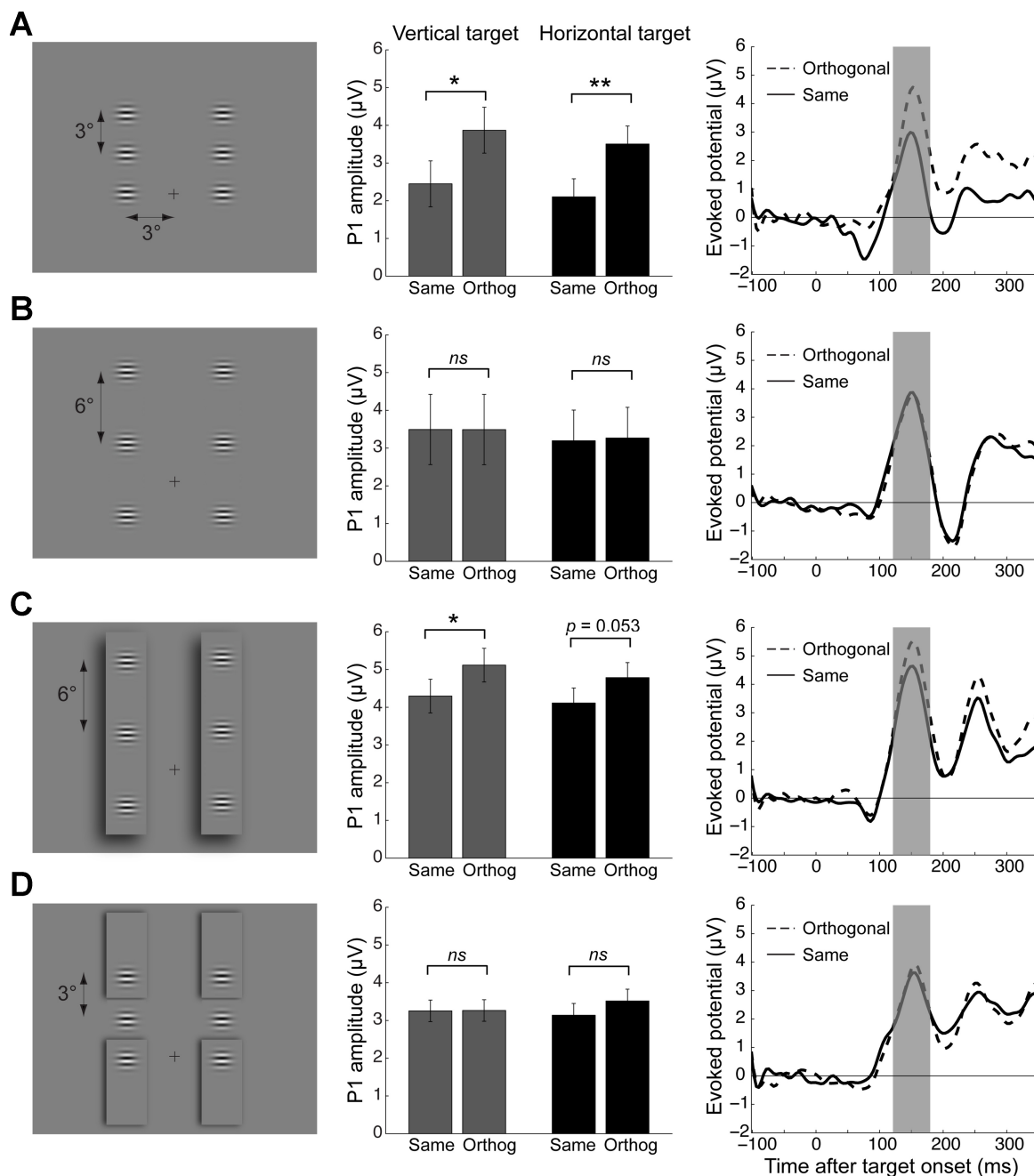


Fig. 4. The stimulus configurations and results of ERP experiments. The *left* column shows the stimulus configurations in each experiment. The *middle* column shows P1 amplitude measured in each condition for each target orientation. Gray and black bars represent P1 amplitudes for the vertical target and horizontal target, respectively. Orthog, orthogonal. The *right* column shows the ERP waveforms averaged across target orientations (vertical and horizontal). Dashed and solid lines represent the ERPs of the orthogonal and same condition, respectively. The shaded areas indicate the P1 amplitude measurement windows. A: *experiment 2A*: near flankers. The center-to-center distance between the target and flankers was  $3^\circ$ . B: *experiment 2B*: far flankers. The center-to-center distance between the target and flankers was  $6^\circ$ . C: *experiment 2C*: far flankers on the same surface as the target. The center-to-center distance between the target and flankers was  $6^\circ$ . D: *experiment 2D*: near flankers on a different surface from the target. The center-to-center distance between the target and flankers was  $3^\circ$ . \* $P < 0.05$ ; \*\* $P < 0.01$ . Error bars represent within-subject 95% confidence interval (Loftus and Masson 1994).

amplitude was suppressed in the same condition compared with the orthogonal condition ( $F_{1,12} = 16.787$ ,  $P = 0.001$ ), consistent with orientation-specific surround suppression. Separate analyses for each target orientation confirmed that the trend was similar for both vertical ( $F_{1,12} = 7.654$ ,  $P = 0.017$ ) and horizontal ( $F_{1,12} = 13.455$ ,  $P = 0.003$ ) targets (Fig. 4A).

After establishing orientation-specific surround suppression in the P1 amplitude of our ERP data, we tested our grouping hypothesis using the same stimulus manipulations used in *experiment 1*. First, in *experiment 2B*, we increased the distance between the target and flankers by doubling the center-to-center distance ( $6^\circ$ ; Fig. 4B) used in *experiment 2A*. We found no difference in P1 amplitude between the same and orthogonal conditions for both target orientations (Fig. 4B; vertical,  $F_{1,14} = 0.013$ ,  $P = 0.911$ ; horizontal,  $F_{1,14} = 0.081$ ,  $P = 0.781$ ).

In *experiment 2C*, we used the distant-flanker configuration of *experiment 2B* but made the target and flankers appear to be grouped on a common surface that was distinct from the background. Note that both the flankers and the cast-shadow surface appeared before the onset of the target using the same timing structure as *experiments 2A* and *2B*. Again, consistent with our grouping hypothesis, P1 amplitude was suppressed in the same condition compared with the orthogonal condition (Fig. 4C; vertical target,  $F_{1,14} = 5.223$ ,  $P = 0.038$ ; horizontal target,  $F_{1,14} = 4.461$ ,  $P = 0.053$ ).

In *experiment 2D*, we used the same spatial parameters of *experiment 2A*, where we observed strong orientation-specific surround suppression but moved the flankers to different surfaces from the target (Fig. 4D). Although the same distance manipulation resulted in strong orientation-specific surround suppression in *experiment 2A* (Fig. 4A), we found no evidence of orientation-specific surround suppression in the P1 amplitude (Fig. 4D; vertical target,  $F_{1,14} = 0.002$ ,  $P = 0.965$ ; horizontal target,  $F_{1,14} = 2.143$ ,  $P = 0.165$ ) when the target and flankers were placed on different surfaces.

Possible low-level, stimulus-based effects of the rendered surfaces on the target response were minimized in *experiments 2C* and *2D* by having the surfaces appear first, before target onset, and remain until well after target offset. Note that we measured the visually evoked potentials to target onset after the visually evoked potentials to flanker/shadow onset diminished. However, there are still important stimulus-based differences to consider. In particular, there are horizontal edges in the proximity of the target (introduced by the surface) in *experiment 2D* that do not exist in the other conditions. Can the lack of surround suppression be explained by low-level stimulus-based differences? If the horizontal surface edge behaved like a flanker, it would have caused less suppression with a vertical target and more suppression with a horizontal target. However, no such differences were observed in our data (see Fig. 4D, *middle*, and compare the responses to the vertical target vs. the horizontal target in the each condition).

To rule out possible low-level effects of the surfaces on the target response further, we examined the single (target-only) condition in *experiment 2D*: when the target was presented without oriented flankers. If the surface was somehow interacting with the target stimulus in a low-level manner, a difference between the vertical and horizontal targets would be expected. Specifically, horizontal surface edges near the target in *experiment 2D* should have resulted in little or no surround

suppression for the vertical target if they acted like horizontally oriented flankers (e.g., like the vertical-target orthogonal condition in *experiment 2A*). On the other hand, horizontal surface edges should have resulted in a suppressed response to the horizontal target (e.g., like the horizontal-target same condition in *experiment 2A*). However, we found no significant difference between the vertical and horizontal targets when presented alone with the surfaces *experiment 2D* (Fig. 5;  $t_{14} = 0.12$ ,  $P = 0.91$ ), further suggesting that the surfaces do not have a simple, low-level effect on the visually evoked potentials to target onset.

We have demonstrated that grouping between the target and flankers was required for orientation-specific surround suppression in early visual cortex by showing that orientation-specific surround suppression occurred in experiments where the target could be grouped with the flankers (*experiments 2A* and *2C*) and that orientation-specific surround suppression did not occur in experiments where the target did not group with the flankers (*experiments 2B* and *2D*). To strengthen our claim, we tested whether there were significant interactions between stimulus conditions (same/orthogonal, a within-subjects factor) and surface manipulations for a given target-flanker distance (grouped/ungrouped, a between-subjects factor). In both the near flanker condition (*experiments 2A* and *2D*) and far flanker condition (*experiment 2B* and *2C*), there was a significant interaction between the stimulus condition and the surface manipulation ( $F_{1,26} = 9.454$ ,  $P = 0.005$  and  $F_{1,28} = 5.596$ ,  $P = 0.025$ , respectively). These results suggest that our findings are not simply due to different statistical power in the individual experiments.

## DISCUSSION

Our results demonstrate that grouping, specifically mediated by the surface placement of the target and flankers, modulates orientation-specific surround suppression. We assume that the surface structure of the images in our experiments is represented in higher stages of the visual system that have neurons with sufficiently large receptive fields and complex tuning properties sensitive to relative depth. This may include regions such as the lateral occipital complex (Kourtzi and Kanwisher 2001; Murray et al. 2002, 2003). Thus it is possible that feedback from these regions modulates orientation-specific surround suppression in early visual areas (e.g., V2–V3). However, the signal that we measured in response to the target, the P1 component, is believed to represent early, feedforward

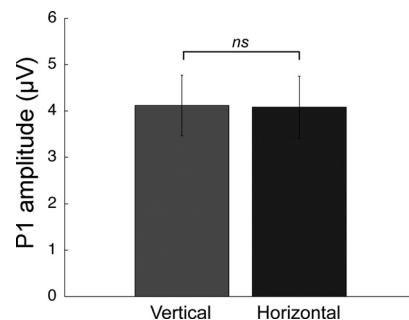


Fig. 5. The response to the single condition in *experiment 2D*. The gray and black bars represent P1 amplitude for the vertical and horizontal targets, respectively. Error bars represent within-subject 95% confidence interval (Loftus and Masson 1994).



neural activity (Luck et al. 2000). Indeed, the onset of the P1 in our experiments (approximately 90–95 ms), although likely too late to originate from V1, closely corresponds to the median onset time (~85 ms) of single unit responses in V2 of the macaque monkey (Schmolesky et al. 1998). Thus how do we reconcile the potential role of feedback with the modulation of an early feedforward neural signal? It is important to emphasize the relative timing of our stimulus presentation. The flankers and the cast-shadow surfaces (in *experiments 2C* and *2D*) were presented first, 1–2 s in advance of the briefly presented target stimulus. Thus there was sufficient time for the putative feedback process to be in place and stabilized before the onset of the target. How our results generalize to other timing configurations, such as the simultaneous presentation of the target and flankers, remains an open question.

In *experiments 2C* and *2D*, we used surfaces defined by cast shadows to perceptually group or ungroup the target and flankers, respectively. It is likely that other grouping cues would serve a similar function and result in a similar modulation of orientation-specific surround suppression. For example, enclosing the target and flankers in *experiment 2B* using lines could serve as a perceptual grouping cue (Palmer 1999). Likewise, we predict that using binocular disparity manipulations to place the target on the same vs. different depth plane as the flankers (Nakayama et al. 1989) would also lead to the presence vs. absence of orientation-specific surround suppression.

We included a demanding central fixation task in *experiment 1* to eliminate specifically any differential effects of attention between the stimulus conditions. Furthermore, in *experiment 2*, the target stimuli were behaviorally irrelevant (i.e., under no specific task instruction), briefly flashed, of unpredictable orientation and peripherally located. Thus it is unlikely that there are any simple confounds related to attention or motivation that could potentially explain our results.

Our stimulus configurations resemble those used to study crowding effects in the periphery where the sensitivity to a target is reduced when the target is surrounded by flankers (Bouma 1970). Indeed, grouping also plays a critical role in crowding (Manassi et al. 2012). Despite some similarity in the stimulus configurations, our results were not due to crowding. First, the stimulus configurations were displayed near the fovea (displaced horizontally from the fixation point by 6° in *experiment 1* and 3° in *experiment 2*), and perceptually the target was clearly visible. Second, we found that orientation-specific surround suppression was modulated by introducing surface structure even in the far-distance condition where the flankers were far removed from the target (6°). Vickery et al. (2009) showed that far-removed flankers that are outside of traditional crowding area could reduce the ability to identify a target when the target was masked. This result suggests that the mask that also affects target visibility interacts with the flankers in a superadditive way. In our experiments, we did not manipulate the target visibility and simply measured the contrast detection threshold for an isolated target after adaptation (*experiment 1*) and VEP for a briefly flashed target (*experiment 2*). Thus it is unlikely that our results were due to reduced target visibility by crowding. However, the question of whether the surface structure manipulations used in our experiments also affect crowding would be an interesting follow-up.

Overall, the high-level surface structure of the image, specifically whether the target and flankers shared a common surface and thus were grouped into a single array, offers the most consistent explanation for our results. Indeed, our results are consistent with behavioral evidence that demonstrate a fundamental role of surface structure in perceptual grouping (Nakayama et al. 1989; Nakayama and Mackeben 1989; Nakayama and Shimojo 1992) and visual detection sensitivity (Huang et al. 2012). The results of the present study, together with our recent findings (Joo et al. 2012), suggest a coding scheme in early visual cortex that is sensitive to high-level image structure.

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## DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the author(s).

## AUTHOR CONTRIBUTIONS

S.J.J. and S.O.M. conception and design of research; S.J.J. performed experiments; S.J.J. analyzed data; S.J.J. and S.O.M. interpreted results of experiments; S.J.J. prepared figures; S.J.J. and S.O.M. drafted manuscript; S.J.J. and S.O.M. edited and revised manuscript; S.J.J. and S.O.M. 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.
- Alitto HJ, Usrey WM. Origin and dynamics of extraclassical suppression in the lateral geniculate nucleus of the macaque monkey. *Neuron* 57: 135–146, 2008.
- 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.
- Angelucci A, Levitt JB, Walton EJ, Hupe JM, Bullier J, Lund JS. Circuits for local and global signal integration in primary visual cortex. *J Neurosci* 22: 8633–8646, 2002.
- 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.
- Bi T, Cai P, Zhou T, Fang F. The effect of crowding on orientation-selective adaptation in human early visual cortex. *J Vis* 9: 13.1–10, 2009.
- Blake R, Tadin D, Sobel KV, Raissian TA, Chong SC. Strength of early visual adaptation depends on visual awareness. *Proc Natl Acad Sci USA* 103: 4783–4788, 2006.
- Blakemore C, Campbell FW. On the existence of neurones in the human visual system selectively sensitive to the orientation and size of retinal images. *J Physiol* 203: 237–260, 1969.
- Blakemore C, Tobin EA. Lateral inhibition between orientation detectors in the cat's visual cortex. *Exp Brain Res* 15: 439–440, 1972.
- Bouma H. Interaction effects in parafoveal letter recognition. *Nature* 226: 177–178, 1970.
- Bradley A, Switkes E, De Valois K. Orientation and spatial frequency selectivity of adaptation to color and luminance gratings. *Vision Res* 28: 841–856, 1988.
- Brainard DH. The Psychophysics Toolbox. *Spat Vis* 10: 433–436, 1997.
- Carandini M, Movshon JA, Ferster D. Pattern adaptation and cross-orientation interactions in the primary visual cortex. *Neuropharmacology* 37: 501–511, 1998.



- 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, 2002.
- Clark VP, Fan S, Hillyard SA. Identification of early visual evoked potential generators by retinotopic and topographic analyses. *Hum Brain Mapp* 2: 170–187, 2004.
- 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.
- Dobbins A, Zucker SW, Cynader MS. Endstopped neurons in the visual cortex as a substrate for calculating curvature. *Nature* 329: 438–441, 1987.
- Dragoi V, Sharma J, Sur M. Adaptation-induced plasticity of orientation tuning in adult visual cortex. *Neuron* 28: 287–298, 2000.
- Engel SA. Adaptation of oriented and unoriented color-selective neurons in human visual areas. *Neuron* 45: 613–623, 2005.
- Fang F, Murray SO, Kersten D, He S. Orientation-tuned fMRI adaptation in human visual cortex. *J Neurophysiol* 94: 4188–4195, 2005.
- Haynes JD, Roth G, Stadler M, Heinze HJ. Neuromagnetic correlates of perceived contrast in primary visual cortex. *J Neurophysiol* 89: 2655–2666, 2003.
- Huang PC, Chen CC, Tyler CW. Collinear facilitation over space and depth. *J Vis* 12: pii: 20, 2012.
- Joo SJ, Boynton GM, Murray SO. Long-range, pattern-dependent contextual effects in early human visual cortex. *Curr Biol* 22: 781–786, 2012.
- 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.
- Kapadia MK, Westheimer G, Gilbert CD. Spatial distribution of contextual interactions in primary visual cortex and in visual perception. *J Neurophysiol* 84: 2048–2062, 2000.
- Kastner S, Nothdurft HC, Pigarev IN. Neuronal correlates of pop-out in cat striate cortex. *Vision Res* 37: 371–376, 1997.
- Knierim JJ, Van Essen DC. Neuronal responses to static texture patterns in area V1 of the alert macaque monkey. *J Neurophysiol* 67: 961–980, 1992.
- Kohn A, Movshon JA. Neuronal adaptation to visual motion in area MT of the macaque. *Neuron* 39: 681–691, 2003.
- Kourtzi Z, Kanwisher N. Representation of perceived object shape by the human lateral occipital complex. *Science* 293: 1506–1509, 2001.
- Larsson J, Landy MS, Heeger DJ. Orientation-selective adaptation to first- and second-order patterns in human visual cortex. *J Neurophysiol* 95: 862–881, 2006.
- Loftus GR, Masson ME. Using confidence intervals in within-subject designs. *Psychon Bull Rev* 1: 476–490, 1994.
- Luck S, Woodman G, Vogel E. Event-related potential studies of attention. *Trends Cogn Sci* 4: 432–440, 2000.
- Maffei L, Fiorentini A. The unresponsive regions of visual cortical receptive fields. *Vision Res* 16: 1131–1139, 1976.
- Manassi M, Sayim B, Herzog MH. Grouping, pooling, and when bigger is better in visual crowding. *J Vis* 12: 13, 2012.
- Mareschal I, Sceniak MP, Shapley RM. Contextual influences on orientation discrimination: binding local and global cues. *Vision Res* 41: 1915–1930, 2001.
- Movshon JA, Lennie P. Pattern-selective adaptation in visual cortical neurons. *Nature* 278: 850–852, 1979.
- Murray SO, Kersten D, Olshausen BA, Schrater P, Woods DL. Shape perception reduces activity in human primary visual cortex. *Proc Natl Acad Sci USA* 99: 15164–15169, 2002.
- Murray SO, Olshausen BA, Woods DL. Processing shape, motion and three-dimensional shape-from-motion in the human cortex. *Cereb Cortex* 13: 508–516, 2003.
- Nakayama K, Mackeben M. Sustained and transient components of focal visual attention. *Vision Res* 29: 1631–1647, 1989.
- Nakayama K, Shimojo S, Silverman GH. Stereoscopic depth: its relation to image segmentation, grouping, and the recognition of occluded objects. *Perception* 18: 55–68, 1989.
- Nakayama K, Shimojo S. Experiencing and perceiving visual surfaces. *Science* 257: 1357–1363, 1992.
- Palmer SE. *Vision Science: Photons to Phenomenology*. Cambridge, MA: MIT Press, 1999.
- Pelli DG. The VideoToolbox software for visual psychophysics: transforming numbers into movies. *Spat Vis* 10: 437–442, 1997.
- Petrov Y, Verghese P, McKee SP. Collinear facilitation is largely uncertainty reduction. *J Vis* 6: 170–178, 2006.
- Priebe NJ, Churchland MM, Lisberger SG. Constraints on the source of short-term motion adaptation in macaque area MT. I. The role of input and intrinsic mechanisms. *J Neurophysiol* 88: 354–369, 2002.
- Sayim B, Westheimer G, Herzog MH. Contrast polarity, chromaticity, and stereoscopic depth modulate contextual interactions in vernier acuity. *J Vis* 8: 12.1–9, 2008.
- Schmolesky MT, Wang Y, Hanes DP, Thompson KG, Leutgeb S, Schall JD, Leventhal AG. Signal timing across the macaque visual system. *J Neurophysiol* 79: 3272–3278, 1998.
- Shapley R. A new view of the primary visual cortex. *Neural Netw* 17: 615–623, 2004.
- Sillito AM, Grieve KL, Jones HE, Cudeiro J, Davis J. Visual cortical mechanisms detecting focal orientation discontinuities. *Nature* 378: 492–496, 1995.
- Solomon SG, Lee BB, Sun H. Suppressive surrounds and contrast gain in magnocellular-pathway retinal ganglion cells of macaque. *J Neurosci* 26: 8715–8726, 2006.
- Vickery TJ, Shim WM, Chakravarthi R, Jiang YV, Luedeman R. Super-crowding: weakly masking a target expands the range of crowding. *J Vis* 9: 12.1–15, 2009.
- Watson AB, Pelli DG. QUEST: a Bayesian adaptive psychometric method. *Percept Psychophys* 33: 113–120, 1983.
- Zenger-Landolt B, Heeger DJ. Response suppression in v1 agrees with psychophysics of surround masking. *J Neurosci* 23: 6884–6893, 2003.
- Zipser K, Lamme VA, Schiller PH. Contextual modulation in primary visual cortex. *J Neurosci* 16: 7376–7389, 1996.