Surround modulation in human vision unmasked by masking experiments

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The responses of neurons in cat and monkey primary visual cortex are modulated by stimuli outside the classical receptive field. Here we report psychophysical evidence from masking experiments for two distinct types of surround modulation, one narrowly tuned to iso-orientation (stimuli with center and surround at the same orientation) and the other broadly tuned to cross-orientation (center and surround at perpendicular orientations). Surround modulation at iso- and cross-orientations showed distinct contrast dependencies, and high-contrast cross-oriented surrounds were able to completely eliminate masking. Surround modulation was modeled by subtracting divisive inhibition that raised the gain of spatial filters.

Responses of V1 neurons to stimuli presented within the classical receptive field are modulated by surround stimuli beyond the classical receptive field[1–5]. Surround modulation suggests that V1 neurons respond to visual features far more complex than single-line segments, and are probably involved in more complex pattern perception. Surround modulation also influences the detectability and appearance of stimuli, as evidenced by psychophysical studies of contrast detection[6–8] and apparent contrast[9,10]. Those studies, which mainly focus on iso-orientation effects, suggest suppressive and facilitative surround modulation. Contrast detection can be facilitated by nearby collinear flanks[6], but apparent contrast is reduced by iso-oriented surrounds[9]. Cross-orientation surround effects are studied much less, probably because a few studies have reported weak or no cross-orientation surround effect on contrast detection[6] and apparent contrast[9,10]. This lack of effect, however, is inconsistent with neurophysiological evidence for strong facilitation by surround stimuli orthogonal to the preferred orientation of visual receptive fields[3,4]. It is also inconsistent with facilitative cross-orientation effects in higher-level visual tasks, such as the pop-out effect of a line segment embedded in orthogonally oriented line segments in visual search[11].

We applied a different approach to investigate surround effects at iso- and cross-orientations. This approach potentially could tie the psychophysical surround effects more closely to their neurophysiological counterparts on a unit-to-unit basis. In psychophysical models of human vision, spatial filters serve as the basic functional units of visual processing, and their organization typically reflects the organization of V1 simple-cell receptive fields[12]. This organization is often studied by masking experiments that measure the influence of a suprathreshold pedestal (such as a grating) on the visibility of a target. The dimensions of spatial filters can be estimated from the dimensions of the pedestal producing maximal masking[13]. Using a spatially localized target and optimized pedestals, our current study revealed psychophysical surround modulation with previously unappreciated scope and complexity.

RESULTS

We measured the effect of a surround grating on the contrast thresholds for a small elongated target centered on a circular pedestal grating (Fig. 1). The size of the pedestal was optimized to produce maximal masking and reflect the spatial extent of the 'perceptive field' of the spatial filters most sensitive to the target[13]. The surround grating abutting the pedestal therefore covered areas beyond the 'perceptive field' of the spatial filter, perceptually analogous to covering surround areas outside the classical receptive fields of visual neurons.

With the surround and pedestal at the same contrast (40%) and spatial frequency (8 cycles per degree, c.p.d.), the surround generally facilitated target discrimination by lowering the contrast threshold over a wide range of surround orientations (Fig. 2). Facilitation was strongest when the pedestal and surround either had the same orientation (iso-orientation), or were orthogonal to each other (cross-orientation). Facilitation at iso-orientation was greatly reduced when the pedestal and surround orientations differed by as little as 7.5°, and gradually recovered after 15° to become maximal again at cross-orientation, at which the pedestal and surround had the highest orientation contrast. The orientation tuning function of surround modulation was nicely fitted (solid curve fitted to mean data) by the linear summation of two Gaussians plus a constant. These two Gaussians, one narrowly tuned to iso-orientation and the other very broadly tuned to cross-orientation, suggest two distinct orientation-tuned mechanisms in surround modulation. The constant reveals a component of surround effect not tuned to orientation, representing facilitative signals from all orientations.

Surround modulation became more complex when the surround contrast was varied. For cross-oriented surrounds, facilitation increased monotonically with surround contrast (Fig. 3, filled circles). Unexpectedly, cross-oriented surrounds at the highest contrast (80%) effectively eliminated pedestal masking, driving contrast thresholds down, equal to the detection thresholds for the same target measured with no pedestal (Fig. 3, dashed lines). Masking by the 40%-contrast pedestal produced a mean contrast threshold

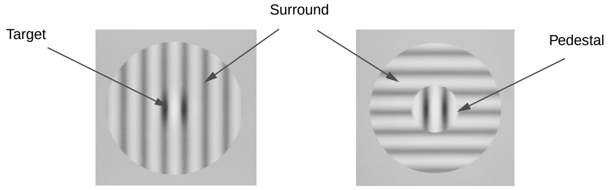

Fig. 1. Stimuli. The stimuli consisted of a D6 grating target centered on a circularly windowed sinusoidal grating pedestal. The pedestal was abutted by an annular sinusoidal grating surround. The surrounds here had the same contrast as the pedestal. Left and right, iso- and cross-oriented surround conditions, respectively.

of 6.2%, which was reduced to 2.9% by the surround, approximately equal to the mean detection threshold with no pedestal (3.0%). This complete unmasking effect was remarkable. It has been known since the nineteenth century that, for a target presented on a suprathreshold pedestal, the incremental threshold for the target is raised in rough proportion to the pedestal contrast[14], following Weber's law. Here we demonstrated that this masking effect can be completely undone with appropriate surrounding stimuli.

Surround modulation at iso-orientation (Fig. 3, open circles) showed a very different contrast dependence. When the surround contrast was lower than the pedestal contrast, facilitation increased monotonically with surround contrast, similar to the cross-orientation data. However, when the surround contrast exceeded the pedestal contrast, facilitation was greatly reduced. At 80% surround contrast, contrast thresholds were more than twice as high as those at cross-orientation, and were similar to thresholds in the pedestal-only condition (about 6% in the mean plot). Experiments described below showed that suppression caused by higher-contrast iso-oriented surrounds might reflect additional inhibition added to facilitation, and their net effect determines the sign of modulation. This complexity of contrast dependence in surround modulation resembles the neurophysiological contrast dependence of surround modulation, in that neural responses can be enhanced by a surround stimulus at one contrast level but inhibited by the same stimulus at a different contrast level[4,15,16].

When the orientation of a high-contrast surround (80%) was varied from iso- to cross-orientation, suppression diminished rapidly after iso-orientation, and facilitation slowly increased at larger relative orientations (Fig. 4a, filled circles). Regardless of the sign of modulation, however, the general orientation tuning properties were similar to the data with 40% surround (Fig. 4a, open circles), in that one phase was always sharply tuned to iso-orientation, and the other was always broadly tuned to cross-orientation. This similarity further confirmed our earlier finding of two surround modulation processes operating within different orientation ranges. Moreover, the distinct contrast dependencies of the two processes indicated that they operate independently.

Surround modulation, either facilitative or suppressive, is always specific to the relative spatial frequency. At both iso- and cross-orientations, facilitative and suppressive surround modulation functions associated with 40% and 80% contrast surrounds were maximized when the surround and center had the same spatial frequency (8 c.p.d.), and almost vanished when the surround spatial frequency was about one octave away from the target spatial frequency (Fig. 4b).

We also studied the effects of the spatial frequency of the overall stimulus pattern (that is, center and surround). The spatial frequency was varied from 2 to 8 c.p.d. by varying the viewing distance with the physical stimuli unchanged. In this way, the physical size of the stimuli was kept constant, and only the retinal scale was changed. Surround modulation (Fig. 5) at cross-orientation with 40% and 80% contrasts as well as at iso-orientation with 40% contrast was facilitative and basically scale or spatial-frequency invariant. However, modulation at iso-orientation with 80% contrast showed less facilitation as spatial frequency increased, although at 2 c.p.d. it was just slightly less facilitative than that under other surround conditions at the same spatial frequency. Surround modulation under this condition is thus not purely suppressive, but rather likely reflects the net effect of general surround facilitation and additional suppression caused by higher-contrast iso-oriented surrounds. This suppression seems to gain in strength at higher spatial frequencies.

DISCUSSION

Our results demonstrate that surround modulation at both iso- and cross-orientations can reduce masking and facilitate contrast discrimination. This facilitation indicates a gain increase in relevant spatial filters so that a smaller criterion (threshold) contrast difference can be detected. Masking is now generally modeled as a result of divisive inhibition contributed by pooled signals from neighboring neurons tuned to all orientations. In Foley's model[17], for example, the spatial filter response R is defined as $R = E^p/(\Sigma I^q + Z)$, where E is a half-wave rectified linear summation of exci-

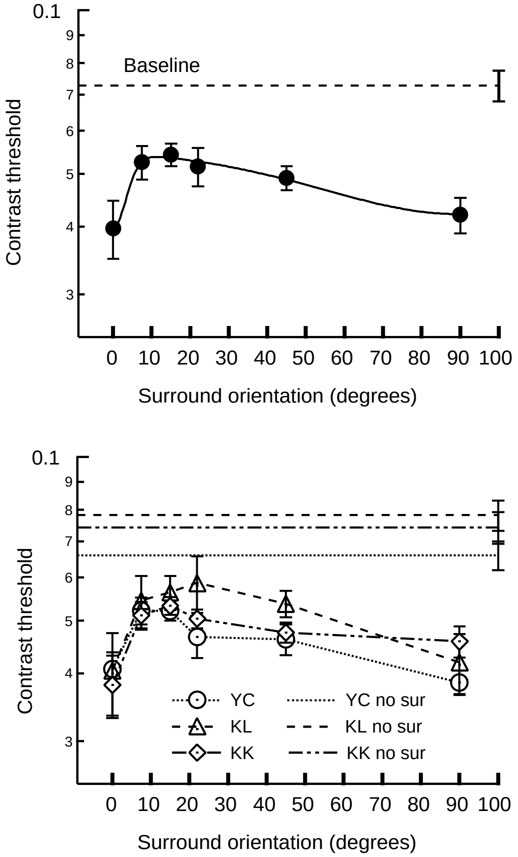

Fig. 2. Effects of relative orientation on surround modulation. Surround effects were indicated by the contrast threshold change from the baseline level (pedestal-only, no-surround condition; dashed lines). Top, mean results (filled circles) and data fitting (solid curve). Bottom, individual data (baselines above); YC, KL and KK, subject identifiers; no sur, no surround.

tation elicited by the stimuli, ΣI^q is the linear pooling of inhibition across different orientations, and Z is a constant. In this model, masking results from divisive inhibition, which normalizes excitation and reduces the gain of spatial filters. Although not intended to account for surround modulation of masking, this model could be conceptually extended to surround effects that might modulate the gain of filters by subtracting divisive inhibition, or $R = E^p/(\Sigma I^q + Z - SM)$, where SM represents surround modulation. Surround modulation can be further broken into $SM = F_{iso} + F_{cross} - I_{iso} + C$, where F_{iso} and F_{cross} are two Gaussian functions representing iso- and cross-orientation tuned facilitation, I_{iso} represents inhibition induced by higher-contrast iso-oriented surrounds, and C, the constant, represents orientation-insensitive facilitation. Because surround signals are pooled from a more distant area than are divisive inhibitory signals, surround modulation is likely weaker than divisive inhibition. This adds an important constraint on the output of the model. Otherwise, the denominator of the equation could become very small, which would make spatial filters oversensitive and the contrast threshold even further below the detection threshold, a possibility not supported by our results.

This extended gain-control model of masking suggests that surround stimuli reduce masking by subtracting suppressive signals, making divisive normalization less effective and increasing the gain of spatial filters. At cross-orientation and high-surround contrasts, surround modulation is strong enough to completely discount divisive inhibition and render the spatial filters as sensitive as in the detection task. When surround modulation itself is weakened by inhibition associated with high-contrast iso-oriented surrounds (I_{iso}), divisive inhibition is less affected, which leads to smaller gain increase in spatial filters and reduced facilitation. This inhibition could be strong enough to completely diminish or even overpower facilitative signals, leaving divisive inhibition unchanged or increased, ultimately leading to unchanged contrast thresholds or contrast suppression.

Facilitation of contrast detection by collinear flanks[6] is reported to disappear when non-collinear flanks are added to form a complete surround[18], much like the iso-oriented surrounds in our experiments. The authors explain their data as follows: the surrounding flanks fall within excitatory and inhibitory lobes of a second-stage receptive field and cancel each other's effect[18]. However, this model would predict zero surround effects on contrast discrimination at iso-orientation in our experiments because of the same cancellation. Moreover, although we also have similar data showing contrast detection little changed by iso-oriented surrounds with contrasts 20% or less (suppressed at higher contrasts), contrast detection can be greatly facilitated by cross-oriented surrounds (C.Y. and D.M.L., unpublished data). Such a cross-orientation effect, however, is specifically deemed unlikely by this second-stage model. On the other hand, the lack of contrast detection facilitation by iso-oriented surrounds may be explained by our model. In the detection case, our model can be simplified as $R = E^p/(Z - SM)$. As detection is a special case of discrimination with a 0% contrast pedestal, iso-oriented surrounds, whose contrasts are always higher than 0%, could produce inhibition as suggested in our study, which actually enhances normalization. However, as spatial filter excitation (E^p) could also be increased because of the surround grating stimulation, increased excitation and enhanced divisive normalization are likely to discount each other under lower surround contrasts, which keeps the final outputs of the spatial filters nearly constant, so that the contrast detection thresholds change little. This, however, does not apply to high-contrast surrounds, which produced strong suppression in our study. Facilitation of

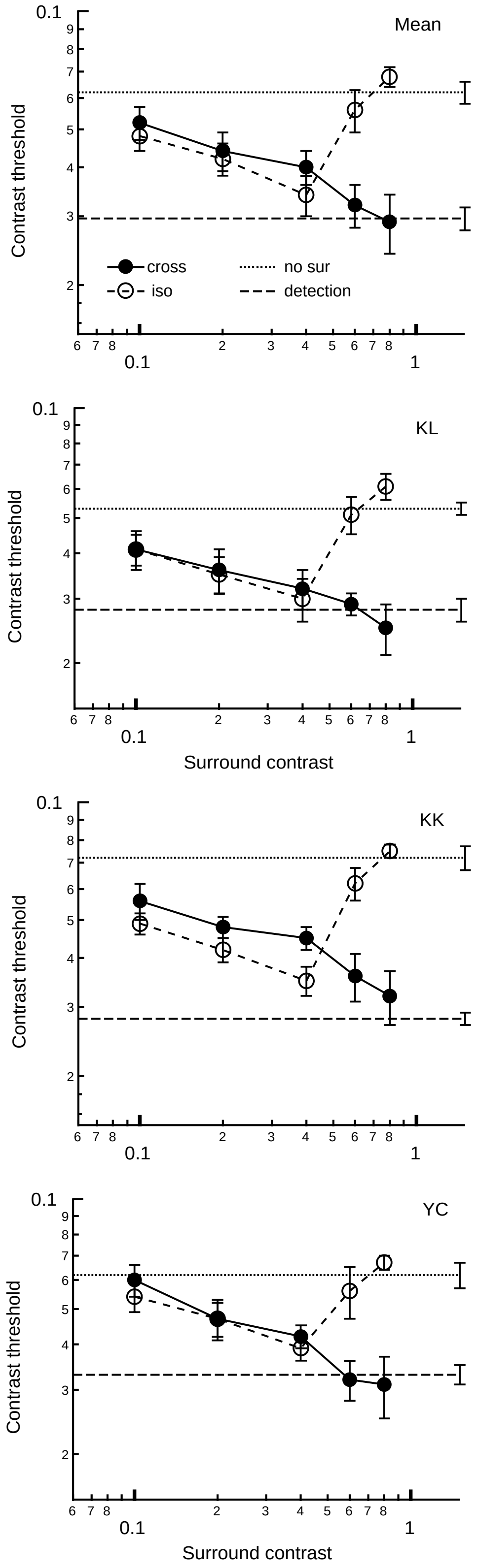

Fig. 3. Effects of surround contrasts on surround modulation. Contrast thresholds at iso-orientations (open circles) and cross-orientations (filled circles). Dotted lines, thresholds in baseline, pedestal-only condition; dashed lines, detection thresholds without the presentation of pedestal and surround. The contrast of the pedestal was fixed at 40%. KK, KL and YC, subject identifiers; no sur, no surround.

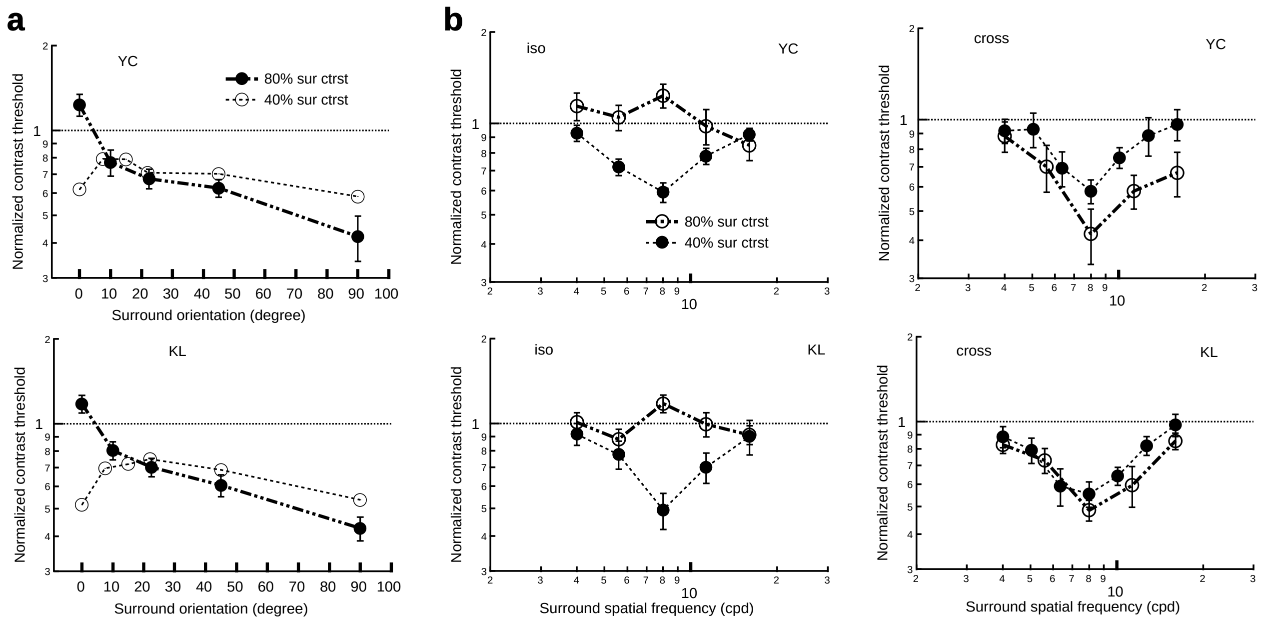

Fig. 4. Effects of relative orientation and spatial frequency on surround modulation at high- and equal-surround contrasts. (**a**) Modulation of contrast thresholds by high-contrast surrounds (80%; filled circles) and equal-contrast surrounds (40%; open circles; from **Fig. 2**) as a function of the relative orientation. Contrast threshold data here were normalized by the baseline pedestal-only thresholds to allow cross-session comparison. (**b**) The effects of relative spatial frequency on contrast thresholds at iso- and cross-orientations. The target frequency was fixed at 8.0 c.p.d. The surround was always in phase with the target and pedestal. Left column, iso-orientation; right column, cross-orientation. YC and KL, subject identifiers; sur ctrst, surround contrast.

contrast detection by just two collinear flanks may be a different story. Because the two flanks produce much weaker signals than does a complete surround, they may behave like a low-contrast surround and elicit facilitative inputs to the spatial filter to improve contrast detection. These effects may prove to be another complexity in psychophysical surround modulation.

As spatial filters have limited orientation-tuning bandwidth, it is proposed[19] that spatial filters with different orientation tuning properties only interact at a second-order stage; that is, signals from these first-order filters are only pooled after a nonlinear rectification. However, our cross-orientation data indicated strong 'cross-talk' among neighboring filters tuned to orthogonal orientations. Such direct 'dialogs' are supported by the recent neurophysiological finding that cross-orientation surround modulation can be mediated by local horizontal connections between neighboring cortical columns within the same neural module but tuned to orthogonal orientations[20]. Thus, orientation pooling could occur at relatively early stages of cortical processing, which would reduce the burden of orientation computation on a later stage in the visual system.

METHODS

Observers and apparatus. Three adults with normal or corrected-to-normal vision were studied. The stimuli were generated by a VisionWorks computer graphics system (Vision Research Graphics, Duham, New Hampshire) and presented on a Px19 monochrome monitor (U.S. Pixel, Framingham, Massachusetts). The monitor had a resolution of 1,024 × 512, a frame rate of 117 Hz, a mean luminance of 62 cd per m^2 and a screen size of 3.8° × 3.0° at a viewing distance of 5.64 m. The luminance of the monitor was made linear by a 15-bit look-up table.

Stimuli. The target was a 10-arcmin-long, spatially localized D6 grating (a sixth derivative of a Gaussian) centered in-phase on a circularly windowed sinusoidal grating pedestal (40% fixed contrast) of the same spatial frequency (8.0 c.p.d. if not otherwise specified) and orientation (vertical). The D6 target was partially blurred by a Gaussian window along its long axis ($\sigma = 4.2'$) and truncated at the target length. The surround was a sinusoidal grating annulus abutting the pedestal. The diameter of the pedestal was 18 arcmin, which produces maximal contrast thresholds for a D6 target 10 arcmin long. The outer and inner diameters of the surround were 45 and 18 arcmin, respectively.

Procedure. Contrast thresholds were measured with a successive two-alternative forced-choice staircase procedure. The pedestal was presented in each of the two stimulus intervals (300 ms each) separated by a 400-ms interstimulus interval. The target was randomly presented in one of the two stimulus intervals with the same onset and offset as the

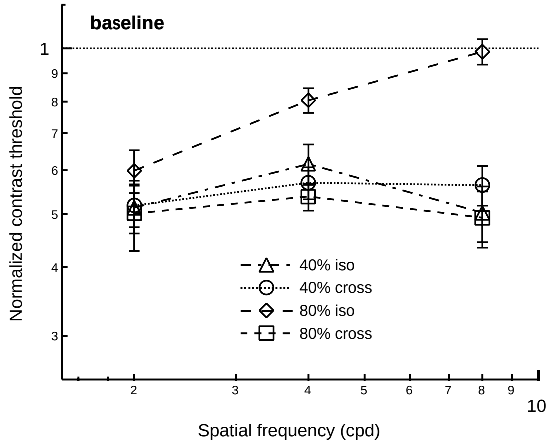

Fig. 5. Surround modulation at different stimulus spatial frequencies. Contrast thresholds were normalized by the baseline pedestal-only thresholds. Data represent mean results from three observers.

pedestal. The observer's task was to judge which stimulus interval contained the target. Each trial was preceded by a fixation cross of 6.3′ × 6.3′ that disappeared 100 ms before the beginning of the trial. Audio feedback was given on incorrect responses. Each staircase consisted of four preliminary reversals and eight experimental reversals. The step size of contrast change in practice reversals was 7.5% of the previous contrast and in experimental reversals was 2.5%. Each correct response lowered the target contrast by one step, and each incorrect response raised the target contrast by three steps, which resulted in a 75% convergence level of the staircase. The mean of the eight experimental reversals was taken as the contrast threshold. Each data point represents the mean of five to six replications, and the error bars represent ± 1 standard error of the mean. Detection thresholds were measured using the same method, with the pedestal contrast set to zero.

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