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Grating and plaid masks indicate linear summation in a contrast gain pool

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In human vision, the response to luminance contrast at each small region in the image is controlled by a more global process where suppressive signals are pooled over spatial frequency and orientation bands. But what rules govern summation among stimulus components within the suppressive pool? We addressed this question by extending a pedestal plus pattern mask paradigm to use a stimulus with up to three mask components: a vertical 1 c/deg pedestal, plus pattern masks made from either a grating (orientation = -45°) or a plaid (orientation = ±45°), with component spatial frequency of 3 c/deg. The overall contrast of both types of pattern mask was fixed at 20% (i.e., plaid component contrasts were 10%). We found that both of these masks transformed conventional dipper functions (threshold vs. pedestal contrast with no pattern mask) in exactly the same way: The dipper region was raised and shifted to the right, but the dipper handles superimposed. This equivalence of the two pattern masks indicates that contrast summation between the plaid components was perfectly linear prior to the masking stage. Furthermore, the pattern masks did not drive the detecting mechanism above its detection threshold because they did not abolish facilitation by the pedestal (Foley, 1994). Therefore, the pattern masking could not be attributed to within-channel masking, suggesting that linear summation of contrast signals takes place within a suppressive contrast gain pool. We present a quantitative model of the effects and discuss the implications for neurophysiological models of the process.

Keywords: masking, suppression, summation, inhibition, spatial vision

Introduction

Typical contemporary models of luminance contrast masking include a contrast gain control stage in which target contrast is divisively suppressed by itself and a more global pool of image contrast signals. For tasks involving judgments of spatial contrast (e.g., Foley, 1994) or fine pattern discriminations (e.g., Thomas & Olzak, 1997), the contrast gain pool appears to be broadly tuned for both orientation and spatial frequency (Ross & Speed, 1991; Ross, Speed, & Morgan, 1993; Foley, 1994; Zenger & Sagi, 1996; Thomas & Olzak, 1997; Olzak & Thomas, 1999; Meese & Holmes, 2002, 2003; Meese & Hess, 2004; Meese, 2004; Chen & Foley, 2004). There is also evidence for suppressive pooling over temporal frequency (Boynton & Foley, 1999), wavelength (Mullen & Losada, 1994; Chen, Foley, & Brainard, 2000), field position (Cannon & Fullenkamp, 1991; Cannon, 1995; Solomon, Sperling, & Chubb, 1993; D'Zmura & Singer, 1996; Snowden & Hammett, 1998; Ellemberg, Wilkinson, Wilson, & Arsenault, 1998; Xing & Heeger, 2000; Chen & Tyler, 2001, 2002; Yu, Klein, & Levi, 2001; Rainville, Scott-Samuel, & Makous, 2002; Zenger-Landolt, & Heeger, 2003; Meese, 2004), and possibly eye of origin (Georgeson, 1988; Meese & Hess, 2004; Meese, Georgeson, & Hess, 2004).

The properties of the spatial gain pool have been assessed primarily by performance measures. In these experiments, the contrast of a cross-channel mask (one that does not excite the detecting mechanism) has been either (i) varied, and contrast detection thresholds measured as a function of mask contrast (e.g., Foley, 1994; Ross & Speed, 1991), or (ii) fixed, and contrast discrimination thresholds measured as a function of pedestal contrast (Foley, 1994; Ross & Speed, 1991; Ross et al., 1993). Here we refer to the first paradigm as pattern masking and the second paradigm as pedestal plus pattern masking.

When there are two or more stimulus components in the gain pool, it is possible to assess the rules that govern their summation (D'Zmura & Singer, 1996). This is of value because it offers insight to the systems' architecture that underlies the masking process and offers constraints on various physiological models of the process (Albrecht & Geisler, 1991; Heeger, 1992; Carrandini, Heeger, & Senn, 2002; Freeman, Durand, Kiper, & Carandini, 2002; Hirsch et al., 2003) that might be linked to the psychophysics. In both paradigms described above, the pattern mask has often contained only a single component. In this case, pattern masking stimuli have only a single high-contrast component in the gain pool (the pattern mask) but pedestal plus pattern masking stimuli have up to two (the pedestal and the pattern mask). As a result, this second paradigm

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allowed Foley (1994) to compare two versions of suppressive summation in a contrast gain control model. In a "full linear suppression model" (Foley's model 2), the suppressive stimulus components were all summed before being passed through an expansive nonlinearity. In a "nonlinear suppression model" (Foley's model 3), the same components passed through expansive nonlinearities before being summed. In fitting his models to an extensive data set gathered using both masking paradigms, Foley found that the nonlinear suppression model produced the best fit.

In an extension of the pattern masking paradigm, Meese and Holmes (2002) measured contrast detection thresholds in the presence of masks containing one or two components (i.e., either a grating or a plaid). They found that masking functions for the two different patterns superimposed when they had the same overall contrast, suggesting strict linear summation of the pattern mask component contrasts in the gain pool. Recognizing that this was at odds with Foley's model, Meese and Holmes offered two alternative models. One of these included a hybrid version of suppression in which (i) the pedestal and (ii) the linear sum of all the other gain pool components each passed through separate nonlinear pathways before summation in the gain pool.

Here we provide a direct test of this model by measuring pedestal masking functions (dipper functions) in the presence of zero-, one-, and two-component pattern masks. This is a particularly diagnostic set of stimuli because the contrast gain pool can contain the pedestal plus zero, one or two further components, allowing a direct comparison of the three different models of suppression described above.

Methods

Equipment

The experiment was run under the control of a PC, and stimuli were displayed from a framestore of a VSG2/3 operating in pseudo-12 bit mode. The monitor was either an Eizo F553-M (mean luminance of 55 cd/m^2) or Sony Trinitron Multiscan 200PS (mean luminance of 65 cd/m^2). Both monitors had a frame rate of 120 Hz. 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 114 cm. A small dark fixation point (4 pixels square) was visible throughout the experiment.

Observers

The two authors (TSM and DJH) served as observers. Both were well practiced with the task and stimuli before data collection began and had normal or optically corrected-to-normal vision.

Stimuli

Fixed contrast pattern mask stimuli had one or two sine-wave components oriented at −45° and ±45°, respectively, each with a spatial frequency of 3 c/deg and had an overall contrast of 20%. (For the plaid mask, the component contrasts were 10% each, and for the grating mask the contrast was 20%). Both types of mask were windowed by a raised cosine function with a diameter at half height of 4.4° and a central plateau diameter of 3.8°. In a third, no-mask condition, the contrast of the mask was 0%.

Test and pedestal stimuli were spatially identical vertical Gabor patches with a spatial frequency of 1 c/deg, a full width at half height of 1.67 cycles, and equal horizontal and vertical Gaussian spreads. All stimulus components (test, pedestal, and the mask) were in sine-phase with a small dark fixation point in the center of the display region, which remained visible throughout the experiment. High-contrast examples of the stimuli are shown in Figure 1.

Stimulus duration was 33 ms.

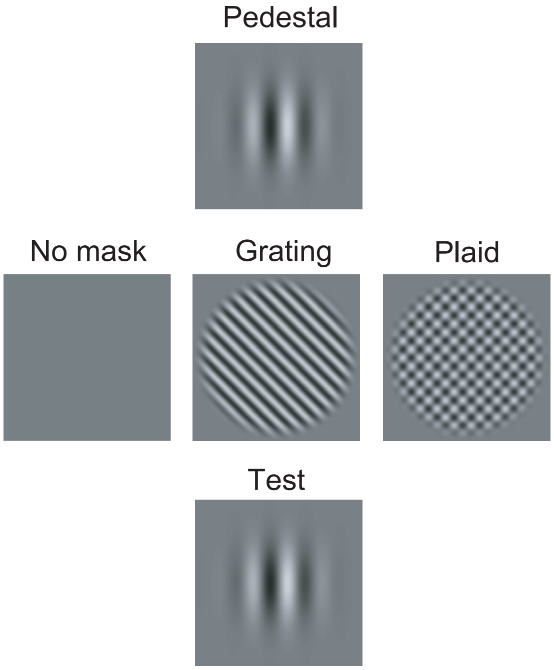

Figure 1. High-contrast examples of stimulus components. The stimulus always had (i) a pedestal (top row) with a contrast between 0% and 32% and (ii) one of three different fixed contrast masks (middle row). The overall contrast of the grating and plaid masks was 20%. The contrast of the test component (bottom row) was adjusted by a staircase procedure and was presented only in the test interval. The observer's task was to detect this component.

Procedure

The contrast level of the test stimulus was selected by a three-down one-up staircase procedure (Wetherill & Levitt, 1965), and a single condition was tested using a pair of randomly interleaved staircases. 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 plus pedestal and the other interval contained the test stimulus plus mask plus pedestal. The onset of each interval was indicated by an auditory tone and the duration between the two intervals was 500 ms (about 15 times longer than the stimulus duration and more than 3 times as long as the temporal impulse response (Georgeson, 1987; Graham, 1989).

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 two intervals was selected randomly by the computer. For each run, thresholds (75% correct) and *SE*s were estimated by performing probit analysis on the data gathered during the test stages and collapsed across the two staircases. This resulted in individual estimates based on around 100 trials (McKee, Klein, & Teller, 1985).

Experimental "contrast-blocs" were repeated 3 times (for TSM) or 5 times (for DJH) and consisted of a set of "mini-blocs" for each of 11 pedestal contrasts selected in a pseudo-random order by the observer. A mini-bloc consisted of an experimental session for each of the three mask conditions (grating, plaid, and no mask), selected in a random order by the computer.

Before data collection began, the following rejection and replacement criterion was set to lessen the impact of unreliable estimates of threshold. If the *SE* of a threshold estimate was greater than 3 dB, 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 around or above 3 × 100 trials per data point for TSM and 5 × 100 trials per data point for DJH.

Results

The results are shown in Figure 2 for both observers. In the absence of a pattern mask, a classic dipper function was found (open triangles), consistent with numerous previous studies (e.g., Nachmias & Sansbury, 1974; Legge & Foley, 1980; Wilson, 1980). The shape of this function is often attributed to two different processes (e.g., Foley, 1994; Olzak & Thomas, 2003). An accelerating transducer on the output of the detecting mechanism (Legge & Foley, 1980) produces facilitation just above detection threshold (the dip). This is caused by within-channel drive from the pedestal, which falls into the same pathway as the test stimulus. On the other hand, suppressive gain control from pedestals with higher contrasts (self-suppression) produce threshold elevation (Foley, 1994; Thomas & Olzak, 1997; Olzak & Thomas, 2003; Meese & Hess, 2004), corresponding here with the dipper handle. This second factor is often thought to be part of a more general gain control process in which suppression also arises from mask components outside of the pass-band of the test pathway (cross-channel suppression).

In the presence of a pattern mask (large circles), the dipper function remained, but the dip region shifted upward and to the right. This indicates two things. First, there was substantial pattern masking when the pedestal contrast was zero or low. Second, on the model described above, this pattern masking cannot be attributed to suprathreshold within-channel drive (self-suppression) from the pattern mask. This is because the low-level excitatory drive that is necessary to produce facilitation was still available from the pedestal (the region of facilitation was shifted but otherwise intact). The implication here is that the pattern masking is due entirely to cross-channel suppression (Ross & Speed, 1991; Foley, 1994; Mullen & Losada, 1994).

At the highest pedestal contrasts, the three masking functions tended to converge. In general, this transformation of the dipper function by a pattern mask is very similar to that found in previous studies where the pattern mask had only a single component (Ross & Speed, 1991; Foley, 1994; Mullen & Losada, 1994). For one of the observers (DJH), there is a distinct cross-over for the masking functions between pedestal contrasts of 12dB and 24dB, meaning that the fixed contrast masks actually facilitated detection of the test for a range of pedestal contrasts. For the other observer (TSM), this cross-over is much less marked and might even be absent.

The results for the two fixed contrast pattern mask conditions were similar: The pedestal dipper function was transformed in very much the same way, regardless of

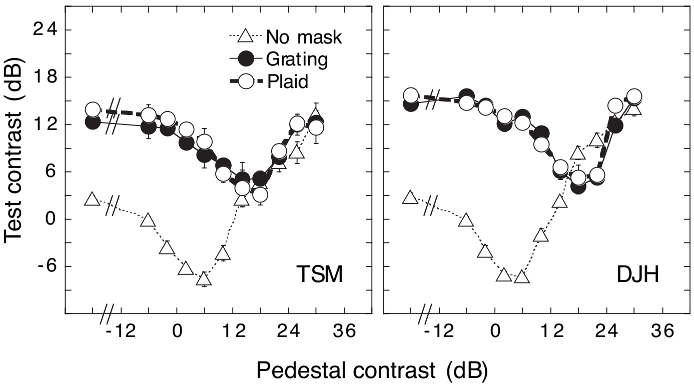

Figure 2. Contrast discrimination thresholds for two observers (different panels). Note that the curves in this figure are not model fits to the data. Where larger than symbol size, error bars show ±1 *SEM*.

	K	p	q	Z	w	β	RMS Error
TSM							
Nonlin	0.21	1.93	1.58	2.71	0.76	-	2.08
Lin	0.27	4.12	3.69	2.09	0.15	-	1.42
Hybrid	0.21	2.04	1.69	2.62	0.64	-	1.89
Compound	0.27	3.34	2.91	2.15	0.28	0.53	1.34
DJH							
Nonlin	0.28	2.63	2.26	2.13	0.72	-	2.04
Lin	0.24	3.59	3.22	2.08	0.24	-	1.81
Hybrid	0.30	3.24	2.85	2.02	0.53	-	1.51
Compound	0.28	3.7	3.32	2.04	0.43	0.15	1.33

Table 1. Best-fitting parameter values and RMS error for two observers and the four versions of the model described in the text. For each observer, from top to bottom, these are nonlinear summation, full linear summation, hybrid, and compound.

whether the fixed contrast mask had one or two components. The equivalence of the two different types of pattern mask suggests linear summation in the gain pool because the sum of the plaid component contrasts (10% each) is exactly equal to the grating mask contrast (20%). On the other hand, a deep cross-over by a pedestal plus pattern mask function with a pedestal mask function hints at nonlinear summation between pedestal and pattern mask in the gain pool (Meese & Holmes, 2002). We provide quantitative examination of these and other versions of suppression summation in the next section.

Models

We assume that the test stimulus is detected when an observer's response difference to the mask and mask plus test stimulus equals a constant K:

$$K = RESP_{\mathrm{MASK+TEST}} - RESP_{\mathrm{MASK}},$$

where K is a free parameter of the model. The observer's response is given by

$$RESP = E/(Z^q + POOL),$$

where the constant Z and exponent q are free parameters of the model and E and $POOL$ are functions of stimulus component contrasts as follows:

$$E = (C_{\mathrm{ped}} + C_{\mathrm{test}})^p$$

where C_{ped} and C_{test} are the pedestal and test contrasts (in %), respectively, and the exponent p is a free parameter of the model.

The function $POOL$ was formulated differently for each of four versions of the model and always included at least two free parameters: an exponent q, introduced above, and a weight w.

Nonlinear summation model (Foley's model 3)

$$POOL_{\mathrm{NONLIN}} = (C_{\mathrm{ped}} + C_{\mathrm{test}})^q + (wC_{\mathrm{mask1}})^q + (wC_{\mathrm{mask2}})^q$$

Full linear summation model (Foley's model 2)

$$POOL_{\mathrm{LIN}} = (C_{\mathrm{ped}} + C_{\mathrm{test}} + wC_{\mathrm{mask1}} + wC_{\mathrm{mask2}})^q$$

Hybrid model (Meese & Holmes, 2002)

$$POOL_{\mathrm{HYBRID}} = (C_{\mathrm{ped}} + C_{\mathrm{test}})^q + (wC_{\mathrm{mask1}} + wC_{\mathrm{mask2}})^q$$

Compound Model

$$POOL_{\mathrm{COMP}} = (1-\beta)(POOL_{\mathrm{HYBRID}}) + \beta(POOL_{\mathrm{LIN}}),$$

where β is a free parameter and $0 \leq \beta \leq 1$.

For $RESP_{\mathrm{MASK}}$, C_{test} was equal to zero. For $RESP_{\mathrm{MASK+TEST}}$, C_{test} was solved numerically. The model was fit simultaneously to all three masking functions (33 data points) for both observers using a downhill simplex algorithm (Press, Flannery, Teukolsky, & Vetterling, 1989). The algorithm was initialized with 100 pseudo-randomly selected initial values, and the fits reported are those that achieved the lowest root mean square (RMS) error (in dB). For the first three models, there are five free parameters (K, Z, t, p, and q) and for the fourth, there is one additional parameter, β. Parameter values and RMS errors are shown for both observers and all four versions of the model in Table 1, and the fits are shown in Figure 3 for TSM and Figure 4 for DJH.

For both observers, the nonlinear summation model does a poor job in fitting the data. Its main failing is it predicts that the two pattern mask stimuli should transform the dipper functions in different ways, in particular, that the grating mask should elevate threshold further than the plaid mask across a substantial part of the function. There was no good evidence for this for either observer. In fact, for TSM there was a very slight tendency for the plaid to produce more masking than the grating at low mask contrasts. The nonlinear summation model also tends to underestimate the depth of the dipper in the no-mask condition. (Forcing the model to capture the depth of the dipper

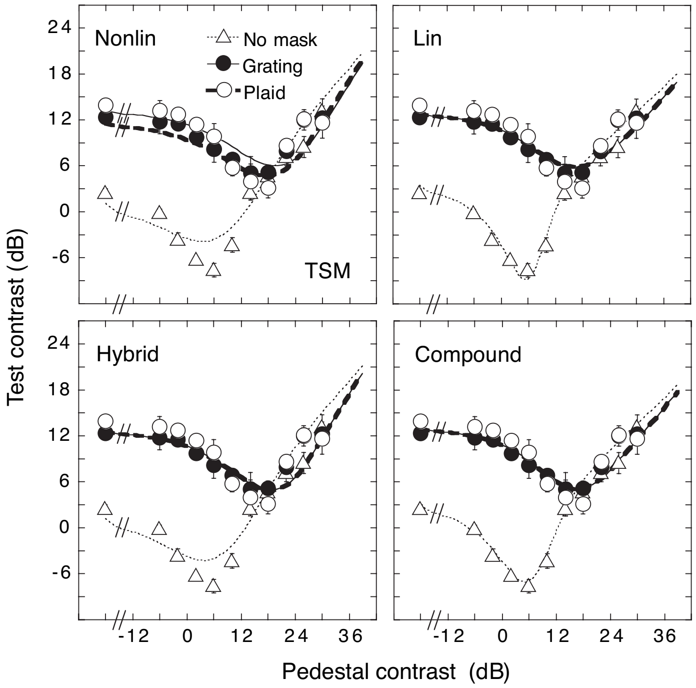

Figure 3. Data for TSM replotted from Figure 2. Curves show model fits described in the text. Each panel is for a different version of the model. For this observer, the best fits were achieved by the compound model (bottom right) and the full linear summation model (top right). The least successful version was the nonlinear model (top left).

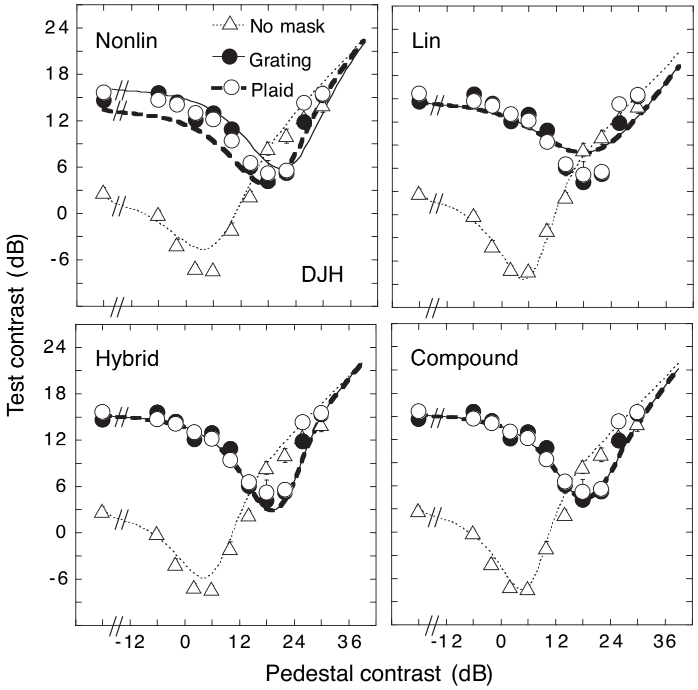

Figure 4. Data for DJH replotted from Figure 2. Curves show model fits described in the text. Each panel is for a different version of the model. For this observer, the best fits were achieved by the compound model (bottom right) and the hybrid model (bottom left). The least successful version was the nonlinear model (top left).

while keeping the dipper handle intact results in a greater separation between the grating and plaid mask curves.)

The full linear summation model does a much better job in fitting the depth of the no-mask dipper and the superposition of the two fixed-mask conditions. (Note the larger value of the exponent *p* in Table 1, which influences the size of the dip.) In fact, it fits the results for TSM quite well. However, for DJH it fails to capture the depth of the cross-over of the pattern mask functions and the pedestal dipper function, a behavior that was actually well described previously by the nonlinear summation model.

The hybrid model of Meese and Holmes (2002) is a compromise between the two models described above. It includes linear summation of the two pattern mask components and correctly predicts the superposition of the two fixed-mask functions. It also processes the pedestal and pattern mask components within separate pathways, each having their own output nonlinearities. This allows the model to capture the dip in the cross-over for DJH, but it does a less good job in fitting the results for TSM.

In sum, the nonlinear summation model fails for both observers, the full linear summation model is best for TSM, and the hybrid model is best for DJH. To try and accommodate these observer differences with a single model, we devised a compound version, whose suppressive gain pool consists of complementary weights of those found in the hybrid model and the full linear summation model. Not surprisingly, with the extra free parameter this produced the best fit of all, tending toward the full linear summation model for TSM and the hybrid model for DJH.

Discussion

Cross-channel masking

The survival of facilitation by a pedestal in the presence of a second (suprathreshold fixed contrast) mask is a well-known signature of cross-channel masking (Ross & Speed, 1991; Foley, 1994; Mullen & Losada, 1994). But three other forms of evidence also point to this conclusion for the stimuli used here. First, detection of the test stimulus is facilitated by a low-contrast pedestal but is not facilitated by a pattern mask alone at any of a wide range of contrasts examined (Meese & Holmes, 2002). Second, unlike the case of within-channel masking (e.g., Legge, 1984; Bird, Henning, & Wichmann, 2002; Kontsevich & Tyler, 1999), it has been found that oblique 3 c/deg mask components do not *linearize* the psychometric function (produce a *d*' slope of one) for the vertical 1 c/deg test component (Georgeson & Meese, 2004; Meese et al., 2004). Third, contrast matching experiments (e.g., Meese & Hess, 2004) have shown that an oblique 3 c/deg mask attenuates the perceived contrast of a superimposed 1 c/deg test grating. These four lines of evidence provide a very strong case that the 3 c/deg mask components were not exciting the detection mechanism for the 1 c/deg target stimulus and rule out a within-channel masking account of the linear summation of pattern mask components. Instead, we conclude that masking arises from cross-channel suppression and that pattern mask contrasts sum linearly within a suppressive pathway, at least for the stimulus configuration used here. We refer to this as linear suppression. Note, however, that this does not disallow an output nonlinearity after summation. In fact, the models considered here work exactly this way, though other possibilities also exist (see the early adaptation model of Meese & Holmes, 2002).

Linear suppression

Others have considered the issue of summation within the contrast gain pool by measuring performance for tasks involving fine spatial discriminations (Thomas & Olzak, 1997). In this work, the preferred model also involved linear summation among suppressive terms (Thomas & Olzak, 1997; Olzak & Thomas, 1999). However, it is unclear how these findings relate to ours because the Thomas/Olzak model produces contrast-independent output at high contrasts, and is, therefore, unsuitable for performing contrast discriminations. One possibility suggested by Thomas and Olzak (1997) is that the two tasks (contrast discrimination and spatial discrimination) might be mediated by different pathways. The results here (and those of Meese & Holmes, 2002) are consistent with this, but the possibility remains that the two putative pathways might share a common suppressive gain pool.

There is, however, one feature of the models tested here (in the model section) that should be considered further. Like several other models in which the gain pool terms are expressed according to component contrasts (e.g., Foley, 1994), the formulations do not address the pooling of image contrast over space. This is an important part of filter-based models, particularly in the suppression stage (e.g., Watson & Solomon, 1997), and poses a problem for extending these models to include linear suppression. This is because summing the absolute values of one or two sine-wave components over space is not the same as summing their amplitudes. For example, the response amplitude of an isotropic linear filter (e.g., a filter with a circular weighting function with excitatory center and inhibitory surround) is the same for our two pattern masks, but the integral of its rectified response is not. It remains unclear what the most appropriate method might be to extend our models to include integration of suppression over space.

Related psychophysical studies

As mentioned in the Introduction, several other investigators have found cross-channel suppression using pattern masking and pedestal plus pattern masking paradigms. Of interest here are those cases where at least two mask components were of sufficiently high contrast to contribute to the gain pool. Foley (1994), Ross and Speed (1991), and Ross et al. (1993) all carried out studies this way. In pedestal plus pattern masking experiments, deep cross-overs of the type found for DJH here (compare the no-mask and mask conditions) were also found by Foley for both of his observers. But Ross and his colleagues found little or no evidence for this; instead, their results more closely resembled those for TSM. The deep cross-over is of interest because it is a feature of models in which the pedestal and mask pass through expansive nonlinearities before summation (e.g., Foley's model 3 and the hybrid model). It seems that there is evidence for this for some observers (e.g., DJH) but not for others (e.g., TSM). The origin of these observer differences is not clear, but one possibility is that linear and nonlinear pathways to suppression are weighted differently between observers. This idea is embodied in what we have called the compound model.

The main aim of the experiments performed here was to improve our understanding of the pathways involved in the contrast gain pool. The strong evidence for linear suppression has contributed to this and extends the results of Meese and Holmes (2002). They performed grating and plaid pattern masking experiments and found linear suppression of mask components over a wide range of mask contrasts (for further discussion, see Meese & Holmes, 2002). As we discuss below, this has particular implications for the physiological substrate, but filter-based image processing models (Watson & Solomon, 1997; Itti, Koch, & Braun, 2000) might also benefit from revision of their suppressive gain control processes.

Finally, the experiments performed here and by Meese and Holmes (2002) address summation of components only in the contrast gain pool. Other studies have found that at detection threshold, the components in a two-component plaid are detected independently (Phillips & Wilson, 1984; Georgeson & Shackleton 1994; Meese & Williams, 2000). Above threshold, the perceived contrast of a plaid is closer to the quadratic sum than the linear sum of its component contrasts (Georgeson & Shackleton, 1994; Cannon, 1995). And the perceived structure of plaids whose components are each subject to a tilt aftereffect strongly implies summation of plaid components after oriented filtering (Meese & Georgeson, 1996) and, presumably, after the output nonlinearities of oriented filters (see below). It would seem that the rules for summation within image control channels (e.g., suppression mechanisms) are different from those within image data channels (e.g., those carrying image structure and contrast). (Though see Fiser, Bex, & Makous, 2003, for an experiment on a related issue in the temporal domain.)

Physiological suppression

Psychophysical evidence for cross-channel suppression is well supported by observations of similar phenomena in orientation tuned cortical cells. In particular, the contrast response is suppressed by a superimposed stimulus with an orientation at right angles to that preferred by the cell. Early work supposed that the suppression arose from cross-channel inhibition in the cortex (Morrone, Burr, & Maffei, 1982; Bonds, 1991). This idea received more formal expression in models where the outputs from a pool of orientation tuned cortical cells were fed-back to produce broad-band divisive inhibition (Albrecht & Geisler, 1991; Heeger, 1992). Certainly, the suppressive effect must occur beyond the output stage in the lateral geniculate nucleus (LGN) because there, non-orientation tuned cells are not suppressed by orthogonal stimuli but are excited by them.

The intracortical inhibition hypothesis has received direct support from the finding that when GABA inhibition in the cortex is blocked pharmacologically, cross-orientation inhibition is abolished (Morrone, Burr, & Speed, 1987). However, Freeman et al. (2002) have challenged this interpretation (see their study for details) as well as the intracortical inhibition account of cross-orientation suppression. They propose that in cat, suppression arises from synaptic depression in the thalamo-cortical projection. Specifically, the effects manifest themselves not in the LGN, but at the first synaptic site in the visual cortex (Freeman et al., 2002; Carandini et al., 2002). On this account, the term cross-channel suppression is a misnomer, because the suppressive influences originate before the channelling of spatial information into different spatial frequency and orientation bands.

Carandini and his colleagues present several empirical-based arguments in support of their view. First, at high drift rates, stimuli can stimulate cells in the LGN but fail to stimulate cortical cells. Nevertheless, fast stimuli can produce cross-orientation suppression in the cortex, suggesting that suppression is not cortical in origin (Freeman et al., 2002). There is also a related psychophysical finding. Meier and Carandini (2002) found that slow (2.7 Hz) and fast (27-38 Hz) drifting gratings both produced high levels of cross-orientation masking, even though their cortical response (inferred from psychophysical data) was much lower at the faster speed. Another well known physiological result is that contrast adaptation causes a substantial rightward shift of the contrast response functions of cortical neurons (e.g., Ohzawa, Sclar, & Freeman, 1985), but has little or no effect on the sensitivity of neurons in the LGN (though see Solomon, Peirce, Dhruv, & Lennie, 2004). Freeman et al. (2002) found that cross-orientation suppression was also untouched by cross-orientation adaptation, implying that adaptable cortical cells do not mediate this form of suppression.

A different account of cross-orientation suppression emerges from recent work by Hirsch et al. (2003), who studied the properties of inhibitory interneurons in layer 4 of primary visual cortex in cat. They found two distinct populations: orientation tuned simple cells and non-orientation tuned complex cells. In particular, they suggested that the complex cells might be the mechanism for broad-band (cross-channel) suppression in the contrast gain control. Whether these cells have properties similar to their thalamic afferents (e.g., whether they are responsive to a wide range of temporal frequencies and whether they fail to adapt) is not known. But it does seem likely that Carandini and his colleagues would not have recorded from this type of non-orientation tuned cell because they rejected cells that had test:mask response ratios less than 1.5.

A physiological substrate for linear suppression?

It remains unclear how the linear suppression seen here might be implemented in visual cortex, but some consideration of the three hypotheses above is worthwhile. The intracortical inhibition hypothesis seems an unlikely candidate because the contrast response of typical orientation tuned cells is not linear with contrast (e.g., Albrecht & Geisler, 1991). It, therefore, seems unlikely that a linear suppressive contrast signal would be achieved by summing the outputs of these cells. On the other hand, a revised version of the intracortical inhibition model in which suppression is fed-back from a subset of orientation tuned cells that behave linearly above threshold (e.g., see the early adaptation model of Meese & Holmes, 2002) might survive. Such cells are certainly not typical in visual cortex, but as V1 cells with previously unknown properties continue to be found (e.g., Hirsch et al., 2003), this possibility should not be ruled out.

The synaptic depression hypothesis initially seems plausible. Here, linear summation of mask signals could take place within the circular mechanisms of the LGN. However, the LGN cells would have to be sufficiently broad-band to respond to signal and mask spatial frequencies that are a factor of 3 apart. Furthermore, synaptic depression is strictly monocular (Freeman et al., 2002), but the results of Meese and Hess (2004) suggest a fast-acting (< 200 ms) dichoptic component of cross-channel masking. They found that a small patch of oblique 3 c/deg grating briefly presented to one eye could mask a small patch of 1 c/deg vertical target stimulus briefly presented to the other eye. It would seem that causes other than synaptic depression are involved in cross-channel masking.

The circular inhibitory complex cells of Hirsch et al. (2003) remain a possible substrate for the linear suppression found here. There is less need to impose constraints on the spatial frequency bandwidth of the suppressive mechanisms in this hypothesis because the inhibitory interneurons would sum across mask component orientation and inhibit orientation tuned cortical cells at lower (and other) spatial frequencies. However, little is known about the properties of the complex cells uncovered by Hirsch et al. (2003), and whether they would achieve what is required of them here awaits elaboration. For example, they would need to respond equally to (a) a plaid with component contrasts of 10% and (b) a grating with contrast of 20%.

Noise sources

Discrimination thresholds do not constrain the form of the noise sources in models of the type we have considered, so we have not made these explicit in the models. However, the models are consistent with at least two possibilities widely discussed in the literature. If the contrast response (*RESP*) is thought of as the magnitude of mechanism response, then the model parameter K relates to constant variance Gaussian noise added at the output stage of the model (i.e., after filtering and interactions, but before the decision variable). However, other models have supposed that noise is multiplicative (e.g., Itti et al., 2000), in which case, *RESP* is better thought of as the signal to noise ratio (Foley, 1994). These two possibilities have prompted some recent debate (Tyler & Chen, 2000; Mortensen, 2002, 2003; Gorea & Sagi, 2001, 2002; Kontsevich, Chen, & Tyler, 2002a; Kontsevich, Chen, Verghese, & Tyler, 2002a) but the picture remains unclear (Georgeson & Meese, 2004). Quite possibly, both types of noise are involved.

Conclusions

Substantial levels of masking of a low spatial frequency test component (1 c/deg) can be produced by other components that fall outside of the spatial frequency and orientation pass-band of the detecting mechanism. We attribute this to cross-channel suppression from a contrast gain pool within which at least one pathway achieves linear summation of stimulus contrast over an orientation difference of 90 deg.

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