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A common contrast pooling rule for suppression within and between the eyes

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Abstract

Recent work has revealed multiple pathways for cross-orientation suppression in cat and human vision. In particular, ipsiocular and interocular pathways appear to assert their influence before binocular summation in human but have different (1) spatial tuning, (2) temporal dependencies, and (3) adaptation after-effects. Here we use mask components that fall outside the excitatory passband of the detecting mechanism to investigate the rules for pooling multiple mask components within these pathways. We measured psychophysical contrast masking functions for vertical 1 cycle/deg sine-wave gratings in the presence of left or right oblique (± 45 deg) 3 cycles/deg mask gratings with contrast $C\%$, or a plaid made from their sum, where each component (i) had contrast $0.5C_i\%$. Masks and targets were presented to two eyes (binocular), one eye (monoptic), or different eyes (dichoptic). Binocular-masking functions superimposed when plotted against C , but in the monoptic and dichoptic conditions, the grating produced slightly more suppression than the plaid when $C_i \geq 16\%$. We tested contrast gain control models involving two types of contrast combination on the denominator: (1) spatial pooling of the mask after a local nonlinearity (to calculate either root mean square contrast or energy) and (2) “linear suppression” (Holmes & Meese, 2004, *Journal of Vision* **4**, 1080–1089), involving the linear sum of the mask component contrasts. Monoptic and dichoptic masking were typically better fit by the spatial pooling models, but binocular masking was not: it demanded strict linear summation of the Michelson contrast across mask orientation. Another scheme, in which suppressive pooling followed compressive contrast responses to the mask components (e.g., oriented cortical cells), was ruled out by all of our data. We conclude that the different processes that underlie monoptic and dichoptic masking use the same type of contrast pooling within their respective suppressive fields, but the effects do not sum to predict the binocular case.

Keywords: Contrast gain control, Psychophysics, Masking, Human vision, LGN, Divisive inhibition

Introduction

Contrast gain control and cross-orientation suppression

Over the past 15 years, our understanding of spatial contrast vision has been heavily influenced by models of suppressive contrast gain control. Accounts have been developed for cortical cells (Albrecht & Geisler, 1991; Heeger, 1992), psychophysical contrast- and pattern-masking in humans (Wilson & Humanski, 1993; Foley, 1994; Watson & Solomon, 1997; Itti et al., 2000), fine spatial judgments (Olzak & Thomas, 1999; Itti et al., 2000), lateral interactions (Chen & Tyler, 2001; Yu et al., 2003; Meese et al., 2007), and texture perception (Graham & Sutter, 1998, 2000). A central component in each of these models is cross-orientation suppression. This involves the suppressive influence of a mask on a target mechanism (Morrone et al., 1982; Bonds, 1989; Foley, 1994; Meese, 2004) and operates principally at low spatial frequencies and high temporal frequencies (Meese & Hess, 2004; Meese & Holmes, 2007; Meese et al., 2007).

In spite of the empirical endeavors above, there is still no consensus on the purpose of cross-orientation suppression, with arguments being marshaled for each of the following. (1) It tightens the orientation and spatial frequency tuning of cortical cells (Ringach et al., 2002b). (2) It protects population codes from the deleterious effects of contrast compression (Albrecht & Geisler, 1991; Heeger, 1992). (3) It removes redundancy (Schwartz & Simoncelli, 2001). One problem for the development of computational theories of the process is that it is still not fully characterized, with fundamental properties continuing to emerge (Meese & Holmes, 2007). Another problem is that suppression might contribute to more than one computational goal. In that case, it becomes difficult to separate out the effects and to understand whether each contributes or interferes with the aims of the others.

Pooling rules for suppression

One aspect of cross-orientation suppression that has received particular attention is the contrast-pooling rule in the suppressive pathway (Derrington & Henning, 1989; Foley, 1994; Meese & Holmes, 2002; Holmes & Meese, 2004; Bonin et al., 2006). There are at least two reasons for this. First, contrast suppression is an

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early visual process, and effective models of it are needed to clarify the input stage to higher order image processing of more natural visual stimuli and tasks. Put another way, since psychophysical performance depends on the contrast-pooling rule that is used (Foley, 1994; Holmes & Meese, 2004), the processes involved need to be properly understood. Second, an understanding of the pooling rule might shed light on the nature of the computations being performed. The general idea is that if a pooling rule can be firmly established, this might offer clues to the purpose of the computation and/or the nature of its neuronal implementation.

Three functional possibilities for pooling are outlined in Fig. 1. In Fig. 1A, one or two mask components each pass through an accelerating nonlinearity (contrast transducer) before being summed. This pooled response is then used to drive a process

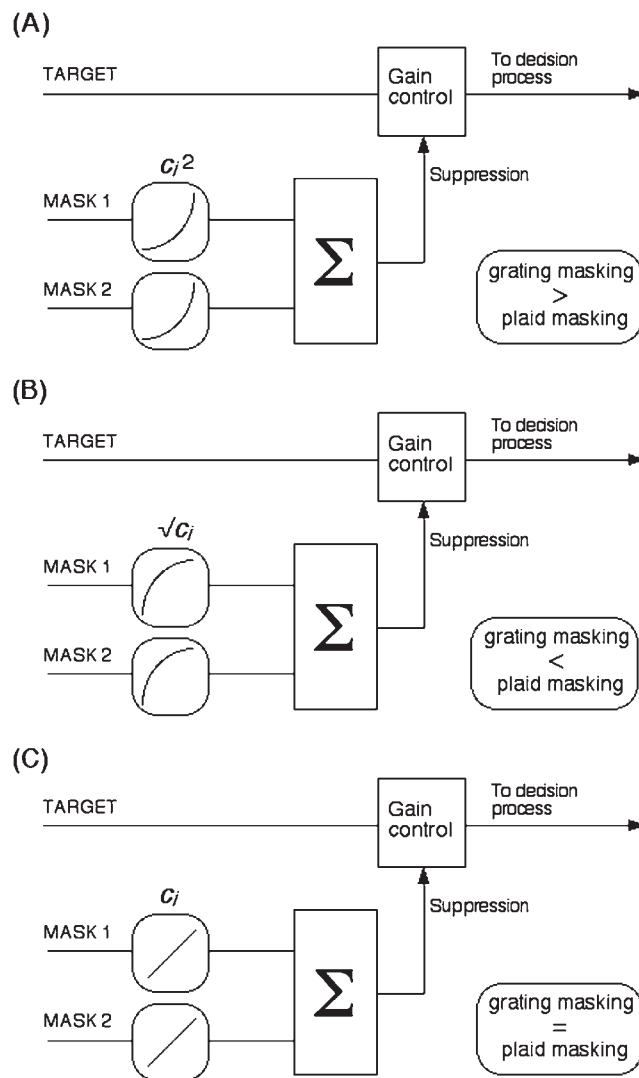


Fig. 1. Arithmetic contrast pooling rules for suppressive contrast gain control. Mask components pass through an accelerating nonlinearity (A) or a compressive nonlinearity (B) or are linear (C) before being summed and suppressing the excitatory pathway (TARGET). Grating masks excite a single suppressive input (MASK1), whereas plaid masks excite two inputs (MASK1 and MASK2). The expressions in the boxes denote the relative strengths of masking by plaids and gratings, where the plaid component contrasts are half those of the grating. Details of spatial pooling and the response nonlinearity in the excitatory pathway are not shown.

that suppresses the target (gain control). The contrast squaring in this arrangement provides the foundation for computing mask energy or mask root mean square (RMS) contrast (Heeger, 1992; Bonin et al., 2006). The arrangement in Fig. 1B is similar, except that the nonlinearity is compressive (Fig. 1B). This is what might be expected if suppression is placed after response compression in the cortex (at higher mask contrasts at least). An alternative arrangement might involve feedback (Heeger, 1992; Wilson & Humanski, 1993), though this raises the complicating issue of mutual inhibition between the mask components. We do not develop such an arrangement here. Finally, in Fig. 1C, there is linear pooling of mask contrast before contrast nonlinearities are involved. This is consistent with the contrast response of a linear filter that responds equally to both mask components.

Importantly, the three forms of pooling in Fig. 1 each make different predictions for the relative masking produced by plaids and grating masks when the overall mask contrast (C) is the same in the two conditions (i.e., the plaid component contrasts are half those of the grating). Thus, for the accelerating (squaring) nonlinearity (Fig. 1A), we have $(0.5C)^2 + (0.5C)^2 = 0.5C^2$ for the plaid and C^2 for the grating; hence, the grating is the more potent masker. For the compressive (square-rooting) nonlinearity (Fig. 1B), we have $\sqrt{(0.5C)} + \sqrt{(0.5C)} = \sqrt{(2C)}$ for the plaid and \sqrt{C} for the grating; hence, the plaid is the more potent masker. When the initial stage is linear (Fig. 1C), we have $0.5C + 0.5C = C$ for the plaid and C for the grating; hence, the two mask types are equally potent.

Gain control and ocular interactions

Models of suppressive contrast gain control have prompted a resurgence of interest in ocular interactions in psychophysics (Meese & Hess, 2004; Maehara & Goryo, 2005; Ding & Sperling, 2006; Meese et al., 2006; Tsuchiya et al., 2006; Medina et al., 2007; Baker et al., 2007a, 2007b; Weiler et al., 2007), electrophysiology (Walker et al. 1998; Truchard et al., 2000; Li et al., 2005; Sengpiel & Vorobyov, 2005), and functional imaging (Büchert et al., 2002). These studies have driven the development of binocular models of masking, where interocular suppression forms part of the divisive contrast gain control (Walker et al., 1998; Meese & Hess, 2004; Maehara & Goryo, 2005; Meese et al., 2006; Baker et al., 2007a).

Studies in cats (Li et al., 2005; Sengpiel & Vorobyov, 2005) and humans (Meese & Hess, 2004; Baker et al., 2007b) have revealed at least two pathways for cross-orientation suppression. In humans, both appear to assert their influence before full binocular summation (Baker et al., 2007b). These pathways have different spatial and temporal properties, where the more broadly tuned one operates within ocular channels (Bonin et al., 2005) and the more narrowly tuned one operates between them (Li et al., 2005; Sengpiel & Vorobyov, 2005; Baker et al., 2007b). Only the interocular pathway is prone to disruption through contrast adaptation (Li et al., 2005; Sengpiel & Vorobyov, 2005; Baker et al., 2007b). And only this pathway has the same temporal characteristics as the contrast detection mechanism (Baker et al., 2007b). All this has been taken to suggest subcortical and cortical loci of the effects, respectively. Specifically, the ipsiocular route is thought to involve the lateral geniculate nucleus (LGN; Solomon et al., 2002; Bonin et al., 2005; Li et al., 2006; Nolt et al., 2008)—and retina (Solomon et al., 2006; Nolt et al., 2008), but possibly also layer 4 of cortex (Hirsch et al., 2003)—whereas the interocular route is placed in primary visual cortex (Li et al., 2005; Sengpiel & Vorobyov, 2005). This led us to anticipate different orientation-pooling rules for monoptic and dichoptic masking.

For example, if the plaid mask components pass through oriented (cortical) filters before feeding into the suppressive gain pool, then each component would be subject to the compressive output nonlinearity of the oriented filter (Sclar et al., 1990) and we would have the situation as in Fig. 1B. On the other hand, if isotropic filters were to drive suppression (Hirsch et al., 2002; Bonin et al., 2005), then the mask components would not be processed independently and we might expect the situation as in Fig. 1C.

Aims and approach

Our aim was investigate the contrast pooling rules involved in contrast gain control within and between the eyes. This was to (1) enrich our models of early vision (see “Contrast gain control and cross-orientation suppression”), (2) try and further untangle the effects within and between the eyes (see “Contrast gain control and cross-orientation suppression” and “Gain control and ocular interactions”), and (3) try and offer insights into the types of computation being performed (see “Pooling rules for suppression”).

We used briefly presented low-spatial frequency gratings as targets, as these are known to be subject to the greatest levels of suppression (Meese & Holmes, 2007). To avoid potentially complicating factors such as multiplicative noise (Burton, 1981; Tolhurst et al., 1983) and/or response compression in the target pathway (Legge & Foley, 1980; Sclar et al., 1990), we wanted to examine the suppression processes without contamination from pedestal masking. Therefore, we used mask components that were substantially different from the target in spatial frequency (1.6 octaves) and orientation (45 deg). We also used a range of identical overall contrasts for our grating and plaid masks so that we could apply the diagnostic approach outlined in Fig. 1.

Materials and methods

Equipment

Stimuli were displayed on a Clinton Monoray monitor (Cambridge Research Systems, CRS). A ViSaGe stimulus generator (CRS) was used in 14-bit mode and controlled by a PC. Stimuli were viewed from a distance of 114 cm through FE-1 ferroelectric shutter goggles (CRS). The combination of monitor and goggles produced a mean luminance of 20 cd/m² at the eye. A central fixation point was present for the duration of the experiment, and gamma correction ensured that the monitor was linear over the full contrast range used. The shutter goggles used frame interleaving to present different images to each eye, giving an image refresh rate of 60 Hz. This procedure was used for all three ocular conditions (monoptic, dichoptic, and binocular), meaning that mean luminance was constant across conditions. The different combinations of mask and target contrasts were determined by the image data written into the frame store. The lookup tables were set to deliver 100% of the contrast contained in the frame store throughout.

Stimuli and conditions

Target and mask stimuli were circular patches of sinusoidal grating, spatially modulated by a raised cosine window with a full width at half height of 4.5 deg and a central plateau diameter of 3.5 deg. Target gratings were vertical and had a spatial frequency of 1 cycle/deg. There were two mask conditions. In the grating condition, a 3 cycles/deg mask was an oblique grating oriented

either left or right (−45 or +45 deg) with contrast $C\%$. In the plaid condition, the mask was a pair of gratings with orientations of ± 45 deg, where each component (i) had contrast $0.5C$. There were three ocular conditions. Target and mask stimuli were presented to both eyes in the binocular condition, just one eye in the monoptic condition, and different eyes in the dichoptic condition. In the monoptic and dichoptic conditions, nonstimulated eyes always saw mean luminance. The experiment was fully counterbalanced across mask grating orientation and the eye tested such that the number of trials was approximately the same in the 2 (stimulus) \times 3 (ocular) conditions after collapsing across mask orientation and eye tested. Stimulus contrast is expressed as the Michelson contrast, which is given by $C = 100(L_{\max} - L_{\min}) / (L_{\max} + L_{\min})$, where L is luminance. Contrast is also expressed in dB (re 1%) given by $20 \log_{10}(C)$. Detection thresholds were measured for seven mask contrasts (0%, 1%, 4%, 8%, 16%, 32%, and 45%).

Procedure

Observers were seated in a dark room with their heads supported by a head-and-chin rest with the goggles attached. The task was to identify which temporal interval contained the vertical target grating in a two-interval, forced-choice (2IFC) procedure. Each interval contained the mask and had duration of 100 ms. The interstimulus interval was 400 ms. Observers used two mouse buttons to indicate their response, and auditory feedback indicated correctness. The experiment was blocked by mask type (left oblique grating, right oblique grating, and plaid) and mask contrast. Ocular condition (monoptic, dichoptic, or binocular) was interleaved across trials within an experimental session. For each condition, a pair of randomly interleaved staircases controlled the contrast of the target grating using a 3-down, 1-up rule (Wetherill & Levitt, 1965). The step size in the test stage changed the contrast by a factor of 1.3 (2.5 dB), and each staircase terminated after 12 reversals with this step size. An initial stage for each staircase used a larger step size (10 dB and then 5 dB after the first reversal), though data from this stage did not contribute to the estimate of threshold. Thresholds (75% correct), psychometric slopes, and standard errors (S.E.) were estimated by probit analysis (McKee et al., 1985). Following our usual practice, when the S.E. of the fit was greater than 1.4 times the threshold (i.e., S.E. > 3 dB), the data were discarded and the session was rerun. This was done for 24 of 840 estimates (2.86%). A single repetition of the experiment consisted of about 16,800 trials and took approximately 10 h to complete. After collapsing data across the eye tested and the orientation of the mask, there were four estimates of threshold for each mask contrast for each of the 2 \times 3 (mask \times eye) conditions for a single repetition of the experiment.

Observers

All three observers were between 20 and 32 years old, had normal stereovision, and wore their normal optical correction where appropriate. Two undergraduate optometry students (M.A.C. and S.P.J.) completed two repetitions of the experiment as part of their course requirement ($n = 8$ per data point after collapsing across eye and orientation). One volunteer postgraduate student (N.R.H.) completed a single repetition ($n = 4$) and was naive to the purpose of the experiment. All observers had approximately 1 h of practice before formal data collection began.

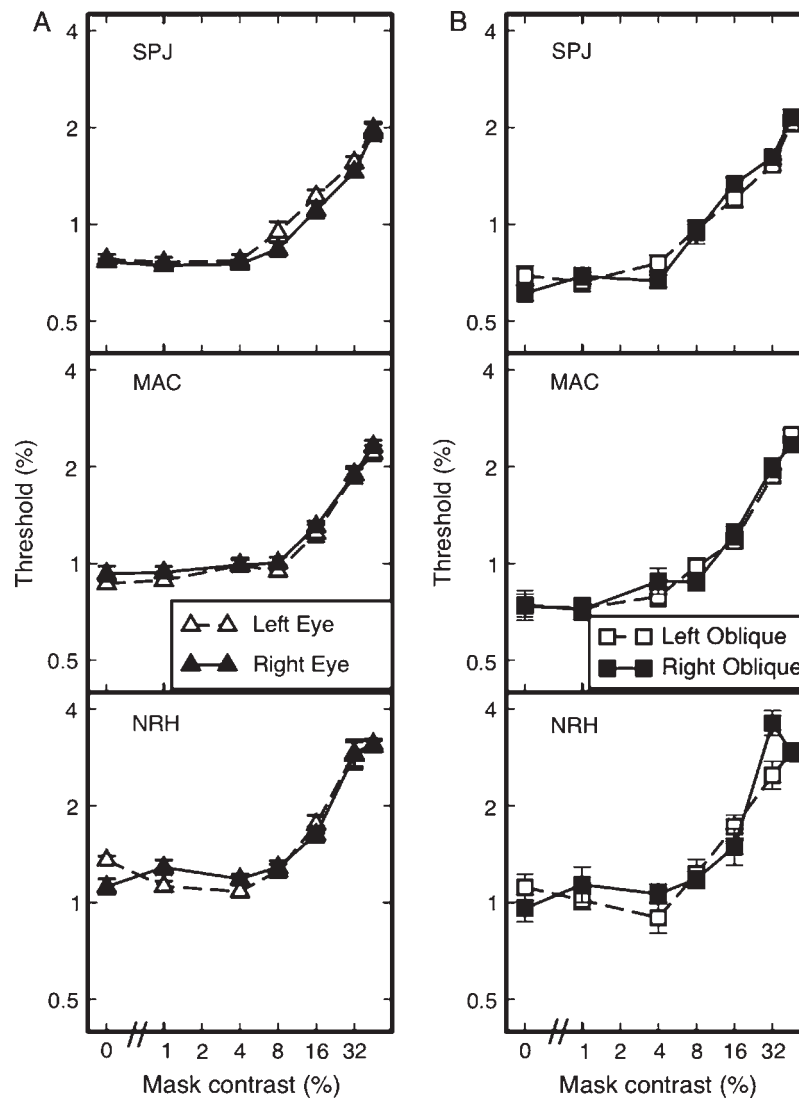


Fig. 2. Preliminary analysis showing masking functions for (A) different eyes (collapsed across monoptic and dichoptic grating and plaid masks) and (B) different grating mask orientations (collapsed across monoptic, dichoptic, and binocular masks for both eyes). Different panels are for different observers, and error bars show ± 1 S.E. where larger than symbol size.

Results

Masking functions

Fig. 2 presents preliminary analysis comparing grating masking functions across eyes (Fig. 2A) and across mask orientations (Fig. 2B). For all three observers, the masking functions were very similar for both eyes and both mask orientations (different symbols within each panel). Therefore, results were collapsed across both of these dimensions for the main analysis.

Figs. 3–5 compare masking functions for the grating and plaid masks for binocular (Fig. 3), monoptic (Fig. 4), and dichoptic (Fig. 5) masks. Overall, the results were similar for the three observers and are summarized by their average in panel D of each figure. The results for binocular masking are very similar to those found by Meese and Holmes (2002). There is little or no effect at low contrast masks, but for mask contrasts of about 8% and above, the mask elevates detection threshold (by an average factor of ~ 4 for a mask contrast of 45%). The amount of masking is the same

regardless of whether the mask was a plaid or grating, implying linear summation of mask contrast across orientation before suppression.

In the monoptic and dichoptic conditions (Figs. 5, 6), sensitivity was less than that in the binocular condition at low mask contrasts. This is to be expected from binocular summation of contrast, which had an average summation ratio¹ of 1.62 (4.2 dB) across observers for a mask contrast of 0%. This compares favorably with other recent estimates of ~ 1.7 (Meese et al., 2006; Baker et al., 2007b; Georgeson & Meese, 2007).

Masking was significantly greater for the grating mask than for the plaid mask for all the three observers in the dichoptic condition and for one of the three observers (S.P.J.) in the monoptic condition (Table 1). For a second observer (N.R.H.), the grating and plaid masking functions crossed over at the highest mask contrast (Fig. 4), resulting in a significant interaction between

¹The binocular summation ratio is the ratio of binocular to monocular contrast sensitivities.

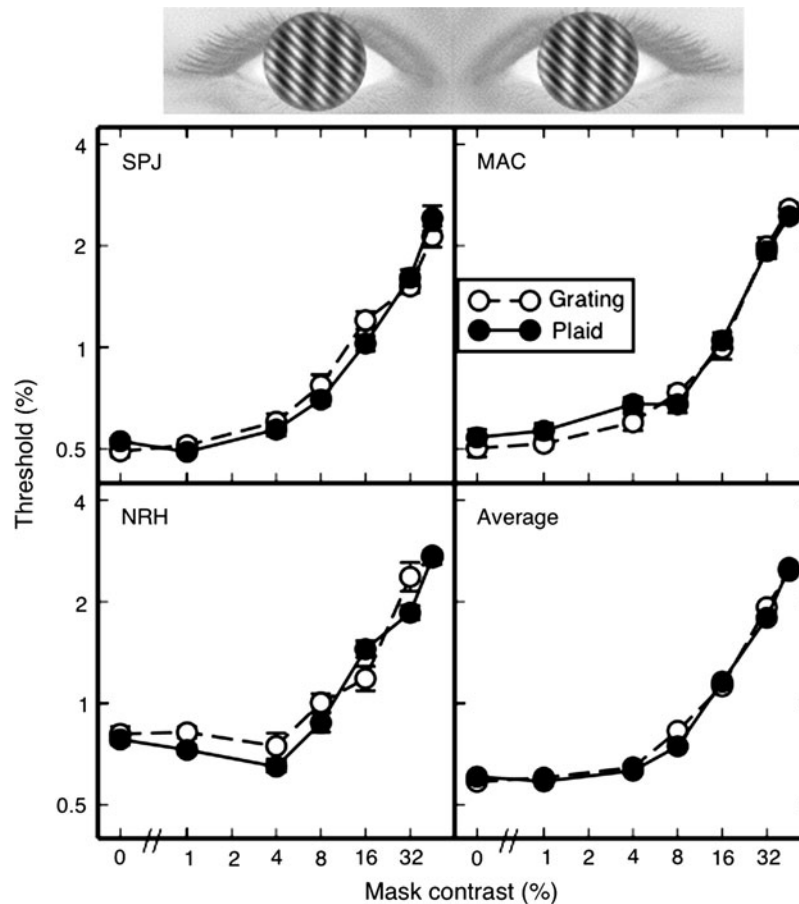


Fig. 3. Binocular masking functions for three observers and their average (different panels). Different symbols are for grating and plaid masks [note that the icon at the top of the figure (also Figs. 4, 5) depicts only the grating condition]. Error bars show ± 1 s.e. where larger than symbol size.

mask type and contrast but no significant main effect of mask type (Table 1). On the other hand, the effect of mask type was significant when the analysis was restricted to mask contrasts of 8%, 16%, and 32% [$F(1,18) = 5.64, P < 0.05$] for this observer.

Pooled over the highest four mask contrasts (Table 1), the average masking functions differ by a factor of 1.14 (1.4 dB) for the monoptic condition and 1.16 (1.3 dB) for the dichoptic condition, indicating deviations away from strict linear summation of mask contrast. However, we note that the deviations are small and diminish at the very highest mask contrast (Figs. 4, 5).

We also note that the overall level of masking is similar in the monoptic and dichoptic conditions (dichoptic masking is 0.7 dB less, averaged across the highest four mask contrasts). At the highest mask contrast, the detection thresholds for all three masking functions are fairly similar (compare Figs. 3–5, far right in each panel). However, the baseline sensitivity is greater for the binocular condition, indicating that at high mask contrasts, binocular masking is more potent than the other two varieties.

The slope of the psychometric function

As we describe below, the slope of the psychometric function provides valuable information about the nature of the interactions that we have studied. Fig. 6 shows the average slopes of the psychometric functions for the six combinations of ocular condition and mask type. In all cases, the slopes are fairly steep and have

Weibull slope parameters around $\beta = 3$ or 4. In particular, there is little or no effect of mask contrast on the slope parameter. [Lu and Dosher (1999) found a similar result using white-noise masks.] If the grating masks here were to excite the mechanism that detects the target (i.e., if the mask were acting as a pedestal), then this would produce a much shallower psychometric function, with a Weibull $\beta \sim 1.3$ (a d' slope of unity; Pelli, 1985, 1987; Tyler & Chen, 2000) due to the linearizing effects of the mask on small-signal increments (Foley & Legge, 1981; Bird et al., 2002; Meese et al., 2006). However, the masks do not affect the slopes of the psychometric functions, implying that the mask components fall outside the passband of the detecting mechanism. The absence of a (distinct) region of facilitation (no “dipper”) in Figs. 3–5 also points to this interpretation (Foley, 1994; Meese & Holmes, 2002)². This makes it unlikely that the masking here is due to conventional pedestal effects (Legge & Foley, 1980; Wilson et al., 1983), leaving cross-channel suppression as the more likely candidate (Ross

²An alternative account of pedestal masking supposes that the transducer is linear and that intrinsic uncertainty is responsible for the steep psychometric function (Pelli, 1985). On this model, a mask reduces uncertainty if it is similar to the target by raising the response of the target channel above that of the other (distracting) noisy channels; this makes the slope of the psychometric function shallow and produces a region of facilitation. On this interpretation, our results indicate that the mask does not reduce uncertainty. Therefore, it is unlikely that the mask produces masking by within-channel excitation on this model either.

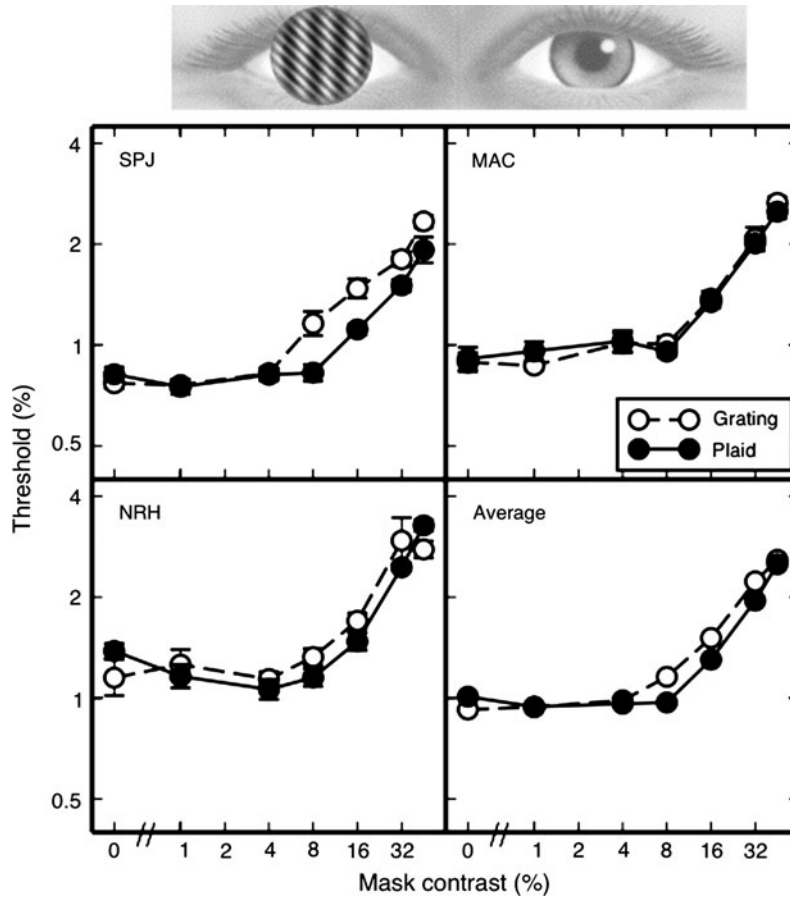


Fig. 4. Monoptic masking functions for three observers and their average (different panels). Different symbols are for grating and plaid masks. Error bars show ± 1 s.e. where larger than symbol size.

& Speed, 1991; Foley, 1994; Olzak & Thomas, 2003; Holmes & Meese, 2004; Meese & Hess, 2004; Meese & Holmes, 2007).

We also note one other aspect to the results in Fig. 6. There is a tendency for the psychometric slope to be a little steeper in the binocular condition (Fig. 6, squares) than in the other two conditions (Fig. 6, triangles and circles). A steep slope can arise for two reasons: uncertainty (Pelli, 1985) and a nonlinear transducer (Foley & Legge, 1981; Lu & Doshier, 1999). This suggests that in the binocular case, either the observer is more uncertain about the stimulus (i.e., the observer monitors a greater proportion of irrelevant noisy channels) or the contrast transduction accelerates more rapidly. Why either of these should be so remains unclear, though the effect is small and probably should be treated with caution.

Analysis

The experiment here provides a general way of assessing the contrast pooling rules of suppressive pathways. In the absence of a pedestal and assuming that the mask components fall outside the passband of the detecting mechanism (Fig. 6; see also “Pedestal masking”), the interactions can be described by dividing an excitatory contrast term (E) by a string of other terms:

$$\text{resp}(\text{stimulus}) = \frac{E}{z^q + E' + w^q \times \text{POOL}}, \quad (1)$$

where z is a saturation constant, E' is a function whose drive is the same as E , and POOL is the pooled response of other components

outside the passband of the detecting mechanism (here they have different spatial frequency and orientation from the target). The exponent q is discussed below. At contrast detection threshold, sensitivity is set by the saturation constant (z) and the weight of POOL (w) controls the contrast at which POOL becomes effective. At contrast detection threshold, E' is usually small compared to $z^q + w^q \times \text{POOL}$. As it plays little role at detection threshold (Legge & Foley, 1980; Wilson, 1980), the modeling is simplified by setting $E' = 0$.

The excitatory drive is given by

$$E = G \times C_{\text{TARGET}}^p, \quad (2)$$

where G sets the gain and is absolved by z and w in eqn. (1).

In the Introduction (see “Pooling rules for suppression”), we presented three arithmetic descriptions of contrast pooling rules for suppression. One of these, involving the compressive non-linearity (Fig. 1B), is not consistent with our results: In no condition did we find plaid masking to be consistently greater than grating masking. We do not give further consideration to this arrangement. The other two possibilities remain viable (Fig. 1A, 1C), and in the following subsections, we develop them to produce four arrangements for pooling mask contrast (POOL). These are then considered in conjunction with two distinct possibilities for the transduction of signal contrast in the excitatory pathway, giving an analysis based on a total of eight different model arrangements. Their behaviors are characterized by the different levels of masking

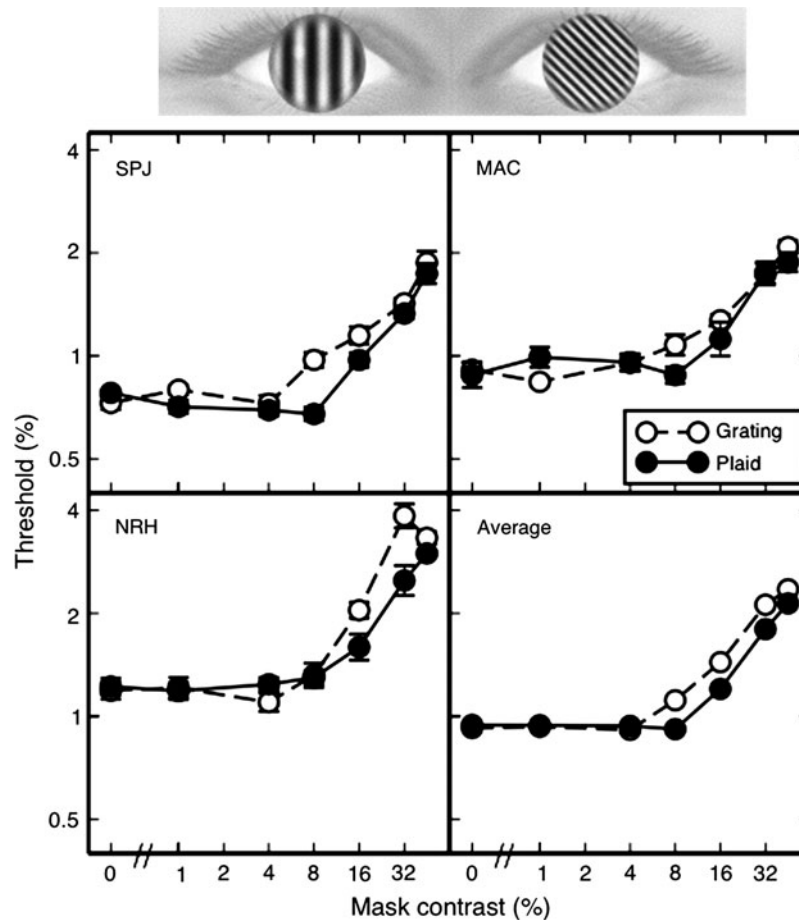


Fig. 5. Dichoptic masking functions for three observers and their average (different panels). Different symbols are for grating and plaid masks. Error bars show ± 1 s.e. where larger than symbol size.

produced by the grating and plaid and the way that suppression increases with mask contrast.

The excitatory response exponent (p)

The exponent p (eqn. 1) is often treated as a free parameter, but there are several values of p worth specific consideration. When $p = 1$, the excitatory contrast transducer is linear. This is not a good model of most cortical cells, which typically have accelerating contrast response nonlinearities at low contrasts (Sclar et al., 1990) but is perhaps a more appropriate approximation in the LGN (Derrington & Lennie, 1984; Sclar et al., 1990). It has also remained a viable model at the system level, where it continues to receive detailed consideration (Solomon, 2007a,b; Summers & Meese, 2007; Wallis et al., 2008), often in conjunction with models of uncertainty (Pelli, 1985; Tyler & Chen, 2000) and multiplicative noise (Burton, 1981; McIlhagga & Peterson, 2006; Solomon, 2007a,b). A long-standing alternative is the accelerating transducer. This is consistent with the contrast response of individual cells at several levels of the visual hierarchy (Sclar et al., 1990) and is a feature of numerous psychophysical models (e.g., Stromeyer & Klein, 1974; Legge & Foley, 1980; Wilson, 1980; Foley, 1994; Watson & Solomon, 1997; Graham & Sutter, 1998; Kontsevich & Tyler, 1999; Lu & Dosher, 1999; Olzak & Thomas, 1999, 2003; Itti et al., 2000; Clatworthy et al., 2001; Chirimuuta & Tolhurst, 2005; Parraga et al., 2005; Meese et al., 2006; García-Pérez &

Alcala-Quintana, 2007; Meese & Summers, 2007). Although estimates of p vary, $p = 2.4$ is a common default, consistent with psychophysical (Legge & Foley, 1980) and electrophysiological data (Sclar et al., 1990). A value of $p = 2.0$ can also be justified on similar grounds and has the benefit of contributing to the calculation of contrast energy (see below).

In the modeling shown here, we used $p = 1.0$ and $p = 2.0$, though models with $p = 2.4$ (consistent with our previous work: Meese et al., 2005; Meese & Summers, 2007; Summers & Meese, 2007) produced very similar fits to those with $p = 2.0$.

Contrast energy of the mask

The contrast energy of a stimulus is the integral over space (and time) of the square of the local contrasts. The computation of contrast energy has a well-established history in vision models at the cellular level (Heeger, 1992; Mante & Carandini, 2005) and at the systems level (Watson et al., 1983; Adelson & Bergen, 1985; Georgeson & Scott-Samuel, 1999; Watson, 2000; Manahilov et al., 2001). One possibility is that suppressive pathways carry the contrast energy of the mask. In our experiments, the grating and plaid masks had the same overall Michelson contrast but very different energies. From Parseval's theorem, the contrast energy of a luminance pattern is equal to the integral of its energy spectrum. This is equal to the squared modulus of its Fourier transform, which for a sine wave grating is proportional to the square of the

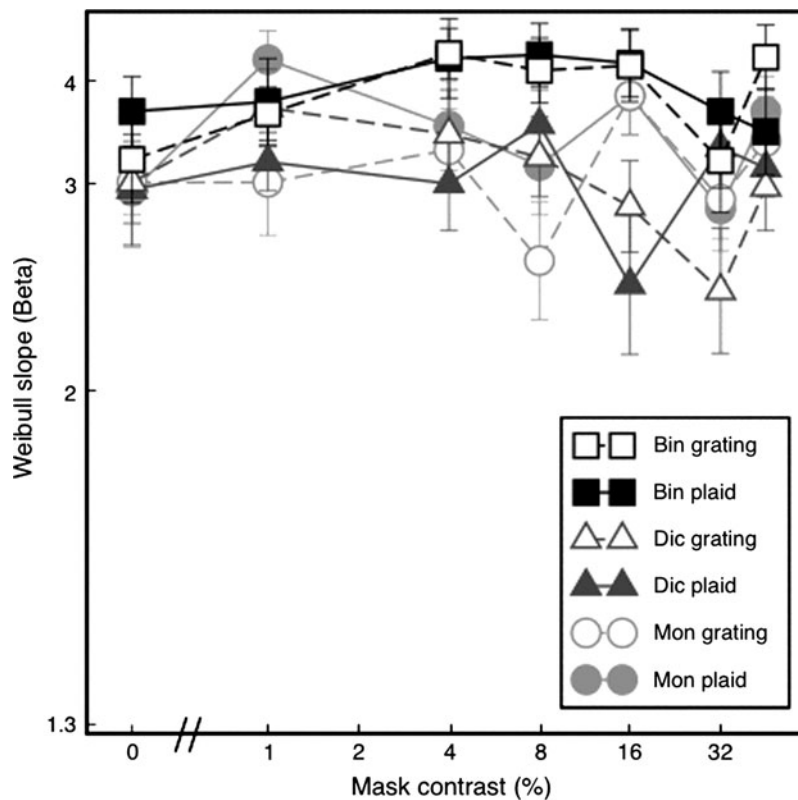


Fig. 6. Slopes of the psychometric functions averaged across observers for each of the three ocular conditions and two mask types.

Michelson contrast of the stimulus. Therefore, since the areas and durations of the plaid and grating masks are the same, energy is proportional to C^2 for the grating mask and $2(C/2)^2$ for the plaid mask. Thus, for the energy model, we say

$$POOL_{GRATING} = AC_{MASK}^2 \quad \text{and} \quad (3)$$

$$POOL_{PLAID} = A \frac{C_{MASK}^2}{2}, \quad (4)$$

where C_{MASK} is the Michelson contrast of the mask stimulus and A is a function of area. This means that the suppressive contribution of POOL is proportional to the square of the Michelson contrast and is a factor of 2 greater for the grating than for the plaid. Note also that the plaid energy is the same whether it is

calculated over the plaid image or summed over that calculated for each of its components.

RMS contrast of the mask

A contrast measure related to energy is RMS contrast. This has been used as the basis for divisive contrast gain control in the LGN and retina in models of single cells (Shapley & Victor, 1981; Bonin et al., 2005, 2006). The derivation of RMS contrast is similar to stimulus energy above, but the squared responses are averaged instead of summed and are followed by a square-root operation. This measure is also equivalent to the standard deviation of the local contrasts, and for a sine wave grating, it scales linearly with the Michelson contrast. Because of the square-root operation, it follows from the previous subsection that the RMS contrast of the

Table 1. Two-factor analysis of variance (highest four mask contrasts \times mask type) for three observers[†]

Eye	Effect	Observer		
		S.P.J.	M.A.C.	N.R.H.
Monocular	T	$F(1, 56) = 33.60^{**}$	$F(1, 56) = 1.42$	$F(1, 24) = 2.09$
	C	$F(3, 56) = 59.60^{**}$	$F(3, 56) = 144.56^{**}$	$F(3, 24) = 66.51^{**}$
	T \times C	$F(3, 56) = 0.75$	$F(3, 56) = 0.05$	$F(3, 24) = 2.40$
Dichoptic	T	$F(1, 56) = 19.33^{**}$	$F(1, 56) = 4.67^*$	$F(1, 24) = 17.06^{**}$
	C	$F(3, 56) = 80.73^{**}$	$F(3, 56) = 45.50^{**}$	$F(3, 24) = 78.26^{**}$
	T \times C	$F(3, 56) = 3.24^*$	$F(3, 56) = 0.83$	$F(3, 24) = 3.56^*$
Binocular	T	$F(1, 56) = 0.16$	$F(1, 56) = 0.54$	$F(1, 24) = 1.17$
	C	$F(3, 56) = 120.42^{**}$	$F(3, 56) = 293.93^{**}$	$F(3, 24) = 111.32^{**}$
	T \times C	$F(3, 56) = 2.27$	$F(3, 56) = 0.57$	$F(3, 24) = 4.48^*$

[†]The asterisks * and ** denote significant ($P \leq 0.05$) and highly significant ($P \leq 0.01$) effects, respectively. C, contrast; T, type.

grating mask here is a factor of $\sqrt{2}$ (3 dB) greater than that of the plaid. Thus, for the RMS model, we have

$$\text{POOL}_{\text{GRATING}} = A' C_{\text{MASK}} \quad \text{and} \quad (5)$$

$$\text{POOL}_{\text{PLAID}} = A' \frac{C_{\text{MASK}}}{\sqrt{2}}, \quad (6)$$

where A' is a function of area. This means that the suppressive contribution of POOL is proportional to the Michelson contrast of the mask and is $\sqrt{2}$ greater for the grating than that for the plaid.

Common equations for energy and RMS contrast

For convenience, we present a further pair of more general equations that can be used for both the energy and the RMS contrast of the masks used here:

$$\text{POOL}_{\text{GRATING}} = A' C_{\text{MASK}}^q \quad \text{and} \quad (7)$$

$$\text{POOL}_{\text{PLAID}} = A' \left(\frac{C_{\text{MASK}}}{\sqrt{2}} \right)^q. \quad (8)$$

When $q = 1$, we have the RMS contrast model, and when $q = 2$, we have the energy model.

Also for convenience, we subject the weight parameter w and the saturation constant z to the exponent q in eqn. (1). This reduces the number of decimal places needed to express w when $q = 2$ and allows more meaningful comparisons of parameter values across different values of q . This does not affect the quality of the fits and has no significant meaning in the models.

Linear suppression

Linear suppression is a descriptive model formulation taken up by Meese and Holmes (2002). Unlike the two models above, it does not integrate over area but simply sums the Michelson contrasts of each weighted (W_i) mask component (i). For the stimuli here, the potency of the mask components is the same ($W_1 = W_2$; Fig. 2B). In the general expression, the sum of mask contrasts is raised to an exponent q , giving

$$\text{POOL}_{\text{GRATING}} = W C_{\text{MASK}}^q \quad \text{and} \quad (9)$$

$$\text{POOL}_{\text{PLAID}} = [W_1(C_{\text{MASK}})/2 + W_2(C_{\text{MASK}})/2]^q = W C_{\text{MASK}}^q. \quad (10)$$

To equate the number of free parameters across the three different models, we fixed $q = 2$ by analogy with the energy model and $q = 1$ by analogy with the RMS contrast model. This means that for the linear suppression model, the suppressive contribution of POOL is proportional to either the Michelson contrast of the mask or its square (depending on q) and is exactly the same for the grating and plaid.

Implementation

As the areas of the masks were always the same, A and A' are constants (eqns. 3–8) and are absorbed by w in eqn. (1). The weight parameter W (eqns. 9 and 10) varies lawfully across spatiotemporal frequency (Meese & Holmes, 2007), but as those parameters were fixed here, W is constant and also absorbed by w .

We make the assumption that the target is detected when the difference between the model responses in the two 2IFC intervals

exceeds the noise level (with standard deviation proportional to σ), giving

$$\text{Resp}(\text{MASK}, \text{TARGET}) - \text{Resp}(\text{MASK}) = \sigma. \quad (11)$$

But by dividing throughout by σ , this parameter is absorbed by z and w . Thus, z and w are the only two free parameters for each of the models.

Model fitting and general observations

The data were averaged across the three observers, and the models (eqns. 1 and 7–11) were fitted to the results for the plaid and grating mask simultaneously for each ocular condition using a downhill simplex algorithm. The fitting procedure minimized the RMS error in the least squares sense expressed in decibel. The fits are shown in Figs. 7 and 8 for $p = 1$ and $p = 2$, respectively, where the different rows are for different models (fit to the same data) and different columns are for the different conditions. Note that in each figure, the top two rows are for eqns. (8) and (7) (RMS contrast and energy) and the bottom rows are for eqns. (10) and (9) (linear suppression). The odd rows (1 and 3) are for $q = 1$, and the even rows (2 and 4) are for $q = 2$.

We consider the quality of the fits in the next subsection, but we begin with some comments about the general properties of the eight different models. First, masking functions are steeper for the lower value of p (compare Figs. 7 and 8) and the higher value of q (compare odd- and even-numbered rows in each figure). Second, for the linear suppression models, masking is always the same for the grating and plaid masks but not for the energy and RMS contrast models. When $p = 1$, the asymptotic difference between grating and plaid masking is 6 and 3 dB for the energy and RMS contrast models, respectively. When $p = 2$, these differences fall to 3 and 1.5 dB, respectively. Third, it follows from this (and Eqs. 1–8) that there is a formal similarity between the RMS contrast model with $p = 1$ and the energy model with $p = 2$ at sufficiently high mask contrasts (i.e., when the influence of z is negligible, which depends on the values of z , w , and mask contrast). However, the models are not identical because of the different rates at which they overcome the influence of z at low mask contrasts. Furthermore, the influences of z and w mean that in some cases, the asymptotic difference described above is not quite reached within the range of mask contrasts in the plots.

Which model is best?

We begin with some general observations. By eye, when $p < q$ (Fig. 7, second and fourth rows), the model masking functions accelerate too rapidly. On the other hand, when $p > q$ (Fig. 8, first and third rows), they are too shallow. The best shapes of the masking functions are achieved when $p = q$.³ This qualitative

³In the psychophysical models of Legge & Foley (1980) and others, an arrangement where the excitatory and suppressive exponents $p = q$ will not do. This is because the contrast response saturates, predicting that contrast discrimination will become impossible at higher contrasts, contrary to empirical observations. Instead, contrast discrimination functions (“dipper” functions) are often fit by breaking the equality between p and q , such that $p \approx q + 0.4$. This has been shown to be consistent with a multiple contrast-mechanism model where $p = q$ for each mechanism, but where progressive values of the saturation constant z give each mechanism a different operating range (Watson & Solomon, 1997). We have confirmed that parameter deviations of the order $p = q + 0.4$ have negligible effects on the quality and character of the fits here (not shown).

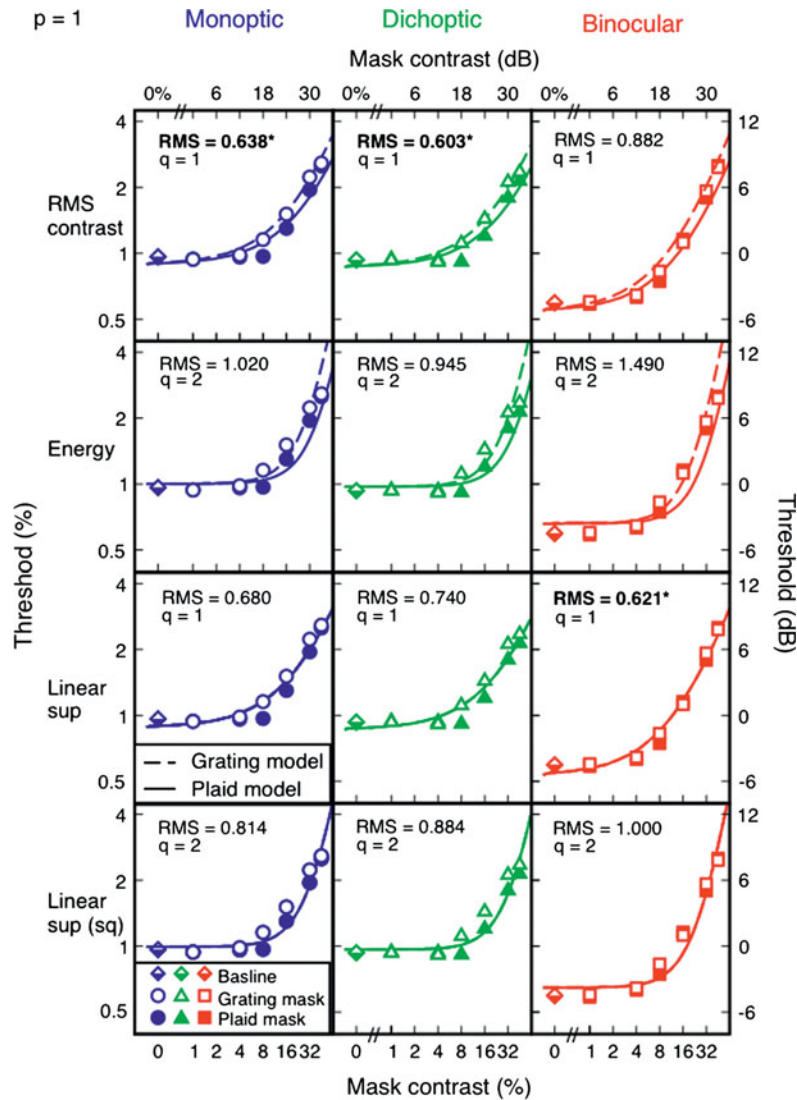


Fig. 7. Fits of four different models (different rows) for the three different ocular conditions (different columns). The models were fit to the grating and plaid mask data simultaneously, requiring two free parameters (z and w) for each panel (Table 2). In all models, the excitatory exponent $p = 1$. Insets show the RMS errors of the fits in dB and the preset values of q in the models (eqs. 7–10). Those set in bold (with the asterisk) are the best fits for each ocular condition. Data are averaged across the three observers. The best fits are found in the first and third rows, where $p = q$.

assessment is confirmed by quantitative comparisons of the RMS errors of the fits (figure insets). Within the top and bottom halves of each figure (Figs. 7, 8), the fits are always better when $p = q$ than when $p < q$ (Fig. 7) or $p > q$ (Fig. 8).

In the behavioral results, there is no systematic difference between the levels of masking produced by the grating and plaid masks in the binocular condition (far right in Figs. 7, 8). This is observed in both the average results and those from individual observers (Fig. 3). The only models (tested here) that behave this way are the linear suppression models; this qualitative success is borne out by the very low RMS errors of the fits for these models (0.62 dB for $p = q = 1$, Fig. 7; and 0.36 dB for $p = q = 2$, Fig. 8). The energy and RMS contrast models cannot produce superimposed masking functions and should not be accepted as adequate models of the binocular masking data here.

In the monoptic and dichoptic cases, the situation is different. The grating mask is generally more potent than the plaid mask at moderate mask contrasts and above. This is consistent with

both the energy model and the RMS contrast model. For these conditions, the fits for the RMS contrast model are best when $p = 1$ (Fig. 7) and those for the energy model when $p = 2$ (Fig. 8), consistent with the $p = q$ preference described earlier. However, as noted above (see “Masking functions”), there is a distinct tendency for the grating and plaid masking functions to converge at higher mask contrasts, casting serious doubt on a strict interpretation of the RMS and energy models.

In general, we conclude that (1) $p \approx q$, (2) linear suppression describes only binocular masking, and (3) the energy and RMS contrast models provide better fits for the monoptic and dichoptic results or, more generally, that suppression is slightly sublinear for these conditions. One exception to this summary of the fits is that the best quantitative fit in the monoptic condition is by the linear suppression model with $p = q = 2$ (Fig. 8) owing, primarily, to the results from MAC (see Fig. 4). However, while this model is a fair approximation of the data, it seems unlikely in detail because it cannot predict the small but significant differences between the

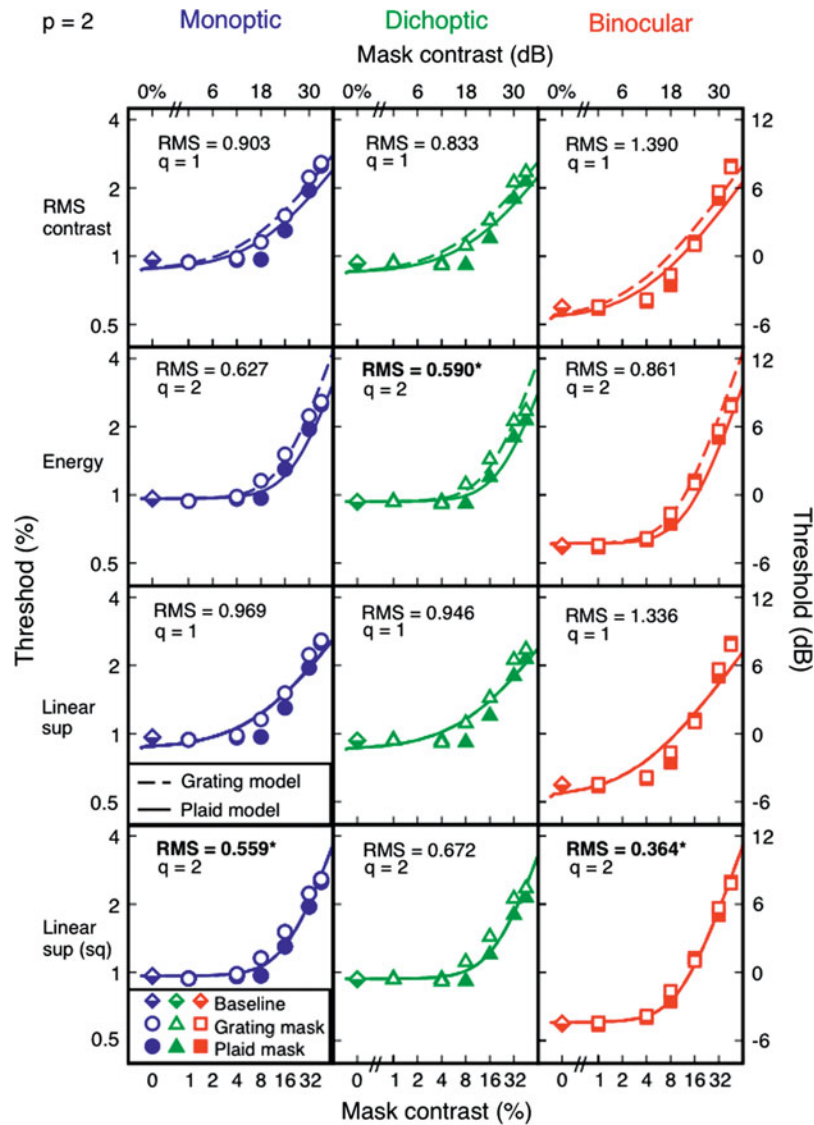


Fig. 8. The same as Fig. 7, except that $p = 2$. The best fits (bold RMS error in dB) are found in the second and fourth rows, where $p = q$.

grating and plaid masks (Table 1). Nevertheless, its quantitative success emphasizes the doubt that we have cast on a strict interpretation of the RMS and energy models.

Discussion

We used grating and plaid masks in psychophysical masking experiments to assess the rules for summing contrast across orientation bands within suppressive pathways in human vision. We confirmed previous work finding that suppressive summation is linear for binocular masks and targets (Meese & Holmes, 2002; Holmes & Meese, 2004) but found similarly small deviations from linearity for monoptic and dichoptic masking. Before discussing the results in the context of our analysis, we first consider two potentially complicating issues.

Pedestal masking

Our mask and target stimuli had very different spatial frequencies (1.6 octaves) and orientations (45 deg) (see icons in Figs. 3–5) and were designed to excite nonoverlapping mask and target pathways in the Fourier domain. Nevertheless, excitatory pathways might involve

some cortical cells that are sufficiently broadband to respond to both the target and the mask (Ringach et al., 2002a), thereby causing the mask to act as a pedestal (i.e., raising the background level of activity against which target increments must be judged). However, we think it unlikely that such broadband mechanisms would have been tapped by the experiments here. First, in psychophysical detection and discrimination tasks (with feedback on correctness), the ideal observer will select the mechanism best suited to their task from the array of outputs that is available to them. Thus, if masking occurs because of excitation of the target mechanism by the mask (e.g., Legge & Foley, 1980), then the observer will restrict the influence of this contamination by using the detecting mechanism with the narrowest bandwidth available. As there are also cortical cells that have bandwidths narrower than the difference between target and mask components here (Ringach et al., 2002a), it seems likely that they will support the mechanisms used by observers in the present experiment.

A related point is that visual neurons in the retina and LGN have very broad selectivity for both orientation and spatial frequency, and this has been suggested as a source of cross-orientation masking (Li et al., 2006; Priebe & Ferster, 2006). However,

this cannot apply to the dichoptic results here, since the mask and target are processed in different ocular pathways prior to the cortex.

Further evidence against a role for pedestal masking in the experiments here comes from direct tests of pedestal behavior (Foley, 1994) using binocular mask and target stimuli very similar to those here. First, when a weak mask excites a target mechanism, it produces marked levels of facilitation (Legge & Foley, 1980), but Meese and Holmes (2002) found no evidence of this, only masking. Second, when a strong mask excites the detecting mechanism, the potential for pedestal facilitation (from a weak mask) is lost. However, Holmes and Meese (2004) found that pedestal facilitation remained in the presence of strong suppression from masks of the type used here. Finally, the analysis of the slope of the psychometric function in the present study is also inconsistent with pedestal masking from our masks. Pedestals effectively linearize the response to small signal increments, producing a shallow psychometric function with a Weibull $\beta \sim 1.3$ (equivalent to a d' slope of unity) (Foley & Legge, 1981; Meese et al., 2006). However, the psychometric functions in the present study all had slopes around $\beta = 3$ or 4 regardless of whether there was masking.

Taken together, these results and arguments pose a serious challenge to those who might wish to attribute the masking in the present study to pedestal (within-mechanism) masking at the system level. This is not to say that the mask and target do not excite the same early components in the system (e.g., this must happen at the level of photoreceptors in the monoptic condition), but it does mean that such coactivation does not translate into classical pedestal effects (Legge & Foley, 1980) at the decision stage.

Multiplicative noise

The models here all make the (simplifying) assumption of late additive noise (eqn. 11). Nevertheless, it is well known that the variance of cellular activity increases with mean response (Tolhurst et al., 1983). This is sometimes referred to as multiplicative noise and is a candidate source of masking because it degrades the signal-to-noise ratio for response increments as mask (pedestal) contrast increases. Whether and how multiplicative noise should be included in psychophysical models has been a topic of much recent debate (e.g., Kontsevich et al., 2002; Georgeson & Meese, 2006; Klein, 2006; Katkov et al., 2006; Solomon, 2007b). Solomon (2007a) assessed psychophysical second responses to small patches of 4 cycles/deg, parafoveal (7.9 deg) gratings and concluded that weak multiplicative noise should be included at least over the lower contrast range. Katkov et al. (2007) performed categorical contrast judgments of centrally placed stimuli that were otherwise similar to Solomon's. They concluded that noise decreased over the initial contrast range and was additive thereafter. Baker and Meese (2007) also concluded that multiplicative noise was not entirely responsible (if at all) for pedestal masking in the dichoptic case for foveal patches of 1 cycle/deg grating. Finally, Meese and Hess (2004) used stimuli similar to those here (dichoptic, monoptic, and binocular grating masks) in a contrast-matching task and found that the masks reduced perceived contrast. Assuming that perception of contrast depends on response magnitude and not variance (Zenger-Landolt & Heeger, 2003), this provides good evidence for the involvement of a suppressive process in the masking here. But how does all this bear on our modeling?

Our experiments here do not involve a pedestal (see "Pedestal masking"), and so it is reasonable to suppose a role for a standing level of additive noise (as we do). But could the masks that we

have used inject multiplicative noise? As they are not summed *within* the detecting mechanism, the most likely route for this would be through divisive inhibition, consistent with the suppressive process here. However, the presence of multiplicative noise would reduce the slope of the psychometric function (Tyler & Chen, 2000; Solomon, 2007b), which is not what we found (Fig. 6). In spite of all this, if mask contrast-dependent noise were injected into the target mechanism and were the sole cause of masking, how would that change our analysis? If the noise from each of the mask components were independent, then the variances would add, and the standard deviation of the noise from the plaid would be $\sqrt{2}$ less than that for the grating (recall that mask component contrast is half that of the grating). Assuming that the multiplicative noise is proportional to mask component contrast, this is formally equivalent to the RMS model. If, on the other hand, the mask noise were simply proportional to the overall contrast of the mask, then the situation is formally equivalent to the linear suppression model (with $q = 1$).

An unexpected result: Orientation pooling is the same for monoptic and dichoptic masks

As outlined in the Introduction, the experiments here were motivated by recent evidence (from psychophysics and single-cell physiology) that different suppressive pathways are involved in monoptic and dichoptic cross-orientation masking, possibly precortical and cortical, respectively. As orientation tuning is a distinct property of the cortex but not subcortical structures, we anticipated that this might have a different influence on the orientation-pooling rules for monoptic and dichoptic masking. For example, if the dichoptic plaid mask components pass through oriented filters before feeding into the suppressive gain pool, then each component would be subject to the output nonlinearity of the oriented filter, and we might expect the result as in Fig. 1B. On the other hand, if monoptic isotropic filters were to drive suppression (Hirsch et al., 2002; Bonin et al., 2005), then the mask components would not be processed independently. This would allow linear summation of the mask component contrasts across orientation, which only then would be subject to the output nonlinearity (if there is one) of the suppressive pathway. Other work has revealed these kinds of difference. In a preliminary report, Challinor et al. (2008) described binocular masking experiments similar to those here, but for a range of mask orientations (0 to ± 90 deg), and with mask spatial frequencies that were the same as the target (1 cycle/deg). For intermediate orientations (± 40 to ± 70 deg), they found that masking was greater for the plaid mask than for the grating mask ("super suppression"), broadly consistent with the scheme in Fig. 1b (see also Derrington & Henning, 1989). Thus, we reasoned that this super suppression might be cortical and might also be revealed by the dichoptic masks here, albeit at a higher mask spatial frequency. However, our results provide no evidence for this or for any differences in masking within and between the eyes: for each of our three observers, the relation between the grating and the plaid masking functions is very similar in the monoptic and dichoptic conditions (compare Figs. 4, 5). We discuss the similarity of these results below.

Origins of cross-orientation suppression

One possibility is that monoptic and dichoptic masking involve the same suppressive process placed *after* binocular combination of signals (Baker et al., 2007b). In that case, (1) similar levels of masking and (2) similar pooling rules should be expected in the

dichoptic and monoptic conditions, as found here. However, we think that this is an unlikely interpretation of our results. Baker et al. (2007b) compared monoptic and dichoptic cross-orientation masking over a range of spatiotemporal frequencies (the mask and target always had the same spatiotemporal frequency) for patches of flickering gratings. The detection thresholds were normalized by the baseline (unmasked thresholds) and analyzed in the context of a contrast gain control model. The monoptic results replicated the binocular results of Meese and Holmes (2007): the weight of suppression was proportional to the square root of the ratio of temporal and spatial frequencies (i.e., masking increased with stimulus speed). However, the dichoptic results were different, being essentially scale invariant over space and time (on normalized axes). These two very different yet lawful results suggest two underlying processes with different constraints or computational goals. Furthermore, as outlined in the introduction, Baker et al. (2007b) found several differences between monoptic and dichoptic masking, including their bandwidths and susceptibility to adaptation. They also found distinct dependencies on stimulus duration (25–400 ms), with monoptic masking tending to be stronger at short durations and dichoptic masking stronger at longer durations, though details varied across observers and mask type. The stimulus duration here (100 ms) was intermediate along the range tested in the previous study and was chosen to try and equate the levels of monoptic and dichoptic masking so that meaningful comparisons could be made across the conditions of interest (plaid vs. grating masking). Thus, we see the similarity in the overall levels of monoptic and dichoptic masking as a mark of success in our experimental design and not an indicator of a common suppression mechanism: the similarity here is the exception⁴ and not the rule.

The main interest in the present study was with the pooling rules in the suppressive pathways within and between the eyes (Figs. 3–5). As these are so similar, it is tempting to suppose that related neurophysiological processes are involved, albeit within different pathways that have otherwise different properties (Baker et al., 2007b).⁵ The two most obvious options are either (1) suppression by isotropic filters (Hirsch et al., 2003; Bonin et al., 2005; Nolt et al., 2008), in which case the orientation pooling is “within-mechanism,” or (2) suppression from a pool of orientation-tuned mechanisms (Albrecht & Geisler, 1991; Heeger, 1992). Primary visual cortex is the first site of orientation tuning, and cortical cells are strongly susceptible to contrast adaptation (Ohzawa et al., 1985; Freeman et al., 2002; Webb et al., 2005; Durand et al., 2007). However, monoptic cross-orientation suppression is immune to adaptation in both cats (Li et al., 2005; Sengpiel & Vorobyov, 2005) and humans (Baker et al., 2007b), making this account seem unlikely for the ipsiocular pathway. Isotropic mechanisms are well known in the retina (Shapley & Victor, 1978) and LGN (Bonin et al., 2005), and also layer 4 of the

cortex (e.g., Hirsch et al., 2003; Martinez et al., 2005), suggesting plausible origins for monoptic and dichoptic masking, respectively. There is also good evidence for a broadband component to suppression in the ipsiocular pathway in cat, where the spatial frequency tuning of the suppressive field in the LGN is broader than its excitatory passband (Bonin et al., 2005; Nolt et al., 2008), consistent with the requirements here. Further support comes from a study by Baker and Meese (2007). They performed a detailed psychophysical investigation of dichoptic masking for 1 cycle/deg targets and ranges of spatial frequencies, orientations, and phases of grating masks. They concluded that two factors were involved in cross-orientation suppression, one tuned and the other broadband and isotropic, similar to that found in the binocular case (Meese & Holmes, 2003). They could not determine whether the two factors arose from different mechanisms, but the isotropic effect was consistent with suppression from a nonoriented mechanism (e.g., Hirsch et al., 2003). Finally, Medina et al. (2007) were able to isolate a suppressive isotropic process using isoluminant (red/green) binocular masks and targets. All this leads us to suggest that the identical monoptic and dichoptic pooling rules here could be attributed to distinct processes of inhibition (Hirsch et al., 2002; Bonin et al., 2005; Solomon et al., 2006; Nolt et al., 2008) from isotropic suppressive fields in ipsiocular and interocular pathways.

The excitatory and suppressive exponents (p and q)

When the mask is a parallel grating, spatially modulated by an annulus, suppression is from the surround and subject to saturation (Petrov et al., 2005; Challinor et al., 2007).⁶ This is to be expected if the suppressive pathway were itself subject to the same or similar sigmoidal contrast transduction (Legge & Foley, 1980) as the target mechanism, as we have proposed (Challinor et al., 2007). In distinction, the masking here is an increasing function of mask contrast.⁷ This is consistent with several other psychophysical studies of cross-orientation masking (e.g., Ross & Speed, 1991; Foley, 1994; Meese & Holmes, 2002, 2007; Meese, 2004; Baker et al., 2007b; Meese et al., 2007) and implies that the pathways underlying cross-oriented, superimposed masking do not saturate, at least for contrasts up to 45%. For $q = 2$ (a square rule for suppression), it is unlikely that this is achieved by a single inhibitory cell because visual neurons do not accelerate with the square of contrast over such a wide range of contrasts. On the other hand, suppression might arise from populations of neurons, each selective for different ranges of contrast. In this case, the square rule could be implemented by increasing the efficacy of inhibitory neurons with contrast. Another possibility is that the requirement for a high dynamic range might be circumvented by using feedback and mutual inhibition (Heeger, 1992). However, regardless of these details, the puzzle remains why there is protection from saturation for superimposed cross-oriented masking but not from parallel surround masking.

One possibility is that cross-oriented masking arises at an earlier stage in the visual system than surround suppression (Petrov et al., 2005; Smith et al., 2006; Durand et al., 2007; though see

⁴Using a very different stimulus design (vertical lines that were superimposed in neither space nor time) Macknik & Martinez-Conde (2004) also found similar levels of masking for monoptic and dichoptic masks. That and further work (Tse et al., 2005) indicated a late component to dichoptic masking that arises after binocular combination. Our results and arguments here do not challenge that conclusion, but Baker et al. (2007b) proposed that the stimulus used in those studies probably involved processes that were different from the contrast phenomena here and elsewhere.

⁵The similarity in the pooling rules for monoptic and dichoptic suppression does not *require* that they both involve the same type of mechanism. For example, for the masks used here, the MAX over space of the linear sum of orientation-tuned linear filters is identical to the MAX over space of a linear isotropic filter.

⁶In human psychophysics, suppressive surround effects are found in the periphery (Petrov et al., 2005), but there is little or no suppression of detection threshold in the fovea (Snowden & Hammett, 1998).

⁷Of the 18 masking functions here, 16 of them were increasing functions of mask contrast above moderate mask contrasts (Figs. 3–5). The two exceptions were for the monoptic and dichoptic grating masks, both for observer NRH. In these cases, the functions became compressive at the highest mask contrast tested.

Webb et al., 2005; Naito et al., 2007), where the contrast response exponents are smaller and saturation is less evident (Derrington & Lennie, 1984; Sclar et al., 1990). For instance, an excitatory exponent of $p = 1$ is consistent with Bonin et al.'s (2005) single-cell model of suppression in the LGN. The arrangement $q \approx p \approx 1$ is also consistent with the results here (Fig. 7, first and third rows) and is similar to the first stage (stage 1) of contrast gain control in the psychophysical binocular summation model of Meese et al. (2006), where $p \approx 1.3$ and $q = 1$. (In Meese et al., the exponent p here was referred to as m and the exponent q here was not explicit). Stage 1 is placed before binocular summation of signals in that model and needs a low excitatory exponent to account for the relatively high levels of binocular summation that we have found (Meese et al., 2006; Baker et al., 2007b). Stage 1 can also accommodate masking from within and between the eyes across a range of orientations and spatial frequencies (Baker et al., 2007b; Baker & Meese, 2007). Elsewhere (Baker et al., 2007b), we have suggested that the two routes to suppression might exert their influence at distinct sequential stages ("stage 1a" and "stage 1b") and speculated (Meese & Holmes 2002; Baker et al., 2007b) that the first of these stages is in the LGN (or retina, or layer 4 of visual cortex), for which there is physiological evidence (Freeman et al., 2002; Bonin et al., 2005; Li et al., 2005; Sengpiel & Vorobyov, 2005; Nolt et al., 2007) and for which the excitatory exponent is low (Derrington & Lennie, 1984; Sclar et al., 1990; Felisberti & Derrington, 1999) [though higher exponents (~2) are also found; Sclar et al., 1990; Felisberti & Derrington, 2001].

The binocular advantage is lost at high mask contrasts

When there is no mask (i.e., mask contrast = 0%), sensitivity is markedly greater with two eyes than with one. However, at the highest mask contrasts, this binocular advantage is diminished or lost (see Fig. 8). This is to be expected if the contrast response to the target has the following form:

$$\text{resp} = \frac{C_{\text{LEFT_TARGET}} + C_{\text{RIGHT_TARGET}}}{z + C_{\text{LEFT_MASK}} + C_{\text{RIGHT_MASK}}}, \quad (12)$$

where we have omitted the exponents p and q (see above) for simplicity. When the mask contrast is low, the contrast terms on the denominator are negligible and a binocular advantage arises from summation on the numerator. However, at higher mask contrasts, z becomes negligible and the binocular combination of mask contrasts on the denominator offsets the binocular advantage on the numerator. This means that the binocular and monoptic expressions become equivalent (for the conditions investigated

here), predicting converging masked thresholds. Thus, masking (threshold elevation) is greater with two eyes than with one because thresholds are raised from a more sensitive baseline, just as we found in the experiment. In the model fitting, a formally equivalent effect was achieved by the expedient of driving the saturation constant (z) to lower values in the binocular condition than in the other two conditions (Table 2). However, as we point out below, the added complexity of the pooling rules found here means that the ocular contrast interactions must be more complicated than eqn. (12) implies.

A puzzle for cascade models of cross-orientation suppression

Overall (Fig. 8), there is an effect of mask type for the conditions where the mask was presented to only one eye (monoptic and dichoptic) but not when it was presented to both (binocular). In other words, by setting suppressive pooling appropriately, a simple feedforward scheme involving a stage of ipsiocular suppression followed by one of interocular suppression could account for the monoptic and dichoptic results but not the binocular results. Thus, regardless of the nature of the nonlinearities within the suppressive pathways, it remains a puzzle how this is effectively removed when stimulation is binocular. The implications are that either plaid masking is selectively enhanced or grating masking is selectively diminished when a binocular match is achieved.

We have established that the form of pooling is the same for the ipsiocular and interocular suppressive pathways, but it remains possible that further suppression arises after binocular convergence. However, a simple form of this arrangement, involving linear summation of monoptic signal pathways, does not solve the puzzle since both types of suppression (pre- and post-binocular) should be tapped by all three ocular conditions. Thus, it would seem that binocular contrast matching of the masks modifies the overall type of suppression (Meese & Hess, 2005). The details of how this is achieved remain unclear, but interocular suppression of the mask components themselves might be important (Baker et al., 2007b).

Conclusions

In human vision, monoptic and dichoptic cross-orientation suppression involve different suppressive pathways (Meese & Hess, 2004; Baker et al., 2007b). However, contrary to our expectations, we found an identical suppressive pooling rule across mask component orientation for monoptic and dichoptic plaid masks. The rule indicated slightly sublinear summation of contrast across orientation. We did not reject models where mask contrast was

Table 2. Free parameter values for the model fits in Figures 7 and 8

	$p = 1$			$p = 2$		
	Monoptic	Dichoptic	Binocular	Monoptic	Dichoptic	Binocular
RMS contrast	$z = 0.892;$ $w = 0.041$	$z = 0.869;$ $w = 0.036$	$z = 0.548;$ $w = 0.047$	$z = 0.868;$ $w = 0.114$	$z = 0.844;$ $w = 0.096$	$z = 0.528;$ $w = 0.095$
Energy	$z = 1.000;$ $w = 0.035$	$z = 0.975;$ $w = 0.032$	$z = 0.660;$ $w = 0.038$	$z = 0.966;$ $w = 0.066$	$z = 0.938;$ $w = 0.059$	$z = 0.612;$ $w = 0.066$
Linear suppression	$z = 0.884;$ $w = 0.035$	$z = 0.866;$ $w = 0.030$	$z = 0.536;$ $w = 0.040$	$z = 0.864;$ $w = 0.096$	$z = 0.852;$ $w = 0.078$	$z = 0.524;$ $w = 0.079$
Linear suppression (square)	$z = 0.995;$ $w = 0.030$	$z = 0.967;$ $w = 0.028$	$z = 0.650;$ $w = 0.033$	$z = 0.966;$ $w = 0.056$	$z = 0.938;$ $w = 0.050$	$z = 0.604;$ $w = 0.057$

expressed as RMS contrast or energy, but these models did affect the choice of excitatory exponent ($p = 1$ for RMS and $p = 2$ for energy). However, the deviation of the data from these model predictions at the highest mask contrasts casts doubt on a strict interpretation of these rules. In any case, the pooling rule is modified for binocular masks. In that situation, the masking cannot be understood in terms of either RMS contrast or energy but requires strict linear summation of the Michelson contrast across orientation. Thus, although binocular masking is more potent than the other two varieties, it is *not* simply their sum. Finally, in no ocular condition were the results consistent with a stage of suppression that followed contrast compression within each mask orientation band.

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