

Identifying separate components of surround suppression

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Surround suppression is a well-known phenomenon in which the response to a visual stimulus is diminished by the presence of neighboring stimuli. This effect is observed in neural responses in areas such as primary visual cortex, and also manifests in visual contrast perception. Studies in animal models have identified at least two separate mechanisms that may contribute to surround suppression: one that is monocular and resistant to contrast adaptation, and another that is binocular and strongly diminished by adaptation. The current study was designed to investigate whether these two mechanisms exist in humans and if they can be identified psychophysically using eye-of-origin and contrast adaptation manipulations. In addition, we examined the prediction that the monocular suppression component is broadly tuned for orientation, while suppression between eyes is narrowly tuned. Our results confirmed that when center and surrounding stimuli were presented dichoptically (in opposite eyes), suppression was orientation-tuned. Following adaptation in the surrounding region, no dichoptic suppression was observed, and monoptic suppression no longer showed orientation selectivity. These results are consistent with a model of surround suppression that depends on both low-level and higher level components. This work provides a method to assess the separate contributions of these components during spatial context processing in human vision.

Introduction

Perception of a visual stimulus depends on its surrounding context; a well-known example of contextual modulation is surround suppression, wherein the perceived contrast of a stimulus is reduced by the presence of surrounding stimuli, compared to when it is viewed in isolation (Cannon & Fullenkamp, 1991; Chubb, Sperling, & Solomon, 1989; Ejima & Takahashi, 1985; Petrov & McKee, 2006; Snowden &

Hammett, 1998; Xing & Heeger, 2000, 2001; Yu, Klein, & Levi, 2001). Studies in animal models have shown that neurons in primary visual cortex (V1) typically show reduced spike rates in response to a stimulus presented with a surround, compared to when a stimulus appears in the receptive field alone (Bair, Cavanaugh, & Movshon, 2003; Cavanaugh, Bair, & Movshon, 2002a, 2002b; DeAngelis, Freeman, & Ohzawa, 1994; Ichida, Schwabe, Bressloff, & Angelucci, 2007; Shushruth, Ichida, Levitt, & Angelucci, 2009; Shushruth et al., 2013; Walker, Ohzawa, & Freeman, 1999). Similar results have been observed in human V1 using functional magnetic resonance imaging (Chen, 2014; Flevaris & Murray, 2015; Joo, Boynton, & Murray, 2012; Nurminen, Kilpelainen, Laurinen, & Vanni, 2009; Pihlaja, Henriksson, James, & Vanni, 2008; Williams, Singh, & Smith, 2003; Zenger-Landolt & Heeger, 2003), suggesting that a reduction in the V1 response may underlie the reduction in perceived contrast observed with surround suppression.

Using electrophysiology in macaques, Webb, Dhruv, Solomon, Tailby, and Lennie (2005) suggested that two neural mechanisms may give rise to surround suppression in V1. They showed that the first is monocular, broadly tuned for stimulus features (e.g., spatial and temporal frequency), resistant to contrast adaptation, and likely operates at the level of the lateral geniculate nucleus (LGN) or the input layers of V1. We will henceforth refer to this first mechanism as “low-level,” given the functional properties and the putative anatomical substrates of this suppression. The second proposed mechanism (“higher level” hereafter) is binocular, narrowly feature-tuned, diminished by contrast adaptation, and most likely occurs at a cortical level beyond the input layers of V1. More recent psychophysical studies in humans have suggested that perceptual surround suppression may also depend on both monocular and binocular processes (Cai, Zhou, & Chen, 2008; Petrov & McKee, 2009). However, it is not

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yet clear to what extent these components are selective for stimulus features such as orientation, or whether they are influenced by contrast adaptation. Thus, the relationship between surround suppression in human vision and the two constituent mechanisms proposed in animals has not been fully established.

The current study was designed to test whether surround suppression during visual contrast perception in humans may be subdivided into distinct components on the basis of feature (orientation) selectivity, sensitivity to contrast adaptation, and the degree of interocular transfer. Indeed, using a contrast adaptation paradigm along with stereoscopic image presentation, we show that two distinct suppression components may be identified that contribute to human contrast perception, which are well matched to the functional properties of the low- and higher level suppression mechanisms described in nonhuman primates (Angelucci & Bressloff, 2006; Webb et al., 2005).

Methods

Participants

Six people (four male and two female, mean age 31 years) completed both experiments after providing written informed consent. Two additional subjects failed to complete the experiments due to difficulty in achieving stable binocular fusion using a stereoscope; data from these subjects were excluded. The experimental protocol was approved by the University of Washington Institutional Review Board, and conformed to the ethical guidelines for research on human subjects provided in the Declaration of Helsinki. All participants had normal or corrected-to-normal binocular vision. All of the subjects were experienced psychophysical observers, and two of the subjects were the authors.

Visual display

Stimuli were presented on a ViewSonic G90fB CRT monitor, and were generated on a PC running Windows XP using MATLAB (MathWorks, Natick, MA) and Psychtoolbox (Brainard, 1997; Pelli, 1997). Subjects viewed the stimuli through a mirror stereoscope at a distance of 50 cm. This allowed us to present images to each eye independently (e.g., images on the left half of the screen were seen only in the left eye). When viewed through the stereoscope, the maximum luminance of the monitor was reduced from 95 cd/m² to 40 cd/m².

The stereoscope was calibrated for each subject before the experiment in order to achieve stable fusion of the images presented to each eye. Subjects were instructed to adjust the relative horizontal position of test images using the stereoscope, to align the images in each eye (a circle within a ring, two collinear vertical lines). Finally, subjects completed a brief task designed to measure sensitivity to horizontal disparity in the alignment of the images presented to each eye. Fixation marks (width = 0.1°, length = 0.5°) were presented centrally in both eyes (left mark oriented vertically, right horizontally). When aligned, these fixation marks form the percept of a plus sign. Subjects were asked to detect whether or not there was a 0.25° horizontal offset between the fixation marks (50% probability). Across 16 trials, subjects averaged 84% accuracy on this task ($SD = 5\%$), indicating that they were sensitive to horizontal disparity between the images in each eye on a fine scale.

Stimuli

Stimuli consisted of sinusoidal luminance modulation gratings presented on a gray background (Figure 1). Fixation marks were presented centrally in each eye, as described above. Two gratings (target and reference) were presented at 5.3° eccentricity. These stimuli appeared 1° below the horizontal meridian (relative to fixation) in order to facilitate future experiments using electroencephalography, for which such an offset is advantageous. Gratings were presented within a circular mask (radius = 0.75°) blurred with a Gaussian envelope ($SD = 0.05^\circ$). Gratings were oriented either vertically or horizontally, and had a spatial frequency of 1.5 cycles/°. In a subset of stimulus conditions (see below), an array of eight circular gratings was presented surrounding the target grating. These surrounding gratings were arranged in a square grid around the target (1° center-to-center distance). Target and surrounding gratings were the same size and spatial frequency, were spatially in-phase, and were all presented at 77% Michelson contrast. This relatively high stimulus contrast was used because previous work suggests that the putative low-level suppression component may dominate at lower contrasts (Cavanaugh et al., 2002b; Webb et al., 2005). The reference grating had the same spatial phase as the target, was always presented without surrounding stimuli, and varied in contrast across trials (see below).

Five different stimulus conditions were used to examine the feature specificity and binocularity of surround suppression during contrast perception. Conditions were defined by the presence and configuration of the surrounding gratings. Surrounding gratings were not presented in the No Surround

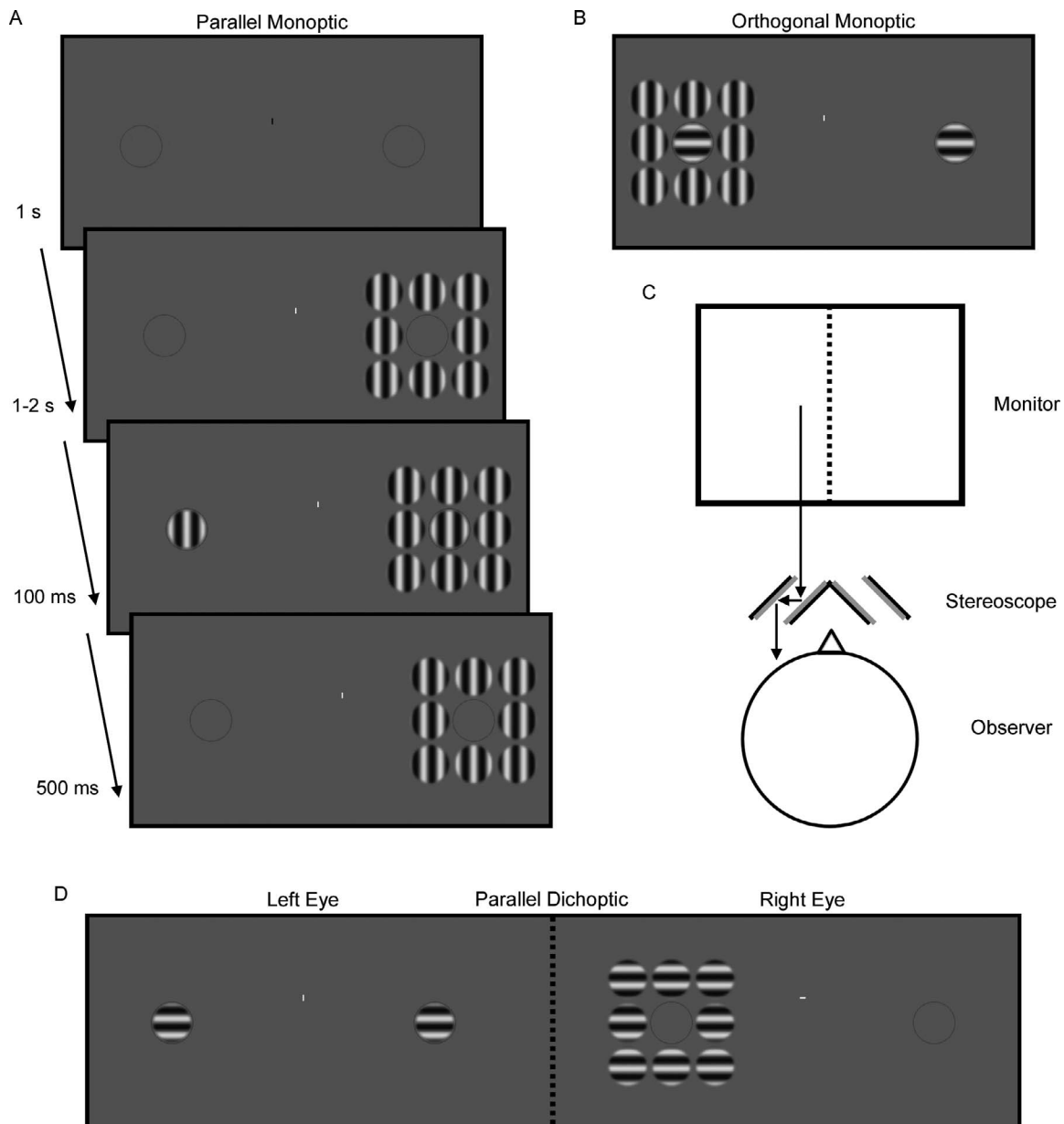


Figure 1. Stimuli and paradigm. (A) Task timing. Each panel illustrates part of the stimulus presentation sequence within a trial. Timing for each portion is indicated at the bottom left. In the third panel, stimuli from the Parallel Monoptic condition are shown as seen in the left eye (right eye blank). (B) Stimuli from the Orthogonal Monoptic condition as seen in the left eye. (C) Illustration of the stereoscopic display. Arrows indicate that images presented on one half of the screen (e.g., left) are seen by the corresponding eye. (D) Stimuli from the Parallel Dichoptic condition, as seen in each eye.

condition. The remaining four conditions were defined by the orientation of the surround relative to the target (Parallel = 0° ; Orthogonal = 90°), and the eye in which the target and surround were presented (Monoptic = same; Dichoptic = opposite). Based on previous work (Cai et al., 2008; Cavanaugh et al., 2002b; DeAngelis et al., 1994; Webb et al., 2005), we expected stronger surround suppression for Parallel and Monoptic surrounds versus Orthogonal and Dichoptic, respectively.

Examples of Parallel and Orthogonal Monoptic stimuli are shown in Figure 1A and B, respectively. Figure 1C illustrates how stimuli on the left and right halves of the screen were presented separately to the corresponding eye using a stereoscope. An example of the Parallel Dichoptic condition is shown in Figure 1D. When viewed through the stereoscope, the target grating appeared in the center of the surrounding gratings.

Paradigm

Experiment 1

The sequence of stimuli presented within a trial is shown in Figure 1A. Each trial began with black fixation marks and circular nonius lines presented in each eye for 1 s. Next, the fixation marks changed from black to white, indicating that the target and reference would appear after a brief delay. The delay length varied from 1–2 s, and was randomized and counter-balanced across trials. During this period, the surrounding stimuli were also presented without the target and reference, except in the No Surround condition where the surrounding region remained blank. The target and the reference then appeared for 100 ms. The surrounding stimuli (or blank background in the No Surround condition) remained for 500 ms after the target and reference gratings disappeared. Finally, the fixation marks changed from white to black, indicating that the trial was over and the subjects could make their response. Response time was not limited.

The subjects' task was to compare the perceived contrast of the target and reference gratings, and respond using the arrow keys to indicate on which side of fixation (left or right) the higher contrast grating appeared. The contrast of the reference stimulus varied across trials using the Psi adaptive staircase method implemented in the Palamedes toolbox (Prins & Kingdom, 2009). In this way the reference contrast was adjusted in order to determine the point of subjective equality between the perceived contrast of the target and reference. Before beginning the main experiment, subjects were shown a series of practice trials in order to ensure task comprehension.

Within one run, 40 trials were presented for each condition in a random order. Subjects completed eight runs in this experiment; the duration of each run was approximately 15 minutes. Independent staircases were used for each of the five stimulus conditions in each run. The target orientation and the eye in which the target was presented were randomized and counter-balanced across trials for each condition within a run. The spatial phase of the gratings and the side of fixation where the target appeared were randomized for each trial.

Experiment 2

The paradigm used in Experiment 2 was identical to that in Experiment 1, except for the following. The major difference was the inclusion of a contrast adaptation paradigm designed to reduce the influence of the surrounding gratings on the perception of target contrast. This paradigm is modeled in part from the psychophysical adaptation method of Joo and colleagues (2012), and closely matches that used by Webb

and colleagues (2005) to examine the effect of adaptation on surround suppression using electrophysiology. Immediately before each run, there was an initial adaptation phase which lasted 30 s. Subjects fixated centrally while the surrounding gratings were presented on both sides of fixation in both eyes. Surrounds were contrast-reversing in a square wave fashion at 1 Hz. Before each trial, there was also a top-up adaptation phase, during which the same contrast-reversing surround stimuli were presented for 5 s in order to maintain the adapted state. Note that during both the initial and top-up adaptation as well as in the trials, surrounding stimuli were always oriented vertically and presented at the same spatial phase (0°), in order to help maintain adaptation. Thus, targets were always oriented vertically in the Parallel conditions, whereas in the Orthogonal conditions they were oriented horizontally. This creates a mild confound between target orientation and surround condition, which raises the question of whether vertical and horizontal targets might be differentially affected by surround suppression. However, we note that Joo and colleagues (2012) found no difference in suppression for vertical and horizontal target gratings. Thus, we believe that this confound is unlikely to have influenced our results in a major way.

The adaptation paradigm roughly doubled the duration of each run, to approximately 30 min. Thus, subjects were given a break to rest their eyes halfway through each run in Experiment 2. The duration of this break was not fixed; subjects were instructed to rest for a minute or two without leaving their seats. Breaks were followed by another 30 s adaptation phase. Subjects completed a total of four runs in Experiment 2. Data from the two experiments were collected in separate sessions on different days; a total of four such hour-long sessions were completed by each subject.

Data analysis

In order to estimate the perceived target contrast in each stimulus condition, we quantified the point of subjective equality between target and reference contrast, in a manner similar to that used by Schallmo, Sponheim, and Olman (2015). This was done by fitting a Logistic function to the responses from all trials in each staircase using a maximum likelihood criterion (Kingdom & Prins, 2010). Guess and lapse rate were both fixed at 4%. The perceived contrast was defined as the reference contrast value reported as higher contrast than the target 50% of the time. Values above 100% or below 0% were excluded. Perceived contrast values were calculated separately for each stimulus condition for all subjects in both experiments.

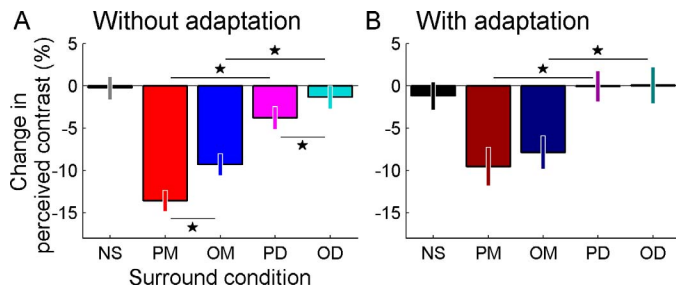


Figure 2. Results from Experiments 1 (A) and 2 (B). Data shown are the mean from all six subjects. Colored error bars show 95% confidence intervals. Different surround conditions are shown along the x axis (NS = No Surround, P = Parallel, O = Orthogonal, M = Monoptic, D = Dichoptic). Asterisks indicate significant differences ($p < 0.05$) as determined by posthoc t tests.

The change in perceived target contrast driven by the surrounding context was calculated by subtracting the veridical target contrast from the perceived contrast values. Negative changes in perceived contrast reflect the anticipated surround suppression effect (Snowden & Hammett, 1998; Yu et al., 2001). Data were normally distributed with equal variance across conditions. Changes in perceived contrast were examined using a repeated-measures analysis of variance (ANOVA). Due to the low sample size, subjects were treated as a fixed effect in our analyses. Although this is common in visual experiments involving a small number of subjects, it limits our ability to generalize the results of our experiments beyond our sample. Following the ANOVAs, planned posthoc comparisons of perceived contrast changes between conditions were made using 1-tailed t tests. The use of 1-tailed tests is justified by our strong a priori expectation of greater surround suppression in the Parallel versus Orthogonal and Monoptic versus Dichoptic conditions (Cai et al., 2008; Cavanaugh et al., 2002b; DeAngelis et al., 1994; Webb et al., 2005). All analyses were performed in MATLAB.

Results

Experiment 1

Using a psychophysical paradigm, we quantified the perceived contrast of a target grating with different surrounding stimulus configurations (Figure 1). We sought to clarify whether or not dichoptically presented surrounds were capable of suppressing the perceived contrast of a target (Cai et al., 2008; Meese & Hess, 2004; Petrov & McKee, 2009). We expected stronger surround suppression for Monoptic versus Dichoptic configurations in Experiment 1, consistent

with the exclusion of a low-level monocular suppression component in the Dichoptic conditions (Cai et al., 2008; DeAngelis et al., 1994; Webb et al., 2005). Stronger suppression for Parallel versus Orthogonal surrounds was also predicted in both Monoptic and Dichoptic configurations, as previous work has suggested that a higher level, feature-selective component operates binocularly (Cai et al., 2008; Webb et al., 2005), although this is not yet clear (Petrov & McKee, 2009).

In Experiment 1, the presence and configuration of surrounding stimuli greatly influenced the perceived contrast of the target (Figure 2A). In the No Surround condition (gray) subjects reported veridical perception of target contrast, while the perceived contrast was generally reduced in the presence of surrounding stimuli, reflecting the expected surround suppression (Snowden & Hammett, 1998; Yu et al., 2001). Perceived contrast was significantly lower when compared with the No Surround condition for the following surround configurations: Parallel Monoptic, 1-tailed paired t test, $t(46) = 6.84$, $p < 0.001$; Orthogonal Monoptic, $t(45) = 5.81$, $p < 0.001$; and Parallel Dichoptic, $t(46) = 1.84$, $p = 0.036$; but not Orthogonal Dichoptic, $t(46) = 0.73$, $p = 0.2$.

The magnitude of surround suppression was next compared across surround conditions in a two-way ANOVA (2 surround orientations \times 2 optical conditions). There were significant main effects of orientation, $F(1, 5) = 10.4$, $p = 0.002$, and optics, $F(1, 5) = 69.1$, $p < 0.001$, but no significant interaction, $F(1, 5) = 0.87$, $p = 0.4$. Planned posthoc comparisons confirmed that perceived contrast was significantly lower in the Monoptic versus Dichoptic conditions [Figure 2A, Parallel Monoptic (red) < Parallel Dichoptic (magenta); $t(47) = 6.54$, $p < 0.001$; Orthogonal Monoptic (blue) < Orthogonal Dichoptic (cyan), $t(46) = 4.38$, $p < 0.001$], as well as in the Parallel versus Orthogonal conditions [Parallel Monoptic (red) < Orthogonal Monoptic (blue), $t(46) = 3.76$, $p < 0.001$; Parallel Dichoptic (magenta) < Orthogonal Dichoptic (cyan), $t(47) = 1.71$, $p = 0.047$]. These results are consistent with the predicted pattern; surrounds that were more similar (i.e., parallel) to the target evoked stronger suppression, as did presenting the target and surrounds in the same eye (Cai et al., 2008; DeAngelis et al., 1994; Webb et al., 2005). The results from Experiment 1 indicate that presenting target and surrounding stimuli in opposite eyes reduces the overall magnitude (but preserves orientation selectivity) of surround suppression during contrast perception. This is consistent with the hypothesis that Dichoptic presentation negates a low-level monocular component of surround suppression, but leaves intact a higher level component that is binocular and feature-selective.

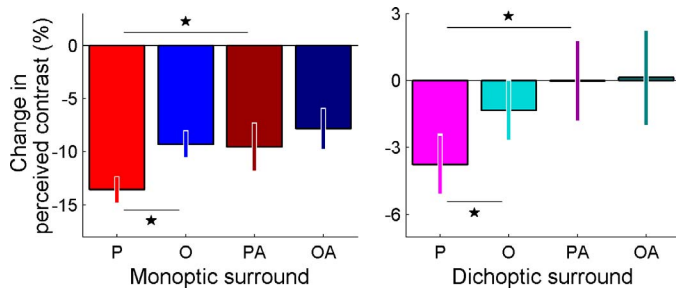


Figure 3. Comparing results from Experiments 1 and 2. Data shown are the mean from all six subjects. Colored error bars show 95% confidence intervals. Different surround conditions are shown along the x axis (P = Parallel, O = Orthogonal, A = with contrast adaptation). Asterisks indicate significant differences ($p < 0.05$) as determined by posthoc t tests. Note that the y axis scale differs between the two panels.

Experiment 2

Experiment 2 used the same psychophysical method and stimulus conditions as in Experiment 1, with the addition of a contrast adaptation paradigm (Methods, Experiment 2). This adaptation was intended to reduce the influence of surrounding stimuli during the perception of target contrast, an effect that has been observed using electrophysiology in animal models (Cavanaugh et al., 2002a; Durand, Freeman, & Carandini, 2007; Patterson, Wissig, & Kohn, 2013; Webb et al., 2005), but has not (to our knowledge) been examined in human psychophysics. Perceptually, adaptation to contrast transfers between eyes, and is specific to the adapted orientation (Blakemore & Campbell, 1969). Adaptation also leads to decreased neural responses in V1 (Carandini & Ferster, 1997). Thus, some have argued that susceptibility to adaptation may serve as a hallmark for visual processes that operate at a cortical level (Durand et al., 2007; Freeman, Durand, Kiper, & Carandini, 2002), although precortical effects of adaptation may not be ruled out (Kim & Rieke, 2001; Smirnakis, Berry, Warland, Bialek, & Meister, 1997). We expected that following adaptation, surround suppression within- and between-eyes would show little or no orientation selectivity, consistent with adaptation mitigating the influence of a higher level, binocular, feature-selective suppression component (Webb et al., 2005).

In Experiment 2, significant suppression of perceived contrast was observed in both the Monoptic conditions, 1-tailed paired t tests, $t(22) > 2.61$, p values < 0.008 , but not in the two Dichoptic surround conditions, $t(22) < -0.64$, p values > 0.7 , when compared with the No Surround condition (Figure 2B). A two-way ANOVA (2 surround orientations \times 2 optical configurations) revealed a significant main effect of

optics, $F(1, 5) = 26.2$, $p < 0.001$, but not orientation, $F(1, 5) = 0.27$, $p = 0.6$, and no significant interaction, $F(1, 5) = 0.23$, $p = 0.6$. Planned posthoc comparisons confirmed that suppression was stronger for Monoptic versus Dichoptic conditions [Figure 2B, Parallel Monoptic (dark red) $<$ Parallel Dichoptic (purple) & Orthogonal Monoptic (navy blue) $<$ Orthogonal Dichoptic (teal); $t(21-22) > 4.14$, p values < 0.001]. However, there was no consistent difference in suppression between Parallel and Orthogonal surrounds, Parallel Monoptic \approx Orthogonal Monoptic and Parallel Dichoptic \approx Orthogonal Dichoptic, $t(21-23) < 0.68$, p values > 0.2 . The results from Experiment 2 indicate little or no orientation selectivity for surround suppression following adaptation to contrast-reversing surrounding gratings, but that suppression remains stronger within- versus between-eyes.

Comparing between experiments

Next we directly compared the results from Experiments 1 and 2 (Figure 3), in order to examine how the contrast adaptation paradigm affected the magnitude of surround suppression. In a three-way ANOVA (2 surround orientations \times 2 optical configurations \times 2 adaptation states) we observed main effects of orientation, $F(1, 5) = 4.96$, $p = 0.027$, optics $F(1, 5) = 81.7$, $p < 0.001$, and adaptation, $F(1, 5) = 7.05$, $p = 0.008$, but no significant interactions between any factors, $F(1, 5) < 1.78$, p values > 0.18 . Planned posthoc comparisons showed that suppression was weaker after adaptation in both Parallel conditions: Figure 3, red $<$ dark red and magenta $<$ purple; 1-tailed independent t tests, $t(69-70) > 1.71$, p values < 0.046 , but no significant differences were observed with and without adaptation in the Orthogonal conditions, $t(68-69) < 0.62$, p values > 0.2 . We also sought to determine whether surround suppression was less orientation-selective following adaptation. To test this directly, we calculated the difference in perceived contrast between Parallel and Orthogonal for all runs in all subjects, in both the Monoptic and Dichoptic conditions of Experiments 1 and 2. When combining Monoptic and Dichoptic data, there was a trend toward a larger Orthogonal-Parallel difference before adaptation versus after, $t(139) = 1.47$, $p = 0.073$, suggesting that surround suppression was less orientation-selective following adaptation. The results from Experiments 1 and 2 together indicate that contrast adaptation reduces surround suppression by parallel (but not orthogonal) surrounds, both within- and between-eyes. This is consistent with adaptation reducing the influence of a higher level component of surround suppression that is binocular and feature-selective.

Discussion

Using a psychophysical paradigm, we examined how surrounding stimuli suppressed the perceived contrast of a target under a variety of stimulus and optical configurations, which were designed to probe whether suppression may be divided into distinct subcomponents with different functional properties. Experiment 1 showed that presenting target and surrounding stimuli in opposite eyes evoked suppression that was weaker than that observed within the same eye. Surround suppression was orientation selective, being stronger for parallel versus orthogonal surrounds regardless of the eye-of-origin. Using the same stimuli and subjects, Experiment 2 demonstrated that after contrast adaptation in the surrounding stimulus region, suppression no longer showed significant orientation tuning, but remained stronger within- versus between-eyes. Comparing between experiments, we see that our results support the existence of (at least) two suppression components: One that we call low-level is monocular, broadly tuned for orientation, and persists after contrast adaptation. The second component that we call higher level is binocular, narrowly orientation-tuned, and greatly diminished by adaptation. Our approach allowed us to firmly establish a link between these two suppression components in human vision, and the neural mechanisms described using similar methods in nonhuman primates (Webb et al., 2005).

Neural mechanisms of surround suppression

Stimuli presented outside the classical receptive field of a V1 neuron do not evoke a response on their own, yet are capable of modulating the response to stimuli presented within the receptive field, typically via suppression (Cavanaugh et al., 2002b; DeAngelis et al., 1994; Henry, Joshi, Xing, Shapley, & Hawken, 2013; Hubel & Wiesel, 1968; Walker et al., 1999). Based on the functional properties of surround suppression observed by Webb and colleagues (2005), they proposed that two suppression mechanisms operated at different stages of visual processing, which they refer to as “early” and “late.” The early mechanism was found to be broadly feature-selective, monocular, and insensitive to contrast adaptation, which suggested a mechanism operating at the level of the LGN or the input layers of V1. In contrast, the late mechanism was sharply tuned, binocular, and diminished by adaptation, all of which were consistent with a level of processing beyond V1 input layers, or in a higher visual area. Attributing the functional mechanisms identified by one study to the anatomical circuits described in another requires some speculation. Nevertheless, it

seems plausible to suggest linking the early mechanism to feed-forward suppression from the LGN (which is believed to be monocular and broadly tuned), and the late mechanism to some combination of local recurrent excitation and horizontal connections within V1, and/or feedback from higher visual areas (which appear binocular and feature-selective; Angelucci & Bressloff, 2006; Angelucci et al., 2002; Shushruth et al., 2012; Shushruth et al., 2013). This proposal is consistent with the interpretation provided by Webb and colleagues (2005), as well as with more recent work (Nurminen & Angelucci, 2014).

Linking neural mechanisms and perception

Dichoptic suppression

Although the mechanisms of surround suppression in human V1 may be assessed using functional methods such as fMRI (Chen, 2014; Zenger-Landolt & Heeger, 2003), a number of psychophysical methods can also be used to noninvasively examine the neural basis of surround suppression in the human visual system. Visual information is processed at early monocular stages (i.e., retina and LGN) before being combined between eyes within V1; by presenting center and surrounding stimuli in opposite eyes (dichoptically), one can examine the extent to which these stimuli interact beyond the binocular integration stage (Cai et al., 2008; Chubb et al., 1989; DeAngelis et al., 1994; Meese & Hess, 2004; Petrov & McKee, 2009; Webb et al., 2005). Note that while stimuli presented to different eyes may *first* interact in visual cortex, precortical suppression mechanisms may still contribute during dichoptic surround presentation, as a significant role for feedback from V1 to LGN during surround suppression has been reported (Sillito, Cudeiro, & Jones, 2006). Studies using electrophysiology in cats (DeAngelis et al., 1994) and macaques (Webb et al., 2005) have shown robust dichoptic surround suppression for many V1 neurons (with a target presented in the neuron’s preferred eye, and a surround in the nonpreferred), which may be slightly weaker than monocular suppression (both target and surround in the preferred eye). Although there is consistent (but limited) evidence to suggest surround suppression operates between-eyes in animal models, the results from psychophysical studies in humans are somewhat mixed.

In the current study, we observed modest but significant suppression of perceived contrast by Parallel Dichoptic surrounds in Experiment 1 (without adaptation; magenta bar in Figure 2A). This agrees with the results of Cai and colleagues (2008), who report suppression of perceived contrast by a (visible) parallel dichoptic surround (average reported suppression index of ~ 0.12 , or a reduction in perceived contrast of

~4%). Dichoptic surround suppression was also reported in studies of spatial masking (Meese & Hess, 2004; see below), and temporal contrast perception (D’Antona, Kremers, & Shevell, 2011). It has been proposed that surround suppression is diminished when the visual system infers that separate objects give rise to center and surrounding stimuli (Coen-Cagli, Dayan, & Schwartz, 2012; Coen-Cagli, Kohn, & Schwartz, 2015); weaker suppression for dichoptic versus monoptic surrounds may be consistent with such an inference for stimuli appearing in opposite eyes.

Our results differ from those of Petrov and McKee (2009), who report a very slight *enhancement* of perceived contrast by a dichoptic parallel surround (though they observed robust suppression of contrast detection by the same surround configuration, see also Petrov & McKee, 2006). Stimulus differences do not appear sufficient to account for this discrepancy, as their stimuli were quite similar to ours (and to those used by Cai et al., 2008). The disagreement may instead be attributed to individual differences in the magnitude and sign of between-eye surround modulation. We note that among our six participants, one showed no change in perceived contrast in the Parallel Dichoptic condition (Mean = -0.4% , $SEM = 4.0\%$), whereas another showed a modest enhancement of perceived contrast (Mean = $+6.5\%$, $SEM = 3.2\%$), similar to the results obtained from the three subjects studied by Petrov and McKee (2009). In an early study of surround suppression, Chubb and colleagues (1989) also reported no effect of a dichoptic surround on the perceived contrast of a target. Although the argument regarding individual differences may also apply in this case given the low sample size ($N = 2$), Meese and Hess (2004) have instead suggested that the lack of dichoptic suppression reported by Chubb and colleagues (1989) may be attributed to their use of high spatial frequency stimuli (5.8–11.6 cycles/°). This proposal is generally in line with the model of surround suppression proposed by Webb and colleagues (2005), wherein the late binocular mechanism responds poorly at spatial frequencies above ~ 6 cycles/°, whereas the early monocular mechanism responds to a greater range of spatial frequencies. Overall, our Dichoptic data lend support to the view that there is a significant higher level component that contributes to surround suppression during human contrast perception, which operates at a level of visual procession after binocular integration. Future studies may examine whether suppression by this component is mitigated by the use of high spatial frequency stimuli.

If dichoptic surround suppression depends solely on a cortical mechanism that is sharply orientation-tuned, one would expect that dichoptic orthogonal surrounds should elicit little or no suppression. However, the orientation-selectivity of dichoptic surround suppres-

sion has not been directly examined in many cases (Cai et al., 2008; Webb et al., 2005), and never to our knowledge following contrast adaptation (see Discussion, Adaptation). The results from Experiment 1 in the current study align with the above prediction; we saw no significant suppression of perceived contrast in the Orthogonal Dichoptic condition, and suppression was significantly greater in the Parallel Dichoptic condition (magenta vs. cyan bars in Figure 2A). Our results in this case agree with those of Petrov and McKee (2009), who found significant suppression of contrast detection by parallel but not orthogonal dichoptic surrounds. These data stand in contrast to those of Meese and Hess (2004), who found significant suppression with a dichoptic surround oriented 45° relative to the target and with a factor of 3 greater spatial frequency. This discrepancy may be explained by the fact that in the latter study, the annular surround partially overlapped the target stimulus (inner diameter of the annulus was the same diameter as the half-height of the Gaussian target envelope). This might be sufficient to preclude stable fusion of the stimuli in each eye into a single percept, thereby evoking an effect such as dichoptic cross-orientation suppression (Baker, Meese, & Summers, 2007), or even binocular rivalry (Tong, Meng, & Blake, 2006), instead of (or in addition to) surround suppression of target contrast perception. Indeed, Meese and Hess (2004) report that for the subject who demonstrated the strongest dichoptic suppression, the target stimulus “often appeared to be invisible.” Finally, dichoptic surround modulation of temporal contrast perception appears to be tuned for relative temporal phase between target and surround (D’Antona et al., 2011), which may be mechanistically similar to the orientation tuned interocular suppression we observed during spatial contrast perception. Our observation of orientation-tuned dichoptic surround suppression lends support to a model of surround suppression that involves a higher level, sharply tuned binocular component (Cai et al., 2008; Nurminen & Angelucci, 2014; Petrov & McKee, 2009; Webb et al., 2005).

Adaptation

Adaptation is a potent form of plasticity in which the neural response to a visual stimulus is reduced following sustained exposure (for reviews, see Kohn, 2007; Solomon & Kohn, 2014). Following adaptation to high-contrast stimuli, neurons in V1 become hyperpolarized and show reduced contrast sensitivity (Carandini & Ferster, 1997). Although contrast adaptation has been observed in the retina (Kim & Rieke, 2001; Smirnakis et al., 1997), this effect is also believed to operate in part at a cortical level; adaptation is somewhat specific to stimulus orientation and may

transfer between eyes (Blakemore & Campbell, 1969; Carandini, Movshon, & Ferster, 1998; Marlin, Douglas, & Cynader, 1991). Contrast adaptation has been used to probe the neural mechanisms underlying specific perceptual phenomena. For example, cross-orientation suppression (in which the response to a test grating is suppressed by a superimposed orthogonal mask) has been shown to be relatively unaffected by contrast adaptation (Freeman et al., 2002), which has been used as evidence to support a precortical locus for this suppression (see also Baker et al., 2007 for a relevant examination of both precortical and cortical mechanisms for cross-orientation suppression).

Conversely, surround suppression in visual cortex is weakened (but not eliminated) following prolonged adaptation to a high contrast surrounding stimulus (Cavanaugh et al., 2002a; Durand et al., 2007; Patterson et al., 2013; Webb et al., 2005), with greater release from suppression found in neurons whose orientation preference matches the adapter (Patterson et al., 2013). Recent work indicates that adaptation may interact with normalization (Solomon & Kohn, 2014), the process by which a neuron's response is reduced by the summed responses of its neighbors (Carandini & Heeger, 2012; Heeger, 1992). Weaker normalization following adaptation has been proposed to account for the different response patterns observed in V1 after adapting to large stimuli (filling the surround), compared with small stimuli (filling only the classical receptive field; Patterson et al., 2013; Wissig & Kohn, 2012). Such an effect may also explain improved behavioral performance during visual search following adaptation to a large grating (Wissig, Patterson, & Kohn, 2013). The above studies suggest that adaptation may attenuate a portion of the surround suppression effect by dampening the response of neurons within early visual cortex (e.g., V1) whose receptive field centers are located in the surrounding stimulus region, and thus form the normalization pool for neurons with receptive fields in the target region. This aligns with the model of surround suppression proposed by Webb and colleagues (2005) who argued that adaptation can reduce the contribution of a higher level (possibly cortical), binocular, sharply tuned suppression mechanism, but spares a low-level one that is monocular and broadly tuned.

Using a combination of surround orientations, stereoscopic configurations, and adaptation states, the current study provided a strong test of this model. Our results from Experiment 2 showed that surround suppression of perceived contrast in humans is weaker and lacks significant orientation selectivity following contrast adaptation in the surrounding region. Adaptation likely reduced the effective contrast of the surrounding stimuli in our paradigm. Previous studies have reported weaker and less orientation-selective

surround suppression for surrounds with much lower physical contrast than the associated center stimuli, with suppression having been abolished altogether in some cases (Henry et al., 2013; Webb et al., 2005; Xing & Heeger, 2001; Yu et al., 2001). Further, significant monoptic but not dichoptic suppression was observed following adaptation. Although we cannot rule out the possibility of some precortical effects of adaptation (Kim & Rieke, 2001; Smirnakis et al., 1997), we observed no significant suppression for the Dichoptic conditions following adaptation in Experiment 2 (Figure 2B), which indicates a strong interocular effect of adaptation and is consistent with a cortical mechanism. Thus, our findings lend support to the proposal that adaptation can specifically weaken a higher level component of surround suppression while preserving a low-level component, and provide evidence for such components in the human visual system.

Stimulus timing

One final technique that has been used to parse different components of surround suppression involves varying the stimulus duration and/or stimulus onset asynchrony between target and surround (Ishikawa, Shimegi, & Sato, 2006; Petrov & McKee, 2009). Results from Ishikawa and colleagues (2006) were consistent with the existence of two mechanisms for “metacontrast masking,” one fast component that persisted at longer asynchronies (surrounds appearing 60–80 ms after targets) and was broadly tuned for orientation and spatial frequency, and another slower component with sharper tuning that operated only at short asynchronies. However, these findings were disputed by Petrov and McKee (2009), who found no suppression by orthogonal surrounds at any asynchrony tested. In another set of experiments from the same study (Petrov & McKee, 2009), these authors found that at short stimulus durations (≤ 100 ms), surrounds viewed binocularly evoke stronger suppression during contrast detection, while suppression is mild at all durations for dichoptic surrounds. In the current study, stimulus timing was quite different; surrounding stimuli were presented for 1–2 s before the appearance of a brief target (100 ms). This paradigm was designed to ensure that processes underlying contextual modulation would already be in place prior to the appearance of the target (Joo et al., 2012; Joo & Murray, 2014). Our results demonstrate that when judging perceived contrast, both low- and higher level components of surround suppression can operate throughout a long delay between surround onset and subsequent target presentation.

Keywords: contextual modulation, contrast perception, mechanisms, dichoptic, contrast adaptation

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