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Suppression pathways saturate with contrast for parallel surrounds but not for superimposed cross-oriented masks

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ABSTRACT

Contrast masking from parallel grating surrounds (doughnuts) and superimposed orthogonal masks have different characteristics. However, it is not known whether the saturation of the underlying suppression that has been found for parallel doughnut masks depends on (i) relative mask and target orientation, (ii) stimulus eccentricity or (iii) surround suppression. We measured contrast-masking functions for target patches of grating in the fovea and in the periphery for cross-oriented superimposed and doughnut masks and parallel doughnut masks. When suppression was evident, the factor that determined whether it accelerated or saturated was whether the mask stimulus was crossed or parallel. There are at least two interpretations of the asymptotic behaviour of the parallel surround mask. (1) Suppression arises from pathways that saturate with (mask) contrast. (2) The target is processed by a mechanism that is subject to surround suppression at low target contrasts, but a less sensitive mechanism that is immune from surround suppression 'breaks through' at higher target contrasts. If the mask can be made less potent, then masking functions should shift downwards, and sideways for the two accounts, respectively. We manipulated the potency of the mask by varying the size of the hole in a parallel doughnut mask. The results provided strong evidence for the first account but not the second. On the view that response compression becomes more severe progressing up the visual pathway, our results suggest that superimposed cross-orientation suppression precedes orientation tuned surround suppression. These results also reveal a previously unrecognized similarity between surround suppression and crowding (Pelli, Palomares, & Majaj, 2004).

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1. Introduction

Masking is the phenomenon where one stimulus (the mask) makes a second stimulus (the target) more difficult to see. In this paper, we restrict our considerations to the situation where the mask is substantially different from the target in one or more dimensions (i.e., it is not a pedestal). This includes situations where (i) the mask and target are superimposed, but have very different orientations (cross-orientation suppression) and (ii) when the mask surrounds the target (surround suppression) (see Meese, Summers, Holmes, & Wallis, 2007; Smith, Bair, & Movshon, 2006 and Petrov & McKee, 2009 for recent reviews).

Studies from single-cell physiology (Kimura & Ohzawa, 2009; Li, Peterson, Thompson, Duong, & Freeman, 2005; Nolt, Kumbhani, & Palmer, 2007; Smith et al., 2006; Tailby, Solomon, Peirce, & Metha, 2007; Webb, Dhruv, Solomon, Tailby, & Lennie, 2005) and psycho-

physics (Meese & Hess, 2004; Paffen, van der Smagt, te Pas, & Verstraten, 2005; Petrov, Carandini, & McKee, 2005; Baker, Meese, & Summers, 2007; Cai, Zhou, & Chen, 2008; Cass & Alais, 2006; Meese & Baker, 2009; Petrov & McKee, 2009) have shown that these forms of masking involve multiple processes of suppression. For example, Petrov et al. (2005) performed contrast detection experiments and found that parallel (co-oriented) surround (doughnut) masking was orientation tuned, and diminished when a cross-oriented mask superimposed the doughnut mask. This implies that for their stimuli, cross-orientation suppression asserts its influence earlier in the processing stream than suppression from parallel doughnuts, because the former interferes with the latter. Petrov et al. also found that when a parallel doughnut mask was added to a superimposed cross-oriented mask, the level of masking increased, consistent with a cascade of suppressive influences.

A striking difference between the two forms of suppression above is that on double-log coordinates, superimposed cross-oriented masking accelerates with mask contrast (Foley, 1994; Medina & Mullen, 2009; Meese, 2004; Meese, Challinor, & Summers, 2008; Meese & Holmes, 2002), whereas masking from a parallel

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Table 1
Matrix of potential results for Experiment 1 and their interpretations. Bold entries indicate previously established results. Entries in italics indicate the factorial combination of the two likely outcomes for the two novel conditions. The last column shows an interpretation for each of the possible outcomes.

Eccentricity (°)	Superimposed cross-oriented masking	Doughnut cross-oriented masking	Doughnut parallel masking	Interpretation
0	Accelerates	Small or no effect	Small or no effect	n/a
4.5	<i>Accelerates</i>	<i>Accelerates</i>	Compresses	Compression is specific to parallel doughnut masking
4.5	<i>Accelerates</i>	<i>Compresses</i>	Compresses	Compression is specific to doughnut masking
4.5	<i>Compresses</i>	<i>Accelerates</i>	Compresses	Complex interpretation required
4.5	<i>Compresses</i>	<i>Compresses</i>	Compresses	Compression is specific to peripheral masking

doughnut saturates¹ (Petrov et al., 2005; Zenger et al., 2000). These different operating characteristics suggest that fundamentally different processes of suppression are involved. However, (substantial) elevation of psychophysical contrast detection threshold has been found for parallel doughnuts only when the entire stimulus is placed away from the fovea (Petrov et al., 2005; Snowden & Hammett, 1998; see also Xing and Heeger (2000) for contrast-matching). Similarly, masking from cross-oriented surrounds has also been found to be weak or absent in the fovea (Meese et al., 2007; Saarela & Herzog, 2008; though see Meese & Hess, 2004). Thus, it is not clear from previous studies whether the saturating characteristic of suppression is specific to parallel masks, doughnut masks or masking in the periphery. We resolve this issue here by measuring contrast-masking functions for parallel and cross-oriented doughnut masks, and cross-oriented superimposed masks for 1 c/deg patches of target grating in central and peripheral vision.

Table 1 summarises the established outcomes from previous studies in bold, the likely possibilities for the unknown outcomes in italics, and their various interpretations in the right hand column. The results of our first experiment are consistent with those in the second row. We present two hypotheses for the cause of the saturating masking functions and test these with a second experiment in which we manipulated the size of the hole in a doughnut mask. The results support the hypothesis that the pathway mediating surround suppression saturates with contrast. They do not support the competing hypothesis in which performance is mediated by dual mechanisms, one very sensitive and subject to surround suppression, the other less sensitive but immune from surround suppression.

The results from Experiment 1 were first presented in abstract form by Challinor, Meese, and Summers (2007).

2. Methods

2.1. Equipment

Stimuli were displayed on a 120 Hz EIZO FlexScan 6600-M 19 in., Gamma corrected greyscale monitor with the use of a VSG 2/5 stimulus generator (Cambridge Research Systems) controlled by a PC and operating in pseudo-15 bit mode. The display had a mean luminance of 40.7 cd/m². Mask and target frames were temporally interleaved giving an image refresh rate of 60 Hz. The mask and target contrasts were controlled using look-up tables. A chin

¹ As pointed out by a reviewer, Petrov et al.'s masking function is non-monotonic (i.e., it declines a little after reaching a maximum level at a contrast of 10%). However, this effect is small and it is unclear whether it was found for all four of their observers (only the average is shown). Zenger, Braun, and Koch (2000) found a similar effect for just one of their four observers. For simplicity, we refer to this type of masking function as asymptotic and/or saturating since this terminology captures the primary characteristic of the effect. The non-monotonicity – if real – appears to be a fairly minor, secondary effect (for detection thresholds at least) and is not of direct interest here. Furthermore, whether this is related to non-monotonic effects that have been found in contrast discrimination (Kingdom & Whittle, 1996; Zenger-Landolt & Heeger, 2003; Zenger-Landolt & Koch, 2001) is also unclear.

and headrest was used to help observers hold fixation at a viewing distance of 70 cm.

2.2. Stimuli and conditions: Experiment 1

All stimuli were 1 c/deg sine-wave gratings modulated by one of two spatial windows and had a duration of 100 ms. The target was a circular patch of horizontal grating in sine-phase with the centre of the display, ensuring that it contained no mean luminance increment. It had a full-width at half-height (FWHH) of 1.26° (36 pixels) (Fig. 1a). The blurring around the edge was done with a raised sine-function with a half-cycle width of 0.28° (8 pixels), giving a central unmodulated target plateau of 1 cycle (28 pixels) and a full target width of 1.54° (44 pixels). The cross-oriented superimposed mask was a vertical grating modulated by the same window as the target (Fig. 1b). The doughnut window used for the surround-masks had an outer diameter of 7.7° (FWHH). The central hole had a diameter of 1.96° (FWHH) and used the same blurring as above. The cross-oriented and parallel doughnut masks are shown surrounding the target in Fig. 1c and d, respectively.

We used a 2 (field position) × 3 (mask configuration) × 8 (mask contrast) factorial experimental design. Stimuli were always rendered in the centre of the monitor and were viewed either centrally

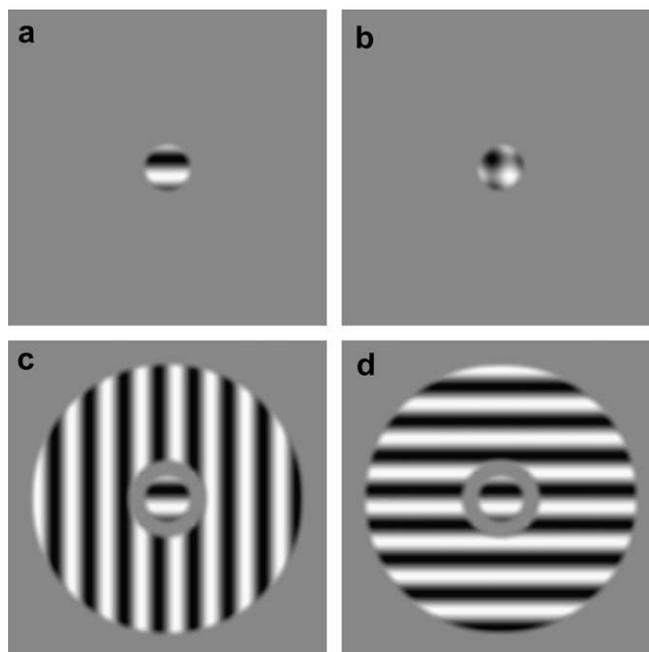


Fig. 1. High-contrast examples of target, and mask plus target stimuli used in Experiment 1. The target was always a small patch of horizontal grating (a), the mask was either a small patch of cross-oriented grating (b), a surrounding doughnut of cross-oriented grating (c), or a surrounding doughnut of parallel grating (d).

(0°) or 4.5° into the periphery. A 1 pixel thick circular ring of 15% contrast surrounded the target and had the same diameter as the hole in the doughnut mask (1.96°). This ring was presented continuously for all experimental conditions to help reduce spatial uncertainty for the target. A central fixation point was not used as this can cause masking for small target stimuli (Meese & Hess, 2007; Summers & Meese, 2009). For the central viewing condition, observers were instructed to fixate the centre of the low contrast ring. For the peripheral viewing condition, observers were instructed to fixate a small dark fixation point that was presented 4.5° directly below the centre of the ring (and centre of the monitor) and was displayed continuously. The height of the monitor was adjusted so that the target was at eye level in each of the two viewing conditions.

Stimulus contrast is expressed as Michelson contrast in percent, given by $C = 100(L_{max} - L_{min}) / (L_{max} + L_{min})$, where L is luminance. Contrast is also expressed in dB given by: $20 \log_{10}(C)$. Detection thresholds were measured for eight mask contrasts (0%, 1%, 2%, 4%, 8%, 16%, 32% and 45%).

2.3. Stimuli and conditions: Experiment 2

The aim of Experiment 2 was to investigate the effect of the doughnut hole diameter, which had values of 1.75°, 1.96° (the same as in Experiment 1), 2.5° and 4°. Otherwise, it was identical to Experiment 1, except that it was performed only with peripheral stimulation (4.5°) and with parallel doughnut masks. All conditions were blocked.

2.4. Procedure

Observers were seated in a dark room and their task was to detect the horizontal target grating using a temporal two-interval, forced choice (2IFC) procedure. Each 100 ms test interval was indicated by an auditory tone and always contained the mask. Only one of the intervals contained the target, chosen at random. The duration between the two test intervals was 500 ms. Observers indicated their response by clicking one of two mouse buttons and received auditory feedback on the correctness of response. The experiments were performed with randomized blocks for field position (central or peripheral) mask configuration (crossed superimposed, crossed doughnut or parallel doughnut) and contrast. For each mask contrast, a pair of randomly interleaved staircases controlled the contrast of the target grating using a 3-down, 1-up rule (Wetherill & Levitt, 1965). The step-size in the test-stage changed the contrast by a factor of 1.3 (2.5 dB), and each staircase terminated after 12 reversals with this step-size. An initial stage for each staircase used a larger step-size (10 dB then 5 dB after the first reversal), though data from this stage did not contribute to the estimate of threshold. Thresholds (75% correct) and standard errors were estimated by probit analysis (McKee, Klein, & Teller, 1985) on data collapsed across each staircase pair (~80 trials per pair) for each run. If the standard error was greater than 3 dB, then the data were discarded and the session was rerun. This was done for less than 3% of the results. The data points and error bars shown in the results are the geometric means and ±1 SE of four independent estimates (runs).

2.5. Observers

All five observers were aged between 23 and 30 years old, and wore their normal optical correction where appropriate. Three observers were authors (KLC, DHB and RJS) and the other two (NRH and LP) were both volunteers, naïve to the purpose of the experiment. Three observers took part in Experiment 1 (KLC, RJS and NRH) and two in Experiment 2 (DHB and LP). One observer,

KLC, had a strabismus and performed the experiment monocularly with her good eye. The other eye was patched. The other four observers had normal vision and performed the experiment binocularly. Before formal data collection began, RJS and KLC had several weeks of practice with this task and stimuli. The other observers had one or 2 h of practice. The practice confirmed that KLC (the strabismic observer) was not anomalous for this task, and this was borne out by the formal data collection.

3. Experiment 1: saturation is specific to parallel surround masking

3.1. Results and discussion

Fig. 2 shows contrast-masking functions for each of three observers (different columns) for central (circles) and peripheral (squares) stimuli for each of the three different spatial configurations (different rows). In all cases, contrast sensitivity was lower in the periphery, as to be expected. There are also several examples of weak levels of facilitation, as found and discussed previously for these types of mask and target configurations (Medina & Mullen, 2009; Meese & Holmes, 2007; Meese et al., 2007). However, our main interest here is in the form of masking. When the stimulus was central (circles) there was only a weak masking-effect for crossed doughnut masks (Fig. 2b) and parallel doughnut

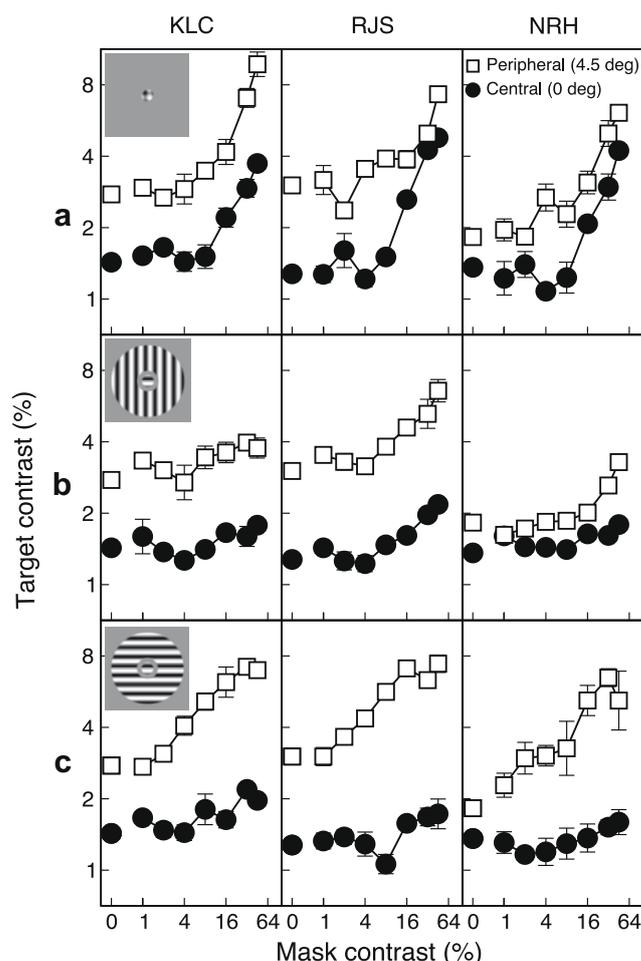


Fig. 2. Masking functions (Experiment 1) for each observer (different columns) for superimposed cross-orientation masking (a), surround cross-orientation masking (b) and surround parallel masking (c). Error bars show ±1 SE when larger than symbol size.

masks (Fig. 2c), consistent with previous work (see Section 1). The superimposed cross-oriented mask (Fig. 2a) produced an accelerating function of masking over the full range of mask contrasts tested (up to 44.6%), also consistent with previous results (see Section 1). The results for central stimulation are summarised in Fig. 3a, which shows the masking functions averaged across observer and plotted as threshold elevation by normalising detection thresholds to the baseline (no mask) measures. This emphasises the similarity between the results for the two doughnut mask conditions (circles), and contrasts them with the strong masking that is found for the superimposed cross-oriented mask (squares). The similarity of the results for the two differently oriented doughnut masks suggests that the underlying process might be isotropic.

For peripheral stimulation (Fig. 2, squares) and the parallel doughnut, masking reached a maximum, followed by no further increase at higher mask contrasts (Fig. 2c), consistent with the results of Petrov et al. (2005). Thus, we have confirmed each of the four different entries in bold in Table 1. The remaining two results are novel to the study here and provide the key to the final column in Table 1. For superimposed cross-oriented masking (Fig. 2a), the masking functions were very similar to those found in the fovea.² For the cross-oriented doughnut mask (Fig. 2b), the results were slightly less consistent. One observer (KLC) showed only weak evidence for masking, whereas the other two observers showed evidence for an accelerating effect. Essentially, the overall pattern of masking for this condition is a slightly more potent version of what was found for central stimulation (compare squares and circles in Fig. 2b). We note that Ishikawa, Shimegi, and Sato (2006) also found surround suppression at detection threshold from peripheral cross-oriented masks, but that Petrov and colleagues did not (Petrov & McKee, 2006; Petrov & McKee, 2009; Petrov et al., 2005). Petrov and McKee attributed this difference to response bias in the Ishikawa study, but that cannot apply to the present study, which used 2IFC. The reason for this difference across studies remains unclear, particularly since the main stimulus parameters were so similar. Perhaps subtle differences such as target phase (sine here, cosine for Petrov and colleagues), or window profile are important, though it is not clear why this should be so. Alternatively, the different results might reflect individual differences amongst observers (e.g., see Zenger et al., 2000).

The peripheral results from Experiment 1 are summarised in Fig. 3b, which emphasises the differences for the three mask configurations described above (different symbols).

Overall, our results (Fig. 3) conform to those outlined in the second row of Table 1. This is to say that if masking is to be found, it accelerates for the cross-oriented case regardless of eccentricity and the relative placement of target and mask (doughnut or superimposed), but asymptotes for the parallel case. However, we proffer this interpretation with some caution. The levels of masking in the peripheral cross-oriented surround condition were comparatively weak (circles, Fig. 3b), never reaching those for the parallel surround. Thus, we cannot rule out the interpretation in the third row of Table 1; it is possible that in the periphery, suppression from the surround arises from a mechanism that is very broadly tuned to the centre orientation such that it is sensitive to orthogonal orientations, but not sufficiently so to drive it into saturation.

² Petrov et al. (2005) also found the same levels of cross-orientation masking for central and peripheral stimulation. However, they did not measure full masking functions, but a single threshold (versus baseline) for a mask contrast of 30%. They found a constant and fairly modest level of this form of masking as a function of eccentricity.

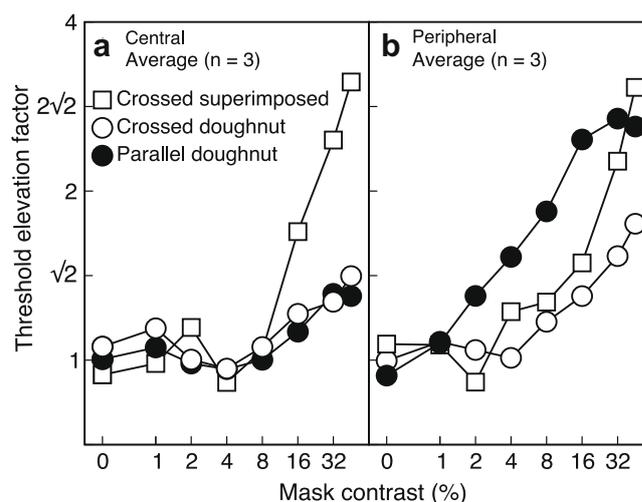


Fig. 3. Results from Fig. 2 averaged across observers ($n = 3$) and normalised to the detection threshold for a mask contrast of 0% for central stimulation (a) and peripheral stimulation (b). Error bars are omitted to avoid clutter. The average standard errors across observers for the three conditions in the order shown in the legend were: 0.62 dB, 0.33 dB and 0.67 dB in (a) and 1.05 dB, 1.84 dB and 0.87 dB in (b). The average standard error within observer was 0.73 dB in (a) and 0.87 dB in (b). (Note that the tick marks on the ordinate have a spacing of 3 dB.)

3.2. Saturation of surround suppression: two hypotheses

We offer two explanations for the saturation of masking from the parallel doughnut. One possibility is that the contrast-response saturates in the pathway that mediates suppression from the surround. Another possibility is that the target is processed by two different mechanisms: one sensitive to low contrasts and subject to surround suppression, the other only operative at moderate contrasts and above but immune from surround suppression. Single-cell evidence provides some support for this idea. Subcortical magnocellular (M) cells are subject to divisive surround suppression, whereas parvocellular (P) and koniocellular cells are either less so, or not at all (Alitto & Usrey, 2008; Solomon, Lee, & Sun, 2006; Solomon, White, & Martin, 2002). Although magnocellular cells have greater contrast sensitivity than parvocellular cells, they are far fewer in number, particularly in the fovea (Derrington & Lennie, 1984), and so we might expect threshold performance to be dominated by the P-system for central stimulation. However, the M:P density ratio increases rapidly with distance from the fovea (Azzopardi, Jones, & Cowey, 1999; Connolly & Van Essen, 1984; though see Gomes, Silveira, Saito, & Yamada, 2005), suggesting that the contrast-sensitive M-system might come to dominate threshold performance in the periphery. Taken together, this might explain why surround suppression is observed at threshold only in the periphery, and why it saturates at moderate contrasts, where the less sensitive but unsuppressed P-stream takes over.

Our next experiment was designed to test the two hypotheses outlined above.

4. Experiment 2: suppressive pathways from the surround saturate with mask contrast

4.1. Introduction and models

Here, we develop two computational models to provide canonical predictions for our two hypotheses. The model equations are closely related to those used in contrast gain control equations by Heeger (1992), Foley (1994) and others.

Our first hypothesis proposes that the suppressive pathways from the surround saturate with contrast. This idea is illustrated by the behaviour of the ‘saturating suppression’ model in Fig. 4a, which was derived from Eqs. (1) and (2) as follows. The saturating response ($Resp_{surround}$) to the surround mask contrast (C_{mask}) is given by:

$$Resp_{surround} = C_{mask}^p / (1 + C_{mask}^p). \quad (1)$$

This provides divisive suppression to the target response ($Resp_{target}$) as follows:

$$Resp_{target} = C_{target}^p / (1 + C_{target}^p + w \times Resp_{surround}^p), \quad (2)$$

where C_{target} is the target contrast and w is the weight of suppression from the surround. For the purpose of illustration we set $p = 2$, but this was not critical. Finally, we assumed that the target was detected when $Resp_{target} \geq 0.5$. (This was not critical though was set less than unity so that the target mechanism did not saturate). Note that the form of the contrast-masking function (Fig. 4a) is unchanged by the magnitude of w , but masking becomes less severe as w decreases. In other words, the masking functions are pressed downwards as the weight of masking decreases.

Our second hypothesis proposes that two mechanisms are involved in the detection process. The most sensitive one is subject to surround suppression, the less sensitive one is not. This idea is illustrated by the behaviour of the ‘dual mechanisms’ model in Fig. 4b, which was derived from Eqs. (3)–(5) as follows. The response of the mechanism that is subject to surround suppression ($Resp_{highsens}$) is given by:

$$Resp_{highsens} = C_{target}^p / (1 + C_{target}^p + wC_{mask}^p), \quad (3)$$

and that of the mechanism immune from surround suppression ($Resp_{lowsens}$) by:

$$Resp_{lowsens} = \alpha C_{target}^p / (1 + \alpha C_{target}^p) \quad (4)$$

The sensitivity of the second mechanism was set lower than the first by arranging that $\alpha < 1$. For the purposes of illustration we set $\alpha = 0.02$, but this was not critical. The overall response ($Resp_{target}$) was determined by Minkowski summation between the two mechanisms, thus:

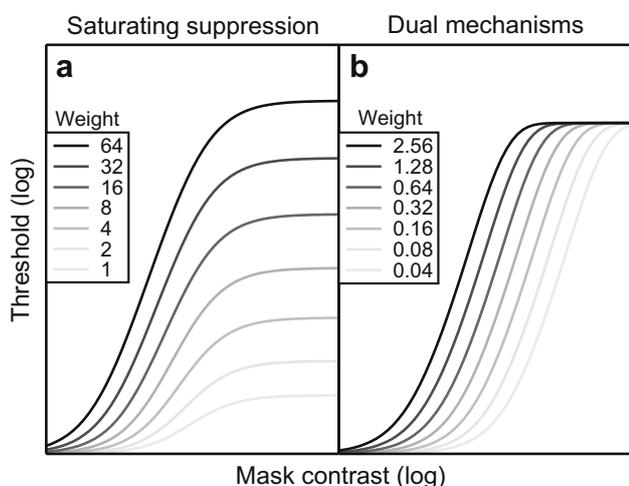


Fig. 4. Canonical model predictions for two models of surround suppression. Masking asymptotes with mask contrast for both models, but varies in different ways with the weight of suppression (w). In the experiments this was assumed to decrease with the size of the hole in the doughnut mask. (a) The ‘saturating suppression’ model (Eqs. (1) and (2)). (b) The ‘dual mechanisms’ model (Eqs. (3)–(5)).

$$Resp_{target} = (Resp_{lowsens}^k + Resp_{highsens}^k)^{1/k}. \quad (5)$$

For the purposes of illustration we set $k = 4$, but this was not critical. As for the previous model, we assumed that $p = 2$ and the target was detected when $Resp_{target} \geq 0.5$. Note that the form of the contrast-masking function is unchanged by the magnitude of w , but the masking functions are shifted rightwards on a log-log plot as w decreases.

The goal of Experiment 2 was to manipulate w experimentally so that psychophysical data could be compared with the two very different families of predictions. We did this by varying the size of the hole (see Fig. 5) in a parallel doughnut mask (Petrov & McKee, 2006).

5. Results

For both observers (DHB and LP) there is clear evidence that the masking functions saturate with contrast (Fig. 6). Note that the ‘2°’ condition is identical to the parallel surround condition used in Experiment 1 (solid circles in Fig. 3b). For the smaller hole

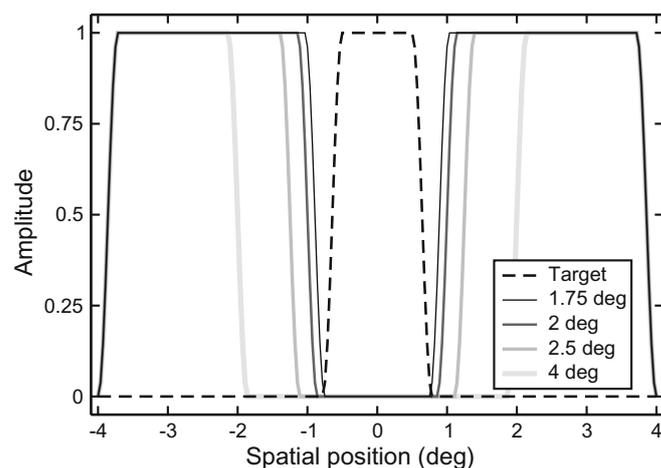


Fig. 5. Cross-sections of the spatial envelopes for the target and doughnut masks used in Experiment 2 in which the diameter of the central hole was varied.

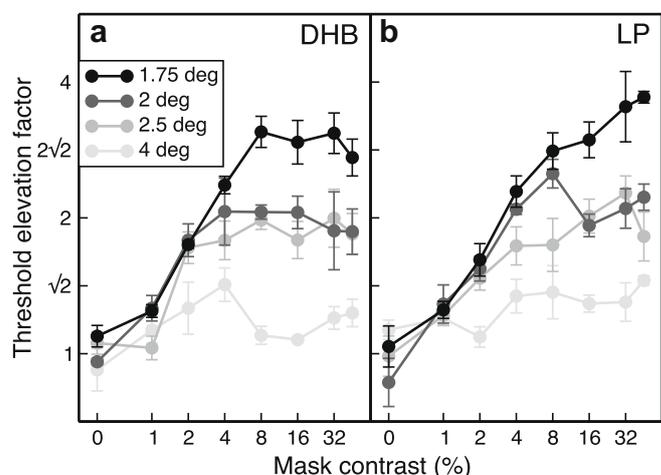


Fig. 6. Results from Experiment 2: threshold elevation for parallel doughnut masks placed 4.5° in the periphery with various diameters of central hole (see Fig. 5 and legend). Results are normalised to the average sensitivity across the four conditions without a mask. Different panels (a and b) are for different observers. Error bars show ± 1 SE.

condition (1.75°), saturation is evident only for DHB (Fig. 6a). However, there is saturation for both observers for the 2° hole and wider. Most notably, the maximum threshold elevation decreases as the diameter of the hole in the mask increases. There is no hint of a lateral translation of the masking functions. These results provide clear support for the 'saturating suppression' model over the 'dual mechanisms' model (compare Figs. 4 and 6).

5.1. Discussion: a similarity with crowding

The relation between masking and crowding has been discussed extensively (e.g., Levi, 2008; Pelli & Tillman, 2008). Although pedestal masking and crowding are clearly very different (Pelli et al., 2004), there are far more similarities between surround suppression and crowding (Petrov, Popple, & McKee, 2007). Although the one cannot be explained completely by the other (Petrov et al., 2007) and spatial integration processes are probably involved (Parke, Lund, Angelucci, Solomon, & Morgan, 2001; Pelli et al., 2004), it is plausible that letter identification is compromised by surround suppression as well as inappropriate summation, as has been proposed for contrast increment thresholds (Meese & Summers, 2007). In any case, it is striking that the form of the contrast-masking functions here (Fig. 6) are very similar to those found by Pelli et al. (2004) for letter spacing and identification (their Fig. 11a). Pelli et al. concluded that the process mediating crowding (from letters in the surround) saturated with mask contrast: the same as our conclusion about surround suppression here. Of course, this does not demand that a common process (or set of processes) mediates the two phenomena, but it does illustrate a new property that the two have in common (Petrov et al., 2007).

6. General discussion

To better understand the suppressive processes involved in contrast masking, we measured masking functions for three different configurations of mask and target in each of two retinal field locations (central and an eccentricity of 4.5°). The only arrangement that produced a saturating masking-function was when the mask and target were parallel (co-oriented) and in the periphery. We confirmed this saturation in a second experiment where we varied the size of the hole in the doughnut mask. In this experiment, the level of masking saturated for nearly all masks, but the strength of masking decreased with the diameter of the hole. This indicates that the asymptotic behaviour of the masking functions owes to the contrast-saturation of the pathway mediating suppression from parallel surrounds.

6.1. Mask contrast range

We found no evidence for asymptotic masking in the cross-oriented cases. It is possible that this would happen at mask contrasts higher than those used here. However, the frame interleaving technique used here (see Section 2) placed an upper limit of 50% for the mask contrast. Using a different method of stimulus construction might have extended this technical limitation a little. However, given the need for headroom for target contrast (in the superimposed condition at least), mask contrasts as high as 100% were not practical, and even a contrast as high as 89.2% would correspond with only one extra data point with the spacing used in most of Fig. 2. Nevertheless, Fig. 3b shows that cross-oriented superimposed masking (open squares) continues to increase at mask contrasts that produce saturation in the parallel surround case (filled circles), ruling out the interpretations in the fourth and fifth rows of Table 1 and pointing to a fundamental difference in operation between these two forms of masking.

6.2. Surround suppression

We interpret the masking by the doughnut masks (circles, Figs. 3a and b and 6) as surround suppression, akin to that from the non-classical surround at the single-cell level. Another possible interpretation is that the detecting mechanisms (excitatory filter-elements) for the target in this study were somewhat larger than the target stimuli, in which case the doughnut masks might also have acted as superimposed masks. However, if this were so then there should be substantial facilitation (a 'dipper') for the parallel surround, owing to the pedestal effect (Foley, 1994; Legge & Foley, 1980) from the accelerating non-linear transducer for contrast detection (Lu & Doshier, 2008; Meese & Summers, 2009). This is not what was found for either of the conditions involving a parallel surround mask (solid circles, Fig. 3) (see also Petrov et al., 2005). For superimposed cross-oriented masking, substantial facilitation is not expected (Foley, 1994) and so this argument cannot be applied. However, it is reasonable to suppose that if the masking from the parallel doughnut is not a manifestation of superimposed masking, then neither is that for the cross-oriented doughnut mask which has an identical spatial configuration. Furthermore, the similarity of the two doughnut-masking functions for central stimulation (Fig. 3a, circles) suggests a common underlying process for the two orthogonal orientations. By comparison to each of the other masking functions in Experiment 1 these are fairly weak, suggesting that they receive little weight in the suppressive pathway that they stimulate. One interpretation of this is that there is a Gaussian weighted (or similar) isotropic suppressive field that superimposes the classical receptive field (CRF) of the target mechanism but whose skirts encroach the surround (Webb et al., 2005).

6.3. Our results require two processes of suppression

At the system-level of psychophysics (Snowden & Hammett, 1998), the component-level of single-cell physiology (DeAngelis, Robson, Ohzawa, & Freeman, 1992) and the intermediate level of functional imaging (Williams, Singh, & Smith, 2003; Zenger-Landolt & Heeger, 2003), it is well established that suppression arises from beyond the CRF (surround suppression) and from components outside the pass-band of the target mechanism (cross-orientation, or cross-channel masking) (see Section 1). In principle, these basic effects could be manifestations of a single suppressive process (Lennie & Movshon, 2005). Target mechanisms could be inhibited by a broadband, isotropic mechanism, such as the inhibitory complex-cells identified by Hirsch et al. (2003), with receptive fields larger than the excitatory mechanism. This would produce self-suppression (Foley, 1994), surround suppression (Snowden & Hammett, 1998), cross-orientation suppression (Meese & Holmes, 2007) and cross-spatial frequency suppression (Holmes & Meese, 2004). However, the orientation tuning of surround suppression (Fig. 3b; see also Ishikawa et al., 2006; Petrov et al., 2005; Zenger et al., 2000) and the different contrast-dependencies of masking in Fig. 3b suggest that parallel surround masking and superimposed cross-orientation masking have different origins. Several previous psychophysical studies (Petrov et al., 2005) and single-cell studies (DeAngelis et al., 1992; DeAngelis, Freeman, & Ohzawa, 1994; Smith et al., 2006; Durand, Freeman, & Carandini, 2007) have led to the same conclusion.

6.3.1. A neuronal framework

Here we describe a framework of neuronal interactions within which our masking results can be placed. The simplest arrangement that we have been able to derive is depicted in Fig. 7 and involves divisive interactions, consistent with previous quantitative analyses (Challinor et al., 2007; Meese & Holmes, 2002) and the modelling here. For central stimulation, the excitatory mechanism

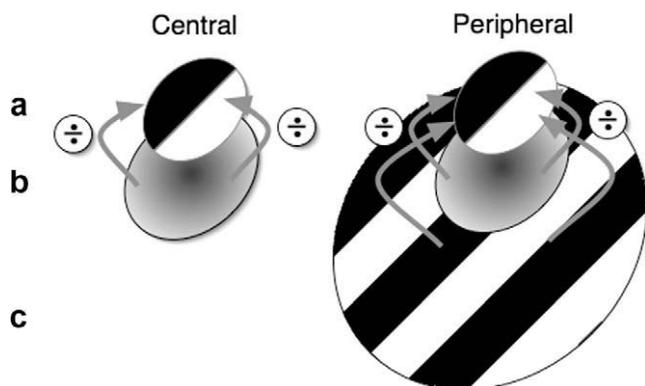


Fig. 7. Suppressive spatial interactions in central and peripheral (4.5°) vision. (a) An excitatory filter-element for detecting the oriented target patch. (b) A broadband isotropic suppression field that is slightly larger than the excitatory filter-element. The suppressive interaction could happen directly, as shown, or indirectly at a stage that precedes orientation tuning of the detecting mechanism. Suppression from this field does not saturate. (c) Large co-oriented suppression field found only for peripheral stimulation at detection threshold. Suppression from this field saturates owing to the saturation of the contrast-response of this field.

is suppressed by a broadband (Baker et al., 2007; Petrov et al., 2005) isotropic field that is slightly larger than the target patch (Fig. 7b). Single-cell physiology in the retina, the lateral geniculate nucleus and the cortex also indicates an isotropic suppression field (DeAngelis et al., 1992; Solomon et al., 2002; Solomon et al., 2006) that is slightly larger than the CRF (Solomon et al., 2002; Webb et al., 2005), and Medina and Mullen (2009) have recently found an isotropic chromatic suppression field using masks with various orientations. The excitatory mechanism in Fig. 7a is shown as orientation tuned, consistent with the detection of oriented gratings (Blakemore & Campbell, 1969), though if the suppression were to take place subcortex then the target mechanism might also be isotropic, at least at this stage of the interaction (Bonin, Mante, & Carandini, 2005; Li, Thompson, Duong, Peterson, & Freeman, 2006). In any case, this type of suppression could account for the substantial superimposed cross-orientation masking and the much weaker isotropic masking from the surround (Fig. 3a).

In the periphery, we suppose a further process that is orientation tuned and much more potent beyond the target region (Fig. 7c). For example, it could have a receptive field that pools over a much larger area than the target mechanism (Petrov & McKee, 2006), thereby delivering substantial surround suppression.

Note that in our illustration (Fig. 7), the larger suppression field extends through the CRF of the target mechanism though we have not performed a specific test of this hypothesis here. However, there is good evidence for an orientation-tuned process of self-suppression from the numerous studies that have investigated this directly using contrast pedestals (e.g., Foley, 1994; Legge & Foley, 1980; Meese & Holmes, 2009; Phillips & Wilson, 1984). How this relates to the contrast-saturation of the suppression field identified here remains unclear, though asymptotic and non-monotonic contrast discrimination functions (pedestal masking) have been reported by others (Kingdom & Whittle, 1996; McIlhagga & Peterson, 2006; Zenger-Landolt & Heeger, 2003; Zenger-Landolt & Koch, 2001). It is plausible that the putative superimposed part of the suppression field was tapped in those studies, particularly by Zenger-Landolt and Koch, who performed their experiments in the peripheral visual field.

For the general arrangement that we propose (Fig. 7), superimposed cross-orientation masking would be similar for central and peripheral stimulation (compare open squares in Fig. 3a and b) and parallel surround masking would be tuned (compare circles in Fig. 3b) and much more potent in the periphery than for central

stimulation (compare solid circles in Fig. 3a and b), just as we found. For peripheral cross-oriented surround masking (Fig. 3b, open circles) we found a slightly greater effect than that for central stimulation (Fig. 3a, open circles). This could be because (i) the weight of surround suppression from the isotropic mechanism (Fig. 7b) is greater in the periphery and/or (ii) because the orientation tuning of the tuned suppressive-mechanism (Fig. 7c) is sufficiently broad for it to receive some drive from orthogonal mask gratings. Our data do not decide between these possibilities.

Finally, it is noteworthy that the peripheral scheme in Fig. 7 is strikingly similar to the spatial components of suppression proposed by Webb et al. (2005) to describe suppression in striate-cells of macaque.

6.3.2. Scope of the framework

While the framework in Fig. 7 is consistent with much psychophysics and physiology, it is limited in scope. For example, there is psychophysical evidence for two stages of cross-orientation suppression (Baker et al., 2007; Meese & Baker, 2009), two stages of surround suppression (Cai et al., 2008) and dual temporal components to surround suppression (Ishikawa et al., 2006; Petrov & McKee, 2009). The study here did not address these issues or those of binocular interactions, and the scheme in Fig. 7 was not designed with them in mind. How this scheme might be extended to embody these complications remains to be seen.

6.4. Possible causes for the different forms of masking

For masking to accelerate with contrast, the effective weight of suppression must accelerate with mask contrast. This can happen if the suppression from masking must overcome an additional standing level of suppression. Mathematically, this is achieved by the saturation constant in many contemporary models of contrast gain control (e.g., Foley, 1994; see Meese et al., 2008 for a variety of implementations). Our psychophysical data here do not imply physiological loci, but the broad spatial frequency and orientation tuning of this effect (Baker et al., 2007; Meese, 2004; Petrov et al., 2005) and its placement before binocular summation (Baker & Meese, 2007; Baker et al., 2007; Meese & Baker, 2009) in the two-stage model of contrast gain control (Meese, Georgeson, & Baker, 2006) are consistent with the broadband isotropic suppression fields identified in the LGN (Bonin, Mante, & Carrandini, 2006; Bonin et al., 2005; Solomon et al., 2006), at least for the monocular contribution of this form of suppression (Baker et al., 2007) (see Baker and Meese (2007) for discussion of the broadband interocular contribution).

Although contrast compression occurs in the LGN (Alitto & Usrey, 2008; Derrington & Lennie, 1984; Li et al., 2006), it is more pronounced in the cortex (Sclar, Maunsell, & Lennie, 1990). The orientation tuning of parallel surround suppression (Fig. 3b; Petrov et al., 2005) its susceptibility to contrast adaptation (Durand et al., 2007) and localisation from functional imaging studies (Williams et al., 2003) also point to a cortical locus, probably V1 (Zenger-Landolt & Heeger, 2003). Thus, if surround suppression were served by inhibitory input from saturating cortical neurons whose useful dynamic range is limited to intermediate contrasts and below, then the masking-effect would saturate, as we have observed.

More generally, assuming that the neuronal contrast-response becomes more compressive (more prone to saturation) as one progresses up the visual hierarchy (Sclar et al., 1990), the absence of saturation for superimposed cross-oriented masking (Experiment 1), and its marked presence for parallel surround suppression (Experiments 1 and 2) suggests an earlier locus for the former. Petrov et al. (2005) also came to this conclusion, but from a very different basis (see Section 1).

6.5. The 'dual mechanisms' model: no support here, but not rejected

At the outset of this study, the dual-mechanisms explanation for the asymptotic behaviour of surround masking had some appeal. It has been suggested that parallel surround suppression might be important for enhancing contour detection and integration in the presence of textured backgrounds (Born & Tootell, 1991; Dakin & Baruch, 2009; Grigorescu, Petkov, & Westenberg, 2003; Kingdom & Prinns, 2009; Petkov & Westenberg, 2003) and that a family of different arrangements between the CRF and the modulatory lobes could be used to produce a population code for higher-order features (Tanaka & Ohzawa, 2009). But if these ideas are correct, why should such an important interaction appear to be absent in the fovea? The proposal of dual mechanisms allows that the neuronal substrate for surround suppression is in fact present throughout the visual field, but that it is not necessarily revealed by the contrast detection task, which picks out the most sensitive population of mechanisms. Thus, surround suppression would be found in the fovea for a suprathreshold contour integration task that taps the suppressed mechanisms (Dakin & Baruch, 2009; Kingdom & Prinns, 2009), but not in a contrast detection task, that does not (Snowden & Hammett, 1998). This proposal also allows for the fact that surround suppression is found in the fovea for the suprathreshold tasks of contrast-matching (Fullenkamp, 1991; Cai et al., 2008; Meese & Hess, 2004; Snowden & Hammett, 1998) and contrast discrimination (Foley, 1994; Meese, 2004).

Zenger-Landolt and Koch (2001) also proposed an arrangement involving two contrast mechanisms (one with and one without divisive surround suppression) to account for their peripheral contrast discrimination functions with flanker masks. Ishikawa et al. (2006) have proposed that M- and P-systems might underpin different processes of psychophysical surround suppression. And other psychophysical work, unrelated to surround suppression, also suggests that multiple contrast-selective mechanisms are involved in processing the full contrast range (Yu, Klein, & Levi, 2004).

Nevertheless, the results from Experiment 2 produced no evidence for the rightward shift of the contrast-masking functions that could have provided the signature for the dual mechanisms arrangement that we have considered. However, although there is no evidence for this arrangement here, this does not rule out the possibility. Our results do show that the surround suppression pathway saturates with contrast, which means that putative peripheral mechanisms that are less sensitive but immune from surround suppression would not have been revealed by the experiments here.

7. Conclusions

We have studied contrast masking in human vision. We conclude that superimposed cross-oriented masking is a different process from parallel surround masking in the periphery. The suppressive pathway that supports the former saturates with contrast whereas that which supports the latter does not. The contrast-response of visual neurons is known to become more compressive moving up the visual hierarchy, suggesting that cross-oriented superimposed masking arises before parallel surround masking. We found no support for the idea that the asymptotic masking from the surround owes to relief from masking at higher mask contrasts by a less sensitive mechanism that is immune from surround suppression. The process of surround suppression identified here has the same contrast-saturating characteristic as that found in crowding.

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