Effects of contrast and size on orientation discrimination

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Abstract

Motivated by the recent physiological finding that a neuron's receptive field can increase in size by a factor of 2–4-fold at low contrast [Nat. Neurosci. 2 (1999) 733, Proc. Natl. Acad. Sci. USA 96 (1999) 12073], we sought to examine whether a psychophysical task might reflect the contrast dependent changes in the size/structure of a receptive field. We postulate that since spatial summation is not contrast invariant, a task that relies on the spatial structure of a receptive field, such as orientation discrimination, should also be affected by changes in contrast. Previously, orientation discrimination thresholds have been reported to be roughly independent of the contrast of a stimulus for most of the visible range of contrasts [i.e. J. Neurophysiol. 57 (1987) 773, J. Opt. Soc. Am. 6 (1989) 713, Vis. Res. 30 (1990) 449, Vis. Res. 39 (1999) 1631]. Here, we found large improvements in orientation discrimination with contrast that were dependent on stimulus area. Furthermore, the apparent constancy of orientation discrimination for large area stimuli is possibly a result of a floor effect on the threshold. Therefore we conclude that there is not strong evidence for contrast invariant orientation discrimination. We interpret these results in the context of recent neurophysiological results about the expansion of cortical cells' receptive fields at low contrast.
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1. Introduction

Recent neurophysiological experiments on neurons in primary visual cortex (V1) suggest that the classical notion of a fixed size receptive field is inadequate (Kapadia, Westheimer, & Gilbert, 1999; Sceniak, Ringach, Hawken, & Shapley, 1999). The main result of these experiments is that the area of a neuron's receptive field, measured with an optimal stimulus at a low contrast, can be from two to fourfold larger than when measured with the same stimulus at a high contrast. An interpretation of this finding is that at low contrast there is a physiological reorganization of the mechanisms subserving the processing of spatial vision. Specifically, there is an increased area of summation over which a neuron pools information when tested with low contrast stimuli. When the cell is tested with a high contrast stimulus, the area of summation is reduced, presumably causing an increase of the cell's spatial resolution. More recently, Sceniak, Hawken, and Shapley (2002) have

examined neurons' spatial frequency tuning and band width at high and low contrast and have reported changes in neurons' spatial frequency tuning curves consistent with changes in the receptive field size. The conclusion from the above studies is that receptive fields undergo a spatial re-organization when probed with stimuli going from high to low contrasts. This physiological result, that receptive fields can vary in size depending on the stimulus properties, suggests that the notion of fixed visual receptive fields needs revision.

Spatial integration has been examined previously in psychophysics (i.e. Graham & Robson, 1987; Jamar & Koenderink, 1983; Legge & Foley, 1980, 1981). However, these experiments were largely explored with the underlying concept of a fixed size, hard wired receptive field (i.e. Hubel & Wiesel, 1962). Given that the experiments of Sceniak et al. (1999) and Kapadia et al. (1999) have demonstrated that receptive fields in V1 cortex are modified with stimulus contrast, we hypothesized that psychophysical tasks which probe basic, low level visual function might display similar contrast dependent changes. There have been more recent reports that contrast can affect observers' judgments on many psychophysical tasks, such as the perceived velocity of a stimulus (i.e. Hawken, Gegenfurtner, & Tang, 1994;

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Stone & Thompson, 1992), its perceived spatial frequency (Gouled Smith & Thomas, 1989; Thomas & Olzak, 1997), the perceived contrast of an embedded stimulus (Polat & Sagi, 1993; Snowden & Hammett, 1998; Solomon & Morgan, 2000; Yu & Levi, 1998) as well as other contextual effects (Mareschal, Henrie, & Shapley, 2002). In this study we sought to examine orientation discrimination as a function of the contrast and size of the test stimulus. We hypothesized that under high contrast conditions, orientation thresholds might not be as influenced by the size of the stimulus (no increased area of pooling) as they would be under low contrast conditions.

Previous experiments have measured orientation discrimination as a function of contrast, but these were carried out at a fixed stimulus size (Bowne, 1990; Reisbeck & Gegenfurtner, 1998; Skottun, Bradley, Sclar, Ohzawa, & Freeman, 1987; Webster, De Valois, & Switkes, 1990; Westheimer, Brincat, & Werhahn, 1999). The general finding was that in the experiments where the stimuli were small, increasing the contrast lowered the orientation thresholds (e.g. Regan & Beverley, 1985; Reisbeck & Gegenfurtner, 1998; McIlhagga & Mullen, 1996), whereas in experiments using larger sized stimuli, orientation discrimination thresholds were fairly contrast invariant (e.g. Bowne, 1990; Skottun et al., 1987). In addition, some experiments have also examined the effect of size on orientation thresholds, although these were always carried out at a fixed contrast (i.e. Heeley & Buchanon-Smith, 1990; Henrie & Shapley, 2001; Orban, Vandenbussche, & Vogels, 1984; Westheimer et al., 1999). However, none of these experiments systematically varied both contrast and size in order to examine their joint influence on orientation thresholds. We sought to examine the role that contrast and size might exert on orientation discrimination thresholds to test the prevailing notion of contrast invariance in orientation discrimination and its theoretical consequences. We consider our results in the context of the above physiological framework of a variable sized receptive field. However, we also consider the changes in signal strength induced by both a reduction in stimulus size and contrast and investigate what effects, if any, these may have on our results.

2. Methods

2.1. Apparatus and stimuli

The stimuli were produced on-line using a Macintosh G3 and displayed in the center of a Sony Trinitron monitor. The monitor was viewed binocularly at varying distances (from 57 to 228 cm), had a mean luminance of 36 cd/m^2, had a video attenuator connected and was calibrated using a UDT photometer. The screen size was 36 cm × 27 cm, the resolution was 1024 × 768 pixels and it was refreshed at 85 Hz. Stimulus generation, presentation, and observers' responses were all computer controlled and stored on-line. Experiments were run from within Matlab, using both Psychtoolbox (Brainard, 1997) and Videotoolbox (Pelli, 1997) routines.

The stimulus consisted of a circular patch of grating varying in size from 0.12° in diameter to 2° in diameter. In order to ensure that at least one cycle of the stimulus was present within the circular aperture, observers varied their viewing distance for the smaller sizes. This resulted in the spatial frequency changing with the viewing distance from 3 c/deg at vd = 57 cm to 12 c/deg at vd = 228 cm. The phase of the gratings was randomized except for the smallest size condition (0.12°) where we ensured that the zero crossing was located in the center of the aperture. Controls were performed to verify that the changes in spatial frequency and band width produced by the changes in viewing distance or size were not large enough to bias the orientation discrimination thresholds. Several studies have examined orientation discrimination thresholds as a function of spatial frequency, and report spatial frequency dependency for the extremes tested (i.e. very high and very low spatial frequencies). Over the mid-range of spatial frequencies used here though, their data display relative invariance with spatial frequency (i.e. Burr & Wijesundra, 1991; Heeley & Buchanon-Smith, 1990; Phillips & Wilson, 1984).

2.2. Procedure

In each experiment, a two-alternative forced choice stimulus procedure was employed. Observers were presented sequentially with two stationary stimuli and were required to judge whether the orientation of the second stimulus was shifted clockwise or counterclockwise relative to the orientation of the first stimulus. The sequence was as follows: a fixation point was presented (100 ms) followed by the first stimulus presentation (250 ms). A brief period (ranging from 500 to 750 ms) where the screen returned to mean luminance ensued prior to the presentation of the second stimulus (250 ms). The observers' task was to indicate by a keypress whether the stimulus shift between the two presentations had been clockwise or counterclockwise. Auditory negative feedback was provided on observers' errors. The orientation shifts that were tested varied between the different observers and were randomly chosen from a pre-determined set of test values. Thresholds were determined using a method of constant stimuli to sample the psychometric function.

Observers initially familiarized themselves with the tasks prior to threshold collection by practicing until the thresholds collected reached a constant plateau. One of the authors and three observers naive to the purpose of

the study served as subjects for these experiments. All observers had normal or corrected to normal vision.

Observers' data on a given condition were pooled across the runs for a given stimulus configuration of size and contrast, and a bootstrapping procedure was used to fit a cumulative Gaussian function to the results (Foster & Bischof, 1991). This procedure yielded the 75% correct point by interpolation as the measure of orientation discrimination thresholds. Error bars on the plots represent the standard deviations of the thresholds at the 75% criterion levels and were derived from the bootstrapping procedure.

3. Results

3.1. Fovea

Orientation discrimination thresholds were measured as a function of contrast for the different sized stimuli in three observers. Stimuli in this experiment were presented at the fixation point. The data for observers IM and AS are plotted in the top panels (left and right, respectively), and SS in the bottom left panel. The averaged data from the three observers are plotted in the bottom right panel. As is clearly captured in the averaged data, all observers display a similar trend of results, mainly that orientation discrimination thresholds are not contrast invariant for the smaller sized stimuli.

For all observers, the threshold curves for the small sized stimuli are not flat. Rather threshold increases as contrast is decreased for stimuli roughly smaller than 0.5°–0.8° in diameter. The data in these plots seem to reveal two types of contrast dependent mechanisms: one which is contrast invariant for large stimuli, and one which is non-contrast invariant using small sized stimuli. This result could reconcile previous experiments on orientation discrimination where some authors report invariance with large sized stimuli only (i.e. Bowne, 1990; Skottun et al., 1987), whereas others report lack of invariance but with, typically, smaller stimuli (McIlhagga & Mullen, 1996; Reisbeck & Gegenfurtner, 1998; Westheimer et al., 1999). These graphs highlight that the behavior of the mechanism underlying performance on this task is dependent on both the size and the contrast of a stimulus. The dependence that is observed could be explained by the following hypothesis. Suppose that the area of spatial summation of neurons doing the task increased with reduced contrast. If this were the case, increasing the size of the stimulus would make it matched to the increased area of summation, possibly enabling a more accurate/better response with larger areas at lower contrast.

The data in Fig. 1 clearly reveal a co-dependency between size and contrast in determining orientation thresholds. In order to highlight this relationship, ori-

entation thresholds have been replotted in Fig. 2 as a function of both the size and the contrast of the stimuli. Examination of the three plots in Fig. 2 illustrates the co-dependency of size and contrast in determining orientation discrimination thresholds. The three dimensional plots are not flat, but rather display a strong peak in orientation thresholds for small sized, low contrast stimuli.

Figs. 1 and 2 both reveal that orientation thresholds are dependent on the contrast of a stimulus for sizes smaller than 0.5°–1° in diameter. At these sizes or smaller, orientation thresholds increase as contrast is reduced, and the area of pooling appears to shift as indicated by the tuning curves becoming steeper. It would be useful to obtain a measure of the breadth of spatial summation of these curves for the different contrasts used. Examination of either Figs. 1 or 2 reveals that the shapes of the curves vary with the different contrasts. In particular, if one were to examine the size of stimulus at which the orientation tuning for a given contrast had reached half of its maximum value (likened to a measure of the spatial summation), this measure would decrease as contrast increased. In order to estimate this area precisely, the midway point (corresponding to (maximum threshold – minimum threshold)/2) of the different contrast curves was interpolated for observers IM and AS.

The data in Fig. 3 are reproduced from Fig. 1, but with size as the abscissa. The data from observer SS have not been included because, for this observer, we were unable to obtain orientation thresholds at the two smallest sizes and the data for the high contrast curves were too shallow to obtain a meaningful measure of spatial summation. For this reason we fit and interpolated the halfway point for only the low contrast curves. We wish to point out that this analysis makes no assumptions about the data beyond that which is presented in the graphs. That is to say that how the curves will diverge beyond the smallest size measured is not addressed, although it is reasonable to assume that they will increase exponentially. Also, it is clear by visual inspection of the graphs that the slopes of the different contrast curves are different. Particularly, the slopes of the 4% and 6% curves are steeper than those of the higher contrasts.

Table 1 reports the halfway threshold values as a function of contrast for two observers. These values decrease as contrast is increased, particularly between 4% and 6%. We interpret this as a reduction in the area of spatial summation with increasing contrast.

3.1.1. Detectability as a function of stimulus size

A clear concern here is how the detectability of the stimuli may affect our results, so in our experiments we measured detection thresholds for the stimuli. This was done using a two alternative forced choice paradigm
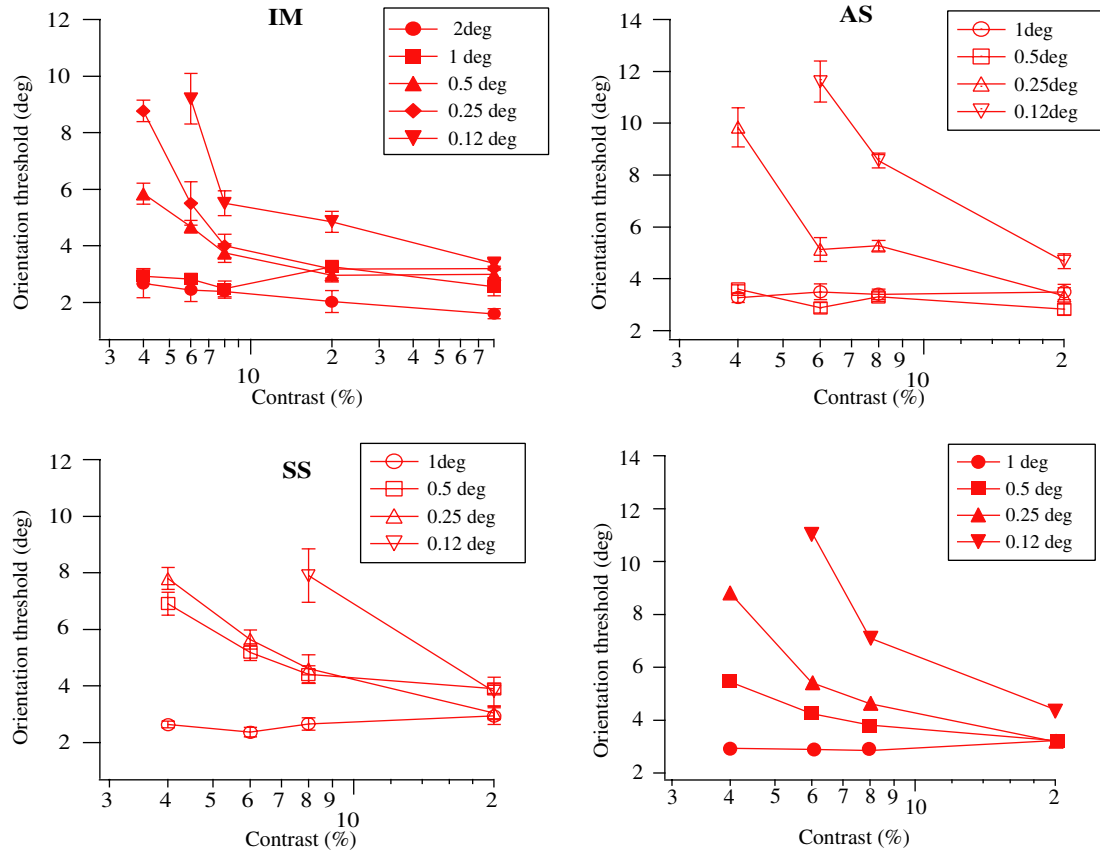
Fig. 1. Orientation discrimination thresholds for observer IM (top left), AS (top right), SS (bottom left) and the averaged data for the three observers (bottom right) at different sizes as a function of the contrast of the stimulus. Spatial frequency = 3 cpd for stimuli sizes of 2°, 1° and 0.5°; spatial frequency = 6 cpd for stimulus size of 0.25°; and spatial frequency = 12 cpd for stimulus size of 0.12°.

where observers had to indicate by a keypress whether the stimulus had been presented in the first interval or the second one. Contrast levels were tested using the method of constant stimuli to sample the psychometric function. The results are reported in Table 2 for subjects IM and AS. There was a close correspondence between these two observers for detection thresholds. For the smallest size tested in the discrimination experiments reported above, the stimulus was 2.4X its detection threshold for IM and 2.8X for AS (note that for this size the lowest contrast used in the experiment was 6%). However, in order to ascertain that detectability was not confounding our data, we measured orientation thresholds for IM on the largest stimulus at 2.4X its detection threshold (corresponding to 0.96% contrast). The orientation threshold measured for this stimulus was 2.43° ± 0.2°. This is not significantly different from the threshold measured at the higher contrasts for this stimulus. This control experiment supports the contention that being a few multiples above detection thresholds for our stimuli was not the limiting factor in orientation thresholds measured in this task, and that probability summation was not solely driving our results. Indeed, for the large sized stimulus we observe

contrast invariance at the same multiple of detection threshold as was used for the smaller sized stimulus, and find no difference in orientation thresholds across the contrast levels tested. This is in agreement with other spatial vision tasks measured as a function of detectability (e.g. Burbeck, 1987).

3.1.2. Control for changes in spatial frequency and band width

In order to examine the effect of stimulus size on orientation discrimination, we had to either change the actual size of the stimulus (which would result in a change in the number of cycles present in the stimulus), or change the viewing distance (which would result in a change in the stimulus' spatial frequency). In our experiment, we decided to keep the number of cycles constant and vary the viewing distance. However, we tested for the effect of spatial frequency differences resulting from the changes in viewing distance on our results. In the data plotted out in Fig. 1, the thresholds measured for a stimulus size of 0.5° and larger were measured with a grating of 3 c/deg. Thresholds for a size of 0.25° were measured with a grating of 6 c/deg, and for a size of 0.12° were with a grating at 12 c/deg. Because
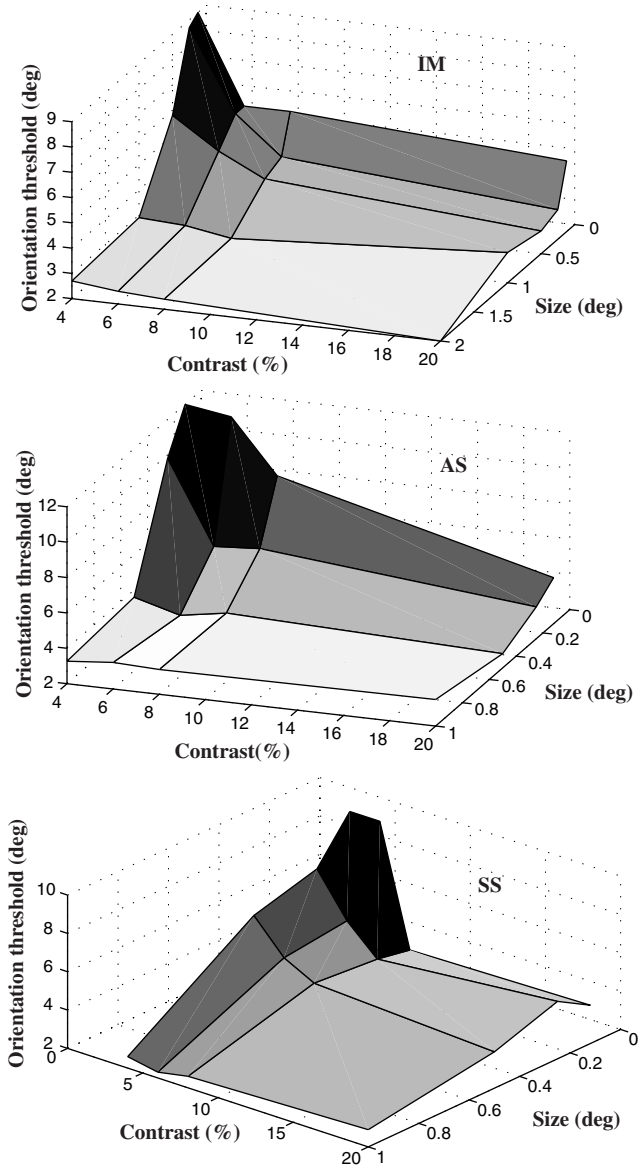
Fig. 2. Co-dependency of size and contrast in influencing orientation thresholds. Orientation discrimination thresholds are plotted as a function of the contrast (front axis) and size (right-hand axis) of the stimuli for the three observers.

there might be some question about the effect of spatial frequency on results measured under these stimulus conditions, we re-measured orientation discrimination thresholds for a size of 0.25° at both 3 c/deg and 12 c/deg. It is impossible to measure thresholds at the smallest size with a grating of 3 c/deg because there would not be a full grating cycle in the stimulus. For this reason, we measured orientation thresholds at different spatial frequencies for the smallest size possible. In addition, we measured thresholds at 4% contrast for the 3 and 6 c/deg gratings (but not 12 c/deg because that condition was not tested in the experiment plotted in Fig. 1) and these were not significantly different (results not on the graph).

Examination of Fig. 4 reveals that orientation discrimination thresholds were not dependent on the spatial frequencies that we used here. There is slightly more variation at 6% than at 20%, but the data are within the standard deviation limits. Also note that thresholds were measured at 6% because for the smallest size stimulus (with a grating of 12 c/deg) this was the lowest contrast tested. This control confirmed previous studies (i.e. Burr & Wijesundra, 1991; Heeley & Buchanon-Smith, 1990; Phillips & Wilson, 1984) that reported that over the range of spatial frequencies used here, orientation discrimination thresholds are constant.

Given that in our main experiment, we varied the viewing distance without changing the spatial frequency of the grating, this resulted in a change in the spatial frequency being tested, but not a change in the number of cycles being presented, except for at the two largest sizes (1° and 2°). Only observer IM measured orientation thresholds using a 2° stimulus and obtained similar values to those measured using a 1° stimulus even though there were twice as many cycles of grating in the 2° stimulus.

3.2. Periphery

A possible concern with collecting thresholds in the fovea is that performance may be plateauing due to potential floor effects. We therefore carried out similar experiments in the near periphery in order to compare the rate of change in orientation discrimination as a function of contrast in the periphery with that measured in the fovea. This would highlight any differences in contrast dependent spatial summation between the brain representations of these two regions of the visual field. In addition, we also sought to operate at a retinal eccentricity at which a potential floor effect would not occur ("floor effect" means the measured performance of a mechanism plateaus before its maximum sensitivity has been reached). For these reasons, we carried out the same task as in the above experiment, but with the stimuli presented 5° laterally from the central fixation point.

Fig. 5 plots the peripheral data measured for subject IM (top left), SS (top right), AJS (bottom left) and the averaged data (bottom right). The data are presented in the same format as in Fig. 1. The absolute orientation thresholds are higher in the periphery than in the fovea. However, as with the foveal data, orientation discrimination thresholds are not contrast invariant. There is an interaction between contrast and size in determining orientation thresholds, with thresholds increasing as contrast is decreased for stimuli smaller than 2°. This finding is also consistent with a recent report by Sally and Gurnsey using lines of different lengths in the fovea and periphery (Sally & Gurnsey, 2003).
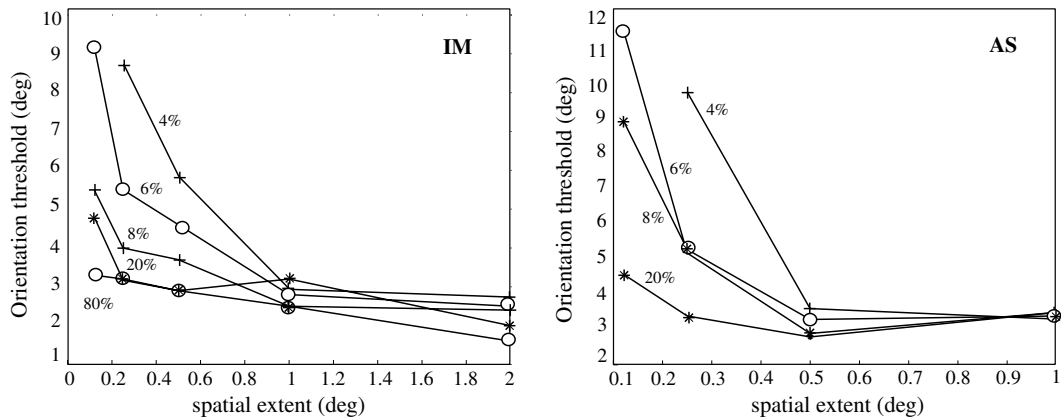
Fig. 3. Orientation discrimination thresholds plotted as a function of size for two observers. Spatial frequency was 3 cpd for sizes of 0.5° and larger, 6 cpd for a size of 0.25° and 12 cpd for a size of 0.12°.

Table 1
Midway threshold values interpolated from the different contrast curves in Fig. 3

	4% contrast	6% contrast	8% contrast
IM	0.7°	0.56°	0.59°
AS	0.5°	0.33°	0.38°

3.3. Contrast invariance or floor effect?

A question which might be raised from our data is whether the invariance in the orientation thresholds measured for large sized stimuli reflects contrast invariance, per se, or is the result of a floor effect. That is to say, does the measured threshold reflect the actual size dependence or contrast dependence of the mechanisms (filters) involved, or is some internal noise limiting performance at high contrast and large size when neural responses achieve a very high signal:noise ratio? In a secondary experiment, we sought to address this by measuring orientation thresholds for large sized stimuli as a function of contrast for stimuli that were spatially jittered. The stimulus could appear in a random spatial location from the central fixation point within a radius of 5° and was presented twice within the same spot (for the two-flash orientation judgment to be made). This procedure was performed on a large sized stimulus for which orientation thresholds were found to be invariant with contrast when there was no uncertainty. The rationale was that by adding spatial uncertainty, we would
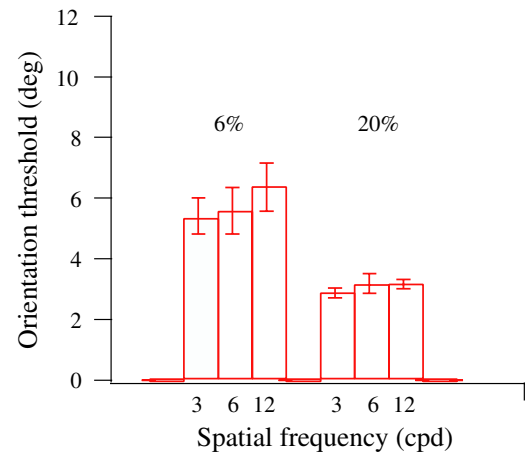

Fig. 4. Orientation discrimination thresholds for observer IM at three different spatial frequencies for a 0.25° diameter stimulus.

raise the absolute orientation thresholds, akin to adding noise. We hypothesized that by doing this while increasing stimulus contrast, two possible outcomes could arise: either orientation thresholds would remain constant (supporting the notion of contrast invariance in the sensory signals) or thresholds would decline with increasing contrast (suggesting that internal, stimulus independent noise might have been limiting performance in the case where the stimuli did not have spatial uncertainty added).

The results of this experiment are plotted out in Fig. 6 for two observers using a large 1° diameter stimulus

Table 2
Contrast detection thresholds for two subjects as a function of the size of the stimulus

	Fovea					Periphery		
	2°	1°	0.5°	0.25°	0.12°	2°	1°	0.5°
IM	0.4%	0.68%	1.01%	0.94%	2.5%	0.72%	1.13%	2.5%
AS	0.45%	0.55%	0.97%	1.2%	2.12%	0.8%	1.2%	2.3%

The first five columns are thresholds measured for stimuli presented in the fovea. The last three columns for stimuli presented 5° peripheral.
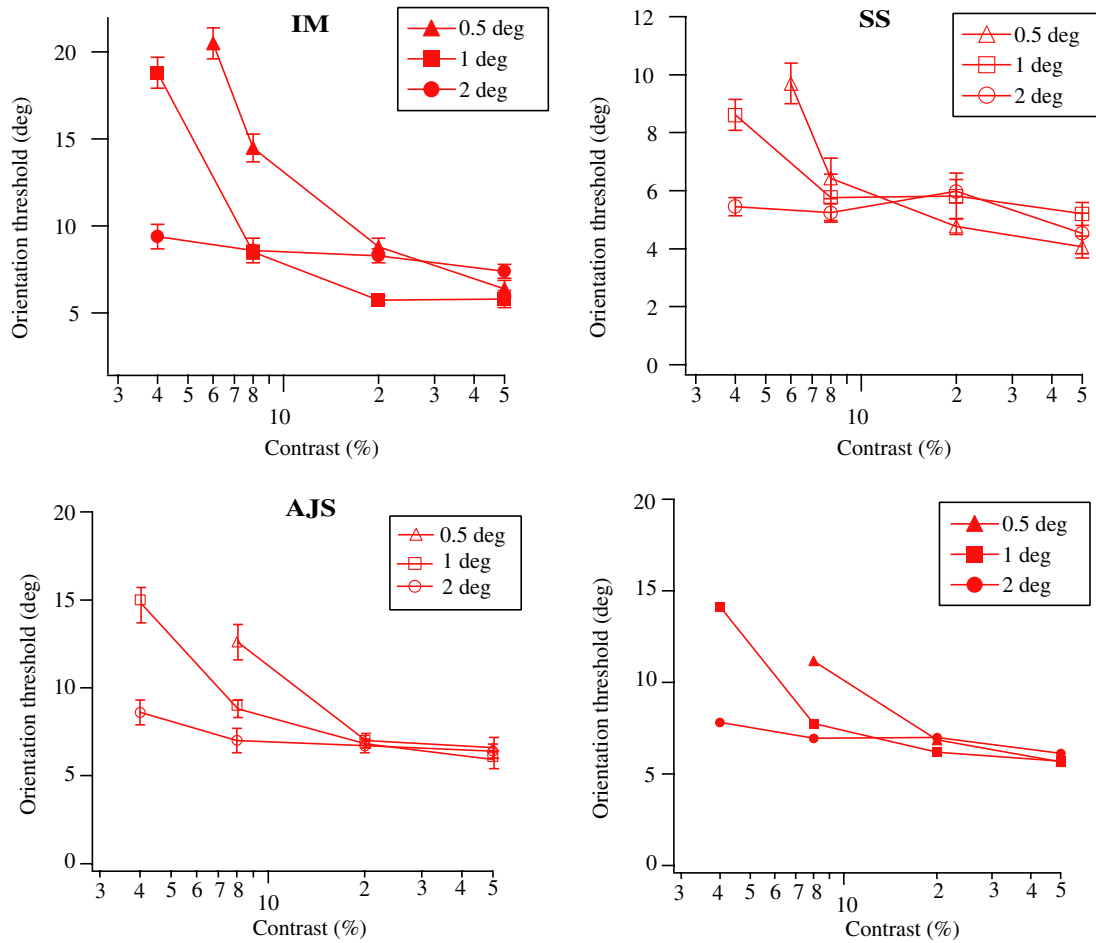
Fig. 5. Orientation discrimination thresholds for observer IM (top left), SS (top right), AJS (bottom left) and the averaged data (right) at different sizes as a function of the contrast of the stimulus, measured in the periphery. Spatial frequency = 3 cpd.
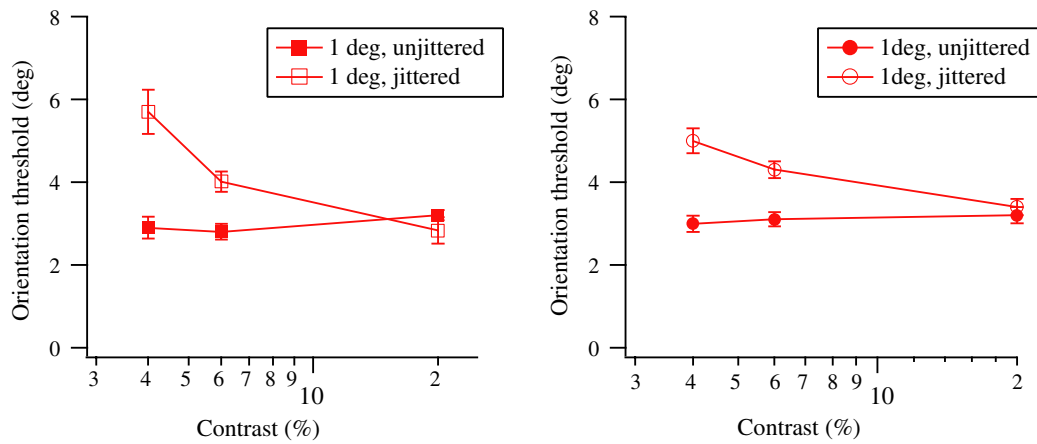

Fig. 6. Effect of spatial uncertainty on orientation discrimination thresholds. Thresholds for observers IM (left) and CL (right) as a function of contrast using a 1° diameter stimulus presented at fixation (filled symbols), or randomly jittered within a 5° radius of fixation (open symbols). Spatial frequency = 3 cpd.

whose contrast was varied. As is apparent from the graph, spatial uncertainty led to an increase in thresholds at low contrast but not at high, suggesting that the invariance that we show in Fig. 1 and that has been

reported by many others (see Section 4) is probably the result of a floor effect. An obvious concern in this experiment is the detectability of the stimulus. Table 2 reports detection thresholds for a 1° diameter stimulus

measured at 5° eccentricity. However, although the stimuli here were not presented that far peripherally, spatial uncertainty had been added which could have increased detection thresholds. For this reason we re-measured the contrast detection threshold for a stimulus of this size with spatial jitter added within a 3° radius (as above). The contrast detection threshold was 1.05% ± 0.12% (IM) and 1.17% ± 0.2% (CL), so that the lowest contrast tested was roughly four times above detection threshold. For this reason we feel that the uncertainty result is not explained by reduced detectability.

3.4. Special case for vertical orientations?

The oblique effect, that observers are more sensitive to variations in orientation around vertical than around oblique orientations, is a well documented phenomenon (e.g. Campbell & Kulikowski, 1966; Heeley, Buchanon-Smith, Cromwell, & Wright, 1997). We sought to investigate whether the contrast/size dependency that we report might be limited to oblique orientations, by examining orientation discrimination thresholds measured about the vertical (±3°) only.

Fig. 7 plots the result of this experiment for observer IM. The solid symbols are thresholds obtained using only vertical orientations, the open symbols are thresholds measured using all orientations between ±45°. In the panel on the left, the stimulus size was 0.25°, in the middle panel the stimulus size was 0.5° and in the right-hand panel the stimulus was 1°. For all three size conditions, the two contrasts tested were 4% and 20%. Clearly the contrast-size dependency reported in this paper also applies to vertical orientations. For the three different sizes used, the vertical data appear to be simply a shifted version of the combined data. This indicates that the dependence of orientation discrimination on contrast is the same with verticals as with obliques for each size. This suggests that there is no oblique effect for contrast's influence on spatial signal summation.

4. Discussion

We find that orientation discrimination thresholds are not contrast invariant but rather depend on both the contrast and the size of a stimulus. We suggest that the area of summation (or, the area used to do the orientation task) changes as a function of contrast. This is reflected by the half height spatial extent varying depending on the contrast of the stimulus used (see Fig. 3). A similar trend of results was obtained for stimuli presented in the near periphery, although the absolute thresholds and summation areas differed. We suggest that our results reflect a change in neural spatial summation that occurs for low contrast stimuli.
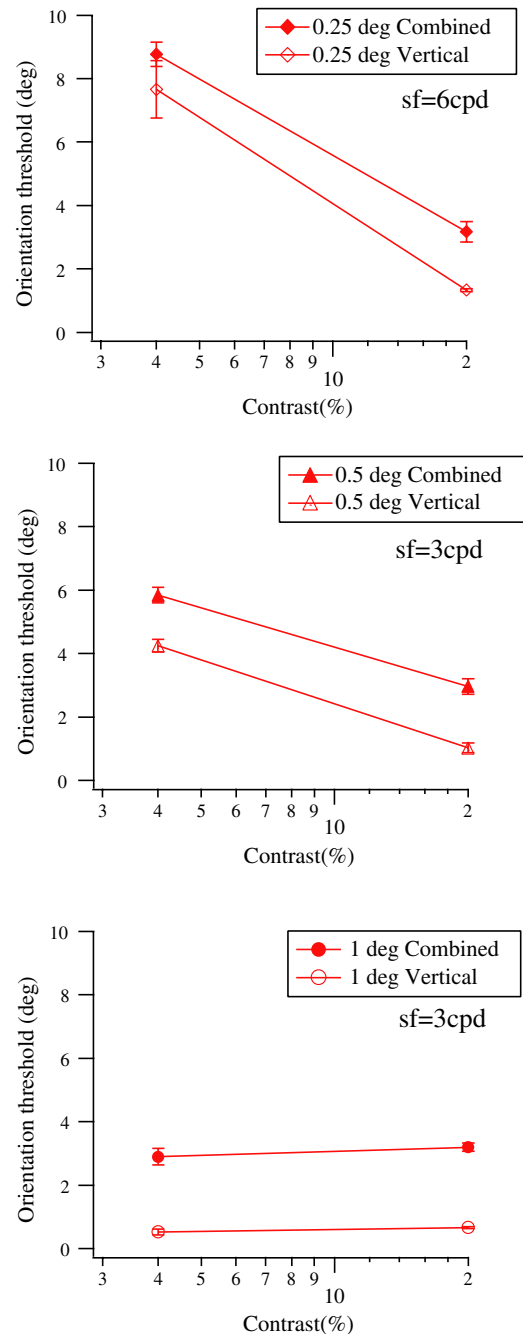

Fig. 7. Orientation discrimination thresholds for observer IM using orientations around vertical only (open symbols) to measure thresholds and combining orientations about vertical and obliques.

A concern that arises from this experiment is that our data simply might reflect the fact that the statistical properties of the stimuli vary at the different sizes and contrasts used in our experiments. In order to investigate this and to examine whether our results might be accounted for by an extension of a model based on the outputs of V1 filters, we modeled our data using conventional models of orientation discrimination based on population coding (i.e. Henrie & Shapley, 2001; Itti,

Koch, & Braun, 2000). Briefly, the modeling consisted of creating a population of 2304 Gabor filters defined by the following function:

$$RF(x,y) = \exp(-x^2/2\sigma_x - y^2/2\sigma_y)\cos(2\pi\omega x + \phi) \qquad (1)$$

where x and y are co-ordinates rotated by the filter orientation. The crucial point we were testing was whether our results on greater summation at low contrast could be accounted for by a model in which the spatial integration within each of the filters was not changed by contrast. Therefore, in this model, the spatial summation characteristics of the filters were invariant with contrast. The filters spanned all orientations and spatial frequencies (±one octave) at 64 spatial positions. The space constants of the Gaussian envelope were chosen to match the stimulus size of 0.25° in diameter. The filters were convolved with the stimulus and the outputs were squared and summed, then fit with the following function resulting in a Gaussian shaped tuning curve (of amplitude a, and variance σ_θ)

$$R(\theta) = a * \exp[-0.5((\theta - \theta')/\sigma_\theta)^2] \qquad (2)$$

The response of each filter was then normalized to the total population response, and Gaussian noise was added to the output of each filter (under the assumption that the variance of the output is proportional to the response magnitude). An orientation discrimination threshold was obtained by calculating d', which is a common measure of the discriminability of two signals in a two-flash task. The model with fixed filter sizes failed to explain the spatial summation in the data. It was then modified such that the filters interacted. In this case, an orientation threshold was obtained after the outputs of the same fixed spatial filters had undergone subtractive inhibitory interactions with surrounding filters so that the response of any one filter would be

$$R = CeFe - CiFi \qquad (3)$$

where Fe = sum of excitatory inputs from filters across orientations, spatial frequency and space (Gaussian space constant = 1°) and Fi = sum of inhibitory inputs from filters across orientations, spatial frequency and space (Gaussian space constant = 2.2°). The excitatory and inhibitory space constants were derived from the work of Sceniak, Hawken, and Shapley (2001). Eq. (3) was implemented at the different contrast levels by changing the gain of the filters for the different sized stimuli. D, taken as a measure of orientation threshold, was calculated from the values of R across the simulated V1 population (for a detailed discussion of d and how it relates to orientation thresholds measured psychophysically see Henrie & Shapley, 2001; Itti et al., 2000). The end product of the modeling effort was the d' derived from the activity of a population of neuronal filters, each of which had a fixed extent of spatial integration of its inputs, but which interacted following Eq. (3).
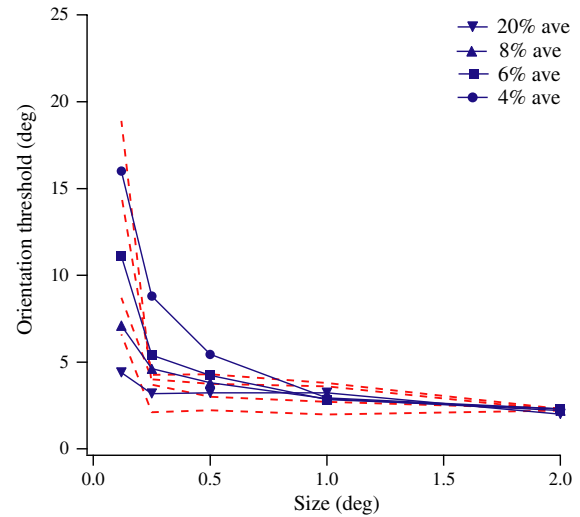

Fig. 8. Orientation thresholds from the model (dashed lines) and observers (filled symbols) as a function of stimulus size at different contrasts.

The results of the modeling are plotted in Fig. 8, with the averaged data for the three observers at the different contrast levels in filled symbols and the model results as dashed lines. Examination of the graph highlights the fact that the model fails to capture the increase in summation displayed at the small sized stimuli at lower contrasts. Because of the failure of the conventional population coding using fixed sized filters, we suggest that changes in stimulus contrast entail changes in the filters required to do the task. Hence, we interpret our psychophysical results as possible manifestations of the contrast related changes that have been reported in single cells (Angelucci et al., 2002; Kapadia et al., 1999; Sceniak et al., 1999). Given that contrast affects the size of a neuron's receptive field, it follows that any task, the performance of which is dependent upon a neuron's receptive field size or structure, should reflect the contrast induced changes, that is to say should not be contrast invariant. We suggest that the size and contrast of a stimulus may influence orientation discrimination thresholds because of the effect of contrast on spatial summation. Performance on the orientation discrimination task (as for any other spatial vision task) is dependent on signal:noise ratios of visual neurons, with performance improving as the signal:noise ratio increases. Two ways in which signal strength can be increased are by raising the stimulus contrast or by summing neural signals over space. For example, an increase in stimulus contrast for small sized stimuli leads to lower thresholds. However, an increase in the area of summation should also lead to lower thresholds, particularly with low contrast stimuli. Indeed, if neurons' receptive fields have increased in size at low contrast, increasing the size of the stimulus will lead to a greater

increase of signal:noise ratio with area than it would at high contrasts.

4.1. How does this fit in with contrast invariance?

Many researchers report contrast invariance of orientation thresholds. However, most previous data were collected along the lower end of our data plots of Fig. 2 and were not typically performed with the smaller sized stimuli that we used (i.e. Bowne, 1990; Gouled Smith & Thomas, 1989; Skottun et al., 1987; Westheimer et al., 1999). Taken at face value, our data could suggest contrast invariance with large stimuli. However we believe that this is a floor effect because measuring orientation thresholds as a function of contrast with jittered stimuli (Fig. 6) revealed that thresholds continue to improve with increasing contrast for large stimuli.

Thresholds measured on any task result from signal:noise ratios. As a signal increases, the S:N ratios will increase and thresholds will decline. In our experiments using small sized stimuli at low contrast, the S:N ratios are initially quite low because the signal is weak and pooling is reduced to a small area (because the stimulus is small) and therefore threshold is high. As contrast is increased, the strength of the signal will rise and S:N ratio will increase, resulting in lower thresholds. However, as contrast is further increased, thresholds plateau. This type of responsivity has been attributed to an hypothetical non-monotonic increase in the strength of the signal with contrast (Gouled Smith & Thomas, 1989). However, we think the plateau might be a consequence of a floor effect caused by internal noise. For large-sized stimuli, the trend of results is different. With large stimuli at low contrasts, S:N ratios are already quite high because the stimulus more than sufficiently covers the receptive fields involved in the task. Because of this, increasing the contrast of the stimulus will not significantly improve the S:N ratios.

4.2. Implications for contrast normalization theories

Contrast normalization models arose from the findings that receptive field properties, such as for example orientation and spatial frequency tuning, appeared to be contrast invariant (i.e. Albrecht & Hamilton, 1982; Bradley, Skottun, Ohzawa, Sclar, & Freeman, 1987; Sclar, Maunsell, & Lennie, 1990; Skottun et al., 1987). Typically, invariance was suggested to occur via a contrast gain control mechanism that normalized the response of a filter (receptive field) by the pooled responses of surrounding filters (Carandini & Heeger, 1994; Carandini, Heeger, & Movshon, 1997). The end result was that the absolute response magnitude of a filter might change as a function of contrast, but its overall selectivity would not because the normalization pool was commensurately affected by the changes in

contrast. Here, we find that invariance does not actually exist in the domain of orientation. This lack of invariance is expected based on the recent finding that receptive fields change in summation size with contrast. This suggests a re-examination of theories pertaining to contrasts' effects on cortical responses. Previous reports have found that contrast actually does affect spatial receptive field properties of V1 neurons (Angelucci et al., 2002; Kapadia et al., 1999; Sceniak et al., 1999), and we confirm that at least in one domain, orientation, contrast can also have strong effects on psychophysically measured discriminability.

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