Masking by fast gratings

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Perception of an oriented pattern is impaired in the presence of a superimposed orthogonal mask. This masking effect most likely arises in visual cortex, where neuronal responses are suppressed by masks having a broad range of orientations. Response suppression is commonly ascribed to lateral inhibition between cortical neurons. Recent physiological results, however, have cast doubt on this view: powerful suppression has been observed with masks drifting too rapidly to elicit much of a response in cortex. We show here that the same is true for perceptual masking. From contrast discrimination thresholds, we estimated the cortical response to drifting patterns of various frequencies, and found it greatly reduced above 15-20 Hz. In the same subjects, we measured the strength of masking by the same patterns and found it equally strong for masks drifting slowly (2.7 Hz) as for masks drifting rapidly (27-38 Hz). Fast gratings thus cause strong masking while eliciting weak cortical responses. Our results might be explained by inhibition from cortical neurons that respond to unusually high frequencies, and yet do not make their signals fully available for perceptual judgments. A more parsimonious explanation, however, is that masking does not involve lateral inhibition from cortex. Masking might operate in retina or thalamus, which respond to much higher frequencies than cortex. Masking might also be due to thalamic signals to cortex, perhaps through depression at thalamocortical synapses.

Keywords: orientation, contrast, suppression, gain control, inhibition, thalamus, cortex

Introduction

Contrast discrimination of oriented patterns relies on neurons in visual cortex. The response of these neurons can be estimated from perceptual discrimination thresholds by ascribing these thresholds to fixed increments in neural response. This method originates with the studies of Fechner (1860), and has been recently shown to estimate correctly the overall responses of neurons in the visual cortex during a contrast discrimination task (Boynton, Demb, Glover, & Heeger, 1999). Indeed, responses in visual cortex correlate with perceptual decisions on a trial-by-trial basis (Ress, Heeger, & Nadell, 2001).

Superimposing an orthogonal mask on an oriented test pattern causes both physiological and perceptual effects. Physiologically, the mask suppresses neuronal responses to the test in the visual cortex of anesthetized cats (Morrone, Burr, & Maffei, 1982; Bonds, 1989) and monkeys (Carandini, Heeger, & Movshon, 1997). This suppression can also be seen in EEG signals evoked in awake humans (Burr & Morrone, 1987; Ross & Speed, 1991; Candy, Skoczenski, & Norcia, 2001). Perceptually, the mask impairs the detection of the test, and worsens contrast discrimination for a wide range of test contrasts (Legge & Foley, 1980; Ross, Speed, & Morgan, 1993; Foley, 1994). Perceptual masking can be easily understood in terms of physiological suppression. Suppression shifts the curve relating neural response to contrast rightward, so that higher contrasts are needed to achieve a given response (Bonds, 1989; Heeger, 1992; Carandini et al., 1997). This effect increases the contrast needed for detection, and shifts to higher contrasts the region where the neurons are most sensitive to changes in contrast (Legge & Foley, 1980; Foley, 1994).

How does the mask reduce the effective contrast of the test? The common interpretation is that the cortical neurons involved receive lateral inhibition from other cortical neurons selective for the orthogonal orientation. From the initial proposals (e.g., Blakemore, Carpenter, & Georgeson, 1970) to current computational models (e.g., Heeger, 1992; Foley, 1994; Adini, Sagi, & Tsodyks, 1997; Watson & Solomon, 1997; Itti, Koch, & Braun, 1999), lateral inhibition between cortical neurons has become the dominant theory.

Recent findings on suppression, however, have cast doubts on the lateral inhibition explanation. If suppression originated from cortical neurons, it would share the properties of those neurons. At least in the cat, however, this does not seem to be the case. First, most neurons in cat visual cortex respond to stimuli from both eyes (Hubel & Wiesel, 1962), whereas suppression is largely monocular (DeAngelis, Robson, Ohzawa, & Freeman, 1992). Dichoptic effects have been observed but appear to operate much more slowly (Sengpiel, Baddeley, Freeman, Harrad, & Blakemore, 1998). Second, visual adaptation strongly reduces the responses of cat cortical neurons (Albrecht, Farrar, & Hamilton, 1984), whereas it

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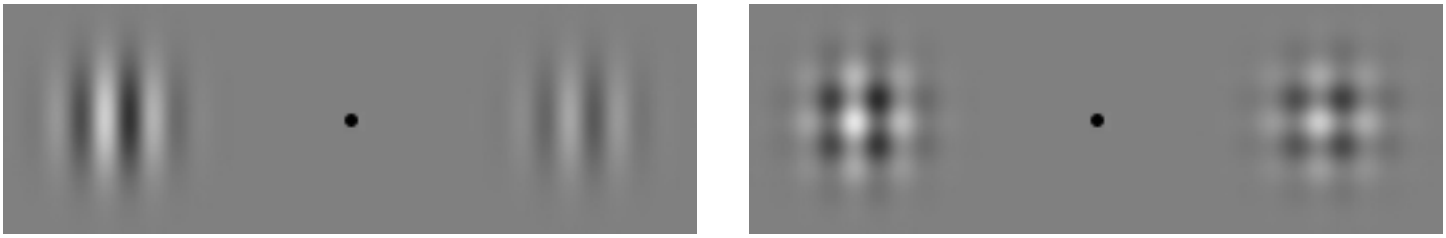

Figure 1. Examples of stimuli in the two experiments. In real experiments, the patches were more distant. Left. A stimulus in the first experiment. Right. A stimulus in the second experiment. In both examples, the increment contrast is on the left side.

does not affect the strength of suppression (Freeman, Durand, Kiper, & Carandini, in press). Third, neurons in cat visual cortex barely respond to stimuli drifting more rapidly than 10-15 Hz (Movshon, Thompson, & Tolhurst, 1978; Saul & Humphrey, 1992), whereas suppression is strong even with mask gratings drifting at rates in excess of 20 Hz (Freeman et al., in press).

Given that lateral inhibition might not explain physiological suppression, we wondered whether it explains perceptual masking. We followed the above argument based on drift rate, and asked whether there are patterns that drift too rapidly to elicit much of a response in cortex but do cause strong masking. From contrast discrimination thresholds, we estimated the cortical response to stimuli drifting at various drift rates. We then examined the masking caused by those same stimuli. We knew that stimuli drifting rapidly would elicit small responses when presented alone. Would they cause masking?

Methods

We measured thresholds for contrast discrimination of a vertical test in the absence and in the presence of a horizontal mask. Test and mask were the product of a drifting sinusoidal grating and a Gaussian window. Subjects performed a 2-alternative spatial forced-choice between stimuli appearing 8 deg to the left and to the right of a fixation mark. Stimuli were observed monocularly from a chin rest placed 80 cm away. The standard deviation of the Gaussian window was 0.5 deg, spatial frequency was 1.5 cycles/deg, and duration was 375 ms.

The first experiment (Figure 1, left) involved simple contrast discrimination of vertical patterns. The subject was presented two test stimuli, one on the left and one on the right, each with the same pedestal contrast (0, 1, 2, 4, 8, 16, or 32%). On one side an increment contrast was added, and the subject reported its location by pressing one of two keys. This measurement was repeated at the following test drift rates: 2.7, 13, 27, 38, and 54 Hz.

The second experiment (Figure 1, right) measured the strength of masking by horizontal masks drifting at various rates. Test stimuli were superimposed to a mask of 30% contrast. This measurement was repeated at the following mask drift rates: 2.7, 13, 27, 38, and 54 Hz. Test drift rate was fixed at the lowest value explored in the previous experiment, 2.7 Hz. As a control, this experiment included the condition in which the mask was absent. The two experiments thus shared the control measurement of contrast discrimination thresholds for a vertical 2.7-Hz test stimulus in the absence of a mask.

Increment contrast was determined by a staircase procedure (QUEST, Watson & Pelli, 1983), which aimed for the contrast yielding 75% correct performance, and was given 30 trials to converge. We then fitted the percentage of correct answers with a Weibull psychometric function using the maximum likelihood method (Watson, 1979), and thus estimated the threshold contrast corresponding to 75% correct.

Experiments took 25-35 min and were each repeated 6-8 times after learning had stabilized. To reduce the effects of involuntary saccades, test stimuli moved in opposite directions, which were randomized from trial to trial. To minimize the effects of adaptation, we also randomized speed, direction, and pedestal contrast. Two subjects participated, one of the authors (L.M.) and a paid naïve observer (S.G.).

Stimuli were generated by the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997) and presented on a calibrated 21" CRT (Sony Multiscan G500, mean luminance 37 cd/m^2) driven by a graphics board with a refresh rate of 159 Hz (MacPicasso 850; VillageTronic, Sarstedt, Germany). Except for the 38- and 54-Hz stimuli, we doubled the resolution of our gray scale from 256 (8 bit) to 512 by interleaving frames. When interleaving, test stimuli with pedestal and increment contrast alternated, whereas the mask was in every frame. With this method, the smallest increment contrast possible was about 0.5%.

Stimuli of 54 Hz were mostly invisible, except for brief flashes. These flashes were most likely artefactual, due to involuntary microsaccades matching the direction of one of the stimuli (Riggs, Armington, & Ratliff, 1954). Microsaccades would improve a subject's chances to guess the right response, leading to an overestimated neural response. While subject L.M. reported sporadic flashes, subject S.G. reported seeing the flashes in all 54-Hz test gratings. We thus did not attempt to measure response to 54-Hz stimuli in this subject, and simply imposed them to be zero.

To estimate the neural response from discrimination thresholds, we followed the methods of Boynton et al. (1999). We took the cumulative response of those neurons that respond to the test to depend on test contrast c as follows:

$$R(c) = K\frac{c^{m+n}}{\sigma^m + c^m}. \quad (1)$$

This function has parameters m, n, σ, and K, and is illustrated in Figure 2B. We made the classical assumption (Fechner, 1860; Legge & Foley, 1980; Boynton et al., 1999; Gorea & Sagi, 2001) that subjects can discriminate between contrasts c and $c+T$ only if these contrasts elicit responses that differ by at least ΔR:

$$R(c+T) - R(c) = \Delta R. \quad (2)$$

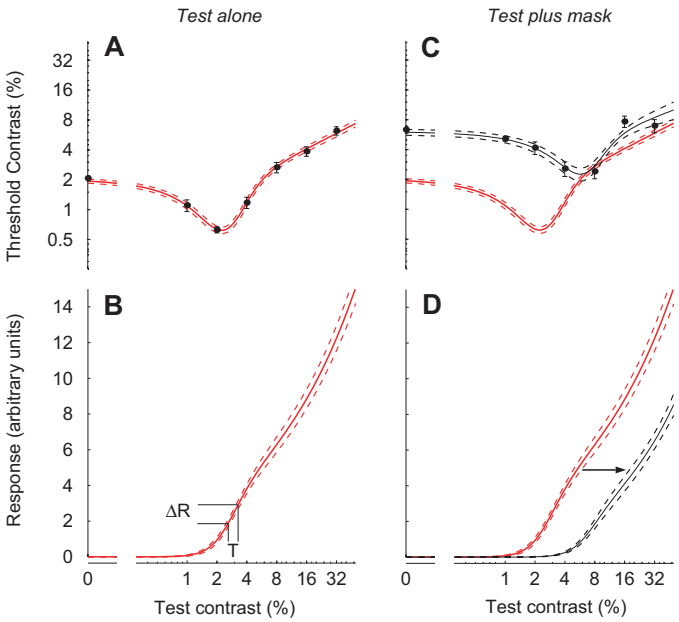

Figure 2. Estimation of neural response and effects of masking. A. Contrast discrimination thresholds for a vertical test pattern. Error bars represent ± 1 standard error (N = 18). Curve is fit of the model; dotted lines indicate one standard error of the fits. B. Neural response estimated from discrimination thresholds. Horizontal and vertical lines illustrate the estimation method: at 2.5% pedestal contrast, the contrast discrimination threshold T that corresponds to $\Delta R = 1$ in neural response is 0.75%. This value is reported on the ordinate of A. C. Effects of masking by a superimposed horizontal mask (N = 6). Red lines are copied from A to facilitate comparison. D. Estimated neural responses. Red lines are copied from B to facilitate comparison. The arrow indicates the effect of masking on the estimated contrast responses. Subject L.M., 2.7-Hz stimuli.

This expression implicitly defines a function $T(c)$, which we fitted to our threshold measurements. The result of one of such fits is illustrated in Figure 2A. We searched for parameters K, σ, m, and n to specify the function $R(c)$, and numerically solved Equation 2 to find the best least square fits of $T(c)$ to the data. Because the units of response are arbitrary, we chose $\Delta R = 1$. To reduce the number of free parameters, we also fixed m to a single value for each subject ($m = 3.55$ for L.M., $m = 3.00$ for S.G., obtained from fits of data with 2.7-Hz test alone). Error bars represent ± 1 standard error (commonly based on 6-8 measurements). Confidence intervals around fitted curves are ± 1 standard error of the fits, which were repeated independently for each set of measurements.

To estimate the strength of masking, we quantify the reduction in effective test contrast caused by the mask. We compute the degree to which the mask shifts the estimated neural responses to the right in the logarithmic contrast axis (Figure 2D). We find the lateral shift s by minimizing the area between $R_{30}(sc)$ and $R_0(c)$, where R_0 and R_{30} are the responses in the absence of a mask and in the presence of a 30% contrast mask. A value of $s = 2$, for example, means that masking has doubled the test contrast needed to obtain a given response. A value of $s = 1$, instead, means that masking had no effect.

Our entire data set is illustrated in supplementary figures. Data and fits of $T(c)$ for measurements of threshold contrast (as in Figure 2A and 2C) are available both for subject L.M. and for subject S.G. The corresponding response versus contrast curves (as in Figure 2B and 2D) are available as well, both for subject L.M. and for subject S.G. The latter figures also illustrate the lateral shift estimated in each masking condition. The extent of this lateral shift is represented by the length of the horizontal bars shown in each panel of the right column.

Results

Our first experiment measured contrast discrimination thresholds for vertical drifting stimuli. As expected, the relation between threshold increment contrast and pedestal contrast (Figure 2A) shows the familiar "dipper" shape, with increment contrast thresholds being lowest when the pedestal contrast is around 2%, the contrast needed for detection (Nachmias & Sansbury, 1974). Also as expected, these data are well fitted by the predictions of a simple model based on a detector with saturating neural response (Legge & Foley, 1980). This neural response (Figure 2B) is estimated from contrast discrimination thresholds by assuming that the subject is at threshold when the neural response increases by a given amount. Increment contrast thresholds are thus lowest where the neural response function is steepest.

Consider now the estimated neural response to test stimuli drifting at different rates (Figure 3A). In line with previous studies (e.g., Robson, 1966; Kelly, 1979; Watson, 1986; Georgeson, 1987), in both subjects the estimated neural response is strong for drift rates of 2.7 Hz and 13 Hz, substantially weaker for drift rates of 27 Hz and 38 Hz, and negligible for a drift rate of 54 Hz.

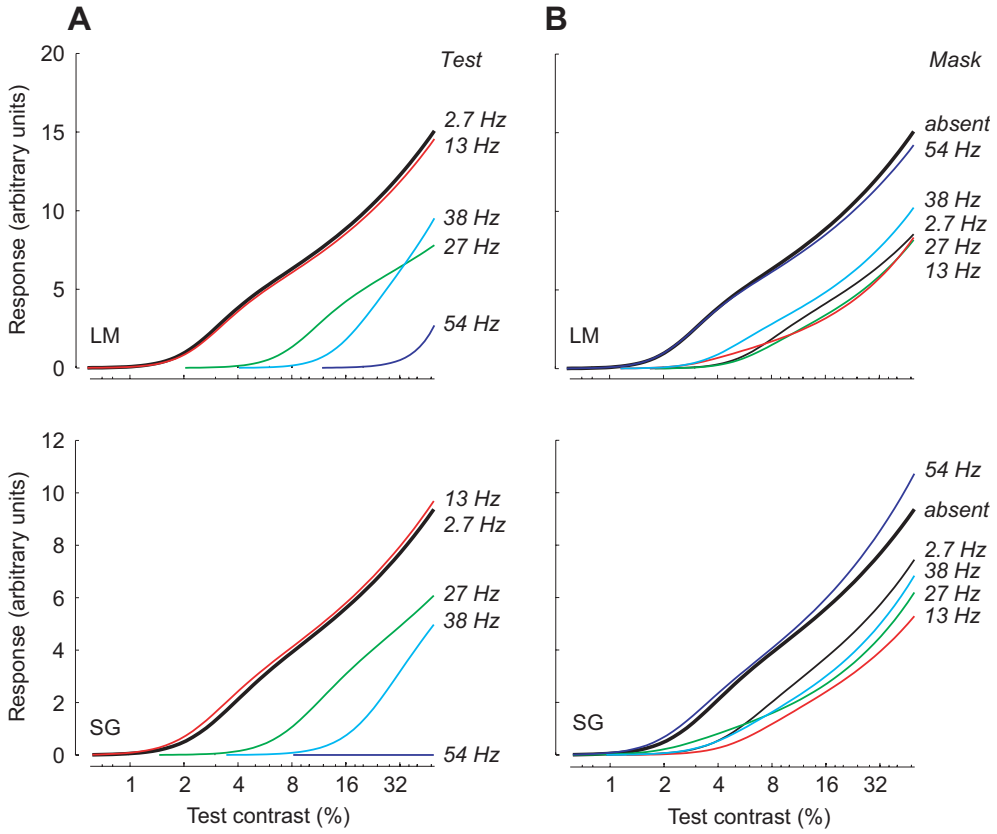

Figure 3. Estimated neural response to test patterns alone and in the presence of an orthogonal mask. A. Responses to test alone, drifting at five different rates. B. Responses to the 2.7 test alone (black) and in the presence of masks drifting at five rates. Top and bottom panels correspond to subjects L.M. and S.G. Confidence intervals are omitted to avoid clutter. An example of their size is in Figure 2.

Our second experiment measured the degree of masking caused by a horizontal mask. Masking had powerful effects (Figure 2C): except for a limited range of pedestal test contrasts, the mask substantially increased the increment test contrast required for discrimination. The mask impaired detection at the lowest test contrasts and impaired discrimination for a broad range of test contrasts (Legge & Foley, 1980; Ross et al., 1993; Foley, 1994).

The effect of the mask on the estimated neural response to the test stimulus (Figure 2D) is largely a rightward shift: the mask increased the test contrast needed to obtain a given neural response. Because the scale in the abscissa is logarithmic, a rightward shift indicates a divisive effect. Just as with physiological suppression, masking divides the effective contrast seen by the neural mechanism (Heeger, 1992; Foley, 1994; Watson & Solomon, 1997).

We now ask our main question: Do masks drifting rapidly cause the same masking as masks drifting slowly? The answer is affirmative for masks drifting as fast as 27-38 Hz. This effect can be seen by comparing the response to the test without a mask with those measured in the presence of masks drifting at different rates (Figure 3B). In both subjects, the response suppression caused by masks drifting at 13 and 27 Hz was strong, similar to that caused by stimuli at 2.7 Hz. Masks drifting at 54 Hz, instead, caused essentially no masking.

This behavior can be quantified by plotting suppression strength as a function of mask drift rate (Figure 4B). We measure suppression strength by the reduction in effective test contrast (see "Methods"). The latter is the degree to which the mask shifts the estimated neural responses to the right in a logarithmic contrast axis (Figure 2D). A value of 2 means that the mask has divided by 2 the test contrast seen by the neural mechanism. Equivalently, it means that the mask has doubled the test contrast needed to obtain a given neural response. Plotting reduction in effective test contrast versus mask drift rate (Figure 4B) confirms the qualitative impression that whether its drift rate is 2.7, 13, 27, or 38 Hz, a drifting mask causes a substantial amount of suppression.

By comparison, we have seen that the neural responses elicited by the mask are reduced above 13 Hz. This dependence can be observed by plotting the estimated neural responses at 30% contrast (the mask contrast) as a function of drift rate (Figure 4A). The slower stimuli (2.7 Hz and 13 Hz) generate an approximately equally strong response, whereas the 27-Hz and 38-Hz stimuli elicit a response that is about half as strong.

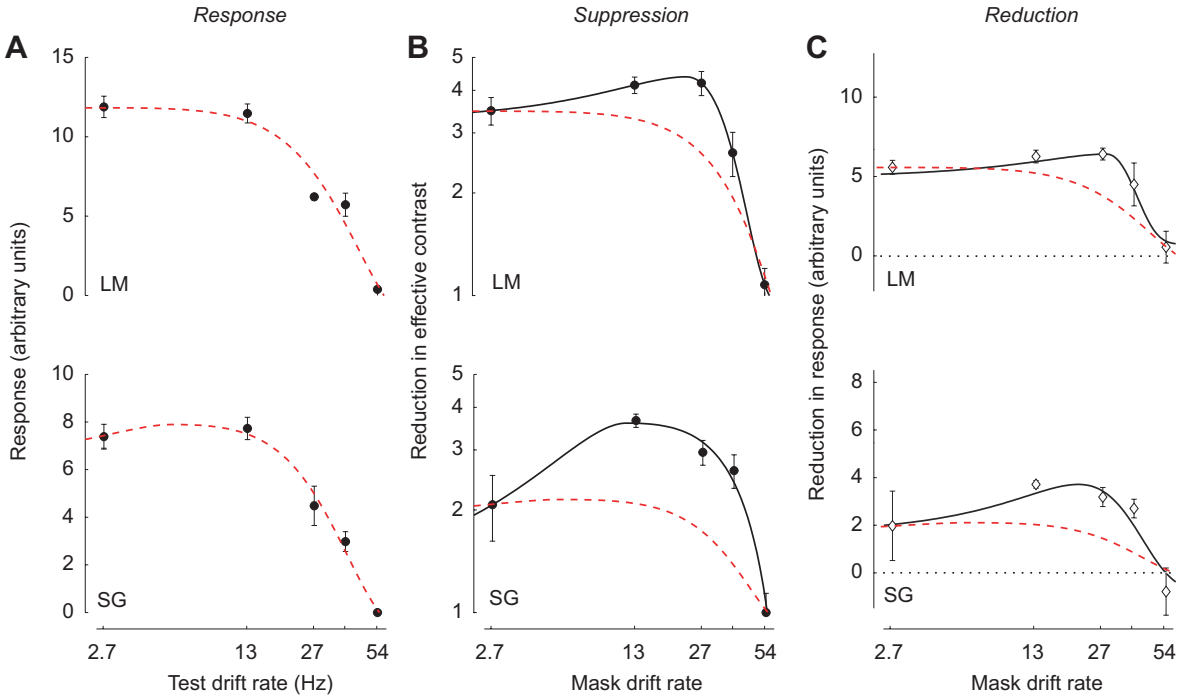

Figure 4. Dependence on stimulus drift rate of estimated neural responses and of suppression strength. Rows are for two subjects, L.M. (top) and S.G. (bottom). A. Estimated neural response to test at 30% contrast, as a function of test drift rate. Data are taken from Figure 3A. Curves are fits by a descriptive function. B. Strength of suppression caused by masks of different drift rates. Suppression is measured as an increase in test contrast needed to obtain a given response (see "Methods"), estimated from Figure 3B. Continuous curves are fits by a descriptive function. Dashed curves are taken from A and rescaled to fit suppression caused by a 2.7-Hz mask. C. Reduction in response to the 2.7-Hz test caused by the mask, as a function of mask drift rate. Data are taken from Figure 3B.

The tuning curves for responses and for suppression are rather different. If one rescales the tuning curve of the responses to account for suppression with the slowest stimuli (Figure 4B, dashed lines), this curve underestimates suppression caused by a 27-Hz mask. If one instead rescales to fit suppression caused by a 27-Hz mask, one overestimates suppression caused by slower masks (not shown). The curve fitted to the responses cannot fit the suppression data because neural responses to a pattern drifting at 27 Hz are half as strong as those elicited by slower patterns (Figure 4A), whereas suppression caused by such a fast pattern is as strong as (or stronger than) that elicited by slower patterns (Figure 4B). Finally, the fitted curves allow a rough estimate of the high frequency cutoff drift rates, where the curves reach half of their maximal value. This cutoff drift rate lies around 32 Hz for the neural response (33 Hz for L.M. and 32 Hz for S.G.), and is higher, around 43 Hz, for suppression (41 Hz for L.M., 46 Hz for S.G.).

A similar conclusion can be drawn if one measures masking by the decrease in estimated neural response to the test. In addition to shifting rightward the curves relating response to test contrast, masking slightly alters the shape of these curves (Figure 3B). Therefore, one might want to measure suppression in additional ways, for example, by measuring the vertical shift rather than the horizontal shift. The results of such a measurement are illustrated in Figure 4C, where we plot the estimated neural response to a 30% contrast, 2.7 Hz test in the presence of a mask, as a function of mask drift rate. Except for the 54 Hz mask, all masks reduced the responses. As for the reduction in effective contrast, the curve relating response and frequency clearly underestimates the reduction in response caused by fast masks.

To summarize, there is a substantial difference between the neural responses elicited by drifting stimuli and the masking caused by these stimuli. Fast gratings cause strong masking while eliciting weak cortical responses.

Discussion

We have found patterns that do not elicit much of a response in cortex but do cause strong masking. We estimated neural responses using a classic method, based on discrimination performance (Fechner, 1860; Boynton et al., 1999; Gorea & Sagi, 2001). We found that 27-38-Hz stimuli elicit substantially smaller neural responses than slower stimuli. In the same subjects, we found that 27-Hz or even 38-Hz stimuli can be as strong in causing masking as slower stimuli.

These results agree well with physiological measurements of suppression in visual cortex. In visual cortex of anesthetized cats, responses vanish at frequencies above 10-15 Hz (Movshon et al., 1978; Saul & Humphrey, 1992), and yet suppression is strong even

with masks drifting at rates in excess of 20 Hz (Freeman et al., in press). Similarly, in EEG signals from human visual cortex, response suppression has been observed with masks having frequencies as high as 30 Hz (Burr & Morrone, 1987).

Our results are also consistent with previous psychophysical studies. Studies of perceptual responses to stimuli of different frequency have established that sensitivity declines rapidly above 10-20 Hz (e.g., Robson, 1966; Kelly, 1979; Watson, 1986; Georgeson, 1987). Studies of masking between stimuli with different temporal characteristics have revealed masking at higher mask frequencies, between 16 and 30 Hz (Anderson & Burr, 1985; Lehky, 1985; Burr, Ross, & Morrone, 1986; Hess & Snowden, 1992; Boynton & Foley, 1999).

Earlier studies of masking differ from ours in a number of ways. First, rather than concentrating on the measurement of thresholds and other psychophysical quantities, we estimate the underlying neural responses. Second, rather than relying on explicit models, we have measured suppression simply by its effect on the estimated neural responses to the test. In particular, we do not assume that test and mask are seen by the same channels (as in Legge & Foley, 1980; Anderson & Burr, 1985; Lehky, 1985; Burr et al., 1986; Hess & Snowden, 1992) or that masking operates through lateral inhibition (as in Foley, 1994; Watson & Solomon, 1997; Boynton & Foley, 1999). Rather, we measure suppression from the shift in contrast responses, as we do in our physiological work (Freeman et al., 2002). Third, we have estimated neural responses to each drifting grating in the presence and in the absence of the mask in the same subjects, so we can compare the two directly.

Still, our study resembles earlier ones, and in particular that of Boynton and Foley (1999). These authors obtained threshold data such as those in Figure 2C for different combinations of test and mask frequency. They fitted these data with a model involving an excitatory mechanism and a divisive inhibitory mechanism (Foley, 1994). The frequency tuning of the inhibitory mechanism was found to be much broader than that of the excitatory mechanism, and to extend beyond 20 Hz. This result is in agreement with our findings, which were obtained using slightly different stimuli. Indeed, in our study (1) test and mask were orthogonal; (2) stimuli were drifting; and (3) except for orientation and (in general) frequency, mask and test had same visual attributes. Our analysis differs from that of the earlier study as well: (1) for each subject we estimated neural responses to the mask alone, to the test alone, and to the test plus mask; (2) we observed the effects of masking directly on the estimated neural responses; and (3) we compared the frequency tuning of masking to that observed for the observer as a whole.

One limitation of our study is the use of a single test drift rate (2.7 Hz). There might be something arbitrary about comparing the visual system's sensitivity to gratings of various frequencies to how various frequencies affect the response to a single frequency. We chose the low value of 2.7 Hz to be conservative, as one might suspect that the responses to faster tests might be reduced by even faster masks than those we found. Indeed, there are indications that if we had repeated our measurements with a test of different drift rate, we still would have found masking by fast gratings. Burr and colleagues (1986) measured the elevation in detection threshold caused by masks of various frequencies; The cut-offs at high frequency appear similar (20-30 Hz) whether the test drifted at 0.3 Hz or at 8 Hz (their Figure 4, c, and d). Likewise, Boynton and Foley (1999) reported similar frequency tuning of their divisive inhibition whether tests flickered at 1 Hz or at 10 Hz (their Figure 9). While these studies employed masks that were parallel to the test, there is little reason to believe that changes in estimated neural response to the test would depend on mask orientation.

One possible interpretation of our results is that suppression originates from lateral inhibition in cortex, and is preferentially caused by neurons selective for high drift rates. The pool of inhibitory neurons would respond well to high frequencies, while for some reason not being as available for contrast perception as neurons responding to lower frequencies. This interpretation, however, does not explain our physiological observations in cat visual cortex (Freeman et al., in press); Here, no neurons have their preferred frequency above 20 Hz, and only a tiny minority of neurons respond at all to gratings drifting so rapidly. Yet, gratings drifting faster than 20 Hz are powerful masks, and often cause the same amount of suppression as masks drifting 10 times slower.

A simpler explanation is that masking is not due to lateral signals from the cortex, but rather to feedforward signals from the lateral geniculate nucleus (LGN). Indeed, both in cat (e.g., Saul & Humphrey, 1990; 1992; Freeman et al., in press) and in monkey (Hawken, Shapley, & Grosof, 1996), LGN responds to stimuli drifting too rapidly to elicit responses in cortex. Moreover, there is a strong similarity between the tuning for frequency of LGN responses and of the strength of suppression (Freeman et al., in press).

But how could a suppressive signal from LGN reach cortex? After all, direct thalamocortical inhibition is not believed to exist. One possibility is that suppression operates already at the level of LGN neurons, or even in the retina. Indeed, responses of LGN neurons are not at all immune to suppression (Freeman et al., in press). Suppression might then be simply inherited by cortex from its afferents. Another possibility is that signals responsible for suppression are relayed from LGN to cortex, for example, by the well known mechanism of synaptic depression (Carandini, Heeger, & Senn, 2002; Freeman et al., in press). To see how, consider the simplified case of a V1 cell that receives all its inputs from LGN afferents, and endow these inputs with synaptic

depression. The V1 cell responds to an optimal grating but not to an orthogonal grating. The individual LGN neurons, however, are not selective for orientation, so depression at their synapses is insensitive to stimulus orientation. Both gratings, then, cause an equally strong synaptic depression. Depression is even stronger in response to the plaid obtained by summing the two gratings, so the resulting responses in the V1 neuron are smaller than those to the test alone.

A feedforward model of suppression makes a number of predictions, which we are setting out to test. First, masking due to thalamic signals would be reduced when the mask surrounds the test, without overlapping it. The masking phenomena that do occur in these circumstances (Polat & Sagi, 1993; Kapadia, Ito, Gilbert, & Westheimer, 1995; Zenger & Sagi, 1996; Adini et al., 1997; Zenger, Braun, & Koch, 2000) could be due to intracortical inhibition, and should be reduced when mask drift rate becomes too high for cortex. Second, masking due to thalamic signals should be immune to pattern adaptation. This prediction was found correct for physiological suppression in anesthetized cats (Freeman et al., in press), and there is evidence that it might be correct also for perceptual suppression (Foley & Chen, 1997). Third, masking due to thalamic signals would be monocular. Masking phenomena that occur dichoptically (with the test in one eye and the mask in the other) would have to be due to intracortical mechanisms. Indeed, dichoptic masking might fall into the category of binocular rivalry, whose effects take quite a long time to develop (Blake, 2001).

Conclusions

We have found that fast drifting patterns do not elicit much of a response in the cortex but do cause strong masking. A similar result was found recently when measuring suppression in the responses of neurons in primary visual cortex. One possible interpretation of our results is that masking originates from lateral inhibition. The inhibitory neurons involved in it would have to be responsive to very high drift rates, and yet their response would be somewhat unavailable for contrast perception. An alternative explanation, more parsimonious, is that masking is retinal or thalamic. In alternative or in addition, it might be due to feedforward signals from the thalamus, perhaps through depression at the very first synapse into the cortex.

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