Low spatial frequencies are suppressively masked across spatial scale, orientation, field position, and eye of origin

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Masking is said to occur when a mask stimulus interferes with the visibility of a target (test) stimulus. One widely held view of this process supposes interactions between mask and test mechanisms (*cross-channel* masking), and explicit models (e.g., J. M. Foley, 1994) have proposed that the interactions are inhibitory. Unlike a *within-channel* model, where masking involves the combination of mask and test stimulus within a single mechanism, this cross-channel inhibitory model predicts that the mask should attenuate the perceived contrast of a test stimulus. Another possibility is that masking is due to an increase in noise, in which case, perception of contrast should be unaffected once the signal exceeds detection threshold. We use circular patches and annuli of sine-wave grating in contrast detection and contrast matching experiments to test these hypotheses and investigate interactions across spatial frequency, orientation, field position, and eye of origin. In both types of experiments we found substantial effects of masking that can occur over a factor of 3 in spatial frequency, 45° in orientation, across different field positions and between different eyes. We found the effects to be greatest at the lowest test spatial frequency we used (0.46 c/deg), and when the mask and test differed in all four dimensions simultaneously. This is surprising in light of previous work where it was concluded that suppression from the surround was strictly monocular (C. Chubb, G. Sperling, & J. A. Solomon, 1989). The results confirm that above detection threshold, cross-channel masking involves contrast suppression and not (purely) mask-induced noise. We conclude that cross-channel masking can be a powerful phenomenon, particularly at low test spatial frequencies and when mask and test are presented to different eyes.

Keywords: human vision, interocular suppression, dichoptic masking, lateral interactions, multiplicative noise

Introduction

Masking is the psychophysical phenomenon where the presence of one stimulus (the mask) interferes with the visibility of another (the test, or target). During the early 1980s the dominant account of this phenomenon was the "within-channel" model of masking. In this model, a target-detecting mechanism is stimulated by the mask stimulus, which reduces the signal-to-noise ratio for the observer, typically by compressing the detecting mechanism's response (Legge & Foley, 1980; Wilson, 1980). The general consensus (e.g., Wilson, Levi, Maffei, Rovamo, & DeValois, 1990; Regan, 2000) was that masking happens only when the spatial properties of the mask and test stimulus are similar (about ± 1 octave in spatial frequency and ± 30° in orientation). However, more recently it has become widely recognized that masks can raise detection thresholds without exciting the detecting mechanism (e.g., Ross & Speed, 1991; Ross, Speed, & Morgan, 1993; Foley, 1994; Mullen & Losada, 1994; Snowden, 1994; Zenger & Sagi, 1996; Dorais & Sagi, 1997; Meese & Holmes, 2003; Meese, in press; Chen & Foley, 2004). One possible explanation of this phenomenon is that "cross-channel" interactions cause the detecting mechanism to be suppressed by inhibitory influences from the masking mechanism (Foley, 1994). This idea owes much to observations of neuronal activity within visual cortex (Bishop, Coombs, & Henry, 1973; Petrov, Pigarev, & Zenkin, 1980; Burr, Morrone, & Maffei, 1981; Morrone, Burr, & Maffei, 1982; Morrone & Burr, 1986; Morrone, Burr, & Speed, 1987; Bonds, 1989; DeAngelis, Robson, Ohzawa, & Freeman, 1992) where suppressive interactions are thought to keep cells of limited dynamic range within the useful region of their operating characteristic (Albrecht & Geisler, 1991; Heeger, 1992), a process sometimes referred to as contrast gain control. Another possibility is that masking occurs because the mask raises the noise level in the detecting mechanism. This idea has received serious attention in the within-channel case (Gorea & Sagi, 2001, 2002; Kontsevich, Chen, & Tyler, 2002a; Kontsevich, Chen, Verghese, & Tyler, 2002b), but in principle it could also apply to the cross-channel case.

More generally, the notion of suppression has had a long history in psychophysical vision research. For example, it has been used to account for several different types of visual illusion (e.g., Carpenter & Blakemore, 1973; Tolhurst & Thompson, 1975; Georgeson, 1980a; Magnussen & Kurtenbach, 1980a), adaptation aftereffects (Klein,

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Stromeyer, & Ganz, 1974; Georgeson, 1976, 1980b; Magnussen & Kurtenbach, 1980b; Greenlee & Magnussen, 1988), and spatial interactions (Olzak, 1986; Polat & Sagi, 1993; Thomas & Olzak, 1997; Ellemberg et al., 1998; Olzak & Thomas, 1999), and has been studied extensively in the context of interocular suppression (e.g., Wolfe, 1986a; Lehky, 1988; Blake, 1989; Westendorf, 1989; Sengpiel, Blakemore, Kind, & Harrad, 1994; Sengpiel, Blakemore, & Harrad, 1995; Kovacs, Papathomas, Yang, & Feher, 1996; Sasaki & Gyobo, 2002) and surround suppression (Solomon, Sperling, & Chubb, 1993; D'Zmura & Singer, 1996; Xing & Heeger, 2001; Snowden & Hammett, 1998; Yu, Klein & Levi, 2001; Zenger-Landolt & Heeger, 2003).

A widespread view has been that within-channel masking can produce large effects (≥ 12 dB) and is easy to obtain (e.g., Wilson, McFarlane, & Phillips, 1983; Phillips & Wilson, 1984), but the picture of cross-channel suppressive effects is much less clear. In some experiments, suppression has been revealed only by recourse to clever manipulations that raise the experimental baseline, providing a pedestal against which inhibitory influences can be seen (Magnussen & Kurtenbach, 1980b; Greenlee & Magnussen, 1988). In situations in which observers detect a target in the presence of a superimposed cross-channel mask, threshold elevation has often been found to be modest (Foley & Chen, 1997) or absent (Campbell & Kulikowski, 1966; Daugman, 1984; Burr & Morrone, 1987; Harvey & Doan, 1990; Lee, Itti, Koch, & Braun, 1999; Itti, Koch, & Braun, 2000). Experiments that have used contrast matching to examine influences from higher contrast surrounds have found small (typically ≤ 6 dB) suppressive effects (Snowden & Hammett, 1998; Xing & Heeger, 2000, 2001) that appear to be spatially tuned (Cannon & Fullenkamp, 1991; Solomon et al., 1993; Chubb et al., 1989; Xing & Heeger, 2001; Yu et al., 2001), implying that lateral suppression is greatest from mechanisms with tuning properties similar to the test mechanism (e.g., Solomon et al., 1993). Threshold elevation can also be found from co-oriented surrounds and is quite marked for peripheral viewing (Snowden & Hammett, 1998), but for foveal viewing is either absent (Snowden & Hammett, 1998) or diminished and seen only at high mask contrasts (Yu, Klein, & Levi, 2003). The situation is further complicated, however, because other detection (Yu, Klein, & Levi, 2002) and discrimination (Yu & Levi, 2000; Yu et al., 2003) experiments suggest that annular surrounds can facilitate the center, particularly when they differ in spatial frequency and orientation (though see Bruce, Green, & Georgeson [2003] and Meese [in press] for further analysis and discussion of these results).

Another type of masking is dichoptic masking, where the test and mask stimuli are presented to different eyes. When spatially superimposed they can produce considerable threshold elevation, even greater than that seen in binocular or monocular cases. Dichoptic masking has been described as tightly tuned to both spatial frequency (Legge, 1979; Levi, Harwerth, & Smith, 1979; Harrad & Hess, 1992) and orientation (Levi et al., 1979; Harrad & Hess, 1992), prompting a within-channel account (Legge, 1984). In this type of model, a spatially tuned binocular mechanism is excited by stimulation from both eyes so that both the mask and the test are seen by the same mechanism when they are sufficiently similar in spatial frequency and orientation (Legge, 1979). This architecture (see "Appendix A") can also accommodate monocular and binocular masking (Legge, 1984) and has been influential, particularly in studies that have used dichoptic stimuli to infer the sequence of visual processing stages (Westendorf, 1989; McKee, Bravo, Taylor, & Legge, 1994; Harris & Willis, 2001).

As mentioned above, one widely held view is that contrast suppression might be part of a contrast gain control process in the cortex. In the binocular case this is thought to underpin cross-channel masking for situations in which (i) a patch of mask grating is superimposed on a patch of test grating (Foley, 1994; Zenger & Sagi, 1996; Itti et al. 2000; Holmes & Meese, 2001; Meese & Holmes, 2002) and (ii) an annulus of mask grating surrounds a patch of test grating (Xing & Heeger, 2001; Snowden & Hammett, 1998; Yu et al., 2001). It is also possible that dichoptic masking is a form of interocular suppression that acts in a similar way, perhaps even at the same site, as other cross-channel suppressive effects (see "Appendix A"). On this model, the finding that a superimposed, cross-oriented mask can elevate contrast detection threshold (by around 3 dB) in normal observers (Levi et al., 1979) is explained by supposing suppression between otherwise monocular channels (for further discussion, see "Dichoptic masking and interocular suppression"). However, while masking has been found for both superimposed and surround masks in the binocular case, this appears not to be so in the dichoptic case. Chubb et al. (1989) found no suppression of perceived contrast using a textured version of an annular mask, even though suppression was found in their monocular conditions. On the other hand, the psychophysical effects of dichoptic annular masks (Chubb et al., 1989) have been explored much less extensively than their binocular and monocular counterparts (Ejima & Takahashi, 1985; Solomon et al., 1993; Cannon & Fullenkamp, 1991, 1996; Snowden & Hammett, 1998; Xing & Heeger, 2000, 2001; Yu & Levi, 2000; Yu et al., 2001, 2002, 2003).

We wished to investigate several points that emerge from the review above. This was not to address a particular over-arching hypothesis, but to explore some of the parameter space that is absent in the literature so that a fuller picture of cross-channel masking of contrast might be seen. We break this down into more specific aims below.

First, if threshold elevation by cross-channel masks is due to cross-channel suppression (e.g., Foley 1994), a superimposed mask should attenuate the perception of contrast above threshold. This prediction is also prompted by observations of cross-orientation inhibition in the primary visual cortex (Morrone et al., 1982, 1987; Bonds, 1989), assuming that perceived contrast is linked to the level of striate cellular activity (Zenger-Landolt & Heeger, 2003). Although numerous psychophysical studies have examined the effects of cross-channel interactions on performance measures (e.g., Ross & Speed, 1991; Ross et al., 1993; Foley, 1994; Zenger & Sagi, 1996; Olzak, 1985, 1986; Olzak & Thomas, 1981, 1991, 1999; Thomas & Olzak, 1997) and the single-cell result has been known for well over 20 years, it is remarkable that (as far as we know) the above prediction has never been tested directly. We remedied this by using a contrast matching paradigm and monocular and binocular stimulus presentation of superimposed test and mask stimuli. This experiment is of particular value because an alternative account of cross-channel masking supposes mask-induced noise in the detecting mechanism. In this case, a cross-channel mask would disturb only the variance of the response from the target mechanism and perception of absolute contrast should not be attenuated.

Second, previous surround- and cross-channel masking experiments have tended to concentrate on mid to high spatial frequencies (Cannon & Fullenkamp, 1991; Solomon et al., 1993; Snowden & Hammett, 1998; Yu et al., 2001, 2002, 2003; Xing & Heeger, 2000; Campbell & Kulikowski, 1966; Daugman, 1984; Harvey & Doan, 1990; Lee et al., 1999; Itti et al., 2000), leaving lower spatial frequencies (≤ 1 c/deg) relatively unexplored. We suspected that suppressive effects might be greater at lower spatial frequencies (Legge, 1979; Xing & Heeger, 2000; Meese & Holmes, 2003), so we concentrated our work in this range.

Third, we wanted to further investigate dichoptic masking, particularly from annular surrounds, where results (Chubb et al., 1989) appear to conflict with those from the superimposed case (Levi et al., 1979). In particular, we wondered whether the cross-channel effects that have been found for binocular masking (e.g., Foley, 1994) might also be found for dichoptic masking.

Finally, we wanted to compare contrast detection and contrast matching experiments to examine whether similar effects are seen both at and above detection threshold. In general, if the mask and test stimuli have similar orientation and spatial frequency and are superimposed, it is not possible to assess the effects of suppression by contrast matching because the mask and test contrasts sum physically. However, this problem is avoided here by restricting our investigation to situations where the mask and test differ in both their orientation and their spatial frequency. Under these circumstances, the mask and test components segment perceptually (Thomas, 1989; Georgeson & Meese, 1997; Georgeson, 1998; Meese & Georgeson, in press), allowing observers to attend to the contrast of the test stimulus and perform the match. Furthermore, binocular masking experiments that have used this configuration (Meese & Holmes, 2002; Holmes & Meese, 2001, 2004; Georgeson & Meese, 2004; Meese, in press) confirm that threshold elevation from these masks is not due to within-channel effects.

Methods

Equipment

Stimuli were generated using the framestore of a CRS VSG2/3 operating in twin palette mode to produce pseudo 12-bit gray-level resolution. Stimuli were presented on a display monitor, which had a mean luminance (L) of 60 cd/m^2 and was gamma-corrected using lookup tables. The experiments were run under the control of a PC. Stimuli were viewed through a mirror haploscope (four pairs of front-surfaced mirrors, set at ± 45°) affording a square monocular field size of 11.5 deg by 11.5 deg and an effective viewing distance of 52 cm. The visible region of the display consisted of a 256 pixel square array for each eye. The frame rate of the monitor was 120 Hz, which gave a picture refresh rate of 60 Hz due to frame-interleaving of mask and test stimuli.

Stimuli

High-contrast examples of our test and mask stimuli are shown in Figure 1. Our basic test stimulus was a sine-phase patch of vertical sine-wave grating, multiplied by a raised cosine function with a central plateau. When the test stimulus had a spatial frequency of 0.46 c/deg, the envelope function had rising and falling parts of 2.25 deg and an intermediate plateau width of either 7.02 deg (Experiment 1; Figure 1a) or 1.08 deg (Experiment 2; Figure 1b). In Experiment 2 this produced a test stimulus with half a cycle of undamped grating and an envelope with full width at half height of 1.5 cycles. When the test stimulus had a spatial frequency of 1 c/deg, the spatial dimensions were scaled accordingly so that the number of cycles was unchanged. The mask stimuli always had a spatial frequency 3 times higher than the test stimulus, an oblique orientation (45°), and had one of three spatial configurations (Figure 1c, 1d, and 1e). In Experiment 1, it had the same envelope as the test stimulus in Experiment 1 (Figure 1c). In Experiment 2 it had either the same envelope as the test stimulus in Experiment 2 (Figure 1e) or an envelope the same as the test stimulus in Experiment 1, but with a

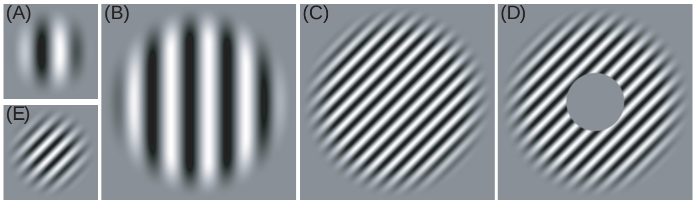

Figure 1. High-contrast examples of test (a, b) and mask (c, d, e) stimuli used in Experiment 1 (b, c) and Experiment 2 (a, d, e). In (d), the inner diameter of the mask is the same as the diameter of the envelope of the test stimulus at half height in (a). In the experiments, the masks had a contrast of 32%. The low spatial frequency was either 0.46 c/deg or 1 c/deg. The high spatial frequency was either 1.38 c/deg or 3 c/deg.

hole cut out to make an annulus (Figure 1d). The diameter of the hole was the same as the full width at half height of the test stimulus envelope (Figure 1a). To achieve anti-aliasing, the inner edge of the annular mask was blurred by a rising part of a raised cosine function with a full width of two pixels. The Michelson contrast ([*L*max – *L*min]/[*L*max + *L*min]) of the grating-type mask stimuli described above was always 32%.

A small fixation spot was displayed binocularly in the center of the display region throughout the experiments and stimulus duration was 200 ms.

Deviations from these basic stimulus conditions are described in the relevant experimental sections.

Contrast detection

In the contrast detection experiments, thresholds were measured using a two-interval forced-choice (2IFC) technique, where the mask stimulus appeared in both test intervals and the test stimulus appeared in one, chosen at random. The duration between the offset of the first interval and the onset of the second interval was 500 ms, and the onset of each interval was indicated by a short auditory tone. Observers used two buttons of a mouse to indicate which interval contained the test stimulus and were given auditory feedback (a short tone) to indicate the correctness of their response. Stimulus contrast was controlled in log steps by a 3-up 1-down staircase procedure (Wetherill & Levitt, 1965).

Contrast matching (nulling)

In the contrast matching experiments, the contrast of the test stimulus was adjusted in log steps by a 1-up 1-down staircase procedure (Wetherill & Levitt, 1965; Meese, 1995) to match the perceived contrast of an unmasked reference stimulus over a range of reference contrasts. (Strictly speaking, this is a nulling technique because the observer is manipulating the test contrast to null the effects of the mask.) The duration between the offset of one stimulus and the onset of the other stimulus was 500 ms, and the onset of each stimulus was indicated by a short auditory tone. The order of test and reference stimuli was randomized and the observer used two mouse buttons to select the test interval that appeared to contain the higher test contrast. No feedback was given. Preliminary contrast detection experiments ensured that the lowest contrast used for the reference stimulus was always above detection threshold.

It has been suggested to us that it can be very difficult, or even impossible, to obtain a perfect perceptual match between a monocular target alone and the same target with a dichoptically presented mask. While this might be true for certain experimental paradigms, typically it was not true here. Both observers found the task natural and straightforward and were able to perform the task quickly and with ease. Specific exceptions to this are noted below.

Psychometric functions

In all cases, psychometric functions were measured using pairs of interleaved staircases so that observers could not track the progress of the experimental procedure (Cornsweet, 1962). The staircase step-size was 3 dB (20 times the log increment/decrement of Michelson contrast) and data were fit using probit analysis (i.e., they were fit by a cumulative log-Gaussian function). For the detection experiment, threshold was taken to be the 75% correct point on the psychometric function. For the matching experiments, the point of subjective equality was the 50% point on the psychometric function. For both types of experiment, the analysis was based on the data gathered from the last 12 reversals of each staircase. Larger step sizes were used for an initial pair of staircase reversals but the data from these preliminary stages were discarded from the analysis (Meese, 1995). For both types of experiment, the analysis was based on the data gathered from between two to six staircases. This produced means and standard errors based on around 100 to 300 trials in the contrast detection experiments and around 60 to 180 trials in the contrast matching experiments (Finney, 1971; McKee, Klein, & Teller, 1985).

In all experiments, the order of conditions was determined using randomized blocs.

Observers

The two authors (TSM and RFH) served as observers. They both wore their normal optical correction, and were well practiced at the tasks before data collection began.

Experiment 1: Large mask and test stimuli

One of our main aims was to explore dichoptic masking from the surround. Our initial intuition was that if this exists then the likelihood of finding it would be enhanced by using a test and mask combination that were known to be potent when superimposed. Thus, in Experiment 1 we used a basic stimulus to establish whether our methods and general stimulus parameters were appropriate for measuring masking. Our basic test and mask stimuli are shown in Figure 1b and Figure 1c, respectively.

Contrast detection

Figure 2 shows threshold elevation for the two observers, two test spatial frequencies (0.46 c/deg and 1 c/deg), and monocular and dichoptic conditions. For both observers there was substantial threshold elevation in the 0.46-c/deg condition (around a factor of 4) for both stimulus conditions. For TSM, the level of masking was similar for the two stimulus conditions, though for RFH it was markedly greater for the dichoptic condition. At a spatial frequency of 1 c/deg, the pattern of results for the two observers was unchanged, though the overall level of masking was reduced by around a factor of 2.

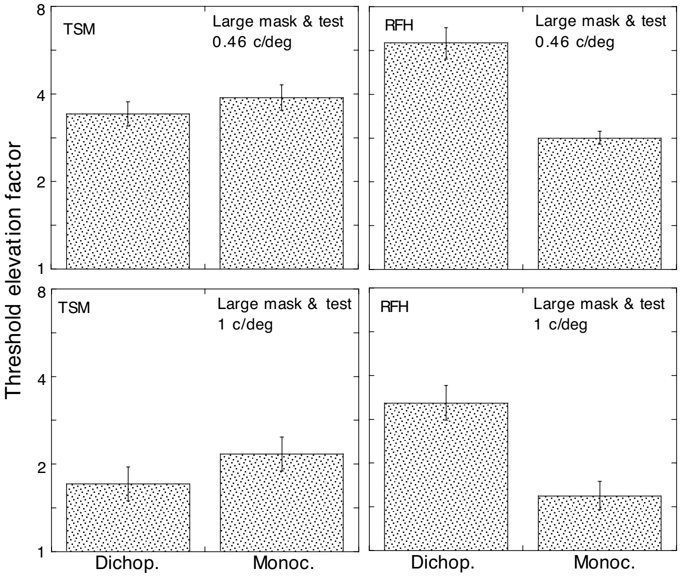

Figure 2. Detection results for Experiment 1. Bars show threshold elevation for a large patch of test grating in the presence of a superimposed mask of the same size but oblique orientation (+ 45 deg) and spatial frequency 3 times higher than the test. (Note that each tick mark on the ordinate represents 3 dB.) Each panel shows results for a monocular condition and a dichoptic condition. In the monocular condition, both stimuli were presented to the observer's dominant (right) eye and the other eye was presented with mean luminance. In the dichoptic condition, the test stimulus was presented to the dominant (right) eye and the mask stimulus was presented to the other eye. The top and bottom panels are for test spatial frequencies of 0.46 c/deg and 1 c/deg, respectively. The left panels are for TSM and the right panels are for RFH. Error bars show ±1 *SE*.

Contrast matching

The results of the matching experiment are shown in Figure 3 where the reference contrast is plotted on the ordinate against the staircase adjusted test contrast. (Our choice of plotting the independent variable along the ordinate is unconventional, but produces a figure in which the perceived contrast is plotted as a function of stimulus contrast consistent with other contrast matching experiments in which the comparison contrast was adjusted: e.g., Hess, Bradley, & Piotrowski, 1983; Georgeson, 1985, 1991.) The oblique lines in our matching figures indicate a veridical match.[1] Data points that fall below this line indicate that the mask reduced the perceived contrast of the test stimulus, and that the test contrast had to be raised to overcome this. Such an effect is consistent with the suppressive account of masking outlined in the "Introduction." For both observers, suppression occurred over a substantial range of the contrasts tested and like in the detection experiments, produced considerably greater effects at 0.46 c/deg than at 1 c/deg. The level of suppression was quite similar for the dichoptic and monocular conditions, with the exception of the 0.46-c/deg condition for RFH, where the suppression was greater for the dichoptic condition than the monocular condition. In all cases, the matching functions tended to approach the contour of veridicality as the reference contrast increased, indicating that suppression from the mask was abolished for matching contrasts around 16% and above.

Discussion

The results from the detection and the matching experiments both suggest that the mask, whose spatial frequency and orientation are quite different from that of the test stimulus, strongly suppresses the test stimulus, regardless of whether it is in the same or the different eye from the test patch. This is particularly marked at the lower spatial frequency (0.46 c/deg). In the dichoptic condition, for example, the test grating had to be increased to a contrast of just over 11% to match a standard contrast of 4% for TSM. For RFH the effect was even larger: a test contrast of 26% was needed to match a standard contrast of only 4%. And for both observers, the standard contrast was at least a factor of 2.8 above detection threshold (see the legend for

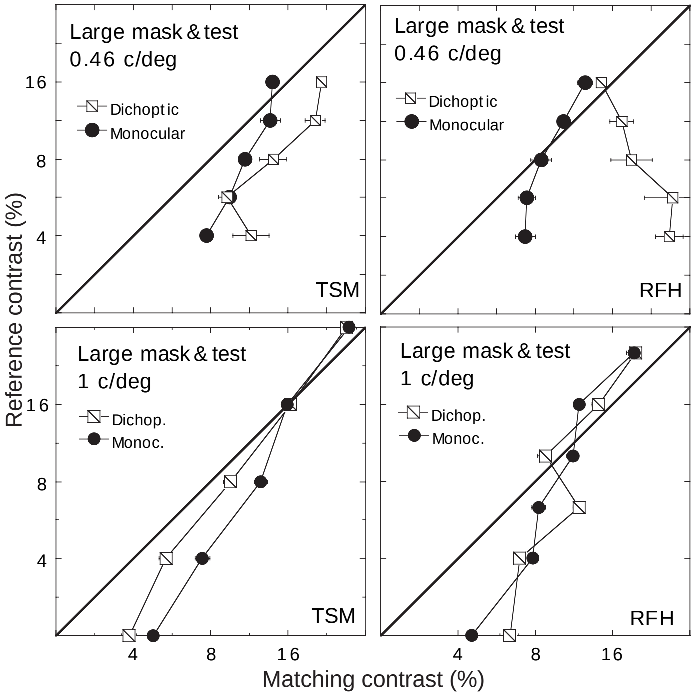

Figure 3. Contrast matching results for Experiment 1 (note the double-log coordinates). The stimulus conditions are the same as for those in Figure 2. The unmasked reference stimulus (ordinate) was always monocular. For the 0.46-c/deg stimuli (top panels), detection threshold for the reference stimulus was 0.98% for TSM and 1.42% for RFH. For the 1-c/deg stimuli (bottom panels), detection thresholds for the reference stimulus were 0.75% for TSM and 1.59% for RFH. Error bars show ±1 *SE*.

Figure 3), indicating that this is a substantial suprathreshold phenomenon. The mask also had a substantial effect on detection thresholds, raising them by around a factor of 4.

One intriguing feature of the dichoptic matching data in Experiment 1 is that there are several instances in which the matching functions fold back on themselves (i.e., have negative slopes); this is particularly notable for RFH at 0.46 c/deg. A backward slope in these matching functions indicates that as the standard contrast is increased, *less* test contrast is needed to achieve a perceptual match (recall that the mask contrast was fixed). We shall return to this seemingly paradoxical phenomenon in the anomalies subsection of the "General Discussion" after encountering it again in Experiment 2.

Having established a general stimulus condition in which masking was clearly evident in both monocular and dichoptic conditions, we turn to the issue of masking from the surround.

Experiment 2: Annular masking and small test stimuli

One limitation of Experiment 1 is that both the mask and the stimuli contained several cycles of luminance grating, so it is unclear whether the suppression came from mechanisms with overlapping or non-overlapping receptive fields (e.g., from within a hypercolumn or from neighboring hypercolumns). In the next experiment we reduced the diameter of the half height of the test stimulus to 1.5 cycles (Figure 1a), which corresponds roughly with the width of the putative detecting mechanism (e.g., Watson, 1982; DeValois & DeValois, 1990; Graham, 1989). The mask stimuli had the same spatial frequencies and orientation as before. The mask spatial envelope was either the same as the small test stimulus (Figure 1e), or was an annulus whose hole had the same diameter as the half height of the test stimulus (Figure 1d). We also wondered whether the absence of luminance contrast in the non-preferred eye was important for obtaining the high levels of monocular masking seen in Experiment 1. To address this we introduced a binocular condition in which test and mask stimuli were presented to both eyes.

Contrast detection

The results from the detection experiment are shown in Figure 4. Like in Experiment 1, considerably more masking was found at the lower test spatial frequency (0.46 c/deg) for RFH, though this was not evident for TSM. When the mask and test were superimposed, masking was roughly similar for the binocular and dichoptic conditions, and for RFH its magnitude was substantial. Clearly then, the absence of luminance contrast in one eye is not a necessary condition to achieve the substantial masking found in these experiments.

When the mask was restricted to the surround (annulus condition), the amount of threshold elevation was reduced considerably in the monocular and binocular conditions, in most cases being either abolished or replaced by a small amount of facilitation (Yu et al., 2002, 2003). Threshold elevation was evident in the dichoptic condition, however, and was substantial for RFH at 0.46 c/deg (greater than a factor of 4). This result contrasts with an earlier experiment on dichoptic surround masking where textured stimuli were used (Chubb et al., 1989).

Contrast matching

The results of the matching experiment are shown in Figure 5 (0.46 c/deg) and Figure 6 (1 c/deg). At a test spatial frequency of 0.46 c/deg, suppression was considerable for both observers in the dichoptic condition, regardless of whether the mask was superimposed on the test or placed in an adjacent surround. In fact, for RFH, the masking was so great in the dichoptic annulus condition that it was not possible to achieve a perceptual match at one of the intermediate matching contrasts (note that there is a data point missing from the plot in this condition). In this case, when the test contrast was raised to the maximum allowable[2] (45%), it was still of insufficient contrast to achieve the

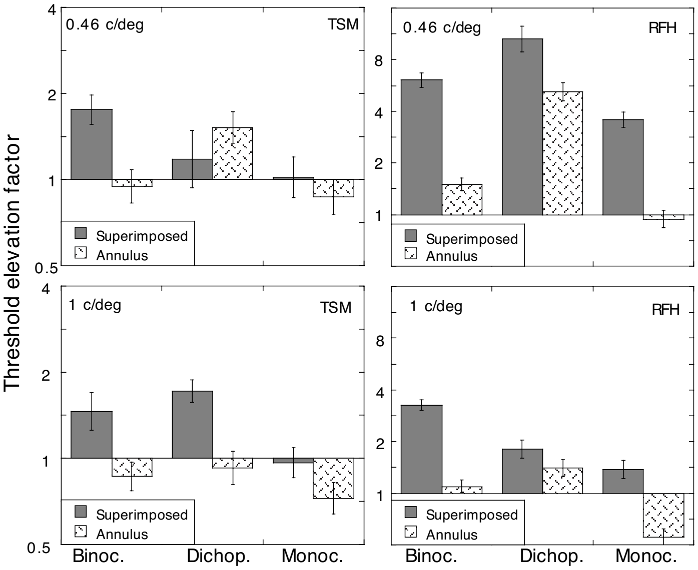

Figure 4. Detection results for Experiment 2. Bars show threshold elevation for a small patch of test grating in the presence of a mask with oblique orientation (45 deg) and spatial frequency 3 times higher than the test. (Note that each tick mark on the ordinate represents 3 dB.) The mask was either a small, superimposed patch (solid shading) or an annulus (hashed shading). Each panel shows results for a monocular condition, a dichoptic condition, and a binocular condition. The top and bottom panels are for test spatial frequencies of 0.46 c/deg and 1 c/deg, respectively. The left panels are for TSM and the right panels are for RFH. Note the different scales for the two observers. Error bars show ±1 *SE*.

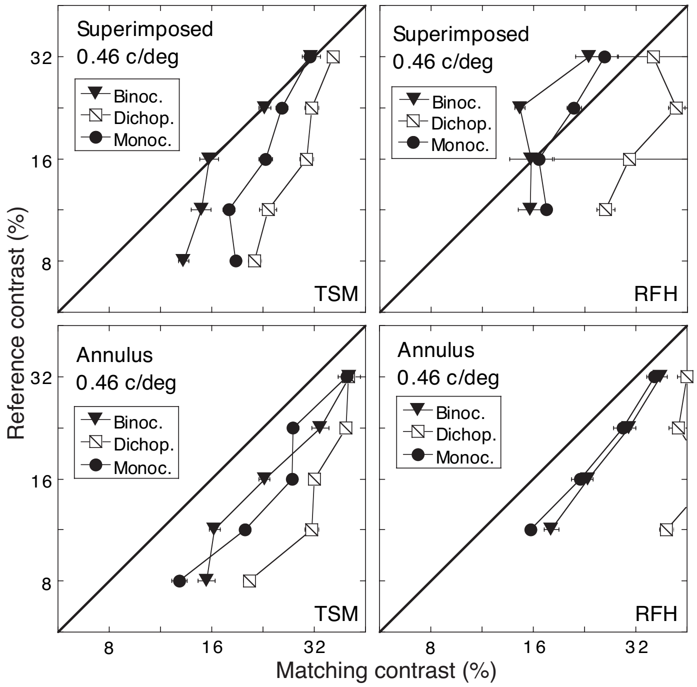

Figure 5. Contrast matching results for Experiment 2 for test spatial frequency of 0.46 c/deg. The test stimulus was a small patch of grating. The unmasked reference stimulus (ordinate) was monocular in the dichoptic and monocular test conditions and binocular in the binocular test condition. Detection thresholds for the monocular reference stimulus were 2.78% for TSM and 2.29% for RFH. Detection thresholds for the binocular reference stimulus were 1.57% for TSM and 1.15% for RFH. Even at the highest possible matching contrast, it was not possible to achieve a perceptual match for the missing data point for RFH in the annulus condition. Error bars show ±1 *SE*.

match and often appeared to be invisible, suggesting that on some trials at least, suppression was total. RFH experienced similar difficulties when the dichoptic mask was superimposed, leading to unusually high standard errors for some of the matches.

At the higher spatial frequency (1 c/deg), suppression was generally much less for both observers, though once again we encountered difficulties in gathering data from RFH. Although the monocular reference stimulus was always well above its detection threshold (2.29%), in preliminary experimental sessions we found that in the dichoptic masking condition the reference patch became very difficult to see. For this reason, we were able to gather data for only the upper region of the matching function. We shall return to this curious phenomenon in the anomalies subsection of the "General Discussion."

For both observers, the monocular and binocular conditions also caused a reduction in the perceived contrast of the test patch, though in some places the effects were quite minor. Broadly speaking, the effects were similar for these two mask conditions, though there are some detailed differences between the observers (see Figures 5 and 6).

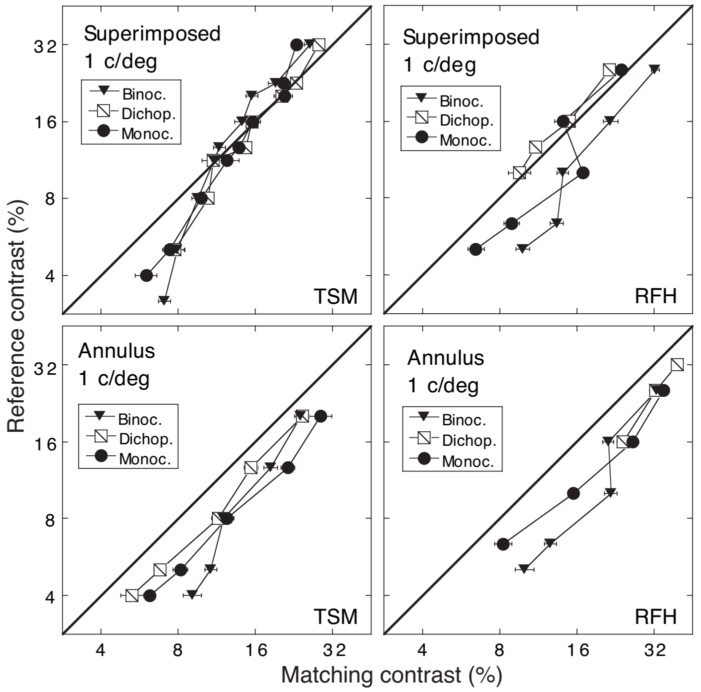

Figure 6. Contrast matching results for Experiment 2 for test spatial frequency of 1 c/deg. The test stimulus was a small patch of grating. The unmasked reference stimulus (ordinate) was monocular in the dichoptic and monocular test conditions and binocular in the binocular test condition. Detection thresholds for the monocular reference stimulus were 2.14% for TSM and 5.13% for RFH. Detection thresholds for the binocular reference stimulus were 1.3% for TSM and 2.01% for RFH. Error bars show ±1 *SE*.

Finally we note that, as we found in Experiment 1, there are several situations in which the masking functions fold back on themselves.

Matching and detection

It is noteworthy that some results from the matching experiment are not readily anticipated by the results from the detection experiment. Consider first the results using a spatial frequency of 0.46 c/deg, which we consider to be our "best" test spatial frequency (compare Figures 4 and 5). For both observers, the results from the detection experiment are consistent with the fairly large matching effects produced by the dichoptic annulus. However, as noted above, the monocular and binocular annular masks produced little or no threshold elevation for either observer yet had a consistent effect across the range of matching contrasts tested. Why this happened is not clear, but one possibility follows. Perhaps both contrast detection and contrast perception of a patch of grating involve a form of summation across several neural mechanisms but only a subset of the mechanisms is suppressed. If summation for perception of contrast were greater than that involved in the detection process (e.g., the Minkowski exponent for perceived contrast were lower than for contrast detection)[3], then the effects would be less for contrast detection than for contrast matching. Alternatively, one might construct arguments involving the same amount of nonlinear summation for both detection and perception, but suppose that the subset of suppressible mechanisms has a lower sensitivity according to a subtractive constant. In this case, suppression would appear more severe as test contrast is increased (from detection threshold to matching levels), because only at the higher contrasts would the responses of the suppressible mechanisms impact the decision variable. Another possibility is that the effects of suppression could apply equally to both signal and noise. As this would not change the signal-to-noise ratio, detection thresholds would be unaffected by the suppression but perceived contrast would be, assuming that perceived contrast depends on signal strength (Zenger-Landolt & Heeger, 2003).

Returning to the data, another unexpected result was that in the superimposed condition for TSM, there was very little threshold elevation at 0.46 c/deg for the monocular and dichoptic conditions, yet these conditions produced the greatest effects in the contrast matching experiment. Again, it is not clear why this is so, but arguments similar to those above could be applied.

Discussion

The detection and contrast matching results from Experiment 2 show that suppression can occur when the mask is either superimposed or adjacent, and in situations where mask and test are presented to (i) the same single eye (monocular), (ii) both eyes (binocular), and (iii) different eyes (dichoptic). The effects were strongest at the lower spatial frequency that we tested (0.46 c/deg) and for the dichoptic condition. Thus, we have found a situation in which a mask exerts considerable suppression on a patch of test grating, yet the test and mask are different in terms of (i) spatial frequency, (ii) orientation, (iii) retinal location, and (iv) eye of origin.

In light of earlier work, this result is surprising. Chubb et al. (1989) used broad-band noise to create a circular test stimulus surrounded by texture. They found suppressive effects from the surround only when the test and mask were presented to the same eye. Although the reason for these different results is not clear, one possibility is that spatial frequency is an important factor. If the masking described here is purely a low spatial frequency phenomenon, it seems likely that the mask stimuli used by Chubb et al. probed spatial frequency bands that were too high to reveal the suppressive effects.

General Discussion

Summary of results

To further our understanding of cross-channel masking, surround masking, dichoptic masking, and suppression in general, we performed experiments with a common target stimulus, but several different types of mask stimulus. In particular, we wished to investigate low target spatial frequencies and address a previous claim that surround suppression is a purely monocular effect (Chubb et al., 1989).

When the mask and test were superimposed, we found threshold elevation and contrast suppression for dichoptic, monocular, and binocular conditions. For TSM, however, the magnitude of the threshold elevation was much reduced when the mask and test stimuli were both reduced in size (compare Experiments 1 and 2, Figures 2 and 4). This effect was much less pronounced for RFH.

Our surround mask was constructed so that the inner edge of the mask was coincident with the half height of the test patch. This mask had little effect on detection threshold (sometimes causing a slight amount of facilitation), other than in the dichoptic condition where elevation was particularly pronounced for RFH at 0.46 c/deg. For both observers, perceived contrast was suppressed for all three modes of presentation (monocular, binocular, and dichoptic), though in contrast to previous work (Chubb et al., 1989), it was greatest for the dichoptic case. In fact, overall, the effects were typically larger for the dichoptic conditions than the monocular conditions, both at and above detection threshold. The effects were also typically much greater for the test spatial frequency of 0.46 c/deg than 1 c/deg.

Controls and extensions

The experiments presented here form part of a larger body of work in which several controls and extensions have been performed. In one set of experiments, Meese and Hess (in press) addressed a specific issue regarding dichoptic masking and perception of depth (McKee et al., 1994). They found that dichoptic masking continued to be effective when the annular surround was replaced by a thin, dark ring. Using this mask they confirmed that masking remained when the configuration was changed so that the test stimulus was presented to the non-preferred eye, and also when the stimulus duration was reduced from 200 ms to 33 ms.

In a series of binocular experiments still under analysis, we have manipulated the orientation of the superimposed cross-channel mask and confirmed that horizontal 1- and 3-c/deg gratings also raise detection thresholds and suppress perceived contrast for a 1-c/deg target stimulus identical to that in Experiment 1.

Masking and suppression

In general, masking refers to the psychophysical effect where one stimulus (the mask) interferes with the visibility of another stimulus (the test). If a mask component suppresses the response to a test component, then this should reduce its perceived contrast and raise its detection threshold (though see earlier caveats). This could be a consequence of inhibitory interactions (e.g., Morrone et al., 1982; Albrecht & Geisler, 1991; Heeger, 1992; Foley, 1994; Zenger & Sagi, 1996), thalamocortical synaptic depression (Carandini, Heeger, & Senn, 2002; Freeman, Durand, Kipper, & Carandini, 2002), or, in the case of detection, compressive transduction if the mask and test components are seen by the same detecting mechanism (e.g., Legge & Foley, 1980; Wilson, 1980). This last possibility is an unlikely account for the stimuli used here because (i) previous experiments have rejected the "within-channel" account of masking when the mask and test components have substantially different spatial frequencies and/or orientations (e.g., Foley, 1994; Ross & Speed, 1991; Ross et al., 1993; Holmes & Meese, 2001), and (ii) if the mask component did excite the detecting mechanism, then perceived contrast would be enhanced, whereas in the experiments reported here it was reduced. Another possibility is that masking could leave the signal intact but increase the noise. This remains a possibility (Gorea & Sagi, 2001; Kontsevich et al., 2002a, 2002b), but not a certainty (Georgeson & Meese, 2004) in the within-channel case and is worth considering for cross-channel cases such as those studied here. Although we cannot rule out this hypothesis in our detection experiments, it cannot be extended to our matching experiments because there an increase in noise should impact only the variability of the contrast match and not its absolute value. In this case, and contrary to our results, no effect on perceived contrast would have been observed.

One recent suggestion (mentioned above) is that cross-orientation masking arises through synaptic depression in the thalamocortical projection (Carandini et al., 2002). Because LGN cells are much more broadly tuned than typical cortical cells, then according to this proposal, what looks like a cross-channel interaction in the cortex is actually a within-channel phenomenon in the LGN. While it remains to be understood whether this intriguing idea is important for related psychophysical phenomena (e.g., Foley, 1994; Meese & Holmes, 2002), it seems an unlikely account for many of our results here because (a) the model predicts that suppression should be monocular (Carandini et al, 2002), and (b) the model requires superposition of the mask and test stimuli, and is not intended to describe surround suppression (Freeman et al., 2002).

In sum, the most likely account of much of the masking found in the experiments reported here is contrast suppression through variously weighted inhibitory interactions. Whether this is from the output of multiple oriented mechanisms (e.g., Morrone et al., 1982; Heeger, 1992; Foley, 1994) or a single broad-band control filter (Hirsch et al., 2003; Holmes & Meese, 2004) is not clear, but certainly the results are consistent with these general types of model (see below for further discussion).

Comparisons with other studies

Our experiments prompt several comparisons with other studies that have investigated the effects of masking from the center and the surround.

Superimposed masking

When mask and test were superimposed, we found that threshold was elevated substantially, in the order of 12 dB (a factor of 4) in some cases (see Figures 2 and 4). This is broadly consistent with other psychophysical reports of cross-channel masking where mid to low test spatial frequencies have been used (e.g., Foley, 1994; Meese & Holmes, 2002, 2003). Indeed, Meese and Holmes (2003) specifically addressed this issue and found binocular cross-orientation suppression to be greatest for transient presentations of low test spatial frequencies. Here, we also found suppressive effects for contrast matching when the mask and test were superimposed (see Figures 3, 5, and 6). We know of no other study in which this type of experiment has been performed, though the results are consistent with some masking experiments at detection threshold (e.g., Foley, 1994; Meese & Holmes, 2002) and the results of single-cell recordings (e.g., Morrone et al., 1982).

Surround masking

Yu et al. (2002) found that cross-channel annular masks with the same spatial frequency (8 c/deg) but different orientations from the test facilitated the detection of a central test stimulus for intermediate levels of mask contrast (around 5% to 20%). Using two flanking patches of mask instead of a surround, Yu et al. (2002) and Chen and Tyler (2002) reported similar effects (Chen and Tyler used a spatial frequency of 4 c/deg). The maximum level of facilitation found in these studies was around 6 dB, though more often it was closer to 3 dB. Facilitation around this magnitude was found in the present experiment for both observers when the vertical test stimulus had a spatial frequency of 1 c/deg, and when the annular surround had a spatial frequency 3 times higher. However, this effect was most clearly evident in the monocular condition, and was either barely seen or was replaced by suppression in the dichoptic conditions (see Figure 4). This suggests an early locus of the facilitatory effect, consistent with the arguments presented by Yu et al. (2002) (see their study for details). Facilitation was not seen in our experiments when the mask was superimposed. This is consistent with the view that the facilitatory effect is due to specific orientation and spatial frequency tuned interactions between center and surround (Yu et al., 2002). However, it would seem that when the test spatial frequency is low (e.g., 1 c/deg), the effect extends over a wider range of mask spatial frequencies than at the higher spatial frequency used by Yu et al. (2002). This is because when the mask and test differed by as much as a factor of 3 (as in the present experiments), Yu et al. (2002) found that facilitation was abolished.

Although the binocular and monocular effects were often much weaker than their dichoptic counterparts, we found that an annular grating surround could suppress the perceived contrast of a central target patch. Most psychophysical studies in which suppression from monocular or binocular surrounds has been found have investigated conditions in which center and surround had similar spatial frequencies and orientations (Ejima & Takahashi, 1985; Cannon & Fullenkamp, 1991, 1993, 1996; Snowden & Hammett, 1998; Olzak & Laurinen, 1999; Xing & Heeger, 2001). However, suppression from orthogonally oriented surrounds has also been found (Solomon et al., 1993; Yu et al., 2001), though facilitation has been seen at certain center/surround contrast ratios (Yu et al., 2001).[4]

In the case of dichoptic presentation of annular masks, the only previous work that we are aware of is that of Chubb et al. (1989). As mentioned previously, these authors used contrast noise stimuli but unlike us found no dichoptic masking. As we suggested earlier in this work, these differences could be due to the different ranges of spatial frequencies involved in the two studies.

Spatial frequency

We have already mentioned that our effects are generally greater at the lower of the two spatial frequencies tested. Elsewhere, this has been found for contrast detection in the presence of superimposed cross-channel masks (Meese & Holmes, 2003) and contrast matching in the presence of cross-channel annular surrounds (Solomon et al., 1993). In particular, Xing and Heeger (2000) performed contrast matching with co-oriented annular surrounds in both the fovea and the periphery. They found only modest effects in the fovea (≤ 6 dB), but much larger effects in the periphery (≥ 12 dB). While this appears to be a genuine effect, the possibility remains that had Xing and Heeger tested at spatial frequencies lower than 2 c/deg in the fovea (as they did in the periphery), they might have seen more substantial effects.

Dichoptic masking and interocular suppression

What kind of scheme might be able to accommodate the many different types of cross-channel masking results reported here? One of our key results is that masks with very different orientation and spatial frequency from the target can attenuate the test stimulus when mask and test are presented to different eyes. However, this result alone does not demand a scheme involving interocular suppression. For example, a scheme in which binocular mechanisms sum information from each eye within fairly narrow bands of spatial frequency and orientation, followed by binocular cross-channel suppression, would also predict this result. However, in this model, the results for the dichoptic conditions should be exactly the same as for the monocular conditions because the same binocular mechanisms would be involved in the suppressive gain control process. While one or two examples of this can be found in our data (e.g., TSM, 0.46 c/deg, Figure 2), there are numerous other examples where the results are at odds with this prediction (e.g., Figure 5). It is also inconsistent with the results of Chubb et al (1989) and those of Meese, Georgeson & Hess (2004), who repeated the monocular and dichoptic, superimposed contrast matching conditions at 0.46 c/deg, and confirmed that dichoptic suppression was greater than monocular suppression, irrespective of which eye was tested. In this context then, a model in which cross-channel suppression follows binocular summation seems unlikely. Instead, we favor a scheme in which linear binocular summation (Truchard, Ohzawa, & Freeman, 2000) comes after cross-channel suppression (contrast gain control) (DeAngelis et al., 1992). In fact, this is consistent with recent conclusions from single-cell work in cat (Walker, Ohzawa & Freeman, 1998; Truchard et al., 2000), though we also allow interocular suppression (both within and across spatial frequency and orientation) at the same stage. In "Appendix A" we show that this kind of scheme can also accommodate monocular, binocular, and dichoptic masking functions, where mask and test stimuli have similar spatial frequency and orientation. This offers a quite different perspective on the masking process considered by Legge (1979, 1984), who attributed dichoptic masking entirely to within-channel excitation. We stress, however, that we are not rejecting the within-channel idea at present, but argue that the entire body of work is consistent with a unifying scheme in which both types of dichoptic masking (Legge's and ours) are described by interocular (cross-channel) suppression. Detailed quantitative features of these models (summarized in "Appendix A") are currently receiving our attention.

Anomalies

There were several unexpected features in our data. An understanding of these features is not essential for the points made in this work, but they are worthy of comment. In several of the contrast matching data sets there are instances where the matching functions have negative slopes, particularly in the dichoptic conditions. This means that as the reference contrast was increased, *less* test contrast was needed to match it. This is inconsistent with most vision models where monotonic contrast response functions are the norm. It is not clear why our functions have negative slope, but one possibility follows. The reference stimulus and test stimulus were presented sequentially at the same retinal location, and therefore stimulated the same target mechanism. Thus, the target mechanism received greater stimulation at the higher reference contrasts. Perhaps, strongly stimulated mechanisms are able to attenuate their suppressive inputs with a time course sufficiently long to extend over the duration of at least one trial. If this were so, the unmasked reference stimulus would lessen the impact of the mask (the mask/test order was random), and negative matching functions would occur.

We encountered a second peculiarity for RFH in Experiment 2, which was almost the opposite of what we have described above. When the matching (unmasked) stimulus contrast was low but well above its independently measured detection threshold, it became very difficult to see and therefore very difficult to match. (Note that there are no data points at lower reference contrasts in the dichoptic conditions for RFH in Figure 6). Conventional accounts of contrast adaptation seem unlikely here because (a) stimulus presentations were brief and (b) the anomaly was noticed only for dichoptic masking. In this case it was as though the suppressive effects of the dichoptic mask were holding over from the low contrast test-plus-mask presentation and occurring even when the reference stimulus was presented alone.

In short, the two peculiarities described here are consistent with a scheme where the extent of dichoptic suppression depends on the recent history of a target mechanism subjected to dichoptic masking. If the target response is low (low match and test contrasts), then suppression continues to act even when the mask is removed, whereas if target response is high (high match and test contrasts), suppression becomes less effective. It was beyond the scope of the present work to address this issue directly, so our suggestion remains speculative, but these anomalies are provocative issues to be explored more fully in the future, by us or by others.

Conclusions

Suppression is a substantial and widespread phenomenon at low test spatial frequencies. It can be observed both at and above detection threshold and is evident when the mask is either superimposed or surrounds the test stimulus. In particular, it can also be found dichoptically, suggesting a cortical site of suppression where information is combined across the two eyes. Typically, however, we find that suppression is greater in the dichoptic condition than corresponding binocular and monocular conditions, suggesting that suppression precedes binocular summation. Whether within-eye and cross-eye suppression arise at different stages or the same stage but with different weights in a suppressive gain pool ("Appendix A") remains unclear.

Appendix A: Two models of binocular summation

Here we consider an "early" binocular summation model inspired by the architecture developed by Legge (1984). We also present a simple alternative that we refer to as the "late" binocular summation model, first described by Meese (2003). We validate the new model by demonstrating its ability to handle monocular, binocular, and dichoptic masking data gathered by Legge, but point out that it also offers a site for cross-channel dichoptic masking, amblyopic suppression, and eye-based accounts of binocular rivalry. The architecture of the early binocular summation model is less well equipped to do this because of its late stage of contrast gain control and binocular suppression. For example, on this model, a binocularly balanced observer should have the same level of cross-channel suppression for comparable monocular and dichoptic conditions. This is at odds with much of our data and those of Chubb et al. (1989). The new model, which evolved from earlier thinking about binocular summation and dichoptic masking (Legge, 1984) in the context of contemporary thinking about contrast gain control (Heeger, 1992; Foley, 1994; Walker et al., 1998; Truchard et al., 2000), is presented in the spirit of a first attempt at achieving both of these demands. Both models are currently receiving detailed quantitative examination and psychophysical testing by us and by Mark Georgeson.

A schematic illustration of a model similar to that proposed by Legge (1984) is shown in Figure A1. Note that, as in Legge's model, binocular summation comes before contrast compression. Mathematically, this model can be expressed as follows:

$$\text{Output1} = (L^2 + R^2)^{1.2}/(Z + L^2 + R^2 + POOLr), \quad \text{(A1)}$$

where L and R are the contrast (%) responses of the left and right eye to a binocularly fusible stimulus (e.g., a patch of vertical grating). The term Z is a constant, sometimes referred to as the semi-saturation constant, and $POOLr$ is a function that describes the suppressive contribution from other (remote) mechanisms in the suppressive contrast gain pool. This term was not a feature of Legge's model, is not fully specified here, and does not form part of the computations behind Figure A3. However, experiments by Foley (1994) and others prompt its inclusion, and we show it here for completeness.

More generally, the values of the exponents in Equation A1 can be free parameters, but here are set to convenient values broadly consistent with the published literature. The behavior of this model for three different types of masking is shown in Figure A3. With $Z = 1$, predictions were made by calculating the responses of the model to (i) a test plus a mask stimulus and (ii) a mask stimulus alone. To derive detection thresholds for the test stimulus, the test contrast was adjusted to give an arbitrary constant difference ($k = 0.4$) between these two responses across all the conditions tested. In the monocular condition, a patch of test and/or mask grating is presented to just one eye. In the binocular condition, the same patch of test and/or mask grating is presented to both eyes. In the dichoptic condition, the patches of test and mask grating are presented to different eyes. The model predicts five distinct features that have been seen in psychophysical masking functions (Legge, 1984): (i) binocular detection thresholds are slightly lower than monocular detection thresholds, (ii) the upper parts of monocular and binocular masking functions are very similar, (iii) monocular and binocular masking functions are dipper shaped, (iv) dichoptic masking has little or no region of facilitation, and (v) dichoptic masking is greater and has a steeper slope than monocular and binocular masking.

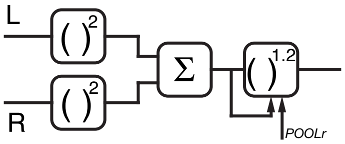

Figure A1. Early binocular summation model, after Legge (1984). In this model, binocular summation precedes contrast gain control. The arrows indicate divisive suppression. The exponents apply to the excitatory terms, which arrive from the left (no arrows). A semisaturation constant that forms part of the formal model is not shown (see Equation A1).

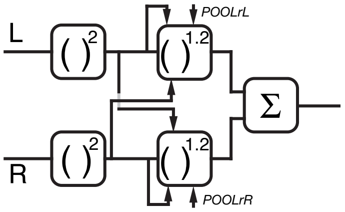

Figure A2. Late binocular summation model, proposed by Meese (2003). In this model, binocular summation comes after contrast gain control. The arrows indicate divisive suppression. The exponents apply to the excitatory terms, which arrive from the left (no arrows). Semisaturation constants and cross-channel weights that form part of the formal model are not shown (see Equation A2).

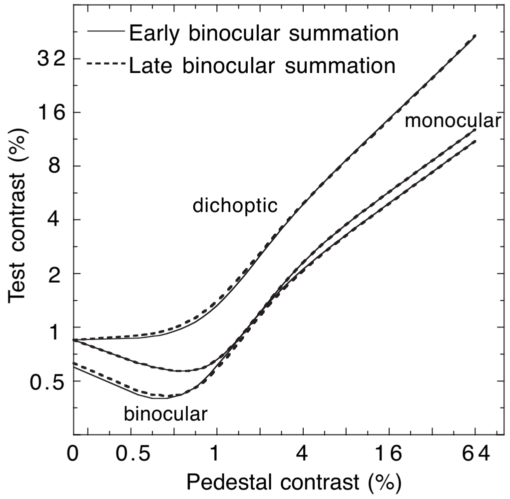

Figure A3. Comparison of masking behavior for the early and late binocular summation models shown in Figures A1 and A2. The three different pairs of functions are for the three different types of masking experiment denoted by the labels. Although unclear in the figure, the functions for monocular and binocular masking do not cross.

An alternative model of binocular summation is shown in Figure A2. Here, contrast gain control, including interocular suppression, is applied to each of the monocular channels prior to binocular summation. Mathematically, this model can be expressed as follows:

$$\text{Output2} = (L^{2.4})/(Z + L^2 + w.R^2 + POOLrL) + (R^{2.4})/(Z + w.L^2 + R^2 + POOLrR), \quad \text{(A2)}$$

where w represents the weight of interocular suppression, and *POOLrL* and *POOLrR* are functions that describe the suppressive contributions from other (remote) mechanisms (including cross-channel interocular contributions) in the contrast gain pools for the left and right monocularly excited channels, respectively. In the simplifying case, where $w = 1$, and $POOLrL = POOLrR$, the number of free parameters is the same as in the early binocular summation model and the equation simplifies to

$$\text{Output2} = (L^{2.4} + R^{2.4})/(Z + L^2 + R^2 + POOLr), \quad \text{(A3)}$$

which is similar but not identical to Equation A1.

In Figure A3, the late binocular summation model (Equation A2) is fit to predictions made by the early binocular summation model (Equation A1). The parameters Z and k were set as before, leaving w as the only free parameter. A simplex algorithm estimated this to be 0.74.

The behavior of the two models is very similar. Specifically, all five of the features seen in psychophysical data and captured by the early binocular summation model are also seen in the late binocular summation model. In the simpler version of the model (Equation A3), the main features of its behavior are preserved but the monocular and binocular masking functions converge at intermediate contrasts and above, and the dichoptic masking function is shifted to the left (not shown). The similarity of these two models is important because it brings into question a previously widespread view (e.g., Westendorf, 1989; McKee et al., 1994; Harris & Willis, 2001) that dichoptic masking is a consequence of binocular summation. This particular point receives further attention elsewhere (Meese & Hess, in press).

The results from our experiments suggest that masking can arise from a form of fast-acting interocular suppression. Here we have shown that this can be accommodated by a contrast gain control model that is also consistent with several well known effects of masking and binocular summation (Legge, 1979; Legge & Foley, 1980; Legge, 1984; Foley, 1994). A notable feature of the model is the early placing of the gain control stages on monocularly excited channels and prior to binocular summation. A similar scheme has also emerged from observations of cellular activity in the primary visual cortex (Walker et al., 1998). We note, however, that contrary to our psychophysical results, single-cell work has found cross-orientation suppression to be weaker for dichoptic presentation than for monocular presentation (DeAngelis et al., 1992; Walker et al., 1998).

Our model might also have some relevance to the study of amblyopia. When the binocular output is "lesioned" in the model and replaced by monocular outputs, binocular contrast summation is abolished but dichoptic masking remains intact, just as has been claimed to happen in some amblyopes (Levi et al., 1979). Finally, our model architecture also offers a route for ocular-based binocular rivalry (Lee & Blake, 2004).

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Footnotes

[1] This was confirmed in a control experiment in which both observers matched the contrast of a variable contrast test stimulus to an identical standard stimulus over a range of contrasts and without the presence of a mask.

[2] The frame interleaving procedure that we used sets a theoretical maximum of 50%. In practice, the actual maximum is a little less than this because the black level of the monitor is slightly higher than zero cd/m^2.

[3] One might consider probability summation for detection and contrast averaging for perception.

[4] The pattern of results was not consistent across observers. The interested reader is referred to Yu et al. (2001) for details.

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