Feature-based attention modulates surround suppression

Anastasia V. Flevaris

Department of Psychology, University of Washington,
Seattle, WA, USA ✉

Scott O. Murray

Department of Psychology, University of Washington,
Seattle, WA, USA ✉

Stimuli appearing in the surround of the classical receptive field (CRF) can reduce neuronal firing and perceived contrast of a preferred stimulus in the CRF, a phenomenon referred to as surround suppression. Suppression is greatest when the surrounding stimulus has the same orientation and spatial frequency (SF) as the central target. Although spatial attention has been shown to influence surround suppression, the effects of feature-based attention have yet to be characterized. Using behavioral contrast adaptation in humans, we examined center-surround interactions between SF and orientation, and asked whether attending to one feature dimension versus the other influenced suppression. A center-surround triplet comprised of a central target Gabor and two flanking Gabors were used for adaptation. The flankers could have the same SF and orientation as the target, or differ in one or both of the feature dimensions. Contrast thresholds were measured for the target before and after adapting to center-surround triplets, and postadaptation thresholds were taken as an indirect measure of surround suppression. Both feature dimensions contributed to surround suppression and did not summate. Moreover, when center and surround had the same feature value in one dimension (e.g., same orientation) but had different values in the other dimension (e.g., different SF), there was more suppression when attention was directed to the feature dimension that matched between center and surround than when attention was directed to the feature dimension that differed. These results demonstrate that feature-based attention can influence center-surround interactions by enhancing the effects of the attended dimension.

Introduction

Neural responses in early visual cortex are modulated by stimuli located outside their classical receptive field (CRF). When a preferred stimulus in the CRF has the same orientation, spatial frequency (SF), and contrast as a stimulus in the surround, the perceived contrast (e.g., Cannon & Fullenkamp, 1991; Chubb, 1989) and neuronal response (e.g., Allman, Miezin, & McGuinness, 1985; Blakemore & Tobin, 1972; Cavanaugh, Bair, & Movshon, 2002; Zenger-Landolt & Heeger, 2003) is reduced. This phenomenon, termed surround suppression, has typically been viewed as a low-level mechanism impermeable to top-down influences, arising from mutual inhibition by horizontal connections within the primary visual cortex (V1; Adesnik, Bruns, Taniguchi, Huang, & Scanziani, 2012; Gilbert & Wiesel, 1990), or from feedforward projections from the retina (Solomon, Lee, & Sun, 2006) or thalamus (Alitto & Usrey, 2008). However, recent research has suggested that feedback to V1 from extrastriate and higher-level areas may play a role in surround suppression (Angelucci et al., 2002; Angelucci & Bressloff, 2006; Bair, Cavanaugh, & Movshon, 2003; Jones, Andolina, Oakely, Murphy, & Sillito, 2000; Nassi, Lomber, & Born, 2013). For example, Nassi and colleagues (2013) showed that reversibly inactivating areas V2 and V3 via cortical cooling led to marked reductions in surround suppression in V1.

The top-down processes manifested in these apparent feedback projections have yet to be determined; one fundamental and largely unanswered question is whether selective attention can modulate surround suppression. Whereas attentional modulation of the response to stimuli in the CRF is well documented (Boynton, 2005; Buracas & Boynton, 2007; Carrasco, 2011; Connor, Gallant, Preddie, & Van Essen, 1996; Connor, Preddie, Gallant, & Van Essen, 1997; Desimone, 1998; Desimone & Duncan, 1995; Hamed, Duhamel, Bremmer, & Graf, 2002; Martinez-Trujillo & Treue, 2004; McAdams & Maunsell, 1999; Moran & Desimone, 1985; Pestilli et al., 2011; Reynolds & Chelazzi, 2004; Reynolds, Pasternak, & Desimone, 2000; Treue, 2001; Treue & Martinez-Trujillo, 1999; Womelsdorf, Anton-Erxleben, Pieper, & Treue, 2006),

only a few studies have examined the effect of spatial attention on surround suppression, (Anton-Erxleben, Stephan, & Treue, 2009; Ito & Gilbert, 1999; Roberts, Delicato, Herrero, Gieselmann, & Thiele, 2007; Sundberg, Mitchell, & Reynolds, 2009), and they have not addressed whether attention to features can influence the suppression. Although surround suppression is generally considered orientation specific (e.g., Mazer, Vinje, McDermott, Schiller, & Gallant, 2002), it has also been demonstrated to be SF tuned (Chubb, 1989; Serrano-Pedraza, Grady, & Read, 2012). For example, a recent study examined the influence of varying surround SF and orientation on contrast detection thresholds of a central grating, and found both factors to modulate surround suppression (Serrano-Pedraza et al., 2012). For orthogonal surrounds, contrast detection thresholds of the central grating did not differ from that of a single grating (i.e., with no surround), indicating little influence of the surround on central contrast detection (i.e., little or no surround suppression). Importantly, this lack of influence of orthogonal surrounds was true for all SFs tested. In contrast, when the surround had the same orientation and SF as the center grating, there was a significant increase in contrast detection threshold (i.e., evidence of surround suppression), and this suppression diminished as the surround SF moved away from that of the center grating. These results suggest that both SF and orientation contribute to surround suppression effects; suppression is greatest when both feature values are shared between center and surround, and suppression is minimal when either feature value differs. The nature of the contrast detection task in that study required participants to attend to the center stimulus. Given evidence that the locus of spatial attention influences surround suppression (e.g., Anton-Erxleben et al., 2009; Sundberg, Mitchell & Reynolds, 2009), in Experiment 1 we confirmed this pattern of results in the absence of spatial attention. We employed a psychophysical adaptation paradigm in which contrast detection thresholds of a single grating were measured before and after adaptation to different center-surround configurations. The increase in contrast detection threshold following adaptation has been previously shown to be a reliable measure of the degree of surround suppression in early visual cortex during the adaptation period (Joo, Boynton, & Murray, 2012). Center-surround configurations that elicit more surround suppression (i.e., a reduced neuronal response during the adaptation period) elicit less adaptation, resulting in little difference between pre- and post-adaptation contrast detection thresholds. In contrast, center-surround configurations that elicit less surround suppression (i.e., a robust neuronal response) result in an increase in contrast detection thresholds to the center stimulus following adaptation. This is an ideal

paradigm for measuring surround suppression in the absence of attention because attention can be directed elsewhere during the adaptation period. In Experiment 1, participants were instructed to ignore the center-surround triplets in the periphery and perform a contrast decrement task at central fixation. Indeed, consistent with prior studies (e.g., Chubb, 1989; Serrano-Pedraza et al., 2012), we found both SF and orientation to contribute to surround suppression.

In Experiment 2, we examined whether attending to a particular feature dimension modulates center-surround interactions. Here, we use "feature dimension" to refer to a particular class of attributes (e.g., color, motion, orientation, SF), and we use "feature value" to refer to a specific value within a dimension (e.g., red, upward motion, 90°, 2 cycles/°; Liu, Larsson, & Carrasco, 2007). If the center and surround share a feature value in one dimension but have different feature values in another dimension, does attending to the similar feature dimension enhance surround suppression, and does attending to the different feature dimension reduce it? An abundance of prior work has shown that attention can select individual feature values and dimensions independent of their spatial locations, referred to as "feature-based attention" (e.g., Liu, Larsson, & Carrasco, 2007; Maunsell & Treue, 2006; Martinez-Trujillo & Treue, 2004; Treue & Martinez-Trujillo, 1999; Yantis, 2000; Zhang & Luck, 2009). Feature-based attention has been shown to enhance the gain of neurons tuned to an attended feature value as early as V1 (e.g., Kamitani & Tong, 2005), to modulate cortical areas specialized for processing an attended feature dimension (e.g., Chawla, Rees, & Friston, 1999; Liu, Slotnick, Serences, & Yantis, 2003; McAdams & Maunsell, 2000; O'Craven, Rosen, Kwong, Treisman, & Savoy, 1997; Shoenfeld et al., 2007), and to enhance processing of feature values at unattended spatial locations (e.g., Saenz, Buracas, & Boynton, 2002, 2003). Additionally, attention to a motion stimulus has been shown to be important for driving directionally selective neurons; attention away from the stimulus led to diminished motion aftereffects (Chaudhuri, 1990).

Whereas it is clear that feature-based attention can *enhance* neuronal responses, this prior work did not investigate center-surround interactions; it is not known whether feature-based attention can also *inhibit* neuronal responses when center and surround stimuli have the same feature value in an attended dimension. Some evidence comes from studies of motion perception, showing that feature-based attention can modulate the influence of surround information on motion perception of a foveally presented stimulus (Tzvetanov, Womelsdorf, Niebergall, & Treue, 2006). When participants judged the direction of a foveally presented motion stimulus surrounded by a parafoveal stimulus containing two opposing directions of motion, the opposing

stimuli cancelled each other out and had no effect on the perception of the foveal stimulus. However, when participants were asked to attend to only one of the two motion directions in the surround stimulus, perception of the foveal stimulus was biased away from the attended direction (Tzvetanov et al., 2006). These results suggest that indeed, feature-based attention biases the processing of center and surround information. In that study, attention enhanced the influence of the attended feature (i.e., motion direction) in the surround. Here, we asked whether attention to a feature dimension across both center and surround stimuli influences center-surround interactions. Using psychophysical adaptation as a measure of surround suppression, in Experiment 2 we examined whether attention to a particular feature dimension (i.e., SF/orientation) can modulate surround suppression when center and surround stimuli have the same feature value in one of the two dimensions, and have different feature values in the other dimension. This paradigm is ideal for measuring the effects of feature-based attention on surround suppression because it allows for dissociation between the contrast detection task on the single center stimulus (carried out during the pre- and postadaptation test phases) and the feature discrimination task (carried out during the adaptation phase). During the adaptation phase, attention was not directed to the center stimulus location per se, but to a particular feature dimension across the center and surround stimuli. We hypothesized that there would be increased surround suppression (i.e., reduced adaptation to the center stimulus) when attention was directed to the feature dimension for which center and surround stimuli had the same feature values (e.g., same orientation, same SF), relative to when attention was directed to the dimension for which center and surround differed. This pattern of results would suggest a flexible, high-level influence on surround suppression mediated by attention.

Experiment 1

The aim of Experiment 1 was to establish the degree of surround suppression for center-surround configurations that differed in orientation, SF, or both. Before investigating the effects of feature-based attention in Experiment 2, here we examined surround suppression effects for orientation and SF in the absence of attention, as measured with our adaptation paradigm.

Methods

Participants

Twelve (nine women) undergraduates from the University of Washington participated for monetary

compensation. All participants had normal or corrected-to-normal vision. All gave written informed consent as approved by the University of Washington Institutional Review Board (IRB), and in accordance with the Declaration of Helsinki.

Stimuli

The stimuli were generated and presented using the MATLAB Psychtoolbox (Brainard, 1997). A central black fixation point subtending 0.45° remained on the screen throughout the experiment. Participants performed a contrast detection task before and after adaptation. A Gabor patch (Gaussian-windowed with $\sigma = 0.72°$) with a SF of 5 cycles/° and vertical orientation served as the target for the contrast detection task. The target location was marked during both the adaptation and task phases by four white corners of an illusory square subtending 2.6°, to remove the effect of location uncertainty on the detection task (Petrov, Verghese, & McKee, 2006). The adapting stimuli consisted of the central target Gabor patch and two flanking Gabor patches that were 25% contrast and counter-phase flickering at 2 Hz. The target and flanking Gabors were all Gaussian windowed with $\sigma = 0.72°$. The center-to-center distance between the target and flankers was 3°. The flankers were either (a) 5 cycles/° and vertical (same SF and orientation as the target), (b) 2 cycles/° and vertical (different SF and same orientation), (c) 5 cycles/° and horizontal (same SF and different orientation) or (d) 2 cycles/° and horizontal (different SF and orientation). Stimulus conditions are shown below the x axis in Figure 2.

Procedure

Contrast detection was measured before and after adaptation by two randomly interleaved QUEST (Watson & Pelli, 1983) staircases. In separate blocks, the target Gabor was presented 6° to the left or right of fixation in a two-interval forced choice (2IFC) task in which participants indicted which of two intervals contained the target. Each interval was indicated by a 200 ms high-pitched tone and separated by a 300 ms blank period. The fixation point and the target marker remained on the screen throughout. Participants maintained fixation and indicated which interval contained the target, as well as their confidence, with one set of buttons used for "sure" responses and a second set for "unsure" responses. These confidence ratings were used to calculate the contrast of the subsequently presented target Gabor in the staircase (Watson & Pelli, 1983). Auditory feedback was given for incorrect responses. There were 41 trials (20 trials per staircase) per contrast detection block, with the first
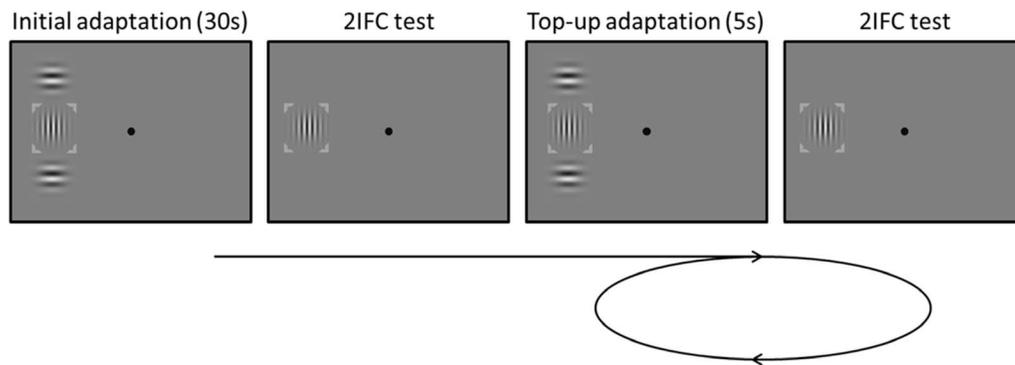
Figure 1. Contrast adaptation experimental procedure. Observers were initially presented with the adapting stimuli for 30 s (counter-phase flickering at 2 Hz), followed by the first 2IFC detection trial (see Methods). Each subsequent 2IFC trial was preceded by 5 s of the adapting stimuli (counter-phase flickering at 2 Hz). The attention tasks were confined to the initial and top-up adaptation periods.

trial discarded. The last contrast values were averaged to estimate each participant's contrast detection threshold for 82% performance.

Following the contrast detection task, participants were presented with the adapting stimuli for 30 s, followed by the first 2IFC task trial. A 5 s top-up adaptation period was presented between subsequent 2IFC task trials to maintain adaptation. The contrast adaptation trial sequence is displayed in Figure 1. Participants performed a contrast decrement task on the fixation point during the adaptation phase, to equate attentional state across conditions. A 10% contrast decrement was presented for 150 ms, and the onset was selected randomly from a uniform distribution between 1.5 and 2 s. Participants were asked to press a button as soon as they saw each contrast decrement. Participants were tested in all four stimulus conditions, in both the left and right visual fields. The amount of adaptation was quantified by calculating the ratio of detection threshold before versus after adaptation ($threshold_{after}/threshold_{before}$). Postadaptation thresholds were assumed to reflect the magnitude of the neural response in early visual cortex to the adapting stimulus (Blake et al., 2006; Blakemore & Campbell, 1969; Carandini, Movshon, & Ferster, 1998; Dragoi, Sharma, & Sur, 2000; Engel, 2005; Kohn & Movshon, 2003; Fang, Murray, Kersten, & He, 2005; Joo et al., 2012; Larsson, Landy, & Heeger, 2006), higher thresholds reflecting higher overall neural activity in response to the stimulus and lower thresholds reflecting lower activity. This is because greater neural activity during the adaptation period would result in more adaptation and increased postadaptation contrast thresholds, whereas lower neural activity would result in less adaptation and lower postadaptation contrast thresholds. Hence, when adapting to the center target, surround stimuli that suppress the response to the target would inhibit adaptation and result in little difference between pre- and postadaptation contrast detection thresholds. In contrast, surround stimuli that do not suppress the response to the target would result in adaptation and thus an increase in postadaptation contrast detection thresholds. Hence, with respect to the target-flanker configuration, lower postadaptation thresholds for the target were taken to reflect greater surround suppression induced by the flankers.
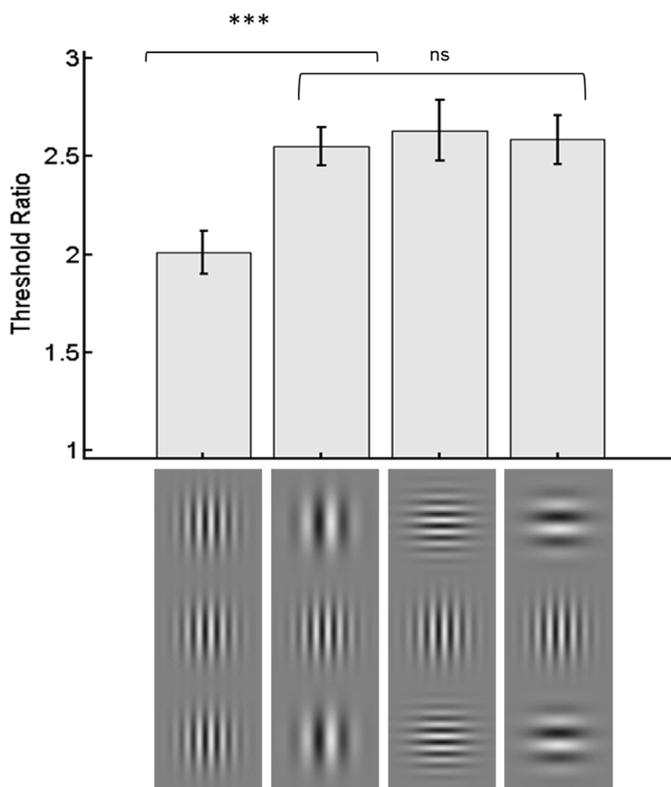
Figure 2. Experiment 1 results. Postadaptation threshold ratios for each adapting stimulus condition. Error bars depict standard errors. Threshold ratios were significantly lower for the same spatial frequency/same orientation adapting stimulus than for the other three stimulus conditions, which did not differ from one another. ***: $p = 0.002$; ns = not significant.

Results

We determined the contribution of SF and orientation to surround suppression in Experiment 1 by comparing differences in postadaptation ratios (i.e., threshold$_{after}$/ threshold$_{before}$) across the four stimulus conditions (Figure 2). Overall, threshold ratios were significantly lower for the same SF/same orientation adapting stimulus than for the other three stimulus conditions, which did not differ from one another. Because postadaptation thresholds are assumed to reflect the magnitude of neural responses to the adapting stimulus in early visual cortex (Blake, Tadin, Sobel, Raissian, & Chong, 2006; Blakemore & Campbell, 1969; Carandini et al., 1998; Dragoi et al., 2000; Engel, 2005; Kohn & Movshon, 2003; Fang et al., 2005; Joo et al., 2012; Larsson, Landy, & Heeger, 2006), the results indicate more surround suppression in the same spatial frequency/same orientation stimulus condition.

A SF (same, different) × orientation (same, different) × visual field (left, right) Analysis of Variance (ANOVA) revealed a main effect of orientation, $F(1, 11) = 6.23$, $p = 0.03$, with the same orientation stimuli yielding a significantly lower postadaptation ratio (2.28) than did the different orientation stimuli (2.61). Although there was no main effect of SF, this was qualified by a significant SF × orientation interaction, $F(1, 11) = 6.19$, $p = 0.03$. Follow-up t tests (Bonferroni corrected) revealed that when SF was the same, there was a significantly lower postadaptation ratio when orientation was also the same (2.01) than when orientation differed, 2.63; $t(11) = -5.38$, $p = 0.0002$, whereas when SF differed, there was no difference between same (2.55) and different (2.58) orientations, $t(11) = -0.16$, $p = 0.77$. Indeed, planned comparisons revealed no significant difference between postadaptation ratios when only SF differed (2.54) versus when only orientation differed, 2.63; $t(11) = -0.36$, $p = 0.80$, and no significant difference between postadaptation ratios when both SF and orientation differed, 2.58, versus only SF differed, $t(11) = 0.16$, $p = 0.88$, or only orientation differed, $t(11) = -0.28$; $p = 0.79$. On the other hand, postadaptation ratios were significantly lower when both SF and orientation were the same (2.00) than when one or both differed, 2.59; $t(11) = -3.94$, $p = 0.002$.

Discussion

Using psychophysical adaptation and comparing contrast detection thresholds to a central target Gabor before and after adapting to a center and two surrounding Gabors, we found lower postadaptation thresholds when the target had the same SF and orientation as the surrounds than when the surrounds differed in orientation, SF, or both. Given previous evidence that postadaptation thresholds reflect response magnitude in early visual cortex (Blake et al., 2006; Blakemore & Campbell, 1969; Carandini et al., 1998; Dragoi et al., 2000; Engel, 2005; Kohn & Movshon, 2003; Fang et al., 2005; Joo et al., 2012; Larsson et al., 2006), lower postadaptation thresholds to the target when it had the same SF and orientation as the surround indicate greater surround suppression in this condition. Moreover, we found that while both orientation and SF contributed to surround suppression, they did not summate; when the target and flankers differed along both feature dimensions, there was no less suppression than when they only differed on one dimension. However, we tested only orthogonal orientations and highly distinct SFs; it is possible that the effects of surround on central adaptation threshold are only all-or-none under these circumstances, but with smaller differences between feature values, a more graded effect could emerge.

Although many models of surround suppression in V1 are limited to orientation selectivity (e.g., Cavanaugh et al., 2002; Mazer et al., 2002), the present results are consistent with recent studies demonstrating reduced suppression for different SF surrounds (e.g., Chubb, 1989; Serrano-Pedraza et al., 2012), suggesting that surround suppression may reflect inhibition by cells tuned to the same SF as the center. Studies examining surround suppression in a single feature dimension (i.e., SF or orientation) have shown the response to be graded, with decreasing suppression as the surrounding SF or orientation moves away from that of the center (e.g., Cannon & Fullenkamp, 1991; Chubb, 1989). The results from the present study suggest that suppression across dimensions is not graded; we found equivalent postadaptation thresholds whether one or both dimensions differed. Despite research demonstrating relatively independent selectivity for SF and orientation in V1 (Glezer, Tsherbach, Gauselman, & Bondarko, 1982; Mazer et al., 2002; Movshon, Anthony, & Lennie, 1979; Webster & De Valois, 1985), the present results suggest that suppressive mechanisms involving cells tuned to SF and orientation interact and yield the same degree of inhibition (or lack thereof) whether one or more feature values differ between center and surround.

These results are consistent with a prior study that measured contrast detection thresholds for center gratings embedded in surrounds of varying SF and orientation (Serrano-Pedraza et al., 2012). Akin to the current results, that study showed that the contrast detection threshold of a center grating was greatest for center-surround configurations that shared the same SF and orientation (i.e., greatest surround suppression). In contrast, there was little or no difference between the detection threshold of a center stimulus

with no surround, with an orthogonal surround, and with a surround of a sufficiently different SF from the target. For a 5 cycles/° target like the one used in the present experiment, Serrano-Pedraza et al. (2012) found almost no surround inhibition for a 2 cycles/° surround, consistent with our results. Whereas Serrano-Pedraza et al. (2012) required participants to attend to the center stimulus, the contrast discrimination task on the fixation dot in the present study discouraged participants from attending to the center-surround configuration during the adaptation phase. Taken together, across these distinct paradigms, the results from the two studies suggests that irrespective of the locus of spatial attention, surround suppression is greatest when the center and surround share both SF and orientation, and is significantly reduced when the center and surround differ in either or both feature dimensions. In Experiment 2, we investigated whether feature-based attention modulates surround suppression.

Experiment 2

In Experiment 2 we used the same adaptation paradigm as in Experiment 1, but changed the focus of attention during the adaptation phase to investigate the effects of feature-based attention. Rather than attending to the central fixation dot during adaptation, participants were asked to attend to either the SF or orientation of the center and surround Gabors and detect subtle changes in the attended feature dimension. We focused on the two conditions from Experiment 1 in which the features in one dimension (e.g., SF) were the same between center and surround and the features in the other dimension (e.g., orientation) differed. These two conditions are the most informative because if our hypothesis is correct and attention to feature dimension influences surround suppression, then attention to one dimension should have the opposite effect than attention to the other dimension. That is, attention to one feature dimension (i.e., in which the feature values are the same between center and surround) should result in more suppression whereas attention to the other dimension (i.e., in which the feature values differ between center and surround) should result in less suppression.

Methods

Participants

A new group of 14 (10 women) undergraduates from the University of Washington participated in Experiment 2, for monetary compensation. All had normal or corrected-to-normal vision and all gave written in-formed consent as approved by the University of Washington Institutional Review Board, and in accordance with the Declaration of Helsinki.

Stimuli

Stimuli were the same as in Experiment 1, with two exceptions. First, only conditions (2) and (3) were included in Experiment 2. Second, all three Gabors periodically changed SF (i.e., increased by 1.5 cycles/°) or orientation (i.e., increased by 10°) during the adaptation phase. Only one dimension (SF or orientation) changed at a time, and the change occurred simultaneously for all three Gabors.

Procedure

The procedure was identical to that of Experiment 2, with the following exception: Participants were tested in the same orientation/different SF and different orientation/same SF conditions in both visual fields, and attended either to the orientation or the SF in separate blocks. During the adaptation phase in Experiment 2, the SF or orientation of the target and flankers randomly changed and participants were asked to attend to either SF or orientation changes in different blocks, by pressing a button as soon as they detected a change in the attended dimension. SF and orientation changes occurred simultaneously for all three Gabors, and only one feature dimension (SF/orientation) changed at a time. Orientation and SF changes were equally likely to occur, regardless of which dimension participants were attending in a given block. Participants were instructed to attend to the target and flankers as a group, and note changes that occurred simultaneously across all three Gabors.

Results

We first determined whether the SF and orientation discrimination tasks were of roughly equal difficulty by calculating d-prime; (Macmillan & Creelman, 1990) for each task. For the same SF/different orientation center-surround configuration, average d-prime; was 3.53 and 3.44 for the SF and orientation tasks, respectively. For the same orientation/different SF configuration, average d-prime; was 3.50 and 3.88 for the SF and orientation tasks, respectively. A stimulus (same SF/different orientation, same orientation/different SF) by attended dimension (SF, orientation) ANOVA of the d-prime; values yielded no significant effects, suggesting little difference in task difficulty.

To evaluate whether feature-based attention contributes to surround suppression, we compared differences in post-adaptation ratios for the stimuli in which
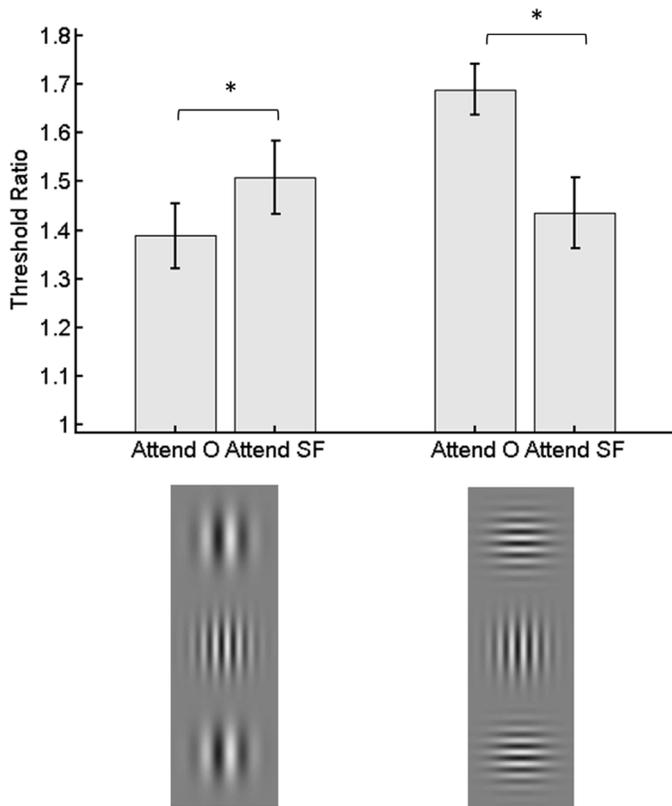
Figure 3. Experiment 2 results. Postadaptation threshold ratios for the two adapting stimulus conditions as a function of attended dimension. Error bars depict standard errors. Threshold ratios were significantly lower for both stimulus conditions when attention was directed to the feature dimension that was the same than to the dimension that differed. (SF: spatial frequency; O: orientation; *: $p < 0.05$).

the target and flankers had different feature values in only one dimension (SF/orientation) and attention was directed to the dimension in which the feature values were the same versus the dimension in which the feature values differed. These data are depicted in Figure 3. Overall, threshold ratios were significantly lower for both stimulus conditions when attention was directed to the dimension in which the feature values were the same compared to when attention was directed to the dimension in which the feature values differed. A stimulus (same SF/different orientation, same orientation/different SF) × attended dimension (same, different) × visual field (left, right) ANOVA revealed only a significant main effect of attended dimension, $F(1, 13) = 7.92$; $p = 0.01$, indicating reliably lower postadaptation ratios when attention was directed to the dimension in which the feature values were the same (1.4) than to the dimension in which the feature values differed (1.6). Planned comparisons revealed that this difference was significant for both stimulus conditions, $t(13) = 2.2$, $p < 0.05$ and $t(13) = 2.3$, $p < 0.05$ for the same orientation/

different SF and different SF/same orientation adapting stimuli, respectively.

Discussion

The results from Experiment 2 demonstrate that selective feature-based attention can influence surround suppression. When the target and surrounding Gabors differed either in SF or orientation, we found lower postadaptation ratios when attention was directed to the feature dimension in which the feature values were the same than when attention was directed to the dimension in which the feature values differed. These results suggest that feature-based attention directly modulates the inhibitory connections for the attended feature dimension.

General discussion

The aim of this study was to investigate whether attending to a particular feature dimension can modulate contextual interactions. Using psychophysical adaptation as an indirect measure of surround suppression, we first established that surround suppression is greatest when both SF and orientation are shared between center and surround, and is reduced when either one or both feature dimensions differ between center and surround (Experiment 1). We then demonstrated that for center-surround configurations that have the same feature value in one dimension and have different feature values in another, directing attention to the feature dimension in which the feature values are the same between center and surround results in less adaptation to the center stimulus relative to directing attention to the feature dimension in which the feature values differ (Experiment 2). Previous studies of feature-based attention have shown that attending to a feature value can enhance the gain of neurons tuned to the attended feature as well as suppress the response of neurons tuned away from the attended feature (Herrmann, Heeger, & Carrasco, 2012; Ho, Brown, Abuyo, Ku, & Serences, 2012; Liu, Larsson, & Carrasco, 2007; Maunsell & Treue, 2006; Serences, Liu, & Yantis, 2005; White & Carrasco, 2011). Previous research has also shown that attending to a specific feature value can bias contextual interactions by enhancing the influence of an attended surround feature value (Tzvetanov et al., 2006). The present results extend these findings by showing that attending to a feature *dimension* can enhance suppression of neurons tuned to a feature in that dimension if surrounding stimuli share a feature value in the attended dimension, relative to when surrounding

stimuli do not share a feature value in the attended dimension.

In our study the feature values in each dimension were stable across the blocks of trials. Hence, it is unclear whether attention selected the feature dimension in general, or the specific feature values in the attended dimension. For example, in blocks when participants were asked to attend to the orientations of the center-surround stimuli and indicate minor orientation changes, the orientations were either all vertical for the entire block, or they were both vertical (i.e., in the center) and horizontal (i.e., in the surround). It is possible that participants generally attended to the dimension (i.e., orientation), but it is also possible that they attended to the specific orientations in the stimuli (i.e., either vertical only or vertical and horizontal). If the specific orientations were attended, then based on prior research of feature-based attention (Herrmann et al., 2012; Ho, Brown, Abuyo, Ku, & Serences, 2012; Liu, Larsson, & Carrasco, 2007; Maunsell & Treue, 2006; Serences et al., 2005; White & Carrasco, 2011), we would expect that neurons tuned to the attended feature values would be enhanced. In the case when both center and surround were vertical, neurons tuned to vertical orientation would be enhanced, including neurons whose receptive fields were on the central as well as the surround stimuli. However, our results suggest that contextual mechanisms can inhibit the general enhancement to vertical orientation, and when both center and surround stimuli had vertical orientation, the central vertical stimulus was suppressed relative to when center and surround had different orientations. A second possibility is that attention selected the feature dimension more generally rather than selecting a particular feature value, leading to an enhancement in the contextual interactions within that dimension. For example, if orientation was selected, when both center and surround stimuli had vertical orientation and different SF, the similarity in orientation was enhanced and led to an increase in suppressive mechanisms. The present paradigm cannot distinguish between these possibilities, but it is clear that attending to a feature dimension can serve to either enhance or reduce surround suppression, depending on the feature values of center-surround stimuli in the attended dimension. Prior studies found different center-surround interactions when spatial attention was directed to the center stimulus relative to when attention was directed to the surround (e.g., Anton-Erxleben, et al., 2009; Sundberg et al., 2009), but a different pattern of results has been found for different brain regions. For example, in V4, attention decreased surround suppression when the center stimulus was attended and increased surround suppression when the surround was attended (Sundberg et al., 2009), but the opposite pattern was found in area MT (Anton-Erxleben et al.,

2009). In the present study we attempted to keep spatial attention distributed across the entire center-surround configuration by presenting feature changes simultaneously across all three Gabors. However, the fact that the threshold ratios in Experiment 2 were much smaller than those in Experiment 1 could suggest that spatial attention to the center-surround configuration increased surround suppression, albeit a different group of participants participated in each study. An interesting avenue for future research is to investigate how spatial attention and feature-based attention interact to mediate contextual interactions. For example, studies of feature-based attention have shown that attending to a feature value automatically enhances processing of feature values at unattended spatial locations, a phenomenon referred to as "global feature-based attention" (Saenz et al., 2002, 2003; Treue & Martinez-Trujillo, 1999). It is unknown whether feature-based attention influences center-surround interactions for unattended stimuli. Overall, the present results not only demonstrate an additional top-down process that influences surround suppression, but point to the importance of the relationship between feature-based selectivity and feature-based attention in mediating the contextual interactions.

Acknowledgments

Commercial relationships: none.
Corresponding author: Anastasia V. Flevaris.
Email: ani.flevaris@gmail.com.
Address: Department of Psychology, University of Washington, Seattle, WA, USA.

References

Adesnik, H., Bruns, W., Taniguchi, H., Huang, Z. J., & Scanziani, M. (2012). A neural circuit for spatial summation in visual cortex. *Nature, 490,* 226–231.

Alitto, H. J., & Usrey, W. M. (2008). Origin and dynamics of extraclassical suppression in the lateral geniculate nucleus of the macaque monkey. *Neuron, 57,* 135–146.

Allman, J., Miezin, F., & McGuinness, E. (1985). Stimulus specific responses from beyond the classical receptive field: Neurophysiological mechanisms for local-global comparisons in visual neurons. *Annual Review of Neuroscience, 8,* 407–430.

Angelucci, A., & Bressloff, P. C. (2006). Contribution of feedforward, lateral and feedback connections to the classical receptive field surround of primate V1 neurons. *Progress in Brain Research, 154,* 90–120.

Angelucci, A., Levitt, J. B., Walton, E. J., Hupe, J. M., Bullier, J., & Lund, J. S. (2002). Circuits for local and global signal integration in primary visual cortex. *The Journal of Neuroscience, 22,* 8633–8646.

Anton-Erxleben, K., Stephan, V. M., & Treue, S. (2009). Attention reshapes center-surround receptive field structure in macaque cortical area MT. *Cerebral Cortex, 19,* 2466–2478.

Bair, W., Cavanaugh, J. R., & Movshon, J. A. (2003). Time course and time-distance relationships for surround suppression in macaque V1 neurons. *The Journal of Neuroscience, 23,* 7690–7701.

Blake, R., Tadin, D., Sobel, K. V., Raissian, T. A., & Chong, S. C. (2006). Strength of early visual adaptation depends on visual awareness. *Proceedings of the National Academy of Sciences, USA, 103,* 4783–4788.

Blakemore, C., & Campbell, F. W. (1969). On the existence of neurons in the human visual system selectively sensitive to the orientation and size of retinal images. *Journal of Physiology, 203,* 237–260.

Blakemore, C., & Tobin, E.A. (1972). Lateral inhibition between orientation detectors in the cat's visual cortex. *Experimental Brain Research, 15,* 439–440.

Boynton, G. M. (2005). Attention and visual perception. *Current Opinion in Neurobiology, 15,* 465–469.

Brainard, D. H. (1997). The psychophysics toolbox. *Spatial Vision, 10,* 433–436.

Buracas, G. T., & Boynton, G. M. (2007). The effect of spatial attention on contrast response functions in human visual cortex. *The Journal of Neuroscience, 27*(1), 93–97.

Cannon, M. W., & Fullenkamp, S. C. (1991). Spatial interactions in apparent contrast: Inhibitory effects among grating patterns of different spatial frequencies, spatial positions and orientations. *Vision Research, 31*(11), 1985–1998.

Carandini, M., Movshon, J. A., & Ferster, D. (1998). Pattern adaptation and cross-orientation interactions in the primary visual cortex. *Neuropharmacology, 37,* 501–511.

Carrasco, M. (2011). Visual attention: The past 25 years. *Vision Research, 51*(13), 1484–1525.

Cavanaugh, J. R., Bair, W., & Movshon, J. A. (2002). Nature and interaction of signals from the receptive field center and surround in macaque V1 neurons. *Journal of Neurophysiology, 88,* 2530–2546.

Chaudhuri, A. (1990). Modulation of the motion aftereffect by selective attention. *Nature, 344,* 60–62.

Chawla, D., Rees, G., & Friston, K. J. (1999). The physiological basis of attentional modulation in extrastriate visual areas. *Nature Neuroscience, 2*(7), 671–676.

Chubb, C. (1989). Texture interactions determine perceived contrast. *Proceedings of the National Academy of Sciences, USA, 86*(23), 9631–9635.

Connor, C. E., Gallant, J. L., Preddie, D. C., & Van Essen, D. C. (1996). Responses in area V4 depend on the spatial relationship between stimulus and attention. *Journal of Neurophysiology, 75,* 1306–1308.

Connor, C. E., Preddie, D. C., Gallant, J. L., & Van Essen, D. C. (1997). Spatial attention effects in macaque area V4. *The Journal of Neuroscience, 17,* 3201–3214.

Desimone, R. (1998). Visual attention mediated by biased competition in extrastriate visual cortex. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences, 353*(1373), 1245–1255.

Desimone, R., & Duncan, J. (1995). Neural mechanisms of selective visual attention. *Annual Reviews of Neuroscience, 18,* 193–222.

Dobbins, A., Zucker, S. W., & Cynader, M. S. (1987). Endstopped neurons in the visual cortex as a substrate for calculating curvature. *Nature, 329,* 438–441.

Dragoi, V., Sharma, J., & Sur, M. (2000). Adaptation-induced plasticity of orientation tuning in adult visual cortex. *Neuron, 28,* 287–298.

Engel, S. A. (2005). Adaptation of oriented and unoriented color-selective neurons in human visual areas. *Neuron, 45,* 613–623.

Fang, F., Murray, S. O., Kersten, D., & He, S. (2005). Orientation-tuned FMRI adaptation in human visual cortex. *Journal of Neurophysiology, 94,* 4188–4195.

Gilbert, C. D., & Wiesel, T. N. (1990). The influence of contextual stimuli on the orientation selectivity of cells in primary visual cortex of the cat. *Vision Research, 30,* 1689–1701.

Glezer, V. D., Tsherbach, T. A., Gauselman, V. E., &

Bondarko, V. M. (1982). Spatio-temporal organization of receptive fields of the cat striate cortex. *Biological Cybernetics, 43*(1), 35–49.

Hamed, B. S., Duhamel, J. R., Bremmer, F., & Graf, W. (2002). Visual receptive field modulation in the lateral intraparietal area during attentive fixation and free gaze. *Cerebral Cortex, 12,* 234–245.

Herrmann, K., Heeger, D. J., & Carrasco, M. (2012). Feature-based attention enhances performance by increasing response gain. *Vision Research, 74,* 10–20.

Ho, T. C., Brown, S., Abuyo, N. A., Ku, E. H., & Serences, J. T. (2012). Perceptual consequences of feature-based attentional enhancement and suppression. *Journal of Vision, 12*(8):15, 1–17, http://www.journalofvision.org/content/12/8/15, doi:10.1167/12.8.15. [PubMed] [Article]

Ito, M., & Gilbert, C. D. (1999). Attention modulates contextual influences in the primary visual cortex of alert monkeys. *Neuron, 22,* 593–604.

Jones, H. E. Andolina, I. M., Oakely, N. M. Murphy, & Sillito, A. M. P. C., (2000). Spatial summation in lateral geniculate nucleus and visual cortex. *Experimental Brain Research, 135,* 79–284.

Joo, S. J., Boynton, G. M., & Murray, S. O. (2012). Long-range, pattern-dependent contextual effects in early human visual cortex. *Current Biology, 22*(9), 781–786.

Kamitani, Y., & Tong, F. (2005). Decoding the visual and subjective contents of the human brain. *Nature Neuroscience, 8,* 679–685.

Kohn, A., & Movshon, J. A. (2003). Neuronal adaptation to visual motion in area MT of the macaque. *Neuron, 39,* 681–691.

Larsson, J., Landy, M. S., & Heeger, D. J. (2006). Orientation-selective adaptation to first- and second-order patterns in human visual cortex. *Journal of Neurophysiology, 95,* 862–881.

Liu, T., Larsson, J., & Carrasco, M. (2007). Feature-Based Attention Modulates Orientation-Selective Responses in Human Visual Cortex. *Neuron, 55*(2), 313–323.

Liu, T., Slotnick, S. D., Serences, J. T., & Yantis, S. (2003). Cortical mechanisms of feature-based attentional control. *Cerebral cortex, 13*(12), 1334–1343.

Macmillan, N. A., & Creelman, C. D. (1990). Detection theory measures of response bias. *Psychological Bulletin, 107,* 401–413.

Martinez-Trujillo, J. C., & Treue, S. (2004). Feature-based attention increases the selectivity of popula-tion responses in primate visual cortex. *Current Biology, 14,* 744–751.

Maunsell, J. H. R., & Treue, S. (2006). Feature-based attention in visual cortex. *Trends in Neuroscience, 29,* 317–322.

Mazer, J. A., Vinje, W. E., McDermott, J., Schiller, P. H., & Gallant, J. L. (2002). Spatial frequency and orientation tuning dynamics in area V1. *Proceedings of the National Academy of Sciences, USA, 99*(3), 1645–1650.

McAdams, C. J., & Maunsell, J. H. R. (1999). Effects of attention on orientation tuning functions of single neurons in macaque cortical area V4. *The Journal of Neuroscience, 19,* 431–441.

McAdams, C. J., & Maunsell, J. H. R. (2000). Attention to both space and feature modulates neuronal responses in macaque area V4. *Journal of Neurophysiology, 83,* 1751–1755.

Moran, J., & Desimone, R. (1985). Selective attention gates visual processing in the extrastriate cortex. *Science, 229,* 782–784.

Movshon, J. Anthony, & Lennie, P. (1979). Pattern-selective adaptation in visual cortical neurones. *Nature, 278,* 850–852.

Nassi, J. J., Lomber, S. G., & Born, R. T. (2013). Corticocortical feedback contributes to surround suppression in V1 of the alert primate. *The Journal of Neuroscience, 33*(19), 8504–8517.

O'Craven, K. M., Rosen, B. R., Kwong, K. K., Treisman, A., & Savoy, R. L. (1997). Voluntary attention modulates fMRI activity in human MT-MST. *Neuron, 18,* 591–598.

Pestilli, F., Carrasco, M., Heeger, D. J., & Gardner, J. L. (2011). Attentional enhancement via selection and pooling of early sensory responses in human visual cortex. *Neuron, 72*(5), 832–846.

Petrov, Y., Verghese, P., & McKee, S. P. (2006). Collinear facilitation is largely uncertainty reduction. *Journal of Vision, 6*(2):8, 170–178, http://www.journalofvision.org/content/6/2/8, doi:10.1167/6.2.8. [PubMed] [Article]

Reynolds, J. H., & Chelazzi, L. (2004). Attentional modulation of visual processing. *Annual Review of Neuroscience, 27,* 611–647.

Reynolds, J. H., Pasternak, T., & Desimone, R. (2000). Attention increases sensitivity of V4 neurons. *Neuron, 26,* 703–714.

Roberts, M., Delicato, L. S., Herrero, J., Gieselmann, M. A., & Thiele, A. (2007). Attention alters spatial integration in macaque V1 in an eccentricity-dependent manner. *Nature Neuroscience, 10,* 1483–1491.

Saenz, G. T., Buracas, G. M., & Boynton, G. M. (2002). Global effects of feature-based attention in human visual cortex. *Nature Neuroscience, 17,* 17.

Saenz, G. T., Buracas, G. M., & Boynton, G. M. (2003). Global feature-based attention for motion and color. *Vision Research, 43,* 629–637.

Serences, J., Liu, T., & Yantis, S. (2005). Parietal mechanisms of switching and maintaining attention to locations, objects, and features. In L. Itti, G. Rees, & J. Tsotsos (Eds.), *Neurobiology of Attention* (pp. 35–41). New York: Academic Press.

Serrano-Pedraza, I., Grady, J. P., & Read, J. C. (2012). Spatial frequency bandwidth of surround suppression tuning curves. *Journal of Vision, 12*(6):24, 1–11, http://www.journalofvision.org/content/12/6/24, doi:10.1167/12.6.24. [PubMed] [Article]

Shoenfeld, M. A., Hopf, J.-M., Martinez, A. Mai, H. M., Sattler, C., Gasde, A., ... Hillyard, S. A. (2007). Spatio-temporal analysis of feature-based attention. *Cerebral Cortex, 17(10),* 2468–2477.

Solomon, S. G., Lee, B. B., & Sun, H. (2006). Suppressive surrounds and contrast gain in magnocellular-pathway retinal ganglion cells of macaque. *The Journal of Neuroscience, 26,* 8715–8726.

Sundberg, K. A., Mitchell, J. F., & Reynolds, J. H. (2009). Spatial attention modulates center-surround interactions in macaque visual area v4. *Neuron, 61,* 952–963.

Treue, S. (2001). Neural correlates of attention in primate visual cortex. *Trends in Neurosciences, 24,* 295–300.

Treue, S., & Martinez-Trujillo, J. C. (1999). Feature-based attention influences motion processing gain in macaque visual cortex. *Nature, 399,* 575–579.

Tzvetanov, T., Womelsdorf, T., Niebergall, R., & Treue, S. (2006). Feature-based attention influences contextual interactions during motion repulsion. *Vision Research, 46*(21), 3651–3658.

Watson, A. B., & Pelli, D. G. (1983). Quest: A Bayesian adaptive psychometric method. *Perception & Psychophysics, 33,* 113–120.

Webster, M. A., & De Valois, R. L. (1985). Relationship between spatial-frequency and orientation tuning of striate-cortex cells. *Journal of the Optical Society of America, 2*(7), 1124–1132.

White, A. L., & Carrasco, M. (2011). Feature-based attention involuntarily and simultaneously improves visual performance across locations. *Journal of Vision, 11*(6):15, 1–10, http://www.journalofvision.org/content/11/6/15, doi:10.1167/11.6.15. [PubMed] [Article]

Womelsdorf, T., Anton-Erxleben, K., Pieper, F., & Treue, S. (2006). Dynamic shifts of visual receptive fields in cortical area MT by spatial attention. *Nature Neuroscience, 9,* 1156–1160.

Yantis, S. (2000). Goal-directed and stimulus-driven determinants of attentional control. In S. Monsell & J. Driver, (Eds.), *Control of cognitive processes: Attention and performance XVIII* (pp. 73–103). Cambridge, MA: MIT Press.

Zenger-Landolt, B., & Heeger, D. J. (2003). Response suppression in v1 agrees with psychophysics of surround masking. *The Journal of Neuroscience, 23*(17), 6884–6893.

Zhang, W., & Luck, S. J. (2009). Feature-Based Attention Modulates Feedforward Visual Processing. *Nature Neuroscience, 12*(1), 24–25.