Effects of binocular suppression on surround suppression

The responses of neurons in the primary visual cortex (V1) are generally inhibited by stimuli surrounding their classical receptive fields (CRF). This surround suppression can influence the visual perception of stimuli. For instance, the presence of a surround stimulus can decrease the apparent contrast of a central stimulus. A recent neurophysiological study in nonhuman primates suggests that two distinct mechanisms, early and late mechanisms, give rise to surround suppression. Here, we used binocular suppression to render the surround stimuli invisible and evaluated the effects of this masking on the two types of surround suppression. We found that the early mechanism was unsusceptible to, whereas the late mechanism was eliminated by, binocular suppression. The distinct effects of binocular suppression on the early and late mechanisms suggest that the two types of surround suppression arise from different neural substrates.

Keywords: psychophysics, surround suppression, binocular suppression


Introduction

Hubel and Wiesel (1965, 1968) found that the response of V1 neurons in cat and monkey was reduced when an otherwise optimal stimulus was extended beyond the neuron’s CRF. Since then, this type of inhibition, now referred to as surround suppression (which we will abbreviate as SS), has been widely explored in physiological and psychophysical studies (Bair, Cavanaugh, & Movshon, 2003; Cannon & Fullenkamp, 1991; DeAngelis, Freeman, & Ohzawa, 1994; Petrov, Carandini, & McKee, 2005; Webb, Dhruv, Solomon, Tailby, & Lennie, 2005). Despite years of research, the mechanism underlying SS remains unclear. Thalamocortical feedforward (Ozeki et al., 2004), intracortical horizontal (Stettler, Das, Bennett, & Gilbert, 2002) and extrastriate feedback (Bair et al., 2003) connections to V1 have been proposed to serve as a possible source of SS. It is assumed that SS is not attributable to a single mechanism but rather a combination of multiple sources (Angelucci & Bressloff, 2006; Séries, Lorenceau, & Fregnac, 2003). Webb et al.’s (2005) recent physiological study supports this hypothesis. They suggested that SS in primate V1 was generated by two distinct mechanisms, one early and one late. The early SS is untuned and monocularly driven and may originate in the lateral geniculate nucleus (LGN) or input layers of V1. The late one, however, is stimulus tuned and binocularly driven and is a cortical mechanism.

Likewise, the findings from psychophysical studies imply that SS in human vision may also result from multiple mechanisms. Chubb, Sperling, and Solomon (1989) found that the suppressive effect induced by random texture could not transfer between eyes, whereas other researchers who used collinear center-surround gratings as stimuli reported opposite results (Meese & Hess, 2004; Petrov & McKee, 2006). In addition, Yu and Levi (2000) showed that iso-surround and cross-surround
had different effects on pedestal masking, although iso-
and cross-surround had similar pattern of suppressive
effects on central targets (Xing & Heeger, 2000). These
psychophysical evidence suggests that a single mechanism
may be insufficient to explain the diverse properties of SS
induced by different stimuli.

Binocular suppression has been an effective method to
determine if the mechanism of a visual process occurs
before or after the neuronal site for the suppression of
rivalry (Blake, 1995; Blake & Fox, 1974; Kim & Blake,
2005; Lehmkühle & Fox, 1975; Moradi, Koch, & Shimono,
2005; Wiesenefelder & Blake, 1990). It occurs
when incompatible images are presented to corresponding
regions of the two eyes. During this process, the stimulus
in one eye is masked from awareness by the stimulus in
the other eye (Blake & Logothetis, 2002). In the present
study, we attempted to explore whether in human vision
there also existed the similar early and late mechanisms of
SS that were found in macaque monkey (Webb et al.,
2005). We dissociated the putative early and late SS by
means of manipulating the relative orientation of central
and surround gratings as well as the way by which the
central and surround gratings were presented, and we
measured the influences of binocular suppression induced
by a dynamic noise on the putative early and late
mechanisms. It was supposed that the early and late SS
should be differently affected by binocular suppression if
they arose from distinct neural substrates. We report that
the early SS is unsusceptible to whereas the late one is
eliminated by binocular suppression, suggesting that the
two types of SS differ in their neural sources.

Method

Apparatus, observers, and stimuli

Stimuli were generated by using Matlab and the
Psychophysics Toolbox (Brainard, 1997; Pelli, 1997) and
were presented on a linearized 19” Dell UltraScan P991
monitor (1024 × 768 resolution; 100-Hz refresh rate).
Four naive observers and the first author participated in
Experiments 1, 2, and 3. Another naive observer and the
first author participated in Experiment 4. All observers
had normal or corrected-to-normal vision. They viewed a
pair of dichoptic displays through a mirror stereoscope
(viewing distance, 72 cm; a region of about 15° × 22°
could be seen). A black fixation point (0.114° × 0.114°)
and a black square frame (5.95° × 5.95°) were always
presented in each display to promote stable binocular
alignment. Three kinds of stimulus were used, namely, a
circular central grating (diameter, 1.42°), an annular
surround grating (inner diameter, 1.42°; outer diameter,
5.68°), and an annulus containing dynamic luminance
noise (see Figure 1). Both gratings were static sinusoidal
grating with a mean luminance of 20.0 cd/m². The
contrast of the surround grating was usually 100%, unless
otherwise noted. The contrast of the central grating was
fixed at 30% (in Experiments 1, 2, and 3) or systemati-
cally varied from 20% to 80% (in Experiment 4). The
spatial frequency of gratings was either 4.84 cycles/degree
(in Experiments 1, 2, and 3) or 7.26 cycles/degree (in
Experiment 4). The noise consisted of small squares of
0.085° × 0.085°, each of which changed in luminance
every 100 ms to a value drawn randomly from 0 to
40.0 cd/m² (with full contrast, in Experiments 1, 2, and 3)
or from 10.0 to 30.0 cd/m² (with contrast of 50%, in
Experiment 4). The border of the circular stimulus and the
inner border of the annular stimuli were blurred by half a
cycle of a raised cosine function. The width of blurred
borders was 0.28°. The remainder of the screen was held
at the mean luminance (20.0 cd/m²).

Procedure

In this study, surround suppressive effects from visible
and invisible surround gratings were measured. In the
invisible condition, the surround grating was presented to
the observer’s non-dominant eye, while an annular
dynamic noise, which was used to suppress the annular
surround grating, was presented to the corresponding
location in the dominant eye (Figures 1B, 1C, and 1D).
Thus, the surround grating was rendered invisible by the
noise in the opposite eye. In the visible condition, stimuli
were identical to those in the invisible condition except
for the replacement of the noise by a blank mean
luminance field.

In Experiment 1, the central and surround gratings were
both vertical and were presented monoptically (i.e., both
appeared in the non-dominant eye). In the invisible
condition (Figure 1A), observers kept fixation and per-
formed a two interval forced-choice (2IFC) contrast
discrimination task. The two intervals that lasted for
500 ms each were separated by a 300-ms blank interval.
Either an isolated central test grating (Control trial,
Figure 1A, right) or an identical test grating surrounded by
an annular grating (Experimental trial, Figure 1A, left) was
displayed in the first interval and an isolated central
comparison grating was displayed in the second interval.
Test and comparison gratings that both appeared in the
fovea were ramped on and off smoothly over a 100-ms
period to reduce any transient artifact. Observers judged
which interval contained the higher-contrast grating. We
used a QUEST staircase procedure (King-Smith, Grigsby,
Vingrys, Benes, & Supowit, 1994) to measure the apparent
contrasts (i.e., the contrast at which the comparison grating
matched the test grating) of the test gratings for both
the experimental and control trials by changing the contrast
of the comparison grating. Each 40-trial run consisted of an
experimental-trial and control-trial staircases that included
20 trials each. The experimental and control trials were randomly presented in each run. A suppression index (SI), defined as $SI = (\text{apparent contrast}_{\text{control trial}} - \text{apparent contrast}_{\text{experimental trial}}) / \text{apparent contrast}_{\text{control trial}}$, was calculated for each run and was used to assess the suppressive effect of the surround grating. Each data point of SI was averaged from at least four repeated runs for each observer. In the visible condition, the stimuli and procedure were the same as those in the invisible condition except for the replacement of the noise by a blank mean luminance field.

To ensure that the surround grating in the invisible condition was effectively suppressed by the noise, the surround grating was presented to the non-dominant eye and came on 1000 ms earlier than the noise in the dominant eye (Wolfe, 1984). In addition, before formal experiments, we conducted a preliminary experiment in which observers reported whether or not they could perceive the surround grating in the non-dominant eye when the dynamic noise appeared in the dominant eye. Three out of five observers (Y.Q.C., W.L.Q., and D.P.) reported that they did not see the surround grating. The other two (Y.C.C. and L.X.H.) claimed that a vast majority of areas but a part of outer border of the surround grating was invisible.

In Experiment 2, the central and surround gratings were mutually orthogonal (i.e., vertical center and horizontal surround) and were presented monoptically (i.e., both appeared in the non-dominant eye; Figure 1C). In Experiment 3, the central and surround gratings were mutually parallel (i.e., vertical center and vertical surround) and were presented dichoptically (i.e., the central grating appeared in the dominant eye while the surround grating appeared in the non-dominant eye; Figure 1D). Other aspects of Experiments 2 and 3 were identical to Experiment 1.
In Experiment 4, we reconducted Experiments 1, 2, and 3 in two observers by varying the center contrast. Four contrast levels (20%, 30%, 50%, and 80%) were used. To lessen potential impacts of the surround noise on the apparent contrast, the noise had a contrast of 50%, instead of the full contrast that was used in Experiments 1, 2, and 3. With this low contrast, the noise could nevertheless mask the surround grating effectively for the two observers.

Results

In the present study, we investigated the surround suppressive effects induced by three types of surround (i.e., Monoptic parallel surround, Monoptic orthogonal surround, and Dichoptic parallel surround). Webb et al.’s (2005) recent electrophysiological study suggested that suppressive effects induced by these types of surround originated from different sources. We tried to test this hypothesis in human vision by evaluating the susceptibilities of the suppressive effects to binocular suppression. We supposed that the SS induced by these types of surround should arise from distinct sources if they were differently affected by binocular suppression.

Experiment 1: SS from a monoptic parallel surround

In this experiment, the central and surround gratings were mutually parallel and were monoptically presented (Figures 1A and 1B). As shown in Figure 2A, the surround grating caused clear suppression in the apparent contrast of the central test grating in both the visible (SI $\pm$ SEM: $0.204 \pm 0.021$; $t$-test, $t(4) = 9.71, p < 0.001$) and invisible (SI $\pm$ SEM: $0.170 \pm 0.013$; $t$-test, $t(4) = 13.00, p < 0.001$) conditions. However, the suppressive effect in the invisible condition was significantly weaker than that in the visible condition (paired $t$-test, $t(4) = 2.80, p < 0.05$). This result shows that when the surround grating was masked by binocular suppression, although still inducing potent suppressive effect on the central target, its effect was weakened.

Webb et al. (2005) suggest that there exist two types of SS: the early mechanism is untuned and monocularly driven; the late mechanism is orientation selective and binocularly driven. According to this hypothesis, the monoptic parallel surround could induce both the early and late mechanisms. Therefore, the suppressive effect observed in this experiment should be attributable to the summation of the two types of SS. This single experiment...
cannot give us information about how binocular suppression interferes with the early and the late SS, respectively. The following experiments bear on this question.

**Experiment 2: SS from a monoptic orthogonal surround (the early mechanism)**

In **Experiment 2**, the central and surround gratings were mutually orthogonal and were monoptically presented (Figure 1C). Because the late SS is narrowly tuned to orientation (Webb et al., 2005), its suppressive effect may decay to a low level once the surround is orthogonal to the target. Therefore, the monoptic orthogonal surround should mainly produce the early SS.

As shown in Figure 2B, the apparent contrast of the test grating in the experimental trial was suppressed in both the visible (SI = SEM: 0.130 ± 0.007; t-test, t(4) = 18.80, p < 0.001) and invisible (SI = SEM: 0.123 ± 0.004; t-test, t(4) = 30.20, p < 0.001) conditions. The magnitudes of the suppressive effect in both conditions were virtually similar (paired t-test, t(4) = 1.51; p > 0.20), indicating that binocular suppression had no effect on this type of SS. However, one might argue that the effect of binocular suppression is concealed by the nonlinearity of the visual system because the visual response could be saturated with the full surround contrast used in **Experiment 2** (Blake, Tadin, Sobel, Raissian, & Chong, 2006). If this is the case, binocular suppression should affect SS evidently when the surround contrast is low. To test this possibility, we reconducted **Experiment 2** on two of the original observers and adopted four levels of the surround contrast that ranged from 30% to 100%. The result shown in Figure 2C indicates that, at each level of surround contrast, binocular suppression nonetheless has no effect on SS. We thus suggest that the early SS is unsusceptible to binocular suppression and this insusceptibility cannot be explained by the nonlinearity of the visual system. That is, the early SS can be induced without perception of the surround stimulus.

**Experiment 3: SS from a dichoptic parallel surround (the late mechanism)**

In **Experiment 3**, we turned our attention to the late mechanism of SS. The late mechanism is binocularly driven while the early mechanism is monocularly driven (Webb et al., 2005). To isolate the late mechanism, the test grating and the surround grating were parallel and were presented dichoptically (Figure 1D).

The result depicted in Figure 2D indicates that, in the visible condition, the surround grating could suppress the test grating that appeared in the opposite eye (SI = SEM: 0.124 ± 0.012; t-test, t(4) = 10.71, p < 0.001). In the invisible condition, however, the suppressive effect completely disappeared (SI = SEM: −0.001 ± 0.010; t-test, t(4) = −0.04, p > 0.90). The suppressive effects of the two conditions were significantly different (paired t-test, t(4) = 6.48, p < 0.005). This result indicates that the suppressive effect of the late SS can be eliminated by binocular suppression.

**Experiment 4: Varying the center contrast**

In this experiment, we systematically varied the central test contrast from 20% to 80%. The surround contrast was fixed at 100%. The spatial frequencies of the central and surround gratings were 7.26 cycle/degree. The three stimulus configurations (i.e., monoptic parallel surround, monoptic orthogonal surround, and dichoptic parallel surround) that were assumed to induce different surround suppressive mechanisms were tested. In invisible conditions, the noise contrast was set to a low level (50%) so as to lessen potential impacts of the surround noise on perceived contrast (see below for details).

The individual results of the two observers were depicted in Figure 3, in which SI was plotted as a function of center contrast. The data demonstrated that, in visible conditions of all stimulus configurations, the surround suppressive effect decreased nearly monotonically with increasing center contrast. This result is consistent with previous reports (Takeuchi & De Valois, 2000; Xing & Heeger, 2000). Similarly, when the surround grating was masked by the noise (invisible conditions), the suppressive effect also varied monotonically as center contrast increased from low to high. However, the visible surround might be more effective than the invisible surround to suppress the central grating, depending on the center-surround stimulus configuration. Specifically, for the monoptic parallel surround (Figure 1B), the suppressive effect was somewhat weaker in the invisible condition than that in the visible condition (Figure 3A); for the monoptic orthogonal surround (Figure 1C), the suppressive effect was comparable for both conditions (Figure 3B); and for the dichoptic parallel surround (Figure 1D), the suppressive effect in the invisible condition was much weaker than that in the visible condition, approaching zero (Figure 3C). These results replicated the findings of Experiments 1, 2, and 3 and further indicated that suppressions from different surround stimuli were influenced by binocular suppression in different ways, suggesting that there exist distinct mechanisms underlying SS.

As shown in **Experiment 3** (Figure 2D) and replicated in this experiment (Figure 3C), the suppressive effect induced by the dichoptic parallel surround grating was (nearly) eliminated by the binocular suppression of the surround noise. In the invisible condition of this stimulus configuration, the surround noise and the central target were actually presented in the same eye (Figure 1D). Previous research has reported that a monoptic high-contrast texture surround would weaken the apparent contrast of a central texture patch (Chubb et al., 1989).
Therefore, a potential concern is that the monoptic noise in Experiment 3 might induce a reduction of the apparent contrast of the central grating (i.e., the monoptic noise also produced SS on the central target), resulting in ceiling effects in SS. It would be possible that the ceiling effects concealed the additional surround suppressive effect of the dichoptic surround grating. To lessen this possibility, the contrast of the noise in Experiment 4 had been set to a low level (50%) instead of the full contrast that was used in Experiment 3. The low-contrast noise might be less effective in producing SS. Furthermore, to evaluate the impact of the noise, we ran a control experiment to measure apparent contrast of a central grating at four contrast levels when the central grating was surrounded only by a monoptic noise. The result depicted in Figure 4 showed that the noise had slight surround suppressive effects that were much weaker than the effects of the dichoptic grating (see the filled dots in Figure 3C), suggesting that the noise surround might not be sufficient to conceal the effect of the dichoptic grating.

**Discussion**

In line with a previous neurophysiological study in nonhuman primates (Webb et al., 2005), the present
results provide psychophysical evidence indicating that, in the human visual system, there also exist two distinct mechanisms of SS. The early mechanism that is monocularly driven and insensitive to orientation is unsusceptible to binocular suppression. The possibility that this insusceptibility resulted from the nonlinearity of the visual system (Blake et al., 2006) was ruled out by a further experiment, in which we systematically varied the surround contrast and nonetheless did not observe any effect of binocular suppression even at low levels of surround contrast. On the other hand, the late mechanism that is binocularly driven and tuned to orientation is completely abolished by binocular suppression. The explanation that the surround suppressive effect of monoptic noise on the target concealed the surround suppressive effect of the dichoptic grating seems inadequate to account for the abolishment of the SS because the monoptic noise was insufficient to produce ceiling effects in surround suppression.

The distinct influences of binocular suppression on the two types of SS imply that they arise from different neural mechanisms. In the invisible condition of the present experiments, surround gratings were nearly suppressed from visual awareness by the noise in the opposite eye. It has been proposed that the extent to which neural activity of visual areas correlates with visual awareness increases along the visual hierarchy (Logothetis, 1998). In line with this proposal, psychophysical evidence shows that some early visual adaptations, such as orientation-dependent adaptation (Blake & Fox, 1974) and translational motion aftereffect (Lehmkuhle & Fox, 1975), can be induced by invisible adaptor; by contrast, more complex adaptations, such as spiral motion aftereffect (Wiesnfelder & Blake, 1990) and face adaptation (Moradi et al., 2005), are eliminated in the absence of visual awareness. The fact that the early SS survives binocular suppression suggests that its mechanism is located at an early stage of visual processing that does not require visual awareness, presumably occurring before the neural site(s) of binocular suppression. In contrast, the elimination of the late SS caused by binocular suppression suggests that the late SS should originate from a later source that should lie beyond the neural site(s) of binocular suppression; the surround information that is exploited to induce the late SS should be cut off before they could travel across the site(s) of binocular suppression.

Electrophysiology of SS has been extensively studied in V1, but the similar suppressive effect has also been observed in other visual areas such as LGN, V2, and MT (Allman, Miezin, & McGuinness, 1985). Given the potential involvement of these areas in the representation of the apparent contrast of the central grating, we are not confident that the early and late SS found in the present study correspond to the early and late mechanisms of SS in V1 reported in Webb et al. (2005). Still, basing on the present results, we could speculate that the early SS might originate from early stages of visual processing such as LGN and/or monocular neurons of V1 where the neural activities are generally thought to survive binocular suppression (Lehky & Maunsell, 1996; Leopold & Logothetis, 1996; but see Haynes, Deichmann, & Rees, 2005; Wunderlich, Schneider, & Kastner, 2005), while the late SS might arise from later stages such as extrastriate cortex where the neural activities are attenuated by binocular suppression (Leopold & Logothetis, 1996; Logothetis & Schall, 1989). However, because neural mechanism underlying rivalry suppression is far from being fully understood (Blake & Logothetis, 2002; Tong, Meng, & Blake, 2006), we cannot determine the exact sites at which the early and late SS transpire. In any case, the current results suggest that the two types of SS are originated from distinct sources—the early SS precedes binocular suppression which in turn precedes the late SS. We thus infer that the two mechanisms operate in series and that the early mechanism precedes the late one.

As described above, the early and late SS should originate from different sources. The distinct properties of the two types of SS should be due to different natures of their sources. Furthermore, their distinct properties may provide insights into their different roles in visual processing. The characteristics of the early SS, e.g., broadly tuned to orientation and spatio-temporal frequency (Cannon & Fullenkamp, 1991; DeAngelis et al., 1994; Webb et al., 2005), monocularly driven (Chubb et al., 1989; Webb et al., 2005), unsusceptible to contrast adaptation (Webb et al., 2005), are much like those of cross-orientation suppression (DeAngelis, Robson, Ohzawa, & Freeman, 1992; Freeman, Durand, Kiper, & Carandini, 2002; Li, Peterson, Thompson, Duong, & Freeman, 2005), which is considered to contribute to a
contrast normalization mechanism that helps the visual system maintain sensitivity to wide ranges of contrasts (DeAngelis et al., 1992; Heeger, 1992). This similarity encourages the idea that early SS may also be involved in the normalization mechanism so that the sensitivity to the target is adjusted depending on its contextual contrast.

In contrast, the late SS is tightly tuned to orientation: the suppressive effect is strongest when the target and the surround share the same orientation and diminishes when the surround is orthogonal to the target (Webb et al., 2005). This property could suggest an important role of the late SS for detection of orientation contrast that is a powerful cue for pre-attentive texture discrimination. Therefore, this orientation-specific suppression may provide a substrate for segregation of figures and objects from the backgrounds of visual images (DeAngelis et al., 1994; Lamme, 1995). Furthermore, the present result that an invisible surround cannot induce the late SS is consistent with previous observations that the contextual modulation related to the figure-ground segregation is prevented in the absence of awareness (Lamme, Zipser, & Spekreijse, 2002; Supér, Spekreijse, & Lamme, 2001). This consistency may corroborate the role of the late SS in the figure-ground segregation.

In the present study, it was observed that the orientation-specific SS (i.e., the late SS) was canceled when its inducer was rendered invisible by binocular suppression. However, it is worth noting that not all orientation-specific center-surround interactions are necessarily eliminated by binocular suppression. For example, tilt illusion, a phenomenon of simultaneous orientation contrast that refers to apparent tilt of a vertical grating when it is surrounded by a tilted inducing grating, is preserved even though the inducer is perceptually suppressed by rivalry suppression (Pearson & Clifford, 2005; Wade, 1980; but see Rao, 1977). The distinct influences of binocular suppression on these orientation-specific center-surround interactions imply that they might arise from distinct neural mechanisms.

In summary, our study indicates that the two types of SS that were found in monkeys also exist in human vision. The early mechanism is unsusceptible to the masking of binocular suppression, while the late one is nearly eliminated by the masking. We suggest that the two mechanisms are mediated through different neural substrates.

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