Remote facilitation in the Fourier domain

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Abstract

To explore spatial interactions between visual mechanisms in the Fourier domain we measured detection thresholds for vertical and horizontal sine-wave gratings (4.4 deg diameter) over a range of spatial frequencies (0.5–23 c/deg) in the presence of grating and plaid masks with component contrasts of 8%, orientations of ±45° and a spatial frequency of 1 c/deg. The mask suppressed the target grating over a range of ±1 octave, and the plaid produced more suppression than the grating, consistent with summation of mask components in a broadly tuned contrast gain pool. At greater differences in spatial frequency (≥3 octaves), the plaid and grating masks both produced about 3 dB of facilitation (they reduced detection thresholds by a factor of about \(2^3\)). At yet further distances (≥4 octaves) the masks had no effect. The facilitation cannot be attributed to a reduction of uncertainty by the mask because (a) it occurs for mask components that have very different spatial frequencies and orientations from the test and (b) the large stimulus size and central fixation point mean there was no spatial uncertainty that could be reduced. We suggest the results are due to long-range sensory interactions (in the Fourier domain) between mask and test-channels. The effects could be due to either direct facilitation or disinhibition.

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1. Introduction

Masking is the phenomenon whereby the presence of one stimulus (the mask) impedes the detectability or response to a second stimulus (the test, or target), and it is usually attributed to suppression between mask and test mechanisms (see Meese & Holmes, 2007 for a recent short review). Facilitation is said to occur when the mask enhances the detectability or response to the test stimulus. At contrast detection threshold, facilitation has been found between patches of mask and test grating that differ in spatial position (Chen & Tyler, 2001; Huang, Hess, & Dakin, 2006; Petrov, Verghese, & McKee, 2006; Polat & Sagi, 1993; Solomon & Morgan, 2000; Solomon, Watson, & Morgan, 1999; Williams & Hess, 1998), spatial frequency (Georgeson & Georgeson, 1987; Stromeyer & Klein, 1974; Tolhurst & Barfield, 1978), orientation (Meese & Holmes, 2007; Meese, Summers, Holmes, & Wallis, 2007; Zenger & Sagi, 1996) and combinations of two (Chen & Tyler, 2002; Meese et al., 2007; Yu, Klein, & Levi, 2002) or three of these parameters (Meese & Hess, 2004; Meese et al., 2007). However, most of these studies have concentrated on a fairly narrow range of spatial frequencies and so the full extent of interactions in the Fourier domain is not known. To build a more complete picture of these interactions we report masking experiments for a greater range of differences between mask and test spatial frequency than has been done in most previous studies. In particular, we were interested in conditions where we anticipated that the test grating would be detected by a mechanism that was not excited by the mask.

2. Methods

2.1. Equipment

Stimuli were displayed on a Sony Trinitron Multiscan monitor with a frame rate of 120 Hz using a VSG2/3 stimulus generator operating in pseudo 12-bit mode and controlled by a PC. Mean luminance of the central display region was 65 cd/m². The display was gamma corrected to ensure linearity...
over the full contrast range, and a frame interleaving technique (60 Hz per image) allowed the contrasts of the mask (grating or plaid) and test grating to be varied independently using lookup tables. A chin- and head-rest were used to help observers hold fixation, and viewing was binocular.

2.2. Observers

Four observers performed the main experiment. These were DJH (one of the authors) and three volunteers. Two of these were psychophysics graduate students (ADP & RJS) and one was a graduate student from another scientific discipline (JFT). The facilitation that we found for DJH was unexpected, and the other three observers were not made aware of this finding.

To become practiced at the task and familiar with the stimuli, DJH performed three complete experimental runs (~10,800 trials) before formal data collection began. The other three observers performed a sub-sample of conditions and one complete run (~1200 trials) as practice. For all observers results are means and standard errors from five experimental runs. A series of further experiments designed as controls and to test the generality of our findings (described in Section 3) was performed by DJH only.

2.3. Stimuli

All stimuli were stationary sine-wave gratings or two-component plaids the were windowed by a circular raised-cosine envelope. The central plateau of this envelope was 4.1° in diameter and the half-height, full-width of the envelope was 4.4°. The gratings were in sine-phase with a central dark fixation point (2 pixels square) that was visible throughout the experiment. The spatial frequency of the mask was always 1 c/deg. The spatial frequency of the test was varied over the range 0.5–23 c/deg. There were two types of mask: a grating mask had an orientation of −45° (left oblique) and a plaid mask had component orientations of ±45°. The orientation of the test grating was typically vertical, though in one experiment it was horizontal and in another it varied between vertical and −45°. Examples of 1 c/deg grating and plaid masks and a 5.7 c/deg test grating are shown in Fig. 1.

Stimulus contrast is expressed as the Michelson contrast of the carrier in percent. In most experiments the masks (both plaids and gratings) had component contrasts of 8%. Because of the frame interleaving (see above) this was achieved by alternating between 16% in the mask frame and 0% in the test frame. Thus, to generate a plaid where each component had a contrast of 8% in the time averaged image, the overall contrast of the plaid in the mask frame was 32%.

2.4. Procedure

A temporal two-interval forced-choice (2IFC) technique was used where observers indicated which of the two intervals contained the target using one of two mouse buttons. The computer determined the temporal interval that contained the target randomly and auditory feedback was used to indicate the correctness of response. The two intervals (100 ms each) were marked by short tones at their onset. The duration between the offset of the first interval and the onset of the second interval was 500 ms. A ‘three-down, one-up’ randomly interleaved staircase procedure was used to control the magnitude of the target contrast in logarithmic steps. A pair of interleaved staircases were used for each condition and terminated after 12 reversals each. The staircases were used only to determine stimulus placement. Threshold and its standard error (SE) were estimated using probit analysis (Finney, 1971) to calculate the 75% correct point on the psychometric function and its standard error (SE). This gave estimates based on about 100 trials for each experimental run. In the rare cases where the estimated SE was greater than 3 dB, these data were rejected and the experimental session was rerun. Experimental trials were interleaved across mask type (no mask, grating mask and plaid mask) and blocked across test spatial frequency.

Threshold elevation is expressed in dB, equal to 20 times the log10 ratio of the detection thresholds with and without the mask. This was derived from approximately 1000 trials for each point (500 trials with the mask and 500 trials without the mask).

3. Results and discussion

Results are shown for DJH in Fig. 2. When the test grating has a similar spatial frequency to the mask (1 c/deg),
threshold elevation occurs and is much greater for the plaid mask than for the grating mask. This has been found before when plaid and grating masks had the same spatial frequency as the test (Derrington & Henning, 1989). At higher test spatial frequencies (~5.7 c/deg) masking from both types of mask gives way to a region of facilitation of about 3 dB. The effect is tuned, since it diminishes at higher spatial frequencies.

The same experiment was performed on three other observers but for a more restricted set of test spatial frequencies (Fig. 3). The main effects are replicated by all three observers: at a test spatial frequency of 1 c/deg, the plaid produces considerably more masking than does the grating, but at higher test spatial frequencies (~4 to 8 c/deg) both masks produce small levels of facilitation (~3 dB). Taken with the results from DJH, there is a suggestion that facilitation is stronger for the plaid than for the grating, though the effect is small.

Fig. 4 shows further results for DJH who repeated the experiment using only the plaid mask, but for vertical and horizontal orientations of the test grating measured in different experimental blocks (square symbols). Masking is less for the vertical grating than for the horizontal grating. However, the open circular symbols, replotted from the earlier experimental sessions in Fig. 2, show that this difference is probably due to a decrease in masking with practice for the vertical condition. Zenger and Sagi (1996) and Dorais and Sagi (1997) found similar orientation-specific effects of practice for the cross-orientation masking measured in their experiments. The level of facilitation is the same for both orientations of the test grating and unlike masking, does not change with practice, at least for this observer. However, the main reason for repeating the experiment with horizontal gratings was to test a concern about adjacent pixel nonlinearity. This is a property of CRT raster monitors (Robson, 1999) and can have the effect of reducing the local mean luminance of vertical high spatial frequency gratings. However, the similarity between the results for horizontal and vertical gratings (square symbols) at high spatial frequencies indicates that this is not a factor here.

Next, we investigated whether the facilitation was specific to the 45° orientation difference between the mask and test components used so far. Threshold elevation was measured for a two-octave range of five test spatial frequencies at each of 10 different test orientations (0–45° in 5° steps) as shown in Fig. 5A. The mask was always a 1 c/deg grating with an orientation of −45° and a contrast of 8%. In all cases we found masking at the lower spatial frequencies and facilitation of about 3 dB at the higher spatial frequencies. The spatial frequency at which masking gives way to facilitation (determined by linear interpolation of the masking functions) is shown in Fig. 5B. As the mask and test orientations become more similar, the region of facilitation moves closer to the mask spatial frequency. When the mask and test have the same orientation, facilitation occurs for
spatial frequency differences as small as one octave. This is consistent with previous work that has found facilitation from masks with the same orientation as the test grating and contrasts well above their own detection threshold (e.g. Nachmias & Weber, 1975; Georgeson & Georgeson, 1987; Stromeyer & Klein, 1974; Tolhurst & Barfield, 1978). Thus, our study here extends the results of previous work by showing that facilitation can be found for a wider range of orientation and spatial frequency differences than had previously been thought. Whether the results in Fig. 5 represent a single process that operates over a continuum in Fourier space, or two or more distinct processes that operate in different regions, is not clear.

Finally, we investigated the effect of mask contrast on facilitation for a test spatial frequency of 5.7 c/deg. For component contrasts of 12%, 14%, 16% and 24%, the level of facilitation was the same for grating and plaid masks and was no greater than that seen in the previous experiments (~3 dB). For a component contrast of 8% we confirmed that facilitation was greater for the plaid than for the grating (see Figs. 2 and 3). This suggests a facilitatory process that saturates at an overall mask contrast of around 12%, at least for DJH.

4. General discussion

We have presented evidence for facilitation from 1 c/deg mask components on test gratings around 2.5 octaves higher in spatial frequency and with orientation differences of up to 45°. These effects would have been missed in several previous masking studies because those that have used test spatial frequencies in the range 4–8 c/deg have not typically used masks as low as 1 c/deg (Daugman, 1984; Derrington & Henning, 1989; Harvey & Doan, 1990; Wilson, McFarlane, & Phillips, 1983; though see Bowen & Wilson, 1994).

4.1. A luminance artefact?

Before discussing possible causes of facilitation we first consider a possible artefact. Our sine-phase grating and plaid masks were presented simultaneously with the test stimulus, both for 100 ms. Thus, there were ‘dark’ regions in the image where the local luminance was less than the mean luminance of 65 cd/m² by c%, where c is the overall contrast of the mask. Therefore, the physical contrast of a high frequency test grating in the ‘dark’ regions would approach a contrast that is a factor of 100/(100 – c) higher than its nominal value. If this were the effective contrast of the test grating available to the detection process (Bowen & Wilson, 1994), then when expressed relative to mean luminance (as it was in the experiments) we should expect facilitation of ~0.72 and ~1.5 dB for c = 8%, and c = 16%, respectively. However, these artefacts are notably less than the maximum experimental effects for the grating mask (c = 8%) in Figs. 2, 3 and 5, and the plaid masks (c = 16%) in Fig. 4, where facilitation typically reached ~3 dB. Furthermore, retinal inhomogeneity (Pointer & Hess, 1989) and a dark adaptation process that takes about 150 ms to saturate (Bowen & Wilson, 1994; Crawford, 1947; Kingdom & Whittle, 1996) are both likely to decrease the size of the effects possible through this route. Finally, if this were a substantial contributing factor to the facilitation in our experiments, then facilitation should have increased markedly with mask contrast. It did not: the empirical effects saturated at a contrast of about 12%.

4.2. Three causes of facilitation

As we outlined in Section 1, facilitatory effects have been found in other types of masking experiment, but there is disagreement about their cause. Three candidate processes have been proposed: (i) within-channel excitation from the mask (Legge & Foley, 1980; Solomon et al., 1999; Williams & Hess, 1998; Zener & Sagi, 1996); (ii) reduction of uncertainty by the mask (Petrov et al., 2006; Williams & Hess, 1998) and (iii) sensory interactions between mask and test mechanisms (Chen & Tyler, 2001, 2002; Meese et al., 2007; Polat & Sagi, 1993). The first account requires that the mask and test both fall within the receptive field of a common mechanism with an accelerating output nonlinearity or hard threshold. This seems plausible in the situation where a test patch is placed between two co-oriented flankers (Solomon et al., 1999) or is superimposed and has a similar spatial frequency and orientation to the mask (Zener & Sagi, 1996), but is much less likely when the mask and test differ substantially in spatial frequency and orientation. This ‘within-channel’ hypothesis can be easily tested because in general, the linearizing effects of excitation by the mask should reduce the slope of the psychometric function to a Weibull β ~ 1.3 (Bird, Henning, & Wichmann, 2002; Georgeson & Meese, 2004; Meese, Georgeson, & Baker, 2006; Pelli, 1985, 1987). However, the slope does not become this shallow for superimposed patches of mask and test grating with orthogonal orientations (Baker & Meese, 2006; Georgeson & Meese, 2004; Meese & Holmes, 2007) even though these stimuli can produce facilitation (Baker & Meese, 2006; Foley & Chen, 1997; Meese & Holmes, 2007; Meese et al., 2007). On the other hand, Petrov et al. (2006) found that flanking patches do reduce the slope of the psychometric function for a central test patch. This might be taken to support the within-channel account of facilitation (Solomon & Morgan, 2000), but Petrov et al. also found the same effect for a low contrast ring surrounding the target. Although within-channel effects could occur for this configuration (Petrov et al. used a cosine-phase test stimulus), this seems unlikely, and other possibilities should be considered. The uncertainty hypothesis also predicts that the mask will reduce the slope of the psychometric function (Pelli, 1985; Tyler & Chen, 2000),

1 In this experiment the orientations of the mask and test gratings were the same and the contrast of the mask was 8%. It is well known that when the mask has much lower contrast—around its own detection threshold—facilitation occurs when the mask and test have the same spatial frequency and orientation (e.g. Legge & Foley, 1980).
though not necessarily as low as $\beta \sim 1.3$), and so this result has been taken to support the uncertainty hypothesis for rings and flanker masks (Petrov et al., 2006). However, the situation is not straightforward. Huang et al. (2006) found that facilitation is abolished when the flankers are presented to a different eye from the test, and Meese and Hess (2004) found a similar result for cross-oriented annular masks. Furthermore, Huang et al. decoupled facilitation from a reduction in the slope of the psychometric function: their flankers reduced the psychometric slope regardless of whether they were presented to the same or different eyes from the test.

In its simplest form, the third explanation of facilitation (sensory interactions) proposes that the mask increases the gain of the detecting mechanism, and this does not change the slope of the psychometric function (e.g. Dao, Lu, & Dosher, 2006). At first glance this seems inconsistent with the experimental evidence that the psychometric slope is reduced by facilitation (Huang et al., 2006; Petrov et al., 2006). However, this effect could arise for other reasons. For example, the psychometric function would ‘blur’ if the mask caused it to be nonstationary. This might happen if the mask caused fluctuations in the observer’s attention or if the interaction between the mask and test fluctuated owing to noise.

4.3. The slope of the psychometric function

As outlined above, the slope of the psychometric function can provide valuable supplementary information in experiments on masking and facilitation. The experiments here were performed circa 1998, before we routinely saved those data, but we have performed similar (unpublished) experiments since, in which vertical or horizontal test gratings were detected in the presence of plaid or oblique gratings. Those experiments included conditions in which the test and mask both had component spatial frequencies of 1 c/deg. Those conditions are of interest because we wondered whether the masking at low spatial frequencies (Figs. 2–4) might have involved excitation of the test mechanism by the mask (Phillips & Wilson, 1984; Wilson et al., 1983).

In a ‘transient’ condition, both mask and test were temporally modulated by a single cycle of a 15 Hz square-wave pulse, the mask contrast was 40%, the orientation difference between mask and test was 40°, the observer was DJH and all conditions were blocked. In this case, threshold elevation was 16.6 dB and the psychometric functions had slopes of $\beta = 3.0$ and $\beta = 3.4$ with and without a mask, respectively. These estimates contrast with the much shallower slope of $\beta = 1.5$ when the mask had the same orientation as the test: a result consistent with linearization of the test mechanism by the mask. In another condition the mask was a plaid ($\pm 45^\circ$) with component contrasts of 11% and stimulus duration was 100 ms (similar conditions to those used here). Threshold elevation was 15.5 and 18 dB for DJH.

\footnote{The slope of the psychometric function was estimated using probit analysis, assuming a cumulative log-normal form (approximated by a fifth-order polynomial). The slope of this curve ($\sigma$) is expressed in dB and was estimated independently for each experimental session (typically 100 trials each). Estimates of $\sigma$ were then averaged across multiple sessions (typically 4 or 5) before converting to the more familiar Weibull $\beta$ using the approximation $\beta = 10.3/\sigma$. This approximation was derived by performing a least squares fit of a Weibull function to the cumulative log-normal over a range of $\pm 3\sigma$.}

Fig. 5. Masking and facilitation for a range of orientation differences between mask and test gratings. (A) Each plot shows a masking function for the orientation difference in the inset. Note that the five test spatial frequencies are not the same in each plot. (B) The difference in spatial frequency of mask and test gratings. Note that the results for an orientation difference of 15° are omitted in this panel because of the ambiguity in the masking function (A). This figure represents results from about 45,000 trials.
and TSM, respectively. Correspondingly, the slopes with a mask were $\beta = 3.0$ and $\beta = 3.6$, and without a mask were $\beta = 3.4$ and $\beta = 3.3$. Therefore, despite considerable levels of masking (up to a factor of $\sim 8$) the slope of the psychometric function remained steep when the difference between mask and test orientations was $40^\circ$ or greater.\(^3\) Thus, assuming that nonlinear contrast transduction is at least part of the reason for the steep psychometric function ($\beta \sim 3.5$) at detection threshold (Kontsevich & Tyler, 1999; Legge & Foley, 1980; Legge, Kersten, & Burgess, 1987; Wilson, 1980), this analysis implies that the masking was not due to excitation of a broadband test mechanism by the mask (Phillips & Wilson, 1984), but is consistent with a suppressive influence from the mask on the test mechanism (Foley, 1994; Meese & Hess, 2004). It seems very likely that the same it true of the masking in Figs. 2–4 here.

We have not measured the slope of the psychometric function under conditions similar to those that have produced facilitation in the experiments here. However, we did record the slopes in cross-oriented masking experiments in which similar levels of facilitation ($\sim 3$ dB) have been found (Baker, Meese, & Summers, 2007; Meese & Holmes, 2007; Meese et al., 2007). Our preliminary analysis suggests that this type of facilitation is associated with a modest decrease in the slope of the psychometric function, though there is much variability across observers and conditions. We are presently investigating this issue further.

4.4. What caused the facilitation here?

We address what caused the facilitation seen in the experiments here by first considering the uncertainty hypothesis in the context of the five dimensions of: temporal location, spatial location, orientation, spatial frequency, and spatial phase. Regardless of whether the mask was present, both 2IFC intervals were marked by auditory beeps and so it is unlikely that there was an appreciable reduction of temporal uncertainty by the mask. A central fixation point was presented continuously and the test gratings had a large spatial extent of $4.4$ deg. Thus, observers were well cued to the location of the stimulus on the monitor. Unlike the mask, the fixation point did not indicate the spatial extent of the stimulus, but we think this is unlikely to be important for two reasons. First, ‘no-mask’ and ‘mask’ trials were randomly interleaved on a trial-by-trial basis meaning that observers were repeatedly reminded of the spatial extent of the target (because the mask and target were the same size). Second, the contribution to detection is less towards the grating’s extremities because sensitivity declines with distance from the fixation point at a rate of about $0.5$ deg per cycle (Foley, Varadarajan, Koh, & Farias, 2007; Pointer & Hess, 1989; Robson & Graham, 1981). For example, for the stimulus in Fig. 1C, sensitivity to the outer region of the stimulus is about half that to the centre.

In the main configurations where facilitation was measured, the grating mask provided no cue to test orientation and neither type of mask provided a cue to test spatial frequency. Furthermore, the central fixation point is expected to have reduced phase uncertainty (the target and masks were always in sine-phase) to an extent at least equal to that available from the mask.

In sum, it is very unlikely that the masks reduced either spatio-temporal uncertainty or uncertainty in the Fourier domain for the test gratings that exhibited facilitation here. But this does not rule out the involvement of uncertainty in other contexts (e.g. Tjan & Nandy, 2006). When uncertainty is increased experimentally it raises contrast detection and discrimination thresholds and increases the slope of the psychometric function at and above detection threshold (Meese, Hess, & Williams, 2001; Shani & Sagi, 2005). It remains possible that the facilitation produced by flanks and rings also involves a reduction of uncertainty (Petrov et al., 2006).

The facilitation found here is also inconsistent with sub-threshold stimulation of the test-channel by the mask because the effects occur at orientation and spatial frequency differences that are far too great to stimulate a single mechanism (Foley, 1994; Holmes & Meese, 2004), and psychometric functions are not linearized at these distances (Georgeson & Meese, 2004; Meese & Holmes, 2007). Furthermore, the finding that the spatial frequency at which facilitation occurred increased as the difference between mask and test orientation increased is also inconsistent with that account (Daugman, 1984). (Also see the previous subsection.)

The remaining explanation of facilitation is that of sensory interactions, and this seems the most likely account for the results here. There are at least two ways in which this could occur. First there could be a pool of mechanisms that provides direct modulatory facilitation of the activity in the test mechanism. In that case, it is plausible that the facilitatory pool overlaps with the well-known suppressive pool (Heeger, 1992), but is hidden by suppression (Meese & Holmes, 2007) over much of its range. Second, it could be that the mask suppresses an intermediate mechanism, which causes it to release its standing level of suppression from the target mechanism. Similar proposals have been made for the facilitation (De Valois, 1977; Greenlee & Magnussen, 1988; Tolhurst & Barfield, 1978) and hallucinated contours (Georgeson, 1980) that are experienced at remote spatial frequencies and orientations during and after adaptation.

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