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Vision Research 42 (2002) 733–745

Vision Research

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Lateral interactions: size does matter ☆

Russell L. Woods *, Alex K. Nugent, Eli Peli

The Schepens Eye Research Institute, Harvard Medical School, 20 Staniford Street, Boston, MA 02114, USA

Received 27 March 2001; received in revised form 31 October 2001

Abstract

Usually a high-contrast, co-local mask increases contrast threshold (inhibition). Interestingly, a laterally displaced mask (flanker) can facilitate contrast detection (Vision Research 33 (1993) 993; 34 (1994) 73). When spatial scaling of these flanker effects was implied, stimulus bandwidth was confounded with spatial frequency (λ^{-1}). Under conditions where at lower spatial frequencies, the size (standard deviation, σ) of the Gabor patch was smaller ($\sigma < \lambda$) than higher spatial frequencies ($\sigma = \lambda$), the effect appeared scale invariant. We replicated the original results for all conditions. However, when Gabor size was fixed ($\sigma = \lambda$), facilitation changed with spatial frequency (range 2–13 cycles/deg). When Gabor size was varied ($\sigma = 0.5$–2λ), usually the combination of larger patch sizes and lower spatial frequencies caused inhibition. We were unable to find any conditions that demonstrated spatial scaling. The size, both λ and σ, of both stimulus and flankers, influenced contrast threshold. Also, facilitation reduced as contrast of the flankers was reduced to detection threshold. Some facilitation was apparent with sub-threshold flankers. These results need to be reconciled with current models of lateral interactions.

Keywords: Lateral interactions; Contrast sensitivity; Stimulus bandwidth; Contrast

1. Introduction

Object detection can be affected by spatial context, other objects facilitating or inhibiting detection. Increment thresholds can be considered as the minimum detectable change in the characteristics of one sub-threshold target superimposed on a second target with matching spatial characteristics. Both sub-threshold and supra-threshold masks can influence contrast detection (Kulikowski & King-Smith, 1973; Legge, 1979; Tolhurst & Barfield, 1978). The second target is called a mask because of its effect at high contrast. At high mask contrasts typically there is inhibition, but as mask contrast decreases detection may be facilitated (threshold lower than with no mask) (Legge, 1979; Tolhurst & Barfield, 1978). More generally, spatial masking is the impact of one target on the detection of another, where the two targets may or may not have matching spatial characteristics. For example, a large, co-centric mask (e.g. a pedestal) may alter contrast threshold, with mask size one of the important parameters (Legge, 1978; Westheimer, 1965, 1967; Yu & Levi, 1997a,b). Using such increment-threshold paradigms, the spatial frequency tuning (Legge, 1978; Tolhurst & Barfield, 1978; Wilson, McFarlane, & Phillips, 1983; Yu & Levi, 1998) and orientation tuning (Phillips & Wilson, 1984; Yu & Levi, 1998) of the mechanisms detecting sine-wave gratings have been investigated. Most masking conditions inhibit (worsen) contrast detection. Contextual effects of masks on contrast detection may be mediated by short-range cortical connections (Das & Gilbert, 1999).

Interestingly, an appropriate flanker—a mask that is laterally displaced from the target (i.e. no longer co-centric)—may facilitate (improve) contrast detection (Morgan & Dresp, 1995; Polat & Sagi, 1993, 1994a; Wehrhahn & Dresp, 1998; Yu & Levi, 1997d). Polat and Sagi (1993, 1994a) reported that the detection threshold of a Gabor patch was lower when the patch was flanked by high contrast Gabor patches. Maximum facilitation (approximately half the non-flanked threshold) was noted when the flankers were laterally displaced from the target patch by a distance equal to two to three wavelengths (λ). Larger displacements (up to 8λ or 12λ) produced measurable facilitation, while short

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☆ Aspects of this study were presented at the Association for Research in Vision and Ophthalmology Annual Meeting, Fort Lauderdale—Woods, R. L., Nugent, A. K., & Peli, E. (2000). Bandwidth affects visual lateral interactions. *Investigative Ophthalmology and Visual Science, 41*(4), S803.

* Corresponding author. Tel.: +1-617-912-2589; fax: +1-617-912-0169/0111.

E-mail address: rwoods@vision.eri.harvard.edu (R.L. Woods).

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PII: S0042-6989(01)00313-3

displacements (e.g. 0λ or 1λ) produced inhibition (short displacements are similar to co-centric masking, as the flankers and stimulus overlap). These effects were reported to be spatial frequency independent (which implies spatial scaling) (Polat & Sagi, 1993). Spatial scaling is important as it implies a general principle of uniform operation of the visual system across all scales. Similar facilitation by laterally displaced objects (flankers) have been noted for other spatially localised (but less well spatial frequency defined) objects (Morgan & Dresp, 1995; Westheimer, 1965; Yu & Levi, 1997d). Flanker effects have been ascribed to long-range connections in the visual cortex (Das & Gilbert, 1995; Gilbert, Das, Ito, Kapadia, & Westheimer, 1996; Kapadia, Ito, Gilbert, & Westheimer, 1995; Polat, Mizobe, Pettet, Kasamatsu, & Norcia, 1998; Polat & Norcia, 1996; Yu & Levi, 1997b).

Careful examination of Polat and Sagi's experimental conditions shows that stimulus spatial frequency and bandwidth were confounded in their demonstrations of the spatial scaling of the facilitation effects (Polat & Sagi, 1993). For example, proportionally the Gaussian envelope used for the high spatial frequency objects and flankers was larger (standard deviation, $\sigma = \lambda$) than for the lower spatial frequency objects and flankers ($\sigma = 0.5\lambda$), thereby altering the bandwidth of both stimulus and flanker. Previously mask size has been shown to alter contrast detection (Legge, 1978; Yu & Levi, 1997c). As the bandwidth of Polat and Sagi's stimuli may have interacted with the change in spatial frequency, we examined size effects by systematically altering spatial frequency (λ^{-1}) and bandwidth (σ). Spatial scaling of these effects has implications for visual processing at low spatial frequencies. Low spatial frequencies are important to people with visual impairment through foveal (or macular) vision reduction, as high spatial frequencies are not detected and many use eccentric retinal locations to view. Low to medium spatial frequencies may be sufficient to mediate many important visual tasks such as letter and face recognition (Parish & Sperling, 1991; Peli, Goldstein, Young, Trempe, & Buzney, 1991; Peli, Lee, Trempe, & Buzney, 1994; Solomon & Pelli, 1994). We report that stimulus size, in terms of grating spatial frequency and Gaussian envelope, influenced measured lateral interactions. The lack of scaling highlights limitations of current models for lateral interactions (Polat, 1999; Solomon & Morgan, 2000; Solomon, Watson, & Morgan, 1999; Yu & Levi, 1997c; Zenger & Sagi, 1996).

Also we studied the impact of flanker contrast. Some facilitation was apparent with flankers that were at or slightly below detection threshold. This extends earlier reports of facilitation with a sub-threshold co-located mask (Kulikowski & King-Smith, 1973; Legge, 1979; Tolhurst & Barfield, 1978) and may be related to the report that sub-threshold stimulation is apparent in cells outside the conventional receptive field and beyond the zone that has spiking activity (Das & Gilbert, 1995).

2. Methods

2.1. Subjects

Five subjects (four males and one female, aged 23–40 years) with normal or corrected-to-normal vision participated in the study. Two of the observers (AN and RW) had extensive previous experience as psychophysical subjects and were aware of the purpose of the experiments while the other three subjects had no prior experience of contrast sensitivity measures or discrimination tasks and were naïve to the purpose of the study.

2.2. Apparatus

The stimuli were generated using a VisionWorks™ computer graphics system (Vision Research Graphics Inc., Durham, NH) and were presented on a Nanao™ EIZO® monitor. The video format was 120 Hz non-interlaced. The video resolution was 1024 × 600 pixels occupying an area of 23.4 cm (vertical) × 40 cm (horizontal) (13.2° × 21.8° at 100 cm). Luminance of the monitor was controlled with a 12-bit look-up table. Mean display luminance was 37.5 cd/m^2 in an otherwise dark environment.

2.3. Stimuli

Sinusoidal gratings in a Gaussian envelope (Gabor function) were presented in a collinear arrangement on the vertical meridian (Figs. 1A and 2A), except where specified otherwise. The luminance of each Gabor patch, $L(x, y, \theta)$, was defined by

$$L(x,y,\theta) = L_0\left\{1 + C\cos\left(\frac{2\pi}{\lambda}[(x-x_0)\cos\theta + (y-y_0)\sin\theta]\right)\exp\left(-\left[(x-x_0)^2 + (y-y_0)^2\right]\Big/\sigma^2\right)\right\}$$

where x is the value of the horizontal axis, y of the vertical axis, (x_0, y_0) is the centre of the Gabor patch, λ is the wavelength and θ is the orientation of the carrier, and σ is the standard deviation of the Gaussian envelope, L_0 is the background luminance and C is the contrast of the patch. A test patch was placed between two flanking patches of 40% contrast (except for control conditions in Experiment 3). Each patch was displayed within a rectangle that was $4\sigma_x$ by $4\sigma_y$. For all experiments, except as indicated, the gratings were vertical and the flanking patches were equidistant above and below the test patch. Test-flanker distance was defined as the distance between the centre of the test patch and the centre of a flanking patch. As our system did not allow

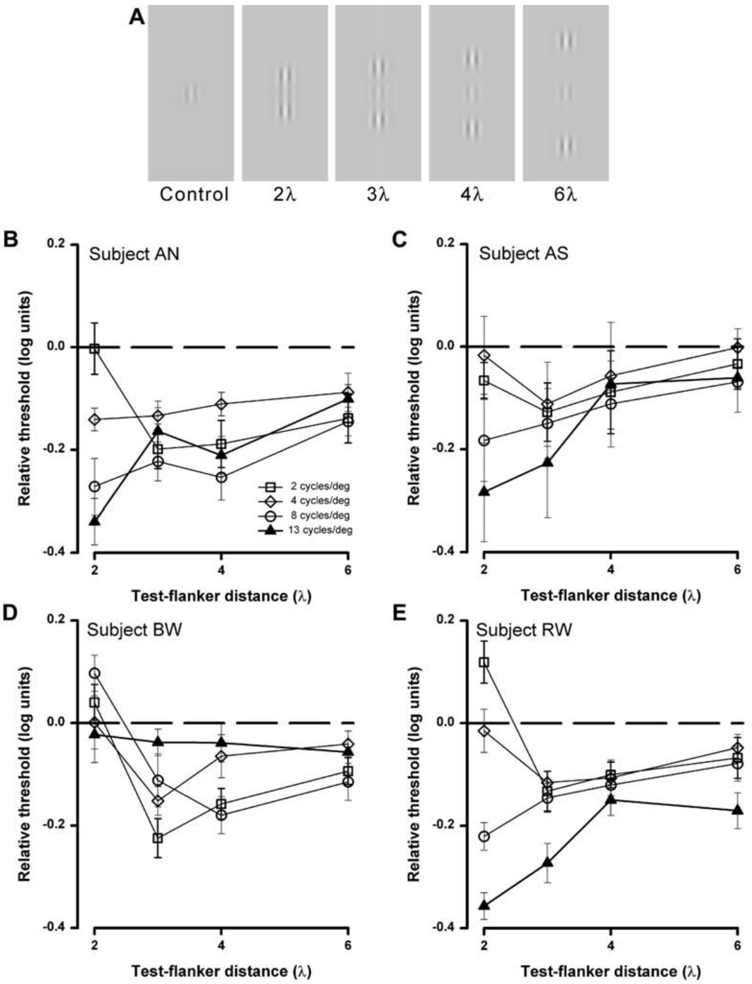

Fig. 1. Experiment 1 investigated spatial scaling of the lateral interaction between the central test stimulus and flankers above and below, (A). Test-flanker distance was varied from 2λ to 6λ, where λ was the wavelength of the contrast grating. Facilitation (lower relative contrast threshold) was found at most test-flanker separations. Relative contrast threshold changed with test-flanker separation and grating spatial frequency in a similar manner for (B) subject AN, (C) subject AS, (D) subject BW, and (E) subject RW. As the contrast threshold differed for the four spatial frequencies, particularly at 2λ, spatial scaling does not occur. Error bars are standard error of the mean.

us to overlap the flanker patches in any one display, the minimum test-flanker distance that we could display was 2σ. To achieve this test-flanker separation it was necessary to display the test patch and the flanking patches in separate interlaced frames (stereo mode: Yu & Levi, 1997c; Williams & Hess, 1998). We did this for all conditions. In this configuration, only half of the maximum contrast was available for any patch because each patch was presented in every other frame only (Yu & Levi, 1997c; Williams & Hess, 1998). Contrast detection with the flanking patches present was compared to a 'standard' condition where detection threshold was determined for a test patch with no flanking patches.

2.4. Procedure

A two-alternative temporal forced-choice staircase procedure was used. Each trial consisted of two 100 ms presentations, each a temporal square wave (abrupt onset and offset), accompanied by audible tones, and separated by 867 ms. Only one presentation contained a test patch, but both presentations contained flanking patches. Audio feedback was given as an indication of an incorrect response. These conditions replicated, as closely as possible, the conditions of the earlier experiments (Polat & Sagi, 1993, 1994a). During the trials subjects were asked to fixate at the position at which the test patch was presented (centre of monitor) without the aid of a fixation point, and report the interval in which they saw the test patch appear. A fixation target could cause masking effects. In pilot studies, we examined the impact of fixation guides using two small dots positioned on both sides of the test patch location or a single moderate contrast dot presented in the location of the test-patch until 500 ms before the test presentation. Neither fixation guide produced a difference in contrast thresholds for the 13.3 cycles/deg condition (the smallest stimulus we used, and for which spatial uncertainty and

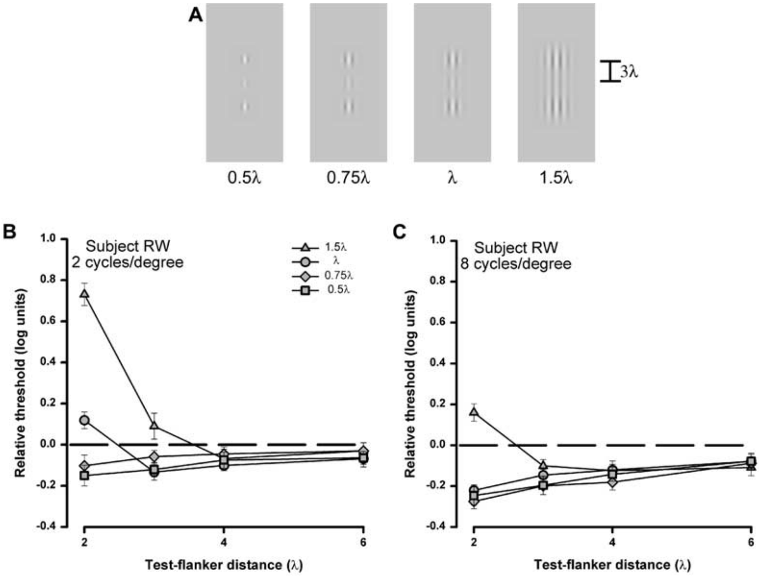

Fig. 2. Experiment 2 investigated the effect of stimulus and flanker size (defined as the standard deviation, σ, of the Gaussian envelope) on contrast detection. As before, test-flanker distance was varied from 2λ to 6λ. Illustrations of stimuli with a test-flanker distance of 3λ and $\sigma = 0.5$–1.5λ are shown in panel A. At both (B) 2 cycles/deg and (C) 8 cycles/deg, a strong interaction between the test-flanker separation and σ (stimulus size) was found for subject RW. Similar results were found for subject AN (Fig. 3). Error bars are standard error of the mean.

unsteady fixation and accommodation would be expected to be greatest).

Each staircase consisted of two practice and 10 experimental reversals or two practice and 40 experimental reversals. The 10-reversal staircases were conducted in sets of four. The geometric mean of 40 experimental reversal contrasts was taken as the contrast threshold (i.e. the average of four 10-reversal staircases or the 40-reversal staircase). Each subject completed 3–6 staircases for each experimental condition. Data is presented as the mean of those staircases, and error bars are the standard error of the mean. The initial contrast of the test stimulus (25%) was easily visible at 2 cycles/deg but just above threshold at 13.3 cycles/deg. During the staircase procedure, the contrast of the test stimulus was decreased 0.30 log units following three consecutive correct responses and increased 0.405 log units for each incorrect response. The staircases are expected to have converged towards the 83% correct point (García-Pérez, 1998).

While replicating some of the earlier experiments, we found that non-linearities in the monitor response (García-Pérez & Peli, 2001; Klein, Hu, & Carney, 1996; Pelli, 1997) can alter the measured effects. In particular, using gratings with few pixels per cycle (e.g. Polat & Sagi, 1993, 1994a,b used 4 pixels per cycle for their 13.3 cycles/deg targets) we found that the relative orientation of the raster and the grating was an important factor on our monitor. As discussed in Appendix A, we found it necessary to use many pixels per cycle (λ) or to arrange stimuli so that relatively large changes in luminance were not required along a raster line. This was achieved by fixing the size of the stimuli on the monitor, so that there were about 23 pixels per cycle, and varying the viewing distance to change grating spatial frequency.

3. Experiment 1: the effect of spatial frequency

To test the spatial scaling reported by Polat and Sagi (1993), the lateral interactions at four spatial frequencies (2, 4, 8 and 13.3 cycles/deg) were tested with test-flanker distances of 2–6λ with all test and flanker Gabors scaled so that $\sigma = \lambda$ (Fig. 1A). Viewing distances were varied from 100 to 654 cm. If there is spatial scaling then similar facilitation or inhibition should be found for each spatial frequency at each test-flanker distance. This will not occur if the different bandwidths of the different spatial frequencies used by Polat and Sagi had an impact on their results.

Facilitation was found for all four spatial frequencies (2 to 13.3 cycles/deg) for all four subjects (Fig. 1). The results for subject BW differed from the other three subjects at the higher spatial frequencies (8 and 13.3 cycles/deg). This is examined in detail in Experiment 3. In general, for test-to-flanker distances of three, four and six λ the facilitation was very similar for all four spatial frequencies. However, substantially different effects were found at the 2λ test-flanker distance, unlike Polat and Sagi (1993). Facilitation was greatest for the higher spatial frequencies (8 and 13.3 cycles/deg), with less facilitation at 2 and 4 cycles/deg. The lateral interaction effects at 8 and 13.3 cycles/deg were very similar to that found by Polat and Sagi (1993) at 6.7 and 13.3 cycles/deg when $\sigma = \lambda$. Any small differences were probably a consequence of monitor non-linearity problems (see Appendix A) and inter-subject differences (Fig. 1). Our results at 2 and 4 cycles/deg were substantially different to those of Polat and Sagi (1993) who used $\sigma = 0.67\lambda$ at 4.4 cycles/deg and $\sigma = 0.5\lambda$ at 3.3 cycles/deg.

As we varied viewing distance to vary the spatial content (visual angle) of our targets, the size of the illuminated field (i.e. the monitor) varied in visual angle. In a control experiment we found that variation in the field size had no effect on the results. This is not surprising given the spatial frequency, position and orientation tuning of these lateral interactions (Polat & Sagi, 1993, 1994a; Yu & Levi, 1998).

Examination of our data did not reveal any learning effects of the sort reported by Polat and Sagi (1994b) that could have confounded the differences between the four spatial frequencies that we tested. However, our study was not designed to evaluate learning effects. Further, when parts of this experiment were replicated a few months later (during Experiments 2 and 3) the lateral interactions had not changed in any systematic manner. However, it was clear that intra-subject variability was larger than we would have liked, but not dissimilar to other groups (Solomon et al., 1999; Williams & Hess, 1998). In conclusion, the lateral interactions did not spatially scale as reported by Polat and Sagi (1993), suggesting that the bandwidth of the stimuli had an important impact.

4. Experiment 2: the effect of test and flanker size

Since, the results at low spatial frequencies found when $\sigma = \lambda$ (Experiment 1) were different from earlier results when $\sigma \neq \lambda$ (Polat & Sagi, 1993), we examined the lateral interactions when Gabor patch size was systematically varied from $\sigma = 0.5$–1.5λ. The Gaussian envelope of both flanker and stimulus were varied simultaneously (i.e. $\sigma_{\text{flanker}} = \sigma_{\text{test}}$) as shown in Fig. 2A. As before, test-flanker distance was defined as the centre to centre distance. Spatial frequencies of 2 and 8 cycles/deg (viewing distances of 100 and 400 cm, respectively) were used to examine whether any effects of patch size scaled with spatial frequency. If patch size is a factor in the lateral interactions, then we expect changes in the lateral interactions as σ is varied.

Contrast sensitivity of the control condition (no flankers) varied with patch size as shown previously (Peli, Arend, Young, & Goldstein, 1993). Facilitation was found for both spatial frequencies at all test-flanker distances tested. In general, for greater test-flanker distances (4λ and 6λ) facilitation was similar for all four patch sizes (Fig. 2). However, at shorter test-flanker distances (2λ and 3λ) substantial effects of patch size are apparent, with facilitation for smaller patches ($\sigma = 0.5\lambda$ and 0.75λ) and inhibition for larger patches. For smaller patches (wider bandwidth) maximal facilitation occurred with a test-flanker distance of 2λ. For the larger patches (narrower bandwidth) maximal facilitation was found at larger test-flanker distances (3λ or 4λ), and inhibition increased with patch size. While these effects of patch size were similar for 2 and 8 cycles/deg, the inhibitory effects for larger patches were greater for the lower spatial frequency. The lateral interactions found with 2 cycles/deg and $\sigma = 0.5\lambda$ were very similar to those reported by Polat and Sagi (1993) at 3.3 cycles/deg and $\sigma = 0.5\lambda$.

It is clear from Fig. 2 that the lateral interactions were not scale invariant when defined in terms of the spatial frequency (λ^{-1}) of the stimulus and flanker. It is possible that the greater overlap of test and flanker for larger patch sizes (Fig. 2A) might be an important factor. As shown in Fig. 3A, the lateral interactions appear to have

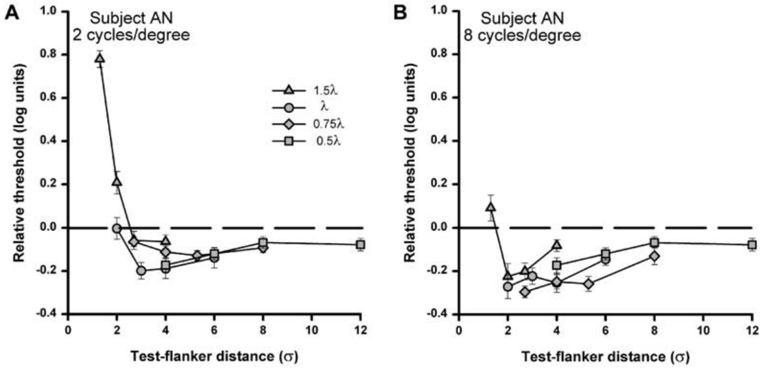

Fig. 3. Results similar to those shown in Fig. 2 (for subject RW) were found for subject AN. Here the results are plotted against the test-flanker distance in units of the σ of the stimulus. When plotted in this manner, the results at (A) 2 cycles/deg could be interpreted as demonstrating spatial scaling. However the results at (B) 8 cycles/deg were less convincing of spatial scaling. Error bars are standard error of the mean.

greater similarities when considered in terms of the size of the patch (σ) for 2 cycles/deg. However, this apparent spatial scaling is probably an artefact, since it is not apparent for 8 cycles/deg (Fig. 3B).

As we used a cosine-phase function, the average luminance of the Gabor patch became slightly brighter than the average monitor luminance for the smaller patches (i.e. when $\sigma < \lambda$) (Cannon & Fullenkamp, 1991; Peli et al., 1993). Therefore, the measured detection threshold may have been luminance detection rather than contrast detection (i.e. detecting the patch rather than the grating). To evaluate this possible artefact, the experiment was repeated at 2 cycles/deg and $\sigma = 0.5\lambda$ using a sine-phase function for test stimulus and flankers. The sine-phase function had an average patch luminance equal to the average monitor luminance. No difference in the lateral interactions was found between the cosine- and the sine-phase function Gabor patches.

Stimulus bandwidth (σ) had an effect on the measured lateral interactions. Facilitation similar to that found with higher spatial frequencies and $\sigma = \lambda$ (i.e. contrast detection with only half the contrast of the patch alone) can be found for lower spatial frequencies when the patch size is reduced (e.g. $\sigma = 0.5\lambda$). This effect of stimulus size explains the difference between our results in Experiment 1 and those of Polat and Sagi (1993) for lower spatial frequencies. Also, this is further evidence of the lack of spatial scaling of these lateral interaction effects at close test-flanker distances ($\leqslant 3\lambda$). Since we altered stimulus and flanker bandwidth simultaneously, it is possible that the effects were not a consequence of the bandwidth alone. The results may have been influenced by the greater overlap of the test stimulus and flankers when the patches were larger (Fig. 2A). This possibly confounding effect is greatest at the smaller test-flanker distances; at a test-flanker distance of 2λ, when $\sigma = 0.5\lambda$ there was no overlap of the test and flanker, while for $\sigma = 1.5\lambda$ there was substantial overlap. This overlap makes the task into a contrast increment detection task rather than the easier contrast detection task (Legge, 1979). Substantial inhibition has been reported when there was no displacement of the flanker (i.e. flanker and test stimulus were co-located) (Polat & Sagi, 1993, 1994a; Williams & Hess, 1998).

5. Experiment 3: the effect of flanker contrast

As noted in Experiment 1, subject BW had little facilitation at the two higher spatial frequencies, 8 and 13.3 cycles/deg, compared to the other three subjects (Fig. 1). Control experiments ruled out uncorrected ametropia and poor fixation as possible explanations. A third possible explanation was that subject BW might not have detected the higher spatial frequency flankers. Subject BW had higher central and peripheral contrast thresholds than subjects AN and RW, and though 40% flankers would have been visible for all conditions, some flankers were very close to her contrast threshold.

As flanker contrast appeared to be a factor in these lateral interactions, we conducted a third experiment in which the flanker contrast was systematically varied from above to below peripheral detection threshold. This was of interest also because Polat and Sagi (1993, 1994a) increased flanker contrast with increasing flanker eccentricity, after stating that the lateral interactions were independent of flanker contrasts between 20% and 80% (Polat & Sagi, 1993). We were able to confirm that independence for 20% and 40% contrast flankers as described below. Finally, the effect of flanker contrast is of interest as increment threshold experiments have demonstrated inhibition at high mask contrasts that reduced to become facilitation at low contrasts (near mask threshold) (Tolhurst & Barfield, 1978; Legge, 1979).

Lateral interactions were measured using the same paradigm as employed in the previous experiments. Flanker contrast was varied from 2.5% to 40% for 4 and 8 cycles/deg (viewing distances of 200 and 400 cm, respectively) and from 1.25% to 20% for 2 cycles/deg (viewing distance of 100 cm). Test and flanker Gabor patches were scaled so that $\sigma = \lambda$, and test-flanker distance was fixed at 3λ, a distance at which there were substantial lateral interactions (Experiment 1). So that any effects of flanker contrast could be evaluated in terms of the threshold for the flanker, detection thresholds were determined for Gabor patches presented in the two peripheral locations of the flankers ($\pm 3\lambda$) and at fixation. A temporal two-alternative forced choice procedure randomly interleaved the threshold determinations for the three tested locations. The same staircase procedure as used for the lateral interaction measurements was employed. A small, low-contrast (31%) fixation target was presented until 300 ms before presentation of the stimulus. This task required a fixation target, as there were no flankers in each presentation to guide fixation.

Fig. 4A and B show that, within the variability of these measurements, facilitation was not different for flankers of 20% and 40% contrast, as stated by Polat and Sagi (1993). As flanker contrast was reduced further, facilitation decreased eventually to zero. Conversely, previous increment-threshold experiments have reported that facilitation increased as the mask contrast was reduced to threshold (Legge, 1979; Tolhurst & Barfield, 1978). The lower panel (Fig. 4C and D) shows the frequency-of-seeing data and fitted cumulative Gaussian functions for the flanker locations. The vertical dashed lines in the upper panel (Fig. 4A and B) represent the thresholds as determined from the staircase (i.e. 83% correct: García-Pérez, 1998). While there are small differences between the two subjects and between spatial

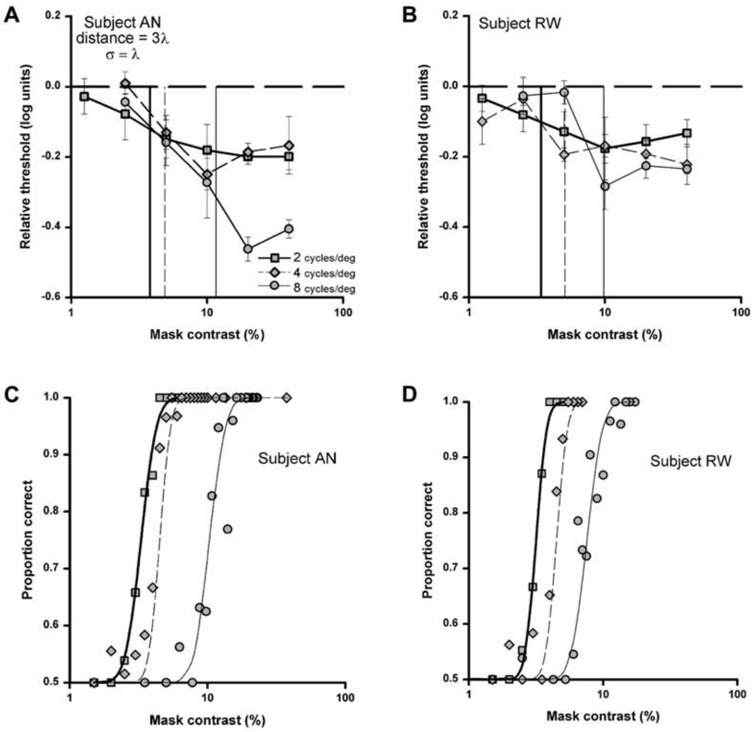

Fig. 4. Experiment 3 investigated the effect of flanker contrast. Test-flanker distance was fixed at 3λ and flanker contrast varied between 1.25% and 40%. Results are shown for (A) subject AN and (B) subject RW. Facilitation was greatest at the highest flanker contrasts (with no difference between 20% and 40% contrast), gradually decreasing to zero as flanker contrast reduced. Contrast thresholds (defined as 83% correct) of the flankers are shown as the vertical lines (same style as for the data). The frequency-of-seeing curves for the flankers are shown for (C) subject AN and (D) subject RW. In many cases sub-threshold flankers produced some facilitation. Error bars are standard error of the mean.

frequencies, it appears that there was some facilitation even with sub-threshold flankers. In most cases, as flanker contrast reduced, the facilitation had begun to decrease before flanker threshold was reached. This seems to offer an explanation for the very limited facilitation found for subject BW at higher spatial frequencies (Fig. 1D). Overall, subject BW had higher contrast thresholds than the other three subjects in Experiment 1, and we suspect that subject BW had similarly higher peripheral detection thresholds for all conditions in Experiment 1. In which case, as the flanker contrast was the same for all spatial frequencies in Experiment 1, the higher spatial frequency flankers were close to her peripheral contrast thresholds, thereby reducing the facilitation.

The reduction in lateral interactions with decreasing flanker contrast is not a complete explanation of the failure to find lateral interactions for subject BW similar to those found for the other three subjects in Experiment 1 (Fig. 1). While we know that the flanker contrast approached BW's peripheral detection threshold for the condition at which the highest peripheral threshold might be expected (13.3 cycles/deg and test-flanker distance 6λ), this explanation is less convincing for 8 cycles/deg and for the shorter test-flanker distances (2 and 3λ). In Fig. 4 there is a trend for the facilitation for the highest spatial frequency (8 cycles/deg) to remain reasonably stable until the flanker contrast was reduced to the peripheral threshold, and then to quickly decrease. Conversely there is a trend for the facilitation for the lowest spatial frequency (2 cycles/deg) to begin to decrease gradually with reducing flanker contrast, even when the flanker was well above the peripheral threshold. On this basis, we might expect more facilitation for subject BW at smaller test-flanker distances at 8 and 13.3 cycles/deg than was found.

6. Discussion

Spatial scaling of these lateral interactions as implied by Polat and Sagi (1993) and equivalent performance in peripheral vision (Polat & Sagi, 1994b) would imply a general principle of operation within the visual system that could be applied across all scales and across the visual field. Such generality is very appealing. We discuss our results in terms of this possible general principle and associated visual models and in terms of the vision of people with central vision impairment.

Clearly the lateral interactions did not spatially scale at all test-flanker distances (Figs. 1 and 2). The size of both the carrier (λ) and the envelope (σ) of the Gabor patch stimuli had an impact on the measured lateral interactions. However, neither could these lateral interactions be characterised only by the separation in terms of visual angle. At larger test-flanker distances ($>3\lambda$) the lateral interactions appear to be independent of spatial frequency (λ^{-1}). In other words, there may be spatial scaling at these longer test-flanker distances. The effects of size become apparent when the flankers are close to the test patch. The impact of proximity was greatest for the lowest spatial frequency (2 cycles/deg). This suggests that this experimental paradigm may involve (at least) two visual mechanisms: one a central (largely) inhibitory zone and the second a more extensive zone that, given the right relationships between the central target and the flanker (often) produces facilitation. Our results suggest that the spatial profiles of the visual mechanisms responsible for these lateral interactions vary with the spatial frequency tuning of the mechanism. In general, it appears the central inhibitory zone is larger, relative to the wavelength to which it is tuned, for the lower spatial frequency mechanisms than the higher spatial frequency mechanisms. This relationship is opposite to that reported by Wilson et al. (1983), who measured increment thresholds, and found that lower spatial frequency sensitive mechanisms had larger bandwidths than higher spatial frequency sensitive mechanisms, since this implies that the spatial extent of spatial frequency filters decreases (relative to λ) with spatial frequency. This difference supports a conclusion that the facilitation is not simply summation within a large filter.

Unlike the stimuli of Polat and Sagi (1993, 1994a) our flankers were not additive. Rather our stimuli were restricted to $4\sigma \times 4\sigma$ squares. Consequently when the test-flanker distances were short, the contrast of the flankers that was co-local with the test patch, was less than that when presented by Polat and Sagi (by as much as half). Given that contrast thresholds increase with spatial frequency over the range tested, and the flanker contrast was fixed, the contrast of the co-local elements of the flankers was closer to contrast threshold of the lower spatial frequency test patches. Over much of the range of mask contrasts, inhibition increases (facilitation decreases) as the contrast of the mask approaches the contrast threshold of the test patch (Legge, 1979). This may be, at least in part, an explanation of the spatial frequency dependent differences in contrast threshold at short test-flanker distances. Given that the contrast of Polat and Sagi's flankers that were co-local with the test patch at short test-flanker distances were higher than ours were, one might expect a greater spatial-frequency dependent effect than in our data, but this is not apparent in their data.

One possible interpretation of our data is that short-range lateral interactions are a function of spatial frequency while long-range lateral interactions are independent of spatial frequency. This differs from the results of Yu and Levi (1997c) who measured increment thresholds. Yu and Levi's stimulus configuration included a mask co-centric with (superimposed on) the test stimulus. Test stimulus height was fixed while mask height was varied. They found for shorter masks that the effect of mask height was independent of spatial frequency and inhibition was greatest at a mask height that was a multiple of the height of the test patch (i.e. a fixed visual angle). The effect of longer masks varied with spatial frequency, with the suggestion that higher spatial frequencies had smaller (in terms of visual angle) end zones. Unfortunately their masks were not long enough at the lower spatial frequencies to make comparisons in terms of λ. Their stimuli were wide-band (clipped) in the vertical dimension. It is possible that the differences in the results of these two studies are a consequence of the complex changes in spatial content with spatial frequency, test-stimulus height and mask height in their stimuli, or a consequence of the task differences (contrast detection versus increment threshold).

As noted by Polat and Sagi (1993, 1994a), these lateral interactions extend well beyond the range of the classical receptive field. Recent studies (Das & Gilbert, 1995; Gilbert et al., 1996) have found that there are substantial supra-threshold and sub-threshold neural interactions in the primary visual cortex over ranges that are consistent with the psychophysical evidence. Cortical pyramidal cells that extend up to 6–8 mm may be involved (Gilbert et al., 1996). Using a 0.5° stimulus, Das and Gilbert (1995) reported a 0.75 mm ($\sim 0.5°$) central zone in which spiking activity was found and a 4 mm ($\sim 4°$) surrounding inhibitory zone in which there was sub-threshold activity. Facilitation due to flanking line stimuli has been reported in parallel psychophysical and electrophysiological studies (Kapadia et al., 1995). Potential models for these lateral interactions include a simple transducer (Solomon et al., 1999), end-stopping (Yu & Levi, 1997c), a two-stage, contrast-gain model (Zenger & Sagi, 1996) and two-stage rectified filters (Polat, 1999; Solomon & Morgan, 2000). Of these models, only Yu and Levi (1997c) measured or tested their model with a range of spatial frequencies and only that model incorporates any specific elements that could account for a lack of spatial scaling. It is possible that these models could be adapted by the addition of a small number of additional parameters that incorporate changes in spatial frequency and patch bandwidth. More problematic is the apparent discrepancy noted above between our results and those of Yu and Levi (1997c) who examined a wide range of spatial frequencies. They interpreted their results as spatial filters with end-stopping that varied with spatial frequency, and length tuning determined by target length. The central inhibitory zone apparent in our data (Figs. 1 and 2) varied as a function of both the spatial frequency (λ^{-1}) and the envelope (σ) of the Gabor test patch. We did not examine a sufficiently wide range of visual angles to evaluate our data in terms of length tuning. Yu and Levi's results can be interpreted as limited confirmatory evidence for a lack of spatial scaling of these lateral interactions, given the relationship between spatial frequency and strength and extent of end-stopping. As noted above, differences between these two studies may be related to stimulus characteristics (e.g. our test patches were not clipped in the vertical dimension) and task (i.e. our flankers did not overlap the target in the same way). End-stopping may be an adequate explanation for short-range lateral interactions (e.g. test-mask distance $\leqslant 3\lambda$) but seems unable to explain the long-range lateral interactions. It seems that new or revised models are required to account for our results. Such models may have to incorporate two different and competing mechanisms and should consider the dynamic nature of receptive fields found electrophysiologically (Kapadia, Westheimer, & Gilbert, 1999).

The different lateral interactions found with changes in patch size (σ) (Figs. 2 and 3) suggest that bandwidth of the stimuli is an important factor for the visual mechanisms responsible for these lateral interactions. However, the simple effect of overlap of the stimuli cannot be disregarded. At the shorter test-flanker distances the narrow-band, larger stimuli (i.e. $\sigma > \lambda$) have more overlap of test stimulus and flankers. As test and flanker begin to overlap, the task changes from contrast detection to increment threshold. When, as in the Polat and Sagi paradigm, the flanker is gradually moved relative to the test stimulus, it becomes difficult to make the classical distinction between contrast detection and increment threshold. For $\sigma = \lambda$ patches, as shown in Fig. 1A, overlap begins at a test-flanker distance of about 3λ. The difference in overlap that was confounded with the change in size of the Gabor patches in Experiment 2 could have had a significant contribution to this reported effect of stimulus size. To examine this possibility, we shall need to systematically and independently vary overlap and bandwidth of the flankers (Woods, Nugent, & Peli, 2002).

The decrease in facilitation with reduction in flanker contrast (Fig. 4) is similar to that reported by Solomon and Morgan (2000) for 13 cycles/deg (same-phase) Gabor patches measured using the Polat and Sagi paradigm. They did not report the peripheral detection thresholds of the flankers. While, for a 3λ test-flanker distance, Polat (1999) reported no difference in facilitation between 10% and 75% flanker contrasts, his data is unconvincing due to the lack of error bars or statistical analysis, and the apparently lower facilitation for 40% than 20% or 75% flanker contrasts. Wehrhahn and Dresp (1998) found that small line stimuli induced by a larger co-linear flanking line with the same polarity showed increasing facilitation as flanker contrast reduced. If we consider our (same phase) stimuli to be equivalent to those same polarity stimuli, this is the opposite of our result. The difference in results may be due to the nature of their stimuli—test stimulus and flanker were dissimilar in size and were wide-band. Interestingly, they reported that when stimulus and flanker had opposite polarity, facilitation was greatest for a high contrast flanker and decreased as flanker contrast reduced (Wehrhahn & Dresp, 1998). This stimulus configuration seems analogous to opposite-phase Gabor patch stimuli. For these opposite phase Gabor patches, Solomon et al. (1999) reported inhibition that decreased as flanker contrast reduced when test-flanker distance was short (2λ) but no lateral interactions with larger test-flanker distances (3 and 4λ; 13.3 cycles/deg). Similarly Williams and Hess (1998) found no effect of opposite phase, 3λ flankers (4.2 cycles/deg). Again, with Gabor patches, the result does not appear consistent with the result found using line stimuli—well spatially localised, but less well frequency-defined (wide-band) (Wehrhahn & Dresp, 1998). It is possible that these differences occur due to the different lateral interaction fields of detectors with different spatial frequency tuning as found in Experiments 1 and 2. Line stimuli would be expected to stimulate a wider range of spatial frequency tuned detectors than Gabor patches. Stimulus contrasts are a factor also. Kapadia et al. (1999) reported that the neuronal receptive field varied with the contrast of line stimuli, being about four times larger for low contrast (10–20%) than high contrast (50–70%) stimuli. Another explanation may be found in the results of Yu and Levi (1997c), who used a paradigm designed to test their end-stopping model of lateral interactions. Yu and Levi reported, for a single spatial frequency (8 cycles/deg), that the effect of phase depended on the distance of the flanker from the text patch. When the flankers were close, same-phase flankers produced inhibition while opposite-phase flankers caused facilitation. However, when the flankers were more distant, both same- and opposite-phase flankers produced facilitation that decreased with reducing flanker contrast. This was explained by their end-stopping model, wherein closer flankers are within the "outer summation zone", while more distant flankers are within the "end zone". These discrepancies between results for stimuli with different spatial characteristics need to be resolved for a better understanding of lateral interactions in human vision.

It is not clear yet whether these lateral interactions occur in the retinal periphery. Williams and Hess (1998) found no facilitation for a limited range of conditions, while in a footnote in one paper, Polat and Sagi (1994b) reported facilitation similar to that found at the fovea (but provided no data). Xing and Heeger (2000), using an annular flanker, reported differences in contrast matching between fovea and periphery. In particular, in peripheral vision the flanker reduced perceived contrast. Since the majority of people with low vision have macular degeneration, and it is these people who would most benefit from image enhancement, further investigation of lateral interactions in peripheral vision is required. Of particular interest in the quest to improve the visual experience of people with macular degeneration are the facilitatory interactions, as these effects may be used to enhance images. In peripheral vision only lower spatial frequencies are visible. Given that in foveal vision these lateral interaction effects do not spatially scale and are influenced by bandwidth, consideration of these aspects of stimulus configuration is required when investigating peripheral vision. In summary, while there may be some general principles that describe these lateral interactions, it appears that any general principle has a layer of complexity not incorporated previously (e.g. it needs to include changes with spatial frequency and bandwidth).

Acknowledgements

Supported by NIH EY05957 and EY12890.

Appendix A. Monitor non-linearity

Many of the lateral interaction effects investigated with this paradigm by Polat and Sagi (1993, 1994a,b) and others (Solomon et al., 1999; Williams & Hess, 1998) were conducted with 13.3 cycles/deg targets. During our early investigations we found that the number of pixels used to represent the grating appeared to influence the results. Polat and Sagi tested spatial frequencies ranging from 13.3 to 3.33 cycles/deg using a 56 Hz non-interlaced display system with 512×512 pixel, viewed from 180 cm (9.6° × 9.6°). Hence, at 13.3 cycles/deg, there were only 4 pixels per cycle. There was a statistically significant difference between the 4-pixels per cycle condition (viewing distance of 118 cm) and the 23 pixels per cycle condition (654 cm), and both facilitation functions appeared slightly different to those reported by Polat and Sagi (1993, 1994a).

We suspected monitor non-linearity, in particular the ability to represent accurately gratings of high contrast and high frequency. Relatively high contrasts were necessary in our experiment (e.g. at 13.3 cycles/deg contrast thresholds were about 10% and the flankers were 40%). To obtain gratings of these nominal contrasts, the required contrast of our display had to be twice these amounts, since each grating was only visible in every second frame (i.e. the perceived contrast was half the contrast of the grating displayed in each frame). As noted by Klein et al. (1996) and Pelli (1997) when a raster scan requires large changes in luminance over a small distance, as occurs when writing across a high-contrast, high-frequency grating, the monitor may fail to represent the change correctly. Presumably the electron gun is unable to change its signal sufficiently quickly (causing low pass filtering: Pelli, 1997). Consequently, the luminance of each pixel is influenced by the luminance of nearby pixels. An additional calibration procedure and look-up table can be used to reduce this problem (Klein et al., 1996). A simpler alternative is to have smaller changes in luminance for subsequent pixels to minimise this non-linearity. This could be achieved by (1) using more pixels to represent the grating (Fig. 5A); or (2) having the raster write along, rather than across the grating (Fig. 5B).

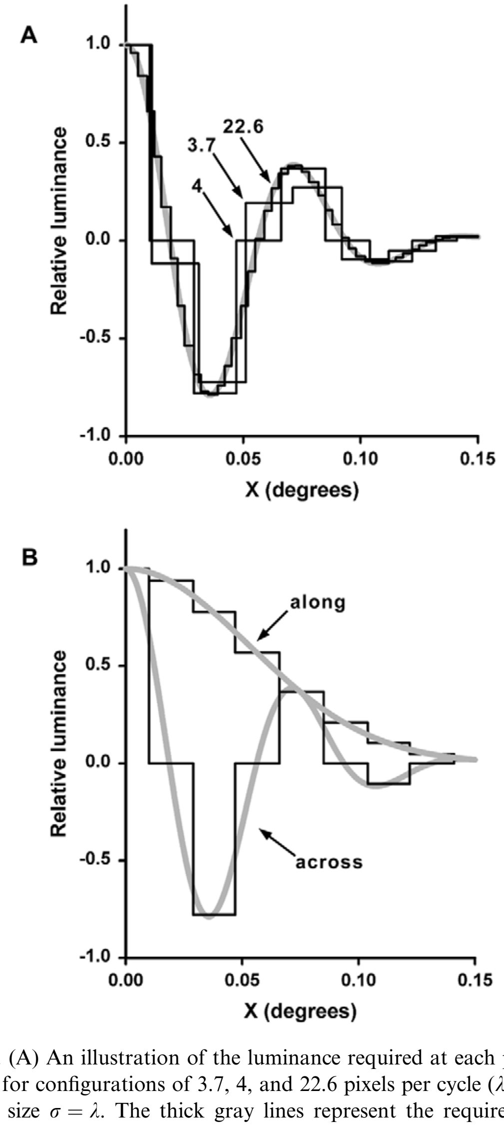

Fig. 5. (A) An illustration of the luminance required at each position (pixel) for configurations of 3.7, 4, and 22.6 pixels per cycle (λ) with a Gabor size $\sigma = \lambda$. The thick gray lines represent the required luminances and the thin black lines represent the nominal luminances at each location. (B) An illustration of the luminance required when the raster line is along or across a 4 pixels per cycle grating of Gabor size $\sigma = \lambda$ (thin black lines) compared with the nominal luminances (thick grey lines). These figures are schematic, as the actual luminance produced by each configuration is influenced by the luminance profile of each pixel and any monitor non-linearity.

The raster on our monitor, as is common, wrote horizontal lines starting from the upper left corner of the screen. Therefore to have the raster write along the grating the gratings need to be horizontal. Alternatively, by placing the monitor on its side vertical gratings with the raster writing along the grating could be produced. To investigate whether our measurements, and possibly those of Polat and Sagi (1993, 1994a), were affected by monitor non-linearity, we measured the lateral interactions with both vertical and horizontal gratings (13.3 cycles/deg. Gabors with 4 pixels per cycle), both with the monitor in its normal orientation and when it was on its side. The facilitation produced by vertical and horizontal gratings was not different (repeated measures ANOVA, $p = 0.49$). As shown in Fig. 6A, on average the facilitation was greater when the raster wrote along the grating than when the raster wrote across the grating ($p = 0.006$) and the shape of the facilitation functions was different (interaction, $p = 0.0009$). In addition, the measured contrast thresholds for the standard condition (no flanking patches) were significantly lower for the raster-along conditions than the raster-across conditions (-0.74 versus -0.58 log units respectively; $p < 0.0001$). Assuming that vision did not change, this means that higher luminance differences between pixels were required for the raster-across conditions to display the same contrast as the raster-along conditions.

Having completed this investigation, we discovered that when the monitor was placed on its side, there were misalignments of the three colour guns (due to the earth's magnetic field) that had not been removed by degaussing. The misalignments caused incorrect irradiation of the three phosphors sufficient to cause changes in colour naming (e.g. dark blue became light green). These effects were not obvious when viewing a screen comprising only shades of grey. As we were concerned that these misalignments of the pixels could make the look-up table inaccurate, we repeated this examination of monitor non-linearity by having the subjects lie on their side while viewing in lieu of rotating the monitor. We found almost exactly the same effects (Fig. 6B). There was a significant effect of raster orientation

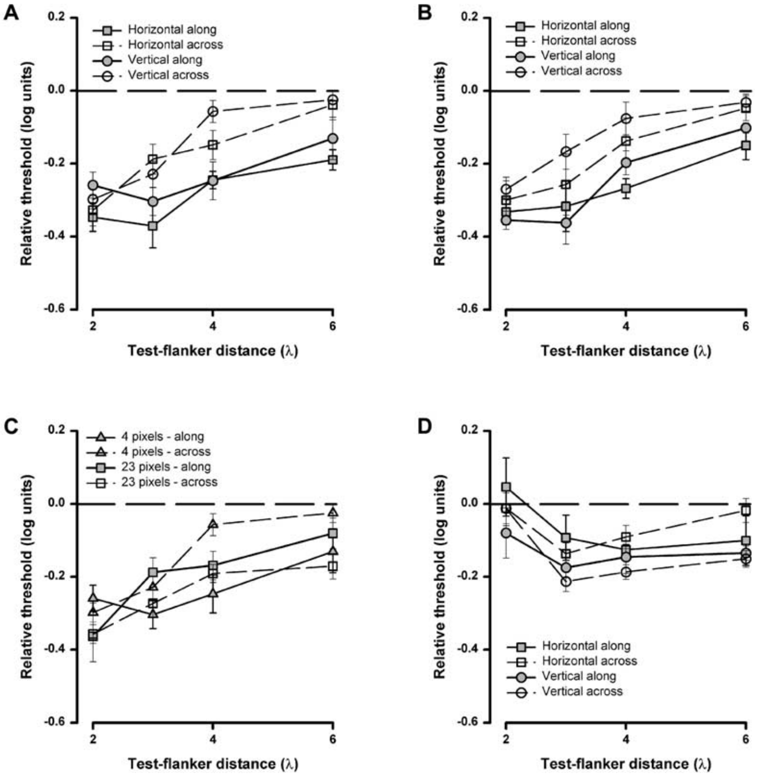

Fig. 6. (A) An evaluation of monitor non-linearity using 4 pixel per cycle, 13 cycles/deg. Gabor patches with $\sigma = \lambda$. Two of the conditions were created by placing the monitor on its side. All conditions produced facilitation (negative relative contrast threshold). There was no difference between the facilitation produced by the vertical and the horizontal gratings. However, the facilitation differed between the raster-across and raster-along conditions. (B) As for A, except the monitor was not rotated, instead the subject lay on his side to create two of the conditions. Again, the non-linearity of the monitor was apparent in the difference between the raster-along and raster-across conditions. (C) An evaluation of monitor non-linearity using vertical, 13 cycles/deg gratings. There was no difference between the facilitation produced by the raster-across and raster-along conditions for the 23 pixel per cycle gratings. (D) As for B, except with 23 pixel per cycle, 2 cycles/deg patches. With this better spatial resolution there was no apparent monitor non-linearity there being no significant differences between the four conditions. Thus, with sufficient spatial resolution the monitor non-linearity could be avoided. Error bars are standard error of the mean.

(repeated measures ANOVA, $p = 0.04$) but no effect of grating orientation ($p = 0.51$) or interaction between raster and grating orientations ($p = 0.27$). García-Pérez and Peli (2001) used a similar approach in a more systematic examination of this and related artefacts associated with monitors.

To investigate the impact of having a larger number of pixels, we compared the 13.3 cycles/deg gratings of 4 pixel per cycle and 23 pixel per cycle vertical gratings, both with the raster-along and raster-across the grating. All four conditions produced facilitation (Fig. 6C). For the 23 pixel per cycle gratings, raster alignment had no effect (repeated measures ANOVA, $p = 0.61$). This suggests that when there was a sufficiently large number of pixels, the monitor could produce equivalent gratings when the raster was writing along or across the grating. For the raster-along condition, the shape of the facilitation function differed slightly between the two resolution conditions (interaction, $p = 0.07$). To confirm this, we repeated the subject-rotating experiment when using 23 pixel per cycle gratings that were 2 cycles/deg when viewed at 100 cm. For this arrangement we found the predicted lack of a significant difference between the raster-along and raster-across conditions (Fig. 6D). Hence, to avoid the non-linearity found when only small numbers of pixels were used to display the grating, we used a fixed target size and varied the viewing distance.

While the number of pixels per cycle was a problem with our system, we do not know whether such problems are found with other systems. However, the monitor that we used was reasonably new and considered of good quality at the time of its purchase. Our experience suggests that care should be taken when evaluating the effects of stimuli created with monitors.

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