Journal of Vision (2004) 4, 930-943 http://journalofvision.org/4/10/8/

Area summation and masking

Tim S. Meese

Neurosciences Research Institute, School of Life and Health Sciences, Aston University, Birmingham, UK

At detection threshold, sensitivity improves as the area of a test grating increases, but not when the test is placed on a pedestal and the task becomes contrast discrimination (G. E. Legge & J. M. Foley, 1980). This study asks whether the abolition of area summation is specific to the situation where mask and test stimuli have the same spatial frequency and orientation ("within-channel" masking) or is more general, also occurring when mask and test stimuli are very different ("cross-channel" masking). Threshold versus contrast masking functions were measured where the test and mask were either both small (SS), both large (LL), or small and large, respectively (SL). For within-channel masking, facilitation and area summation were found at low mask contrasts, but the results for SS and LL converged at intermediate contrasts and above, replicating Legge and Foley (1980). For all three observers, less facilitation was found for SL than for SS. For cross-channel masking, area summation occurred across the entire masking function and results for SS and SL were identical. The results for the entire data set were well fit by an extended version of a contrast masking model (J. M. Foley, 1994) in which the weights of excitatory and suppressive surround terms were free parameters. I conclude that (i) there is no empirical abolition of area summation for cross-channel masking, (ii) within-channel area summation can be abolished empirically without being disabled in the model, (iii) observers are able to restrict the area of spatial integration, but not suppression, (iv) extending a cross-channel mask to the surround has no effect on contrast detection, and (v) there is a formal similarity between area summation and contrast adaptation.

Keywords: human vision, spatial summation, suppression, masking, surround, adaptation, contrast discrimination

Introduction

Early vision is specialized for detecting and representing luminance contrast across the retinal image. Spatial filtering of different bands of spatial frequency and orientation (e.g., Robson, 1980; Watson, 1983) is implemented by parallel convolution of the image with sets of spatial filter-elements (sometimes called “filter kernels”). Each set is sometimes called a filter or, when additional output processes such as nonlinearities are also considered, a channel. Each element sees just a small patch of the retinal image, which is spatially weighted according to the filter’s scale and preferred orientation. Of course, visual features often extend over a much greater distance of the retina than the spatial footprint of a single filter-element (the classical receptive field), suggesting the need for higher order spatial integration of visual information. Recent work suggests that summation might occur across (i) multiple filter-elements at a single retinal location (Georgeson & Meese, 1997; Meese & Georgeson, 1996; Meese & Georgeson, in press; Olzak & Thomas, 1999) and (ii) that linking occurs between different filter-elements at different retinal locations (Field, Hayes, & Hess, 1993). But the experiments presented here concentrate on the summation of information within a single filter. There is good psychophysical evidence for within-channel area summation of this kind (sometimes called spatial summation). At contrast detection threshold, sensitivity increases with the number of cycles in a grating (Legge & Foley, 1980; Howell & Hess, 1978; Robson & Graham, 1981), the height of a grating (Howell & Hess, 1978), the number of grating patches (Bonneh & Sagi, 1998; Meese & Williams, 2000), and the diameter of a circular foveal patch of grating (Cannon, 1995; Meese, Naik, & Dattani, 2003). In most cases, so long as the stimulus is greater than a critical size (Graham, 1989), the rate of improvement is close to the fourth-root of stimulus area and has been interpreted as probability summation amongst multiple filter-elements (Howell & Hess, 1978; Legge & Foley, 1980; Meese & Williams, 2000; Robson & Graham, 1981; Tyler & Chen, 2000). However, other interpretations are possible. Fourth-root summation could represent nonlinear physiological summation (Cannon, 1995; Graham, 1989) through a cascade of contrast squaring mechanisms (Laming, 1988), some other combination of physiological nonlinearities and optimal or suboptimal detection strategies (e.g., Itti, Koch, & Braun, 2000), or facilitatory interactions (Bonneh & Sagi, 1998, 1999; Usher, Bonneh, Sagi, & Herrmann, 1999).

Intriguingly, though, when the area summation experiment is repeated using a variable contrast pedestal (and so the task is contrast discrimination), inspection of the data shows that summation survives at low pedestal contrasts but is effectively abolished at intermediate contrasts and above (Legge & Foley, 1980). One possibility is that the area summation process is disabled for the suprathreshold task of contrast discrimination (Legge & Foley, 1980; Swanson, Wilson, & Giese, 1984; Thomas & Olzak, 1997; Verghese & Stone, 1996). Another possibility, however, is that the empirical loss of area summation does not represent extinction of the summation process but

doi:10.1167/4.10.8 Received March 22, 2004; published November 8, 2004

that it is obscured by a complementary process with opposite effect, one that depends on stimulus size and that operates above detection threshold (Bonneh & Sagi, 1999; Legge & Foley, 1980; Meese et al., 2003). One candidate process that might achieve this is surround suppression (Cannon & Fullenkamp, 1991; D'Zmura & Singer, 1996; Olzak & Laurinen, 1999; Snowden & Hammett, 1998; Solomon, Sperling, & Chubb, 1993; Xing & Heeger, 2000). Luminance contrast that surrounds a central target patch is thought to attenuate the response to the central patch through divisive suppression in a contrast gain pool (Bruce, Green, & Georgeson, 2003; Foley & Chen, 1999). In the experiment of Legge and Foley (1980), this could have gone unnoticed because the size of the test and mask stimuli were confounded: The benefits of increasing test size could have been hidden by the detrimental effects of increasing mask size (Bonneh & Sagi, 1999).

The first aim of this work was to test the idea above by measuring contrast masking functions where both the test and mask are small (SS), where the test is small but the mask is large (SL), and where both the mask and test are large (LL). The initial expectation was that if the area summation process survives contrast masking, then it should be visible in a comparison between SL and LL, because the size of the test stimulus changes across these conditions but the size of the mask does not. Another expectation was that a comparison of SS with SL should reveal the suppressive effects of the surround directly because only the contribution to the gain pool changes across these conditions. As shown in Appendix A, however, detailed quantitative analysis reveals that a contrast gain control model can behave unexpectedly in these respects and that great care is needed when interpreting data from visual inspection alone. In particular, it can be misleading to suppose that small increments in test contrast make a negligible contribution to the suppressive gain pool.

The main experimental observation above is that empirical area summation is abolished by contrast masking when the mask stimulus has the same orientation, spatial frequency, and phase as the test stimulus. However, masking is not restricted to this within-channel situation. Stimuli with orientations and spatial frequencies that are very different from the test stimulus can also cause substantial masking (Foley, 1994; Holmes & Meese, 2001; Meese & Holmes, 2002, 2003; Olzak & Thomas, 1999, 2003; Ross, Speed, & Morgan, 1993; Thomas & Olzak, 1997). This is sometimes referred to as cross-channel masking.[1] Therefore, another main aim of this work was to establish whether the empirical loss of area summation is a general masking phenomenon (applying to both within- and cross-channel situations), or whether it is specific to the situation where the mask stimulus excites the detecting mechanism (within-channel masking).

Methods

Equipment

The experiment was run under the control of a PC, and stimuli were displayed from a framestore of a VSG2/4 operating in pseudo-15 bit mode on a 120 Hz gray-scale monitor (either an Eizo F553-M [mean luminance of 55 cd/m^2] or Sony Trinitron Multiscan 200PS [mean luminance of 65 cd/m^2]). Contrast is expressed in dB and is given by 20 times the log of Michelson contrast (c) given by $c = 100\ (L_{\max} - L_{\min})/(L_{\max} + L_{\min})$ where L is luminance. Gamma correction used lookup tables and ensured that the monitor was linear over the entire luminance range used in the experiments. A frame interleaving technique was used for test and mask stimuli, giving a picture refresh rate of 60 Hz. Observers were seated in a darkened room and sat with their heads in a chin and head rest at a viewing distance of 57 cm. A small dark fixation point (4 pixels square) was visible throughout the experiment.

Stimuli

All stimuli were windowed by a raised cosine function with a central plateau. The rising and falling parts of these functions were each 1 deg. The central plateaus were 1 deg or 16.5 deg for small (S) and large (L) stimuli, respectively. The test and mask were either both small (SS), small and large, respectively (SL), or both large (LL). The test stimulus was always a vertical patch of 1 c/deg grating in sine phase with the fixation point. A within-channel mask always had the same phase, orientation, and spatial frequency as the test stimulus. A cross-channel mask was either a patch of horizontal 1 c/deg grating or an oblique (45 deg) 3 c/deg grating. High-contrast examples of the test and mask stimuli for the three different configurations (SS, SL, and LL) are illustrated in Figure 1. Stimulus duration was 100 ms.

Procedure

Test contrast level was selected by a 3-down 1-up staircase procedure (Wetherill & Levitt, 1965), and a single condition was tested using a pair of randomly interleaved staircases (Cornsweet, 1962). After an initial experimental stage in which larger step-sizes were used (12 dB and 6dB), a test stage consisted of 12 reversals for each staircase using a contrast step size of 3 dB. A two-interval forced-choice (2IFC) technique was used, where one interval contained only the mask and the other contained the test plus mask. The onset of each interval was indicated by an auditory tone and the duration between the two intervals was 500 ms. The observer's task was to select the interval that contained the test stimulus using two buttons to indicate their response. Correctness of response was provided by auditory feedback, and the order of the intervals was selected randomly by the computer. For each run, thresholds (75% correct) and standard errors were estimated by performing

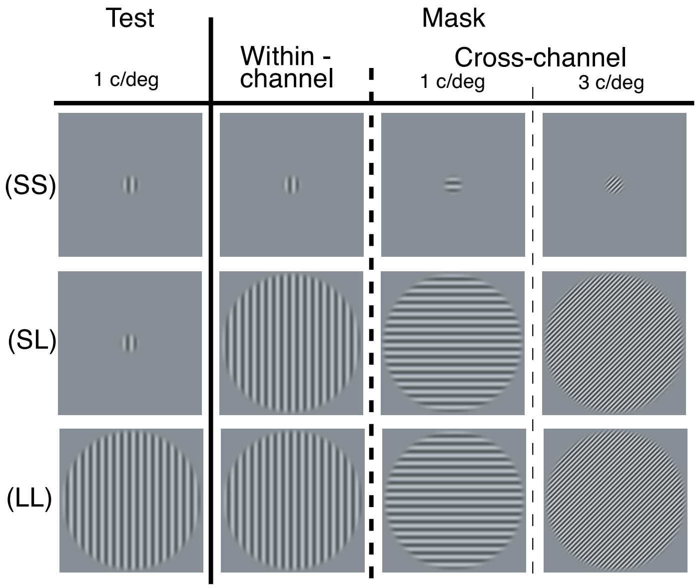

Figure 1. Test and three different mask stimuli used in the small/small (SS) configuration (top), the small/large (SL) configuration (middle), and the large/large (L/L) configuration (bottom). The test stimulus in the SL and SS configurations is identical. The mask stimuli in the SL and LL configurations are identical.

probit analysis on the data gathered during the test stages and collapsed across the two staircases. This resulted in individual estimates for each psychometric function based on around 100 trials (McKee, Klein, & Teller, 1985).

Experimental "contrast-blocs" were alternated between the cross-channel conditions and the within-channel condition, and were repeated 3 times. A contrast-bloc consisted of a set of "mini-blocs" for each of 11 or 12 mask contrasts. Observers were instructed to select the mask contrasts in a random order, but to try and spread their selections evenly across the range. A mini-bloc consisted of an experimental session for each of the three size configurations (SS, SL, and LL), selected in a random order by the computer (using a random number generator).

Before data collection began, the following rejection and replacement criterion was set to lessen the impact of unreliable estimates of threshold. If the standard error of a threshold estimate within a mini-bloc was greater than 3 dB (estimated by probit analysis), the data for that condition were discarded and the mini-bloc was rerun. Estimates of threshold were averaged across all the replications giving results based on around 300 trials per data point.

Observers

Two undergraduate students (PN and SK) served as observers and performed the experiment as part of their course requirement. The author (TSM) was a third observer. All observers had substantial practice in all the stimulus conditions before data collection began and had normal or optically corrected-to-normal vision. TSM performed the experiment using both types of cross-channel masks. For PN the cross-channel mask was the oblique 3 c/deg grating and for SK it was the horizontal 1 c/deg grating.

Model fitting

The model equations were solved numerically using a Pentium PC. I attempted to optimize the fits by using a downhill simplex method (Press, Flannery, Teukolsky, & Vetterling, 1989) initialized with 100 different pseudo-randomly selected sets of parameters. The reported fits are those that achieved the lowest root mean square (RMS) error in dB, though very similar results were achieved from many of the different starting points.

Results

Within-channel masking

Contrast masking functions for the within-channel masks (pedestals) are shown in Figure 2. In all three con-

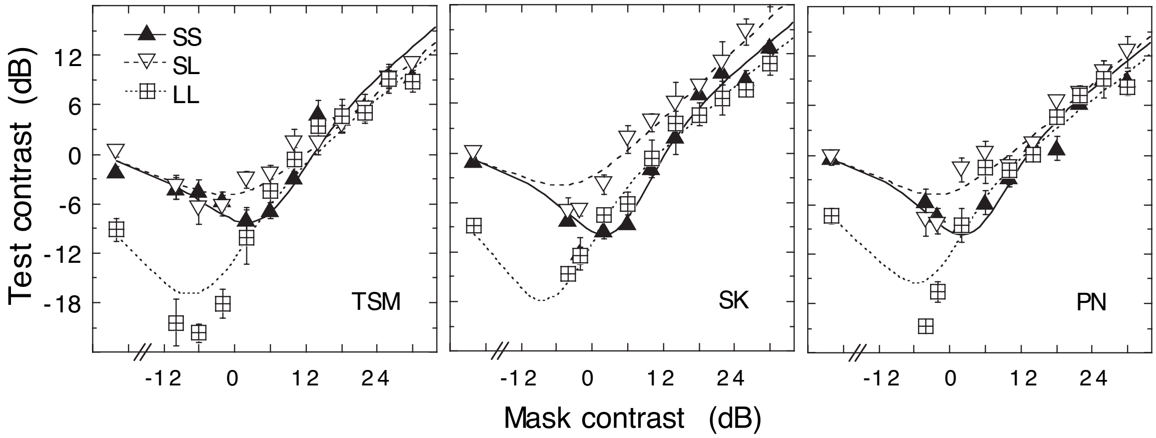

Figure 2. Within-channel masking functions. Different panels are for different observers. Within each panel results are shown for three different spatial configurations (SS, SL, and LL). Error bars show ±1 *SE* where larger than symbol size. The curves are for the model fits described in the text (version 2B).

figurations (SS, SL, and LL), the functions have a classic dipper shape (Legge & Foley, 1980; Nachmias & Sansbury, 1974; Wilson, 1980), meaning that detection of the test stimulus is facilitated by low-contrast pedestals and masked by higher contrast pedestals. A comparison of the SS and LL configurations reveals the effects of increasing the size of the entire stimulus. This causes a reduction in detection thresholds, but only at very low mask contrasts. At intermediate contrasts and above, the upper limbs of the masking functions tend to converge, indicating an absence of empirical area summation in this region. The results for this comparison are very similar to those for Legge and Foley's (1980) observer, who performed the experiment using two stimuli with different widths.

A comparison of the SS and SL configurations reveals the effects of increasing only the size of the pedestal. For TSM and PN, detrimental effects of the surround are seen primarily in the dipper region of the masking functions where the magnitude of facilitation is reduced toward the right-hand side of the dip. A similar effect was reported by Foley (1994). For SK, however, a detrimental effect is evident across the entire range of mask contrasts above −4 dB (0.63%). This is similar to an effect reported by Foley and Chen (1999).

A comparison of the SL and LL configurations reveals the effects of increasing the size of only the test stimulus. For TSM and PN, this is qualitatively similar to the comparison between the SS and LL configurations. Increasing the size of the test stimulus increases contrast sensitivity at low mask contrasts but not at intermediate contrasts and above. For SK, however, the benefit of a larger test stimulus extends across the entire range of mask contrasts. At first sight it would seem that area summation survives within-channel masking for SK, but not for PN and TSM. This empirical difference appears much less puzzling, however, in the light of the quantitative modeling performed in the next main section (also see Appendix A).

Cross-channel masking

The results from the cross-channel conditions are shown in Figure 3. They were very similar for all three observers and for the two different types of cross-channel mask (compare left and right panels). In all cases, threshold was elevated by masks with contrasts around 12 dB (4%) or above and there was no region of facilitation (Foley, 1994). When the size of the mask was increased (e.g., compare SS and SL), this had no effect on the masking functions. When the size of the test was increased, however (compare SL and LL), performance improved across the entire range of mask contrasts. Thus, the empirical abolition of area summation is strictly a within-channel phenomenon.

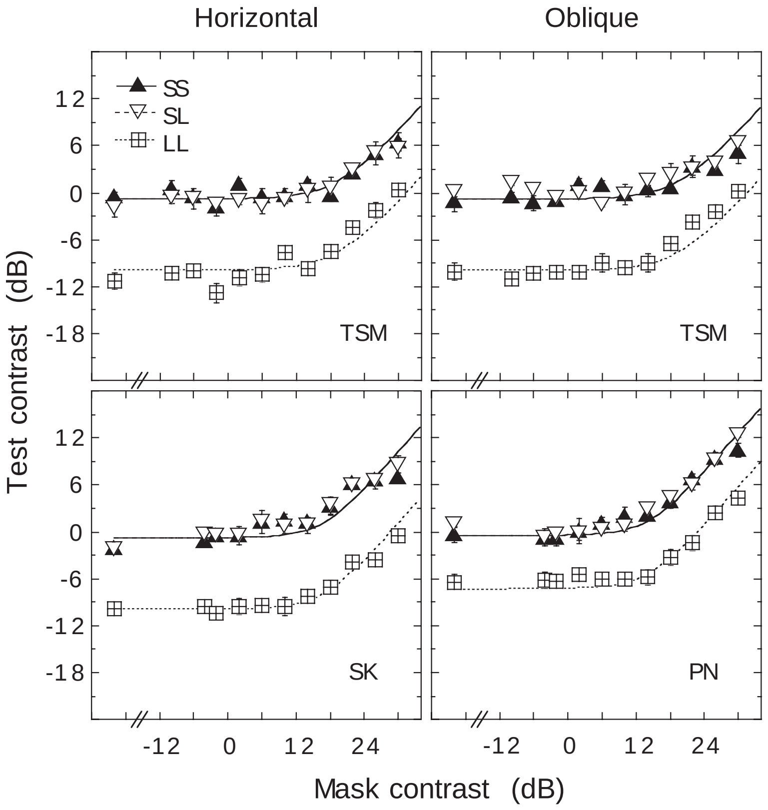

Figure 3. Cross-channel masking functions. Left panels are for the horizontal 1 c/deg mask and right panels are for the oblique 3 c/deg mask. The top row is for TSM, who performed both conditions. The bottom row is for two different observers who performed one condition each. Within each panel, results are shown for three different spatial configurations (SS, SL, and LL). Error bars show ±1 *SE* where larger than symbol size. The curves are for the model fits described in the text (version 2B). Note that the model fits for the SS and SL configurations are superimposed.

Area summation model

Model architecture

For each observer, I have fit the results of the entire experiment with each of several variants of a contrast gain control model. These were inspired by Foley's (1994) recognition that a nonlinear equation for a static output nonlinearity could be extended to include suppressive contributions from nonexcitatory pathways. The generic model below extends that used by Foley (1994) by replacing each contrast term with a pair of terms, so that contributions from center and surround can be handled separately and area summation (between center and surround) can take place.

The internal response of the observer to the stimuli used in this work is given by the following equation and illustrated schematically in Figure 4:

$$RESP = \frac{E_{wc}c_{wc}{}^{p} + E_{ws}c_{ws}{}^{p}}{Z + S_{xc}c_{xc}{}^{q} + S_{xs}c_{xs}{}^{q} + S_{wc}c_{wc}{}^{q} + S_{ws}c_{ws}{}^{q} + S_{hc}c_{hc}{}^{q} + S_{hs}c_{hs}{}^{q}} \tag{1}$$

The parameters p and q are exponents of the various contrast terms and set the character of the response nonlinearities. E and S are the coefficients of excitatory and suppressive terms, respectively. The first letter of the subscript identifies whether the coefficient is a within-channel weight (w), an oblique cross-channel weight (x), or a horizontal cross-channel weight (h). The second subscript denotes whether the weighted term applies to luminance contrast in the center of the display (c) or the surround (s). The constant Z does not represent a degree of freedom and is set to unity.

The variable c is stimulus contrast (in %) and is subscripted using the same convention as for the coefficients. (The reader is alerted to the fact that the letters c and s have each been used to convey different meanings when used as subscripts [center and surround] from when used elsewhere in the model equation [contrast and suppression]). The level of stimulus contrast depends on the mask and test contrasts (c_m and c_t) and the spatial configuration as shown in Table 1.

I assume that the test stimulus is detected when the difference in responses to mask ($RESP_{mask}$) and mask plus test intervals ($RESP_{mask+test}$) is equal to a constant K. In the formulation used here, K does not represent a degree of freedom and was set to 0.1. Formally, this gives

$$K = 0.1 = RESP_{mask+test} - RESP_{mask}\ . \tag{2}$$

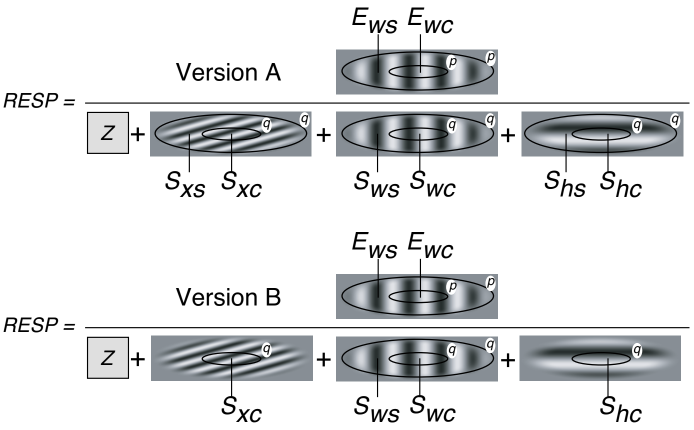

Figure 4. Schematic illustration of the models used in this study. Versions A and B are shown separately to clarify their differences. Versions 1, 2, and 3 allowed the weight parameters (E and S) to vary in different ways as described in the text and Figure 5. Version B contains fewer free parameters than version A but provided a comparable quality of fit to the data in this work.

	Oblique cross-channel	Within-channel	Horizontal cross-channel
SS condition			
c_{xc}	c_m	0	0
c_{xs}	0	0	0
c_{wc}	c_t	$c_m + c_t$	c_t
c_{ws}	0	0	0
c_{hc}	0	0	c_m
c_{hs}	0	0	0
SL condition			
c_{xc}	c_m	0	0
c_{xs}	c_m	0	0
c_{wc}	c_t	$c_m + c_t$	c_t
c_{ws}	0	c_m	0
c_{hc}	0	0	c_m
c_{hs}	0	0	c_m
LL condition			
c_{xc}	c_m	0	0
c_{xs}	c_m	0	0
c_{wc}	c_t	$c_m + c_t$	c_t
c_{ws}	c_t	$c_m + c_t$	c_t
c_{hc}	0	0	c_m
c_{hs}	0	0	c_m

Table 1. Assignment of mask (c_m) and test (c_t) contrasts to the stimulus contrast variables used in the model.

For each observer the model was fit to the entire data set from all conditions tested, and Equation 2 was solved numerically for c_t. In six different versions of the model (versions 1A, 2A, 3A, 1B, 2B, and 3B), different sets of the surround weights were permitted to vary across the SL and LL configurations (these are summarized in Figure 5; see legend for further details).

In version xA, the weights of the cross-channel suppressive surrounds (S_{xs} & S_{hs}) were allowed to take on different values for the SL and LL configurations. In version xB, S_{xs} & S_{hs} were preset to zero, as suggested by visual inspection

			Version A	Version B
			Cross-channel suppression region	
			Variable	No surround
Version 1	*Within-channel integration and suppression region*	Variable integration region Variable suppression region	6(3)	4(2)
Version 2		Matched integration region Variable suppression region	5(2)	**3(1)**
Version 3		Matched integration region Matched suppression region	4(1)	**2(0)**

Figure 5. Summary of six versions of the model used in this work. The bold highlights indicate the two versions that receive the greatest emphasis (version 2B and version 3B). Where the integration or suppression regions are described as "variable," the surround weights were permitted to vary across the three size configurations (SS, SL, and LL). Where they are described as "matched," excitatory and suppressive regions were restricted to the size of the test and mask stimuli, respectively, and their weights were the same for each configuration. This was implemented by fixing the model weights across the size configurations but resetting the excitatory surround weight (E_{ws}) to zero in the SL configuration. The numbers in the right part of the figure refer to the free parameters in the model. A Foley (1994)-type model that includes one cross-channel mask component requires five free parameters. In each cell, the first integer indicates the number of extra free parameters required by the respective model version here. The number in parentheses indicates the number of extra free parameters over and above those that are mandatory in describing excitatory and suppressive sensitivities to within-channel surrounds (versions A and B) and suppressive sensitivities to cross-channel surrounds (version A). In this sense, version 3B is among the simplest models of the Foley-type possible. (Note, for TSM, one further parameter was required [outside the parentheses] because he performed two different cross-channel conditions.) Two further versions of the model (2’B and 2”B) that do not form part of this figure had the same number of free parameters as version 2B. In version 2’B, the within-channel integration region was matched to the size of the mask instead of the test stimulus. In version 2”B the within-channel integration region was variable, and the suppression region was matched to the size of the test stimulus.

of the data. At a cost of two extra free parameters, the version xA models produced only marginally better fits than their version xB counterparts (the difference in RMS errors was never greater than 0.15 dB) and will not be considered further.

Nested within the variation above were three versions of the model in which the excitatory and suppressive within-channel weights from the surround (E_{ws} and S_{ws}) were allowed to vary across the SL and LL configurations. Permitting E_{ws} to vary allows for the possibility that observers were unable to restrict contrast integration to the target area in the SL configuration. (Alternatively, setting E_{ws} to zero means contrast integration is restricted to the target area in the SL configuration.) Permitting S_{ws} to vary allows for the possibility that the level of surround suppression might change with the area of signal integration. In version 1, both E_{ws} and S_{ws} were allowed to vary. In version 2, E_{ws} was set to zero in the SL configuration, but S_{ws} was allowed to vary. In version 3, E_{ws} was set to zero in the SL configuration and S_{ws} did not vary. (See Figure 5 for a summary.) Best-fitting parameter values and RMS error of fit are shown for all three version xB models in Table 2. In general, the fits are very good.

Version 2B showed little degradation in performance over version 1B, and qualitatively, the fits of the two different models looked similar (version 1 not shown here). This suggests that observers were able to restrict the spatial extent of contrast integration to the signal area in the SL configuration. This conclusion was corroborated by the results of an alternative model (version 2’B, not shown), in which the within-channel integration region was matched to the size of the mask instead of the test stimulus. This was achieved by equating S_{ws} for the SL and LL configurations. For all observers, performance (mean RMS error) of this model was worse than for any other model version tested. Qualitatively, it failed badly in several respects, particularly in underestimating sensitivity for the within-channel SL configuration for TSM and PN.

In contrast to the conclusion above, the nonzero weights of the surround suppression terms (S_{ws}) in version 2B suggest that observers were unable to control the spatial extent of suppression as they were the extent of integration. This conclusion was corroborated by the results of an alternative model (version 2”B, not shown) in which the within-channel suppression region was matched to the size of the test stimulus and the within-channel contrast integration region was allowed to vary across size configurations. The performance (mean RMS error) of this model was worse than for any other model version shown in Figure 5. Even when model testing was restricted to the SS and SL con-

	Version 1B			Version 2B			Version 3B		
Observer	TSM	SK	PN	TSM	SK	PN	TSM	SK	PN
Number of data points	108	66	66	108	66	66	108	66	66
Number of functions	9	6	6	9	6	6	9	6	6
Number of free parameters	10	9	9	9	8	8	8	7	7
Mean RMS Error (dB)	1.44	1.27	1.45	1.46	1.41	1.52	1.63	1.45	1.50
p	2.92	2.85	3.46	2.43	2.83	2.91	2.39	2.73	3.12
q	2.51	2.46	3.03	2.05	2.45	2.49	2.02	2.35	2.68
E_{wc}	0.176	0.170	0.135	0.157	0.161	0.149	0.170	0.184	0.146
E_{ws} (SL)	0.128	0.291	0.263	0	0	0	0	0	0
E_{ws} (LL)	3.309	3.012	1.600	1.836	3.041	1.359	1.379	2.477	1.337
S_{wc}	0.383	0.352	0.298	0.309	0.315	0.316	0.304	0.364	0.316
S_{ws} (SL)	1.453	0.699	1.448	1.056	3.396	1.993	1.656	3.917	2.428
S_{ws} (LL)	4.871	4.976	2.918	2.556	4.800	2.393	1.656	3.917	2.428
S_{xc}	0.0042	-	0.0048	0.0101	-	0.0167	0.0109	-	0.0109
S_{hc}	0.0039	0.0080	-	0.0098	0.0080	-	0.0100	0.0106	-
$(E_{wc}/E_{ws}\,[\text{LL}])\times(S_{ws}\,[\text{LL}]/S_{wc})$	0.676	0.798	0.826	0.707	0.807	0.830	0.672	0.799	0.837

Table 2. Parameter values and other details for three versions of the model. Note that the mean RMS error is never worse than 1.63 dB. Model parameters *Z* and *K* did not represent degrees of freedom and were set to 1 and 0.1, respectively. The bottom line in the table is relevant for a comparison between the area summation model and a contrast adaptation model discussed in the text.

figurations, this version of the model failed to capture the differences in within-channel facilitation across the configurations. This confirms that the reduction of facilitation caused by extending a within-channel mask from the center to the surround (compare SS and SL) is not caused by integrating the surround mask with the test stimulus, but by the influence of suppression from the surround.

Model version 3B showed little degradation of performance over version 2B, suggesting that the weight of within-channel suppression from the surround might be the same, regardless of the size of the test stimulus. Because version 3B has the smallest number of free parameters, it might be the preferred model. However, for TSM only, this version of the model failed quite strikingly in one notable respect for the within-channel conditions. It correctly predicted that the SS and SL functions should almost converge at the upper region of the masking function, but incorrectly that masking for these configurations should be more than 3dB greater than for the LL configuration. Qualitatively, at least, this is at odds with the data. For this reason the fits are shown for version 2B, though version 3B remains an attractive alternative and model fits for a restricted set of results can be seen by looking ahead to Figure 6.

Note, however, that in version 2B, the surround suppression parameter increases for all three observers as the size of the test stimulus increases [compare S_{ws} (SL) and S_{ws} (LL) in Table 2]. It is not clear how to interpret this. One possibility is that the greater suppressive influence from the surround is exerted directly on the center. But an equally valid interpretation is that the additional suppression is directed to the surround, which contributes to the detection process for the LL configuration and not the SL configuration.

In general, the model provides a very good account of several features of the data. For the cross-channel conditions, area summation is evident across the entire masking function. For the within-channel conditions, the dipper region is most shallow for the SL configuration and area summation is marked at low pedestal contrasts. At higher contrasts, area summation for the target is almost abolished for two of the observers (TSM and PN), but not a third (SK) (compare SL and LL). This represents a particularly interesting feature of the model: Subtle differences in parameter values are able to accommodate fairly gross differences (the presence or absence of area summation above threshold) in empirical observations.

A final point is that for all three observers, there is a small region just after the dip for the LL configuration where the SS and LL functions crossover and performance is slightly better in the SS configuration. This feature is also evident in Legge and Foley's (1980) data and was commented on by the authors. All versions of the model presented here accommodate this crossover, which has also been seen using twin-mask paradigms (Foley, 1994; Holmes & Meese, in press) and adaptation paradigms (Ross & Speed, 1991).

Discussion

Area summation

Empirically, area summation survives cross-channel masking but can be abolished by within-channel masking.

However, this does not require that the area summation process is literally disabled, as it was for Legge and Foley (1980). A contrast gain control model whose parameters are fixed across mask contrast is able to provide good quantitative fits to all of the data reported here. Similar models having only four free parameters are widely used to model basic dipper functions, such as those measured in the SS configuration. For observers PN and SK, five further masking functions were modeled here with the addition of only three further parameters. For TSM, a further eight functions were modeled at the cost of only four further parameters. To accommodate all of the qualitative features in the data for TSM, one extra parameter was also used (model version 2B).[2] This allowed the level of surround suppression to vary with the size of the test stimulus.

The model proposed here has some features in common with a model proposed by Cannon (1995). In particular, Cannon's model describes the smooth transition from empirical area summation at detection threshold to the absence of area summation for perception of contrast (assessed by matching) at intermediate contrasts and above. In Cannon's formulation this is achieved by allowing stimulus area to modify the parameter referred to as *Z* (the semisaturation constant) in the model here.

Surround masking

A comparison of the SS and SL configurations indicates the effects of increasing the size of the mask stimulus. For within-channel masking, the effects were typically small and they varied among observers, being greatest at the fairly low mask contrasts around the dipper region of the masking function. This has been modeled here by supposing a suppressive influence from the surround, consistent with previous suggestions (e.g., Bruce et al., 2003; Foley & Chen, 1999; Snowden & Hammett, 1998;). In other work that has used an SL configuration, the surround region has been found to facilitate the detection of the central target on a pedestal (Yu & Levi, 2000; Yu et al., 2003). However, this effect is not universal (Foley, 1994; Foley & Chen, 1999), and there was little or no evidence for this phenomenon here (i.e., for no observer were the contrast increment thresholds for the SL configuration markedly lower than for the SS configuration). This suggests that experimental differences such as stimulus spatial frequency (1 c/deg here; 1 or 2 c/deg for Foley; 8 c/deg for Yu & Levi) or the precise configuration of the mask and test stimuli (see Yu et al., 2003) might be important. However, the existence of Yu and Levi's phenomenon might not require substantial modifications to the model. As shown in Appendix A and elsewhere (Bruce et al., 2003; Yu et al., 2003), the type of model considered here can in fact enhance contrast discriminability using suppressive interactions alone.

In cross-channel masking, performance was unchanged when the mask was extended from the center to the surround. Other work has found that a cross-channel annular surround can facilitate the detection of a central target stimulus at 8 c/deg (Yu, Klein, & Levi, 2002) and at 1 c/deg (Meese & Hess, 2004). This raises the possibility that at detection threshold, these cross-channel facilitatory effects require that there be a hole in the center of the mask stimulus. Why this should be so is not clear, but there are at least three possibilities.

1. Interactions between a cross-channel center and surround might eradicate the facilitatory effect.
2. The contour produced by an annular surround (or flanking patches of grating; see "related work" below) might be an important part of the mask stimulus.
3. The stimuli used here might have been inappropriate for achieving facilitation. Further experiments are needed to address these possibilities.

Although Appendix A shows that the present model can accommodate surround facilitation of contrast discrimination, this does not extend to facilitation of detection threshold. However, this can be achieved by a straightforward modification to the model as follows. An additional surround term whose magnitude is constrained to be less than *Z*, is subtracted from the denominator of Equation 1. No doubt, there are several interpretations of negative suppressive terms, but one is disinhibition. For example, if *Z* is seen to represent standing inhibition from mechanisms with spatially overlapping receptive fields, then perhaps its effective reduction by the negative term proposed above is due to a suppressive influence on those mechanisms from the lateral masks (see also Yu & Levi, 1997).

Experimental design and model predictions

The rationale behind the choice of the three stimulus configurations (SS, SL, and LL) was outlined in the Introduction of this work. The idea was that increasing the size of a mask stimulus should reveal the level of suppression from the surround, and that increasing the size of the test stimulus should reveal the weight of spatial integration (see Figure 4). But in the within-channel case, area summation across the entire masking function was evident in the data for only one of the observers (compare SL and LL in Figure 2). Even so, a single model in which area summation occurs at all mask contrasts (numerator terms in Equation 1) was able to accommodate the full set of results for all three observers. This is considered further in Appendix A where it is shown that the model does not always behave in the intuitive way outlined above. For example, increasing mask size can improve performance and increasing test size can degrade performance. The point here is that simple qualitative assessments of contrast discrimination data risk misinterpretation of the underlying processes if they are not accompanied by detailed mathematical modeling.

Other related work

Bonneh and Sagi (1999) also performed experiments using configurations similar to the SS, SL, and LL configurations used here. In their experiments, the stimuli were presented parafovealy (2.4° deg), only a single mask contrast was used (30%), and the spatial frequency was much higher (12.5 c/deg) than that used here (1 c/deg). Bonneh and Sagi found that for both of their observers, the results from the SS and LL configurations were very similar. They also found that discrimination thresholds were higher for the SL configuration than for the other two configurations. One possibility is that Bonneh and Sagi's two observers were simply more similar to observer SK than observers PN or TSM, but another possibility is that model parameter weights vary as a function of spatial frequency and/or retinal field position. For example, if the sensitivities (weights) of the various terms were much less toward the periphery (e.g., Wilson & Bergen, 1979), this would have the same effect as attenuating stimulus contrast. If this were sufficiently severe, then the experiment would move into the dipper region of the functions in Figure 3. In this region, observer and model performance for LL is similar to SS and better than for SL, just as for Bonneh and Sagi's observers.

Other results also suggest examples of model parameter variations with the stimulus parameters above. Snowden and Hammett (1998) found that an annular surround increasingly raised detection threshold as the whole stimulus was moved into the periphery, and Xing and Heeger (2000) found a similar result using contrast matching. Meese and Holmes (2003) found that cross-orientation suppression from a superimposed mask was greatest at lower spatial frequencies, and Meese and Hess (2004) found a similar result in matching and detection experiments using brief dichoptic annular surround masks.

Another type of experiment that has explored the influence of stimuli from the surround is one in which two (or more) flanking patches are used. Chen and Tyler (2001, 2002) measured dipper functions for a central vertical target patch in the presence of a pair of high-contrast (50%) flankers placed above and below the target patch. Like several earlier reports (e.g., Polat & Sagi, 1993), facilitation was found for a zero-contrast pedestal. But as the contrast of the pedestal was increased, contrast increment thresholds became higher than they had been in the absence of the flankers (Chen & Tyler, 2001). For one of their observers this was also true for cross-channel flankers (Chen & Tyler, 2002). Chen and Tyler offered a model of these results in which the test and pedestal terms are modulated by the surround in a contrast gain control equation. This model appears to have been motivated by two factors: first, the finding that the surrounding flanks could facilitate detection of a central target patch (but see "surround masking" above), and second, that the flanks could shift the entire dipper handle laterally (to the left). As neither of these effects were found here (in the second and possibly the first case, the stimulus conditions were inappropriate), the present model was not similarly motivated. Nevertheless, it remains a challenge for future research to reconcile these various findings and models.

Area summation and contrast adaptation

A particularly striking comparison is available between the SS and LL configurations of the present experiment and the effects of contrast adaptation on contrast masking functions. Foley and Chen (1997) found that adapting to a high-contrast target stimulus raised the entire masking function for cross-channel masking, but only the dipper region of the function for within-channel masking. Their results are replotted in Figure 6 next to those from observer SK for the SS and LL configurations here. The functions are very similar in shape, but the aftereffects of adaptation go in the opposite direction to those of area summation.

Meese and Holmes (2002) proposed a simplified model of Foley and Chen's results in which adaptation effectively lowered the within-channel excitatory and suppressive weights for the SS configuration by the same factor (E_{wc} & S_{wc}). (In fact, the formulation offered by Meese and Holmes (2002) was expressed rather differently, but formally it is identical to the proposal stated above.) In the area summation model, the weights of the excitatory and suppressive surrounds (E_{ws} & S_{ws}) were fit independently, so this model has one more degree of freedom than the adaptation model. It is noteworthy, though, that the product ($[E_{wc}/_{ws}]\times[S_{ws}/_{wc}]$) is close to unity for the LL configuration (see bottom line of Table 2). Had this quantity been equal to 1, then the SS and LL model predictions would have converged exactly, and the area summation model (for the SS and LL configurations) would have been formally equivalent to the adaptation model of Meese and Holmes (2002). Specifically, the model parameter that controls the state of adaptation would be the same as that which controls the influence of stimulus size.

Conclusions

Empirically, measures of area summation assessed by contrast increment thresholds survive cross-channel masking but can be abolished by a within-channel mask. However, it does not follow from this that the area summation process is disabled. A contrast gain control model that integrates stimulus contrast over retinal field position can accommodate all of these effects, including individual differences in empirical area summation for within-channel masking. The modeling also implies that observers are able to restrict contrast integration to the region of the test stimulus but are unable to restrict suppressive influences from within-channel surrounds in the same way. On the other hand, the level of masking produced by a superim-

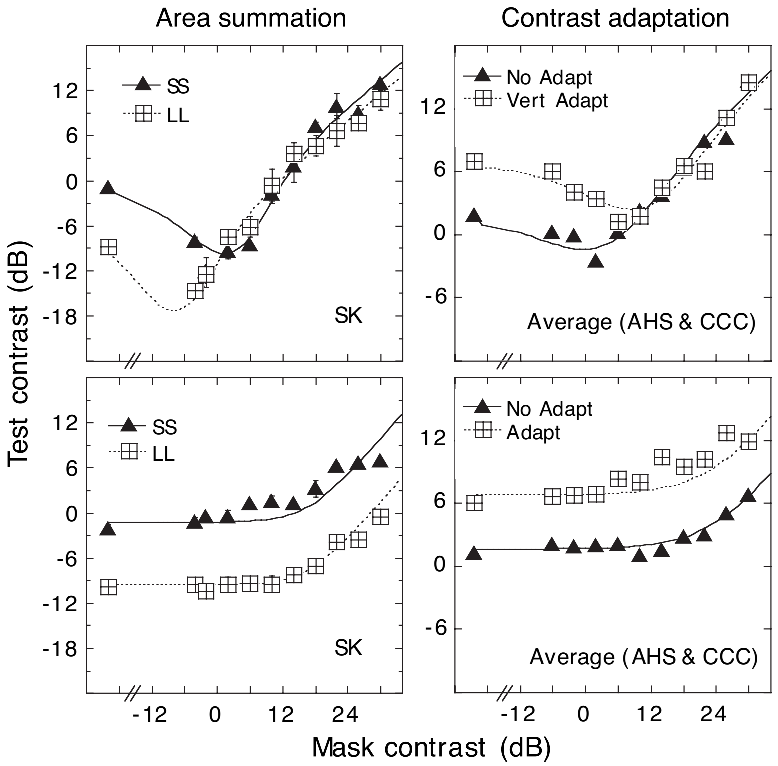

Figure 6. Comparison between area summation results for the SS and LL configurations and contrast adaptation results replotted from Foley and Chen (1997). (These are the averages of two observers.) (Note the different scales on the ordinate and the identical scales on the abscissa.) The model fitted to the area summation data is version 3B (parameter values are reported in Table 2), though other versions could have been used to make the same point. The model fit to the adaptation data is the simplified adaptation model of Meese and Holmes (2002). The similarity of the two models is discussed in the text.

posed cross-channel mask is not changed by extending it to the surround. This suggests that when cross-channel surround effects have been found previously, the hole in the annular masks might be a critical feature of the stimulus. Finally, a striking feature of the model and the data is their formal similarity with results from contrast adaptation experiments. To a first approximation, area summation is the opposite of contrast adaptation.

Appendix A: Facilitation by suppression and masking by target contrast (suprathreshold effects)

The character of the within-channel model predictions in the main body of this work depends on the parameter values in interesting ways. The plots in Figure A1 are for $K = 0.1$ as before, and $p = 2.4$ and $q = 2.0$. (These exponent values are not critical but p should be a little greater than q.) All the weights were set to unity with the exception of the surround weights (E_{ws} & S_{ws}), which were set to 2, 4, and 6, in panels a, b, and c, respectively. The semisaturation constant Z was equated with these weights. This was not necessary for observing the effects discussed here, but helped to center the curves on a common set of axes.

The excitatory surround weight (E_{ws}) was always reset to zero in the SL configuration. This assumes that the observer is able to restrict contrast integration to the target region in each of the three configurations. This set of constraints is consistent with model version 3B.

The main effect of the different weights is to change the behavior of the model in the upper region of the masking functions (the dipper handles). In Figure A1a, discrimination thresholds are similar for SS and LL and higher than for SL. In this case, spatially extending the mask to the surround improves performance (SS and SL). In other words, adding a purely suppressive component can result in facilitation (similar points have been made by Bruce, Green, & Georgeson, 2003, p. 157, and Yu, Klein, & Levi, 2003). I call this *facilitation by suppression*. However, this improvement can be offset by extending the spatial extent of the test stimulus, which causes performance to degrade again (SL and LL). In other words, extending the size of only the test increment can produce a net loss in performance. I call this *masking by target contrast*. Both of these counter-intuitive behaviors are further illustrated by worked examples below.

In Figure A1b, the suppressive weights are increased and the three functions (SS, SL, and LL) superimpose (similar to observers TSM and PN in the experiment). This

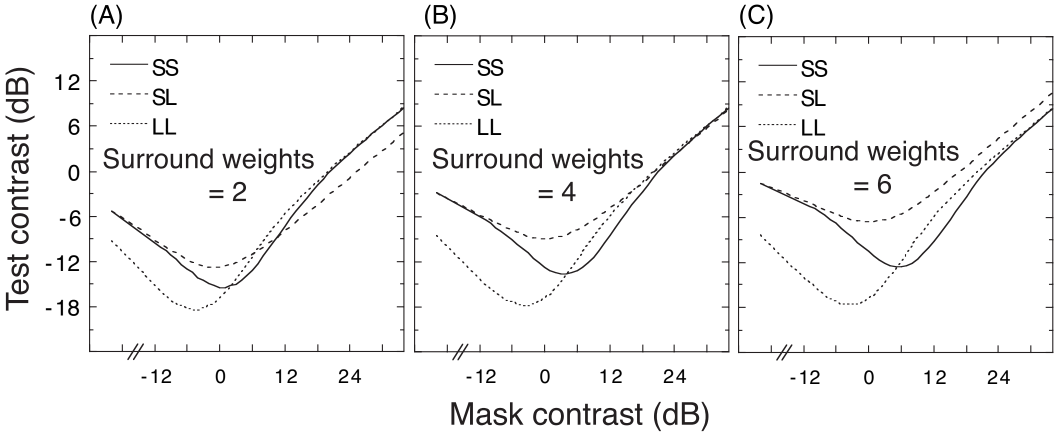

Figure A1. Within-channel model predictions (version 3B) for each of the three area configurations (different curves) and three different sets of surround weights (different panels). Note that only one degree of freedom is manipulated in the model across the different panels. This changes the order of the three functions in the upper region of the masking functions.

illustrates an important point that is easily overlooked. It is sometimes thought that the summation process can be investigated directly by holding mask parameters constant and manipulating only the test stimulus. This argument supposes that the procedure holds the suppressive contribution from the gain pool effectively constant (see Introduction here and Discussion in Bonneh & Sagi, 1999). But in fact, increments in the test stimulus should also contribute to the gain pool, and the modeling here shows that this is not always negligible, particularly above detection threshold. For example, in Figure 1Ab, the benefit of increasing the size of the test stimulus (SL and LL) is exactly cancelled by a concomitant increase in the gain pool. This point is not just theoretical, but is evident in the data of TSM and PN when the mask contrast is around 4% (12 dB) and above.

In Figure A1c, the weights are increased still further, and now performance is worse for SL than it is for SS and LL (similar to observer SK in the experiment). So here, a suppressive surround degrades performance (SS and SL), and increasing the area of the test increment improves performance (SL and LL), exactly the opposite of what is seen in Figure A1a.

So if masking and summation are not simply predicted by the level of suppression or the extent of summation, on what do they depend? The important thing here is to realize that an observer's performance depends on the slope of their internal response to the test stimulus (Bruce et al., 2003; Yu et al., 2003). (In Foley's [1994] model, this is why adding a fixed contrast mask can enhance performance over some regions of the masking functions.) Although it is easy to formulate intuitions about how the absolute level of the contrast response might change with the addition of test and mask components, seeing how this translates to the slope of the contrast response in a contrast discrimination task is much less obvious, and detailed modeling is called for. The modeling here implies that manipulations of both test and mask can, in principle, make the slope of the internal response either more steep, more shallow, or leave it untouched, depending on the parameter values in the model.

The crucial point of all this is that, within the context of models like the one discussed here, adding either a mask or a test component can facilitate or cause masking, depending on factors (i.e., weights) that the experimenter has no direct control over. This poses serious problems for trying to make qualitative predictions prior to performing an experiment.

Worked examples

Let $p = 2.4$, $q = 2.0$, $Z = 1$ and all weights = 1, except for the SL configuration where the excitatory surround weight (E_{ws}) was reset to zero (e.g., model version 3B). Consider only the within-channel masking case. This simplifies Equation 1 to

$$RESP = (c_c^{2.4} + c_s^{2.4})/(1 + c_c^2 + c_s^2).$$

Let the mask contrast (c) be 10% and consider a contrast increment (c) of 1%.

SS Configuration

For the response to the mask stimulus we have

$$RESP_{mask} = (10^{2.4} + 0^{2.4})/(1 + 10^2 + 0^2),$$

$$RESP_{mask} = 251.2/101 = 2.487.$$

And for the response to the mask plus test stimulus we have

$$RESP_{mask+test} = (11^{2.4} + 0^{2.4})/(1 + 11^2 + 0^2),$$

$$RESP_{mask+test} = 315.75/122 = 2.588.$$

This gives a response difference of 2.588 – 2.487 = 0.101.

SL Configuration

For the response to the mask stimulus we have

$$RESP_{mask} = (10^{2.4} + 0^{2.4})/(1 + 10^2 + 10^2),$$

$$RESP_{mask} = 251.2/201 = 1.249.$$

And for the response to the mask plus test stimulus we have

$$RESP_{mask+test} = (11^{2.4} + 0^{2.4})/(1 + 11^2 + 10^2),$$

$$RESP_{mask+test} = 315.75/222 = 1.422.$$

This gives a response difference of 1.422 – 1.249 = 0.172.

LL Configuration

For the response to the mask stimulus we have

$$RESP_{mask} = (10^{2.4} + 10^{2.4})/(1 + 10^2 + 10^2),$$

$$RESP_{mask} = 502.4/201 = 2.499.$$

And for the response to the mask plus test stimulus we have

$$RESP_{mask+test} = (11^{2.4} + 11^{2.4})/(1 + 11^2 + 11^2),$$

$$RESP\ _{mask+test} = 631.5/243 = 2.599.$$

This gives a response difference of 2.599 – 2.499 = 0.099.

The response difference for the SL configuration is greater than for the SS configuration, illustrating facilitation by suppression. The response difference for the LL configuration is less than for the SL configuration, illustrating masking by target contrast.

Footnotes

[1] The term cross-channel masking might be a misnomer. Carandini, Heeger, and Senn (2002) and Freeman, Durand, Kiper, and Carandini (2002) have suggested that the suppressive effects of a superimposed cross-channel mask might be due to synaptic depression in the projection from broadly tuned mechanisms in the LGN to more tightly tuned mechanisms in the cortex.

[2] In fact, for TSM, very good fits could be achieved by equating the weights for the two types of cross-channel mask (S_{hc} & S_{hc}), reducing the total number of free parameters to eight and seven for model versions 2B and 3B, respectively, for this observer. However, this fortuitous simplification is not easily justified.

Acknowledgments

I would like to thank Priya Naik and Saadia Khaler for their enthusiasm and commitment to data collection during the running of this project. I would also like to thank two anonymous referees for their constructive comments. This work was supported in part by an Engineering and Physical Sciences Research Council project grant awarded to TM and Mark Georgeson and a Wellcome Trust project grant awarded to TM.

Commercial relationships: none.

Corresponding author: Tim Meese.
Email: t.s.meese@aston.ac.uk.
Address: Neurosciences Research Institute, School of Life and Health Sciences, Aston University, Birmingham B4 7ET, UK.

References

Bonneh, Y., & Sagi, D. (1998). Effects of spatial configuration on contrast detection. *Vision Research*, *38*, 3541-3553. [PubMed]

Bonneh, Y., & Sagi, D. (1999). Contrast integration across space. *Vision Research*, *39*, 2597-2602. [PubMed]

Bruce, V., Green, P. R., & Georgeson, M. A. (2003). *Visual perception: Physiology, psychology and ecology* (4th ed.). Hove: Psychology Press.

Cannon, M. W. (1995). A multiple spatial filter model for suprathreshold contrast perception. In E. Peli (Ed.), *Vision models for target detection and recognition*. London: World Scientific.

Cannon, M. W., & Fullenkamp, S. C. (1991). Spatial interactions in apparent contrast: Inhibitory effects among grating patterns of different spatial frequencies, spatial positions and orientations. *Vision Research*, *31*, 1985-1998. [PubMed]

Carandini, M., Heeger, D. J., & Senn, W. (2002). A synaptic explanation of suppression in visual cortex. *Journal of Neuroscience*, *22*, 10053-10065. [PubMed]

Chen, C. -C., & Tyler, C. W. (2001). Lateral sensitivity modulation explains the flanker effect in contrast discrimination. *Proceedings of the Royal Society of London B*, *268*, 509-516. [PubMed]

Chen, C. -C., & Tyler, C. W. (2002). Lateral modulation of contrast discrimination: Flanker orientation effects. *Journal of Vision*, *2*(6), 520-530, http://journalofvision.org/2/6/8/, doi:10.1167/2.6.8. [PubMed][Article]

Cornsweet, T. N. (1962). The staircase-method in psychophysics. *American Journal of Psychology*, *75*, 485-491.

D'Zmura, M., & Singer, B. (1996). Spatial pooling in contrast gain control. *Journal of the Optical Society of America A*, *13*, 2135-2140. [PubMed]

Field, D. J., Hayes, A., & Hess, R. F. (1993). Contour integration by the human visual system: Evidence for a local "association field." *Vision Research*, *33*, 173-193 [PubMed]

Foley, J. M. (1994). Human luminance pattern vision mechanisms: Masking experiments require a new model. *Journal of the Optical Society of America A*, *11*, 1710-1719. [PubMed]

Foley, J. M., & Chen, C. -C. (1997). Analysis of the effect of pattern adaptation on pattern pedestal effects: A two-process model. *Vision Research*, *37*, 2779-2788. [PubMed]

Foley, J. M., & Chen, C. -C. (1999). Pattern detection in the presence of maskers that differ in spatial phase and temporal offset: Threshold measurements and a model. *Vision Research*, *39*, 3855-3872. [PubMed]

Freeman, T. C. B., Durand, S., Kiper, D. C., & Carandini, M. (2002). Suppression without inhibition in visual cortex. *Neuron*, *35*, 759-771. [PubMed]

Georgeson, M. A., & Meese, T. S. (1997). Perception of stationary plaids: The role of spatial features in edge analysis. *Vision Research*, *37*, 3255-3271. [PubMed]

Graham, N. V. S. (1989).*Visual pattern analyzers*. New York: Oxford University Press.

Holmes, D. J., & Meese, T. S. (2001). Linear summation for remote masks in a contrast gain pool [ECVP Abstract]. *Perception*, *30*, 81.

Holmes, D. J., & Meese, T. S. (in press). Grating and plaid masks indicate linear summation in a contrast gain pool. *Journal of Vision.*

Howell, E. R., & Hess, R. F. (1978). The functional area for summation to threshold for sinusoidal gratings. *Vision Research*, *18*, 369-374. [PubMed]

Itti, L., Koch, C., & Braun, J. (2000). Revisiting spatial vision: Toward a unifying model. *Journal of the Optical Society of America A*, *17*, 1899-1917. [PubMed]

Laming, D. (1988). Precis of sensory analysis. *Behavioural and Brain Sciences*, *11*, 275-339.

Legge, G. E., & Foley, J. M. (1980). Contrast masking in human vision. *Journal of the optical Society of America*, *70*, 1458-1471. [PubMed]

McKee, S. P., Klein, S. A., & Teller, D. Y. (1985). Statistical properties of forced-choice psychometric functions: Implications of probit analysis. *Perception & Psychophysics*, *37*, 286-298. [PubMed]

Meese, T. S., & Georgeson, M. A. (1996). The tilt aftereffect in plaids and gratings: Channel codes, local signs and 'patchwise' transforms. *Vision Research*, *36*, 1421-1437. [PubMed]

Meese, T. S., & Georgeson, M. A. (in press). Carving up the patchwise transform: Towards a filter combination model for spatial vision. In *Advances in Psychology Research,* Vol. 34. New York: Nova Science Publishers.

Meese, T. S., & Hess, R. F. (2004). Low spatial frequencies are suppressively masked across spatial scale, orientation, field position and eye of origin. *Journal of Vision*, *4*(10), 843-859, http://journalofvision.org/4/10/2/, doi:10.1167/4.10.2. [Article][PubMed]

Meese, T. S., & Holmes, D. J. (2002). Adaptation and gain pool summation: Alternative models and masking data. *Vision Research*, *42*, 1113-1125. [PubMed]

Meese, T. S., & Holmes, D. J. (2003). Orientation masking: Suppression and orientation bandwidth [Abstract]. *Perception*, *32*, 388.

Meese, T. S., Naik, P., & Dattani, R. (2003). The loss of area summation in contrast masking is a "within-channel" effect [Abstract]. *Perception*, *32*, 48-49.

Meese, T. S., & Williams, C. B. (2000). Probability summation for detecting multiple patches of luminance modulation. *Vision Research*, *40*, 2101-2113. [PubMed]

Nachmias, J., & Sansbury, R. V. (1974). Grating contrast: Discrimination may be better than detection. *Vision Research*, *14*, 1039-1041. [PubMed]

Olzak, L. A., & Laurinen, P. I. (1999). Multiple gain control processes in contrast-contrast phenomena. *Vision Research* , *39*, 3983-3987. [PubMed]

Olzak, L. A., & Thomas, J. P. (1999). Neural recoding in human pattern vision: Model and mechanisms. *Vision Research*, *39*, 231-256. [PubMed]

Olzak, L. A., & Thomas, J. P. (2003). Dual nonlinearities regulate contrast sensitivity in pattern discrimination tasks. *Vision Research*, *43*, 1433-1442. [PubMed]

Polat, U., & Sagi, D. (1993). Lateral interactions between spatial channels: suppression and facilitation revealed by lateral masking experiments. *Vision Research*, *33*, 993-999. [PubMed]

Robson, J. G. (1980). Neural images: The physiological basis of spatial vision. In C. S. Harris (Ed.), *Visual coding and adaptability* (pp. 177-214). New Jersey: LEA.

Robson, J. G., & Graham, N. (1981). Probability summation and regional variation in contrast sensitivity across the visual field. *Vision Research*, *21*, 409-418. [PubMed]

Ross, J., & Speed, H. D. (1991). Contrast adaptation and contrast masking in human vision. *Proceedings of the Royal Society of London B*, *246*, 61-69. [PubMed]

Ross, J., Speed, H. D., & Morgan, M. J. (1993). The effects of adaptation and masking on incremental thresholds for contrast. *Vision Research*, *33*, 2051-2056. [PubMed]

Snowden, R. J., & Hammitt, S. T. (1998). The effects of surround contrast on contrast thresholds, perceived contrast and contrast discrimination. *Vision Research*, *38*, 1935-1945. [PubMed]

Solomon, J. A., Sperling, G., & Chubb, C. (1993). The lateral inhibition of perceived contrast is indifferent to on-center/off-center segregation, but specific to orientation. *Vision Research*, *33*, 2671-2683. [PubMed]

Swanson, W. H., Wilson, H. R., & Giese, S. C. (1984). Contrast matching data predicted from contrast increment thresholds. *Vision Research*, *24*, 63-75. [PubMed]

Thomas, J. P., & Olzak, L. A. (1997). Contrast gain control and fine spatial discriminations. *Journal of the Optical Society A*, *14*, 2392-2404. [PubMed]

Tyler, C. W., & Chen, C. -C. (2000). Signal detection theory in the 2AFC paradigm: Attentional, channel uncertainty and probability summation. *Vision Research*, *40*, 3121-3144. [PubMed]

Usher, M., Bonneh, Y., Sagi, D., & Herrmann, M. (1999). Mechanisms for spatial integration in visual detection: A model based on lateral interactions. *Spatial Vision*, *12*, 187-209. [PubMed]

Verghese, P., & Stone, L. S. (1996). Perceived visual speed constrained by image segmentation. *Nature*, *381*, 161-163. [PubMed]

Watson, A. B. (1983). Detection and recognition of simple spatial forms. In O. J. Braddick & A. C. Sleigh (Eds.), *Physical and biological processing of images* (pp. 100-114). New York: Springer-Verlag.

Wilson, H. R. (1980). A transducer function for threshold and suprathreshold human vision. *Biological Cybernetics*, *38*, 171-178. [PubMed]

Wilson, H. R., & Bergen, J. R. (1979). A four mechanism model for threshold spatial vision. *Vision Research*, *19*, 19-32. [PubMed]

Xing, J., & Heeger, D. J. (2000). Centre-surround interactions in foveal and peripheral vision. *Vision Research*, *40*, 3065-3072. [PubMed]

Yu, C., & Levi, D. M. (1997). Spatial facilitation predicted with end-stopped spatial filters. *Vision Research*, *37*, 3117-3127. [PubMed]

Yu, C., & Levi, D. M. (2000). Surround modulation in human vision unmasked by masking experiments. *Nature Neuroscience*, *3*, 724-728. [PubMed]

Yu, C., Klein, S. A., & Levi, D. M. (2002). Facilitation of contrast detection by cross-oriented surround stimuli and its psychophysical mechanisms. *Journal of Vision*, *2*(3), 243-255, http://journalofvision.org/2/3/4/, doi:10.1167/2.3.4. [PubMed][Article]

Yu, C., Klein, S. A., & Levi, D. M. (2003). Cross- and iso-oriented surrounds modulate the contrast response function: The effect of surround contrast. *Journal of Vision*, *3*(8), 527-540, http://journalofvision.org/3/8/1/, doi:10.1167/3.8.1. [PubMed][Article]