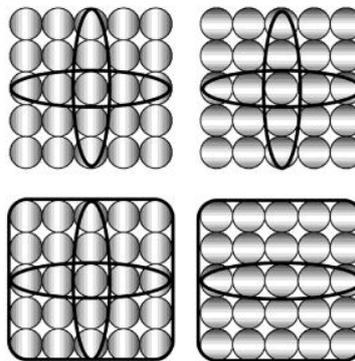




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Anisotropy for spatial summation of elongated patches of grating: A tale of two tails

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Abstract

Studies of spatial summation often use sinusoidal gratings with blurred edges. When the envelope is elongated (i) along the grating stripes and (ii) at right angles to the grating stripes, we refer to the stimuli as skunk-tails and tiger-tails respectively. Previous work [Polat & Tyler, 1999; *Vision Research*, 39, 887–895.] has found that sensitivity to skunk-tails is greater than for tiger-tails, but there have been several failures to replicate this result within a subset of the conditions. To address this we measured detection thresholds for skunk-tails, tiger-tails and squares of grating with sides matched to the lengths of the tails. For foveal viewing, we found a contrast sensitivity advantage in the order of 2 dB for skunk-tails over tiger-tails, but only for horizontal gratings. For vertical gratings, sensitivity was very similar for both tail-types. When the stimuli were presented parafoveally (upper right visual field), a small advantage was found for skunk-tails over tiger-tails at both orientations, and spatial summation slopes were close to that of the ideal observer. We did not replicate the findings of Polat & Tyler, but our results are consistent with (i) those of Foley et al. [Foley, J. M., Varadharajan, S., Koh, C. C., & Farias, C. Q. (2007) *Vision Research*, 47, 85–107.] who used only vertical gratings and (ii) those from modelfest, where only horizontal gratings were used. The small effect of tail-type here suggests an anisotropy in the underlying physiology.

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1. Introduction

Most image-processing models of spatial vision use filters with receptive fields that are either circular or elongated slightly along the filter's preferred orientation. Aspect ratios (width:height) of between 1:1 and 1:1.6 are fairly typical (Daugman, 1984; Watson, 1982). These filters are selective for spatial frequency and orientation and have typical weighting functions (measured physiologically, or inferred psychophysically) with two or three lobes that alternate between excitatory and inhibitory influences (see Polat & Norcia, 1998 for a brief review). This type of model predicts that sensitivity to sinusoidal gratings

increases with area. As the area of the grating grows within the smallest receptive field, sensitivity is assumed to improve linearly, but thereafter more slowly, consistent with probability summation amongst multiple receptive fields (Howell & Hess, 1978; Robson & Graham, 1981). This scheme has been successful in fitting psychophysical results on spatial summation of multiple grating patches (Meese & Williams, 2000) and gratings extending over many stimulus cycles (e.g. Howell & Hess, 1978; Meese, Hess, & Williams, 2005; Robson & Graham, 1981). In contrast, Polat and Tyler (1999) reported evidence for extensive spatial summation along the length of the receptive field (the dimension aligned with the preferred orientation) that had not been observed previously (Howell & Hess, 1978). Performance improved as a square-root rule (sometimes called quadratic summation or Pythagorean summation) up to grating bar lengths dimensionally equivalent to

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8 cycles, but this level of summation did not extend beyond two cycles in width. The square-root rule suggests physiological summation of signal and noise across an array of mechanisms with smaller receptive fields, thus producing a higher-order filter with a longer receptive field. This form of summation is sometimes referred to as ideal because when contrast transduction is linear, it is the strategy that will optimally improve the signal to noise ratio. Other psychophysical studies that have investigated spatial summation over small regions of the retina have also found greater than fourth-root summation. Rovamo and his colleagues (Rovamo, Luntinen, & Nasanen, 1993; Rovamo, Mustonen, & Nasanen, 1994) reported quadratic summation for hard-edged patches of grating within about 4 cycles in the fovea and Kersten (1984) found a similar result over that range. Using 12 c/deg arced strips of grating 3.5 deg into the parafovea, Mayer and Tyler (1986) found substantial levels of spatial summation up to 8 or 16 stimulus cycles and Manahilov, Simpson, and McCulloch (2001) found that quadratic summation extended up to 8 cycles for flickering (6 Hz) Gabor patches in the parafovea. The aspect ratio of 4:1 for the summation region found by Polat and Tyler is much greater than that of receptive fields used in most psychophysical models of early spatial vision, though it is reminiscent of the elongated receptive fields that have been found in layer 6 of primary visual cortex (DeAngelis, Freeman, & Ohzawa, 1994; Gilbert & Wiesel, 1985) and the collator/collector units of Moulden (1994) and Morgan and Hotopf (1989). Polat and Norcia (1998) measured human VEPs using stimuli similar to those of Polat and Tyler, and found a minimum aspect ratio of 6:1, with summation extending over a stimulus length equivalent to 12 cycles (though it should be borne in mind that evoked potentials are at best mass potentials vulnerable to cortical geometry). More recently, Chen and Tyler (2006) concluded that stereoscopic discriminations also involve elongated receptive fields, though at first glance, this is at odds with the very broad orientation tuning recently shown for stereo (Hess, Wang, & Lui, 2006).

However, Polat and Tyler's (1999) report of elongated receptive fields is surprising in the light of several earlier and later studies where this effect was not found. Howell and Hess (1978) found only probability summation when extending the bar length of vertical gratings that were five cycles in width and reported equivalent summation for cycles and height. Foley, Varadharajan, Koh, and Farias (2007) failed to find any evidence of the long receptive fields reported by Polat and Tyler in a study using various sizes and shapes of Gabor patches. Manahilov et al. (2001) found that sensitivity was the same for circular patches and both types of elongation for 2 c/deg Gabor patches at an eccentricity of 7 deg when stimulus size was expressed in terms of area. Finally, thresholds in the model dataset are very similar for Gabors elongated either along or orthogonal to the orientation of the carrier (Carney et al., 1999; Carney et al., 2000).

Here, we report a series of experiments to examine the issue of spatial summation at threshold to try and resolve the discrepancies above. To do this we identified several design issues and other points of clarification, which we outline below.

1.1. Summary of summation rules

The level of summation is characterised by the log–log slope of sensitivity (or thresholds) against area. Assuming that subunits respond to the signals with equal strength (resp_i), different slopes (possibly over different regions) can arise for several reasons, including the following. A slope of 1 occurs for linear summation of signals, but with no further summation of noise (i.e. the limiting noise is constant across size conditions, as in the case where it is added after the summation stage). A slope of 0.5 (a quadratic, or square-root rule) occurs for linear summation of both signal and noise, consistent with ideal summation (Tyler & Chen, 2000). A slope of around 0.25 (a fourth-root rule) is broadly consistent with probability summation across multiple linear mechanisms limited by independent noise (independent detectors) (Tyler & Chen, 2000). These three rules are described by Minkowski summation ($\text{resp}_{\text{total}} = \sum_i (\text{resp}_i^k)^{1/k}$) with exponents (k) of 1, 2 and 4, respectively. Summation slopes fall less steeply than these canonical forms if the individual contrast responses are subject to an accelerating nonlinearity prior to spatial summation and/or a decline in sensitivity over the region of summation (Meese, 2007). For example, another interpretation of a slope of 0.5 is energy summation (Manahilov et al., 2001), which can be achieved if half-wave rectified linear filter outputs are followed by a squaring transducer, linear summation and late additive noise. More generally, any level of summation can be achieved with the appropriate setting of a nonlinear response exponent before linear summation.

1.2. Terminology: orientation and tail-type

We refer to patches of grating with their envelopes elongated along their widths (i.e. by increasing the number of stripes) as 'tiger-tails' (Morgan, Mason, & Baldassi, 2000; Morgan & Tyler, 1995). By analogy, we refer to patches of grating with their envelopes elongated along their lengths (i.e. by increasing the length of the stripes) as 'skunk-tails'.¹

When we refer to stimulus orientation we refer to the orientation of the grating's stripes (i.e. the carrier orientation), not the orientation of the envelope (i.e. not tail orientation).

¹ Much to our chagrin we could not identify a well-known animal that is indigenous to the UK or Australia that has a tail with stripes along its length.

1.3. Retinal field location and orientation

How should our stimuli be constructed? One approach is to use the same stimulus orientation for skunk-tails and tiger-tails, in which case the different tail-types extend into different retinal field locations (Foley et al., 2007; Polat & Tyler, 1999). Another possibility is to use the same field locations but orthogonal stimulus orientations for the two tail-types (Manahilov et al., 2001; Polat & Norcia, 1998; Polat & Tyler, 1999). Both of these methods have been used before, but both involve confounds. As neither is ideal on its own we use both methods with the same observers.

1.4. Envelope shape

In typical spatial summation studies sinusoidal carrier gratings have been modulated by a two-dimensional Gaussian to produce Gabor stimuli with various aspect ratios (Carney et al., 2000; Foley et al., 2007; Polat & Norcia, 1998; Polat & Tyler, 1999). One problem with this is that as the length of a tiger-tail is increased, the Michelson contrast of the stimulus also increases, particularly over shorter lengths. Expressing stimulus contrast as Michelson contrast after the contrast modulation can compensate this (e.g. Polat & Tyler, 1999, Tyler personal Communication), but typically this is not what is done (e.g. modelfest) and the issue is picked up at the modelling stage instead (e.g. Foley et al., 2007; Manahilov et al., 2001; Watson & Ahumada, 2005; Yang, 2007). Here we sidestep this problem by generating envelopes from the product of vertical and horizontal raised cosine functions having central plateaus at least one cycle in width. Consequently, the Michelson contrasts of our stimuli are identical to the contrasts of the carriers.

1.5. Spatial inhomogeneity of summation?

If sensitivity improves with a fourth-root rule when both length and height of a grating are increased (Meese et al., 2005; Robson & Graham, 1981), and a square-root rule when only the length of a tiger-tail is increased (Polat & Tyler, 1999), then the implication is that performance will not change at all when the width of a tiger-tail is extended to match its length. To test this possibility we measured sensitivity to tiger-tails, skunk-tails and square patches (Rovamo et al., 1993) whose sides were matched in length to those of the tails (Polat & Tyler, 1999).

1.6. Experimental design

A requirement for the ideal observer is that the signal is known exactly; in which case, trials from the different conditions should be blocked. On the other hand, a preferred design when probability summation is involved is to interleave trials across different conditions so that the observer monitors the same mechanisms in the conditions that are to be compared (Graham, 1989). Previous results suggest that

this is probably of no practical concern here (Foley et al., 2007; Meese et al., 2005), but in any case we extend the generality of the present study by using both types of experimental design.

1.7. Other parameters

As it is possible that different summation rules exist at different spatial frequencies we performed our study using gratings with carrier frequencies of 4 c/deg (the same as Foley et al., 2007; Polat & Tyler, 1999) and 1 c/deg. To address the possible effects of retinal inhomogeneity, we also compare summation for patches placed in the fovea and parafovea. One final issue that emerged from our study is the influence of different configurations of fixation points. We develop this in the results section.

2. Methods

2.1. Equipment

Stimuli were generated using the framstore of a Cambridge Research Systems (CRS) VSG2/3 operating in twin palette mode to produce pseudo 12-bit grey-level resolution. Stimuli were presented on a display monitor having a mean luminance (L) of 60 cd/m² and a frame rate of 120 Hz. The monitor was gamma-corrected using lookup tables. The experiments were run under the control of a PC.

2.2. Stimuli

The stimuli were rectilinear patches of either vertical or horizontal sine-wave gratings with a spatial frequency of either 1 or 4 c/deg and were viewed binocularly. The gratings were always in sine-phase with the centre of the display screen and, unless otherwise stated, there was also a centrally placed dark fixation point visible throughout the experiment. Other fixation regimens were as described in the results section. Stimulus contrast is reported in dB given by $20\log_{10}(C)$ re 1%, where $C = 100[(L_{\max} - L_{\min})/(L_{\max} + L_{\min})]$. The gratings had their edges smoothed by a half period of a raised sine function. The sigmoidal ramp of the window was 1 cycle wide, and the width and height of the plateau was varied to produce stimuli of different sizes. The dimensions of the plateaus were: 1, 5 and 11 cycles. Nominal width and height are given by the full-width at half-height of the square of the envelope. These dimensions were 1.73, 5.73 and 11.73 cycles. The area of the stimulus is given by the product of the nominal width and height, and is plotted as 20 times the log of this value, to produce an axis that is directly comparable to detection threshold expressed in dB. Fig. 1 shows all of the stimuli used in our experiments. The stimuli fall into three categories: tiger-tails (top), skunk-tails (middle) and squares (bottom). Note that stimuli from the three categories are identical for the shortest width or height dimension used (far left). Consequently, stimuli were selected from only one of the categories for this dimension (nominally 'squares'). These patches had the smallest area and were 72 pixels square to the outer reaches of the modulation.

In all experiments, stimulus duration was 83 ms and the viewing distance was either 57 cm (for a spatial frequency of 1 c/deg) or 228 cm (for a spatial frequency of 4 c/deg). The fixation points were 5' (2 pixels) wide at 1 c/deg and 1.25' (2 pixels) wide at 4 c/deg.

2.3. Procedure

A temporal two-interval forced-choice (2IFC) technique was used where observers indicated which of the two intervals contained the target using one of two mouse buttons. The computer determined the

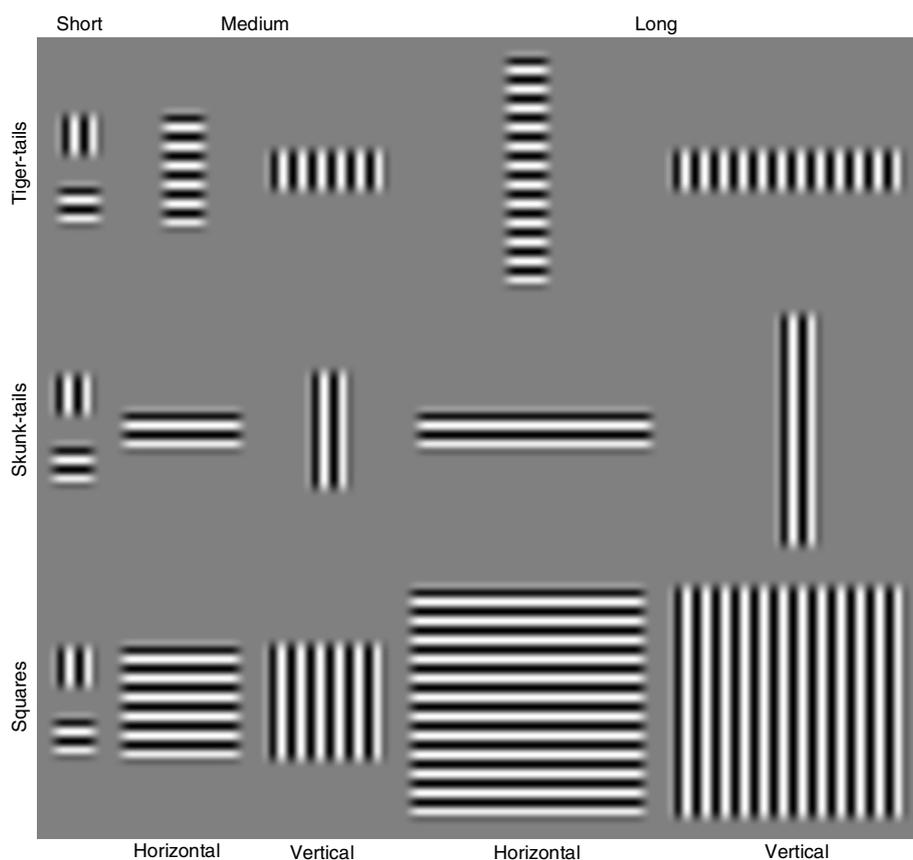


Fig. 1. High contrast examples of all of the stimuli used in the experiments. The three length dimensions are 1.73, 5.73 and 11.73 cycles. Experimental sessions were either blocked or interleaved across pattern, but always used the same carrier orientation.

temporal interval that contained the target randomly and auditory feedback was used to indicate the correctness of response. The two temporal intervals were marked by short tones at the onset of the stimulus. The duration between the offset of the first interval and the onset of the second interval was 500 ms. A 'three-down, one-up' randomly interleaved staircase procedure was used to control the magnitude of the target contrast. Estimates of threshold were made using probit analysis (Finney, 1971) to calculate the 75% correct point of psychometric functions based on about 100 trials accumulated over the last twelve 'reversals' for each of a pair of interleaved staircases tracking the same condition. The data gathered up to the first pair of staircase reversals was always discarded. In different experiments, trials for different shape conditions (Fig. 1) were either blocked or randomly interleaved. Runs for different orientations were always blocked, and the blocks were alternated across orientation. Thus, in the interleaved design there were up to seven pairs of staircases tracking the seven different shape conditions, where each staircase could be selected at random on each trial. In the blocked design, the staircase pairs were selected sequentially in a random order (i.e. a new staircase pair was not selected until both in the previous pair had terminated). Both observers took part in at least four replications of each of the conditions they performed in the various experiments. The data in the figures are the means and standard errors of these four replications and typically are based on ~400 trials per point. Observers took breaks between the replications but not within a session of blocked or interleaved shape conditions.

2.4. Observers

The two authors (TSM & RFH) served as observers and both wore their normal optical correction.

3. Results

3.1. 1 and 4 c/deg, interleaved

Fig. 2 shows the results for a spatial frequency of 1 c/deg and an interleaved design. The different columns are for different observers and the different rows are for vertical (top) and horizontal (bottom) orientations. The two solid lines have absolute slopes of 0.5 (square-root rule) and 0.25 (fourth-root rule), and provide fiducial contours against which the level of summation can be judged. Moving from left to right in each panel (of this figure and others): The first solid square is for the smallest stimulus size on the left of Fig. 1, the open symbols are for the medium and long tails and the solid squares are for the medium and long (large) square stimuli.

When the stripes (carrier orientation) were vertical, the stimulus shape had little effect on summation. For both observers, sensitivity improved with stimulus area to an extent slightly greater than the fourth-root rule. However, when the orientation of the stripes was horizontal, summation was stronger for the skunk-tails than the tiger-tails.

The effect of orientation on tail-type was also found when the spatial frequency was increased to 4 c/deg (and the retinal angle of the stimuli were scaled down accordingly), as shown in Fig. 3. However, for RFH the effect

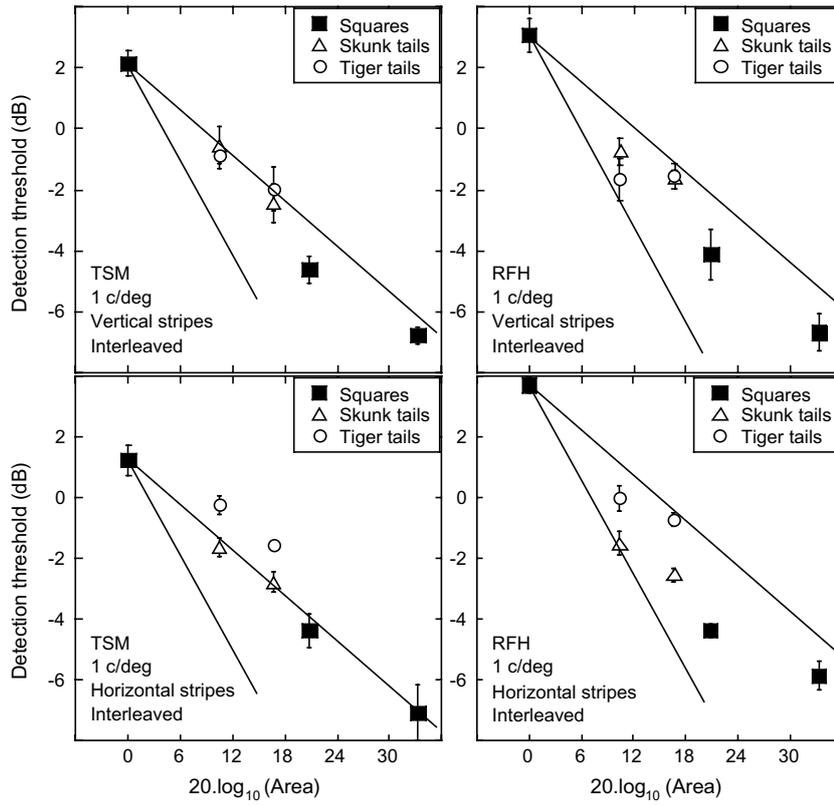


Fig. 2. Summation for the 1 c/deg patches of grating shown in Fig. 1. Error bars show ± 1 SE.

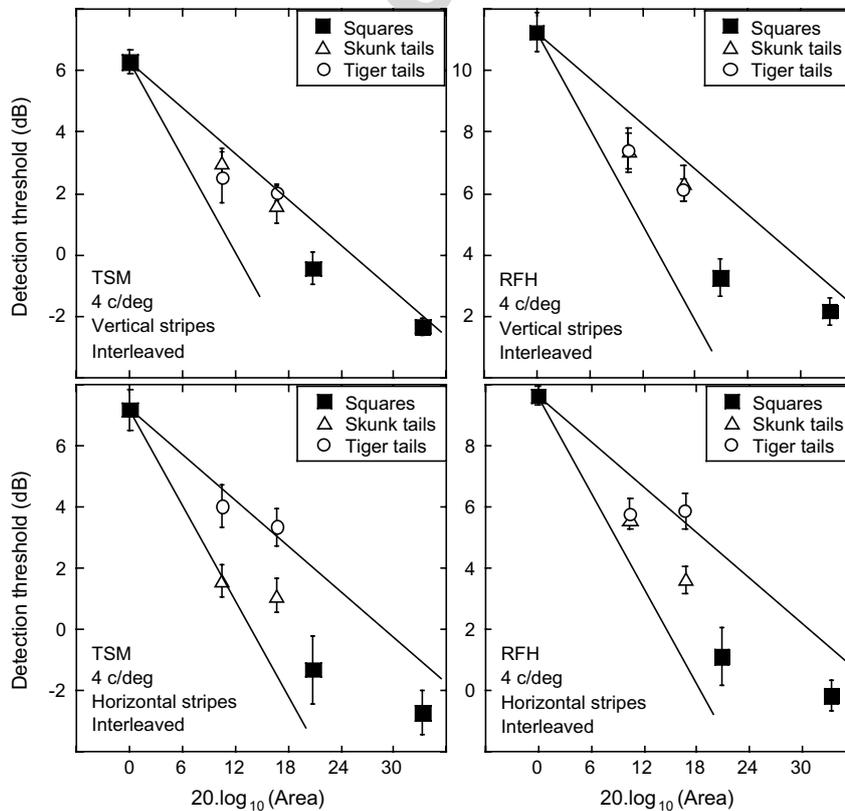


Fig. 3. Summation for the 4 c/deg patches of grating shown in Fig. 1. Error bars show ± 1 SE.

of tail-type was no longer evident at medium lengths (5.73 cycles), though it was present at the longest length (11.73 cycles).

3.2. Fixation point effects

Contemporary models of masking involve a pathway that causes suppression without any concomitant excitation (Foley, 1994). We wondered whether the fixation point might stimulate this pathway and exert a suppressive influence on the target. If this were so then, presumably, the effect would be greater for smaller stimuli located close to the fixation point than for larger stimuli, where parts of the stimulus are more distant from the fixation point. A consequence of this is that it would inflate the steepness of the summation slopes. To test this, TSM repeated the experiment with the central fixation point replaced by a square quad of points placed around the central patch, 45' (3 cycles; 72 pixels) apart along their virtual square edge. Four further pairs of points (45' between each point in the pair) were placed about the extremities of the longest stimulus tails (5 cycles to the right, left, above and below the points of the central quad). We refer to this as a quad-cross of fixation points, or for brevity 'quad fixation'. This arrangement provided a clear indication of the spatial extent of the targets, but spatially encroached only the medium and large square stimuli. Both observers found it

quite natural to hold central fixation using this arrangement.

Results are shown for TSM in Fig. 4 where the interaction between tail-type and orientation is replicated. However, there is a tendency for the data to sit higher in the plot (compare the symbol locations with the fiducial contours in Figs. 3 and 4 for TSM). This implies less summation here, and suggests that our concerns outlined above were justified. Further support for this comes from the observation that threshold for the smallest stimulus (left most square in the figures) is lower with quad fixation (Fig. 4) than with central fixation (Fig. 3). On the other hand, these conditions were performed about 9 months apart, and so a strict comparison is not valid. To check this more carefully, thresholds were measured again for the smallest patch and the method of fixation was blocked. We found that sensitivity was greater for quad fixation by 1.76 dB ($T = 3.92$; $p = 0.0029$, $DF = 10$; two-tailed). We also found that the slope of the psychometric function was very similar for the two fixation conditions, suggesting that uncertainty did not change across the two methods (the geometric means of the Weibull β were 3.49 and 3.58 for central and quad fixation, respectively).

As we have suggested already, one interpretation of this result is that the central fixation point might suppress the detection of a small, superimposed patch. But another interpretation is that the quad of points exerts a facilitatory influence on the central patch (cf. Chen & Tyler, 2001; Meese, Summers, Holmes, & Wallis, 2007; Yu, Klein, & Levi, 2002). We performed one final manipulation, which was to rerun the experiment (for the horizontal condition alone) with no fixation points. In this case, the results cannot be influenced by either suppression or facilitation from the fixation marks. There is a risk that uncertainty will increase and that the loss of an accommodation cue might raise detection thresholds, but this should neither favour nor disadvantage one tail-condition over another. The results in Fig. 5 show that the tail-type effect survives the removal of the fixation point. But the experiment sheds little light on the overall level of summation, which is close to a fourth-root rule for TSM, but in some cases much closer to a square-root rule for RFH.

Note that sensitivity to the smallest patch was about 1 dB less without quad fixation. (We confirmed this by measuring thresholds for this condition again and by blocking the type of fixation). This could be due to facilitation from the fixation marks, or loss of sensitivity due to an increase in uncertainty without them. If it were due to an increase in uncertainty then the slope of the psychometric function should be steeper with no fixation marks (Pelli, 1985). In fact, we found that it was slightly shallower ($\beta = 2.84$ and 3.34, for no and quad fixation marks, respectively), which brings this explanation into question.

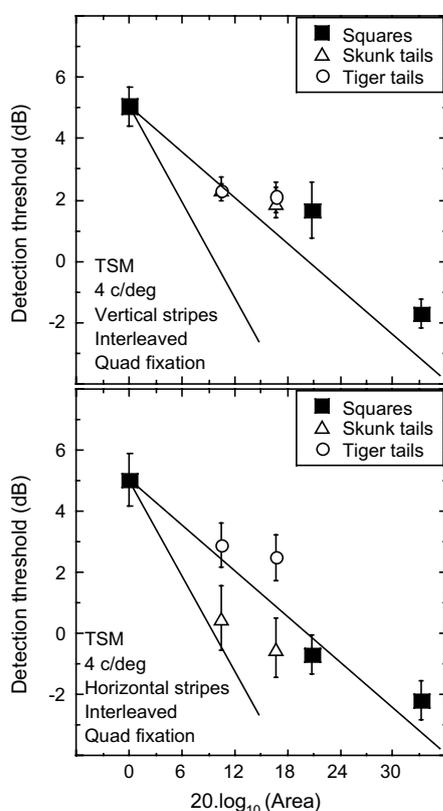


Fig. 4. The same conditions as in Fig. 3 for TSM, but with the central fixation point replaced by a quad-cross of fixation points. See text for details. Error bars show ± 1 SE.

3.3. Blocked design

As outlined in the introduction, ideal summation requires that the signal be known exactly, and this cannot

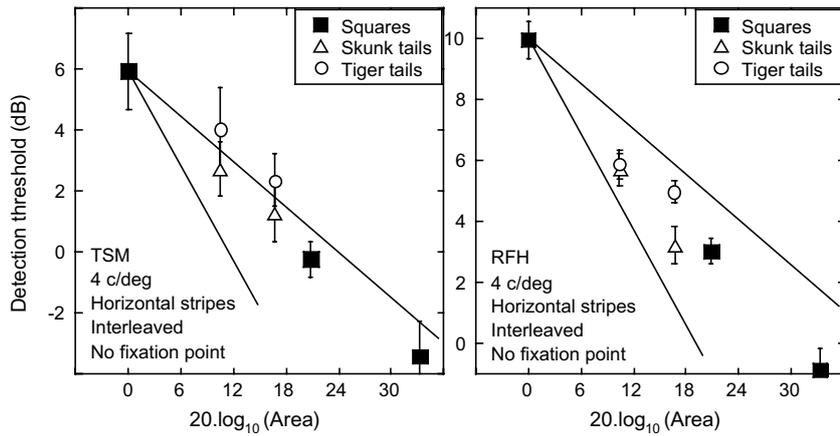


Fig. 5. The same horizontal conditions as in Fig. 3 (bottom), but with no fixation points. Error bars show ± 1 SE.

occur with an interleaved design. Fig. 6 shows summation results using a blocked design (and quad fixation) for the smallest patch and the ‘tails’ conditions only. Using this method, the only condition that approached the square-root rule was the medium length skunk-tail for RFH. However, there is a clear interaction between stimulus orientation and tail-type, with summation being greater for skunk-tails when the stripes were horizontal (as before).

A comparison between the results for TSM in Fig. 6 and those in Fig. 4 shows that whether trials were blocked or interleaved had little affect on summation, consistent with Meese et al. (2005).

3.4. Parafoveal stimulation

One problem with performing summation experiments in the fovea is that sensitivity declines at a rate of approximately 0.5 dB per cycle, with distance from the fovea (Foley et al., 2007; Pointer & Hess, 1989; Robson & Graham, 1981). Thus, as stimulus length is increases, the additional stimulation becomes less effective because of the drop in sensitivity, and the summation slope decreases. To overcome this problem we repeated the present experiment (using the quad fixation points and a blocked design), but shifted the stimulus centres away from the fovea (to the

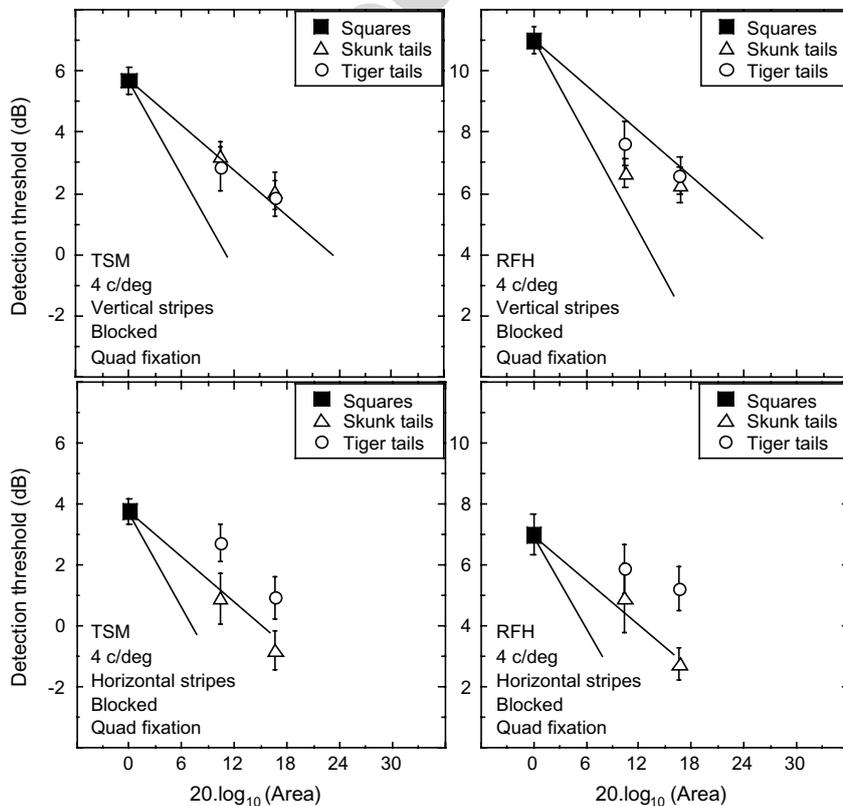


Fig. 6. The same conditions as in Fig. 3, but using a blocked design, quad fixation and for a restricted set of stimulus sizes. Error bars show ± 1 SE.

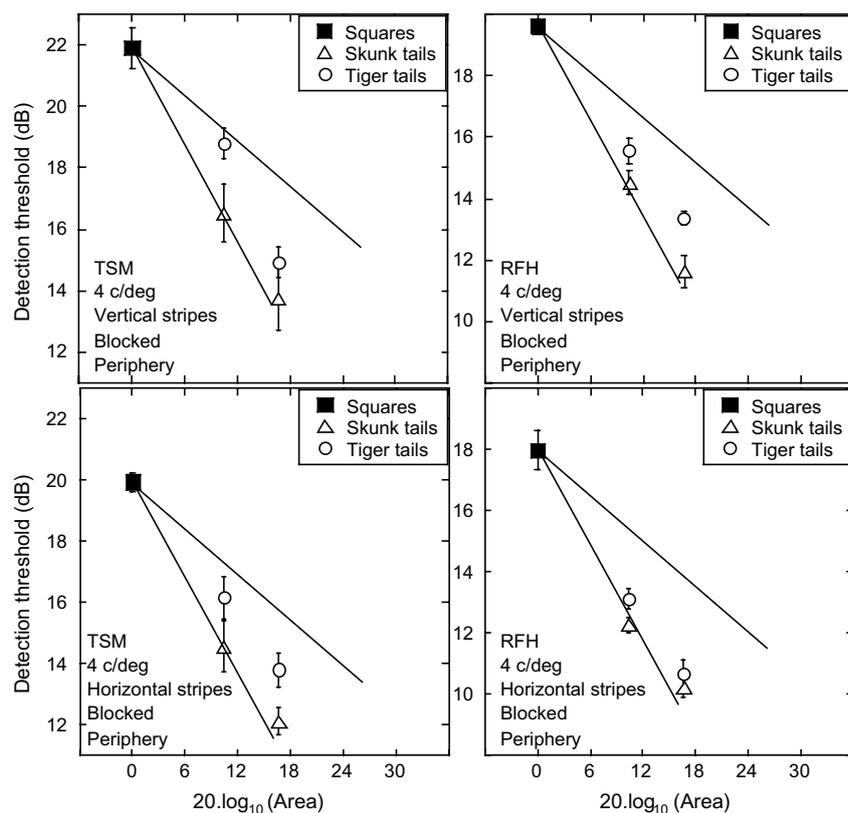


Fig. 7. The same conditions as in Fig. 6, but for stimulation in the upper right visual field (6.75 deg. away from the centre of the fovea). Error bars show ± 1 SE.

upper right quadrant) by a distance of 6.75 deg. (27 cycles). We did this by placing a large fixation point below and to the left of the display region. Although this arrangement is not immune to the effects of retinal inhomogeneity, the effects are not as severe as for foveal viewing (Robson & Graham, 1981).

Fig. 7 shows that this manipulation had a substantial effect on the level of summation. For both observers and both orientations, performance improved according to a square-root rule for skunk-tails. The improvement for tiger-tails was less than this in all cases, but markedly greater than the fourth-root rule. These results suggest that there are visual mechanisms performing summation of stimulus contrast up to about 12 grating cycles. This result is broadly similar to that of Manahilov et al. (2001), who measured summation of elongated 2 c/deg Gabor patches 7 deg above the fixation point. They found summation consistent with a square-root rule over 8 grating cycles.

4. Discussion

We have performed a series of experiments on spatial summation of luminance contrast. Our main aim was to investigate the claim that human vision contains visual mechanisms that sum luminance contrast within long receptive fields over lengths equivalent to eight stimulus cycles (Polat & Norcia, 1998; Polat & Tyler, 1999). Our

results raise two main issues for discussion: (i) the level of summation involved and (ii) the differences between skunk-tails and tiger-tails.

4.1. Level of spatial summation

Other than tail-type, at least two experimental factors affected the level of summation that we measured. These were the type of fixation point (more summation with a central point) and whether stimulation was foveal or parafoveal (more summation parafoveally). Taken with the differences between the two observers (e.g. Figs. 2 and 5), it is difficult to draw a firm conclusion regarding the shape of the spatial summation function for foveal stimulation. However, the parafoveal results provide a strong indication that for both tail-types, summation is greater than that predicted by probability summation over about 12 stimulus cycles. Mayer and Tyler (1986) came to a similar conclusion and Manahilov et al. (2001) found evidence for quadratic spatial summation in the parafovea using Gabor patches. In contrast, Robson and Graham (1981) found nothing more than probability summation in their study. They stimulated the retina much more peripherally (an eccentricity equivalent to 42 grating cycles of their stimulus) than Manahilov et al. or us, though at the same distance (in terms of stimulus cycles) as Mayer and Tyler

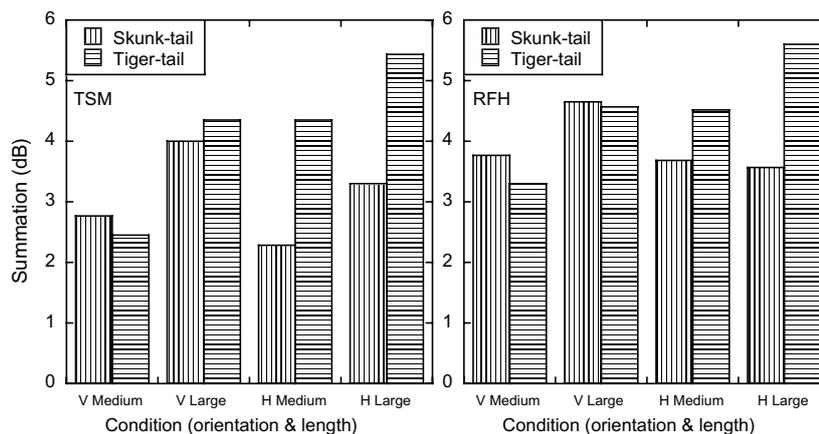


Fig. 8. Summation for the medium (5.73 cycles) and large (11.73 cycles) square patches relative to vertical (V) and horizontal (H) skunk-tails and tiger-tails (different shading) of the same length as the squares. Different panels are for different observers. (For TSM, data are averaged from Figs. 2–4. For RFH data are averaged from Figs. 2 and 3.)

(1986). It remains unclear why Robson & Graham's results are so different from the rest.

For all of the experiments here where thresholds for square patches were measured, mean sensitivity to the tails was always less than for the square whose side was the same length (Figs. 2–5), though in some cases the differences were small for skunk-tails (Fig. 4). To quantify this, Fig. 8 shows the average difference in thresholds between tails and their corresponding squares (i.e. it shows the amount of summation at right-angles to each tail's length). For vertical carriers the effects were similar for both tail-types but for horizontal carriers, the effects were larger for tiger-tails than skunk-tails. This is largely because the orientation anisotropy here is specific to tail stimuli, and not a general anisotropy in summation (see next subsection). However, regardless of these details, spatial summation of large fields cannot be attributed to summation within elongated fields alone.

4.2. Skunk-tails versus tiger-tails

Although design details can affect the steepness of the summation slope (see above), it is unlikely that they are responsible for our universal finding that sensitivity is greater for horizontal skunk-tails than for horizontal tiger-tails. Other than in the parafovea, we also have a consistent finding that sensitivity for different tail-types was the same for vertical gratings. But how do these results compare to those from other studies? Part of the problem here is that some laboratories (see Introduction) fixed carrier orientation across tail-type, whereas others co-varied carrier orientation with tail-type. We did both, but always plotted results together for the same carrier orientation. To provide a more general overview of our findings, normalised averages across the various experiments in which both orientations and tail-types were used are shown for both observers in Fig. 9. This confirms the effect of tail-type for horizontal carriers and the absence of this effect for vertical carriers. This also shows

how the conditions compare across carrier (stripe) orientation. Broadly speaking, summation for horizontal skunk-tails is strongest, that for horizontal tiger-tails is weakest, and the two vertical conditions are intermediate. Further analysis (not shown) confirmed that for both observers, average summation for the largest square conditions was very similar for the two carrier orientations. For the medium squares, summation was very slightly greater (<1 dB) for the horizontal orientation.

Our first comparison is with Polat and Tyler (1999), where the data were gathered under two sets of conditions. The experiments from the Tyler laboratory were performed using vertical sine-wave carrier gratings (Tyler, personal communication), and substantially more summation was found for skunk-tails than tiger-tails. For one observer, the effects were in the order of 8 dB, whereas for the other they were around only 2 dB. We have not replicated that result here, as we found no difference across tail-type for vertical carriers (triangles in Fig. 9). The reason for the discrepancy is not clear. Both studies used the same spatial frequency (4 c/deg) and similar mean luminances (54 cd/m², versus 60 cd/m² here). Both expressed overall stimulus contrast as Michelson contrast and included conditions where the fixation marks surrounded the target. The stimulus duration was longer for Tyler's experiments (600 ms raised cosine envelope there, versus 83 ms pulse here). However, Tyler's summation bias for skunk-tails is not limited to long stimulus durations because results from the Sagi laboratory (Polat & Tyler, 1999) confirmed the effect (in the order of 4–6 dB) using an 80 ms pulse. The envelopes had different profiles in the two studies (raised-cosine here, Gaussian for Polat and Tyler), but this is unlikely to be the explanation because Foley et al. (2007) used very similar stimuli to Polat and Tyler (vertical Gabor patches) but found little difference in summation across tail-type. Finally, comparing across similar stimulus lengths, Howell and Hess (1978), Foley et al., and our study all found summation slopes that were typically less

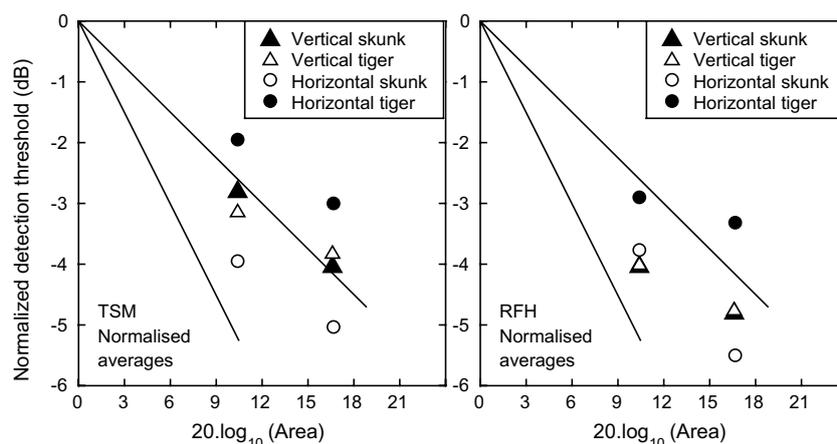


Fig. 9. Average results from all experiments where data were gathered for both tail-types and both carrier orientations and foveal stimulation. (For TSM, data are averaged from Figs. 2, 3, 4, and 6. For RFH data are averaged from Figs. 2, 3 and 6.) Results were normalised to the detection threshold for the smallest patch before averaging. Experiments from Foley et al. (2007) and the Tyler laboratory in Polat and Tyler (1999) should be compared with the open and closed triangles. Experiments from the Sagi laboratory in Polat and Tyler (1999) should be compared with the solid circles and triangles. The appropriate conditions from modelfest should be compared with the open and closed circles.

steep than those for the skunk-tails in the Polat and Tyler study. In sum, the lack of tail-effect for vertical carriers here (triangles in Fig. 9) is consistent with the results from Howell and Hess and Foley et al., but not Tyler.

The experiments from the Sagi laboratory (Polat & Tyler, 1999) involved comparisons across vertical skunk-tails and horizontal tiger-tails. Here we confirm the difference in summation across those conditions (solid symbols in Fig. 9), but the size of the effect here is much less than that found by Polat and Tyler (1–1.5 dB here; 4–6 dB for Polat and Tyler). Again, it is unclear what is responsible for these differences.

At first sight our results might also seem at odds with those from modelfest (e.g. Carney et al., 2000) where thresholds have been measured for various types of horizontal (and other) gratings for 16 observers. (The relevant modelfest conditions are: ‘Baguettes’ 18, 19, 20 and 21 and ‘GaborPatch’ 12). When their one-octave wide Gabor patch was doubled in either length (a skunk-tail) or height (a tiger-tail), sensitivity improved by about 3 dB, consistent with a square-root summation rule (for an earlier analysis on a smaller dataset see Carney et al., 2000). However, as noted before (Carney et al., 2000), further increases resulted in much slower improvement, inconsistent with the very long receptive fields suggested by Polat and Tyler. Notably, sensitivity to the longest skunk-tail was only 0.76 dB greater than for the longest tiger-tail. However, the stimuli used in that study are subject to transformation of Michelson contrast by the Gaussian windowing described in the Introduction: the peak to trough amplitude of the tiger-tail was about 1.3 dB greater than the skunk-tail. So this translates to a sensitivity difference of 2.06 dB across tail-types, which is remarkably consistent with the results for horizontal carriers reported here (see Fig. 9). The modelfest group did not investigate a similar variety of vertical gratings.

Our last comparison is with Manahilov et al. (2001) who are in agreement with us that summation is substantial

(~square-root rule) for parafoveal stimulation. However, they found no effect of tail-type, whereas we found small effects using both carrier orientations (Fig. 7). It is possible that this difference across the studies is also due to the effect of Gaussian windowing discussed above.

4.3. Mechanisms for spatial summation

As outlined in the Introduction (also see below), a failure to find steep summation curves (slope $\sim 1/2$) in the fovea does not stand as evidence against dedicated summing circuits. Meese (2007) considered the situation where the smallest stimulus was a circular grating patch with a diameter of one cycle. He showed that a filtering stage followed by spatial inhomogeneity, accelerating contrast nonlinearity and summation of both signal and noise produces a summation curve that begins steep ($\sim -1/2$) but declines rapidly. This is consistent with experimental results where the areas of circular and square patches of grating have been varied over a similar range (Foley et al., 2007; Meese, 2007; Rovamo et al., 1994; Rovamo et al., 1993). There is also good physiological evidence for higher-order spatial summation of contrast across length in V1 (Gilbert & Wiesel, 1985) and up to 16 cycles of length and width in V4 (Pollen, Przybyszewski, Rubin, & Foote, 2002). Studies in which summation has been measured over small distances (Kersten, 1984; Rovamo et al., 1993; Rovamo et al., 1994; modelfest) have reported evidence for foveal contrast summation of up to about 4 grating cycles, and structural information can be integrated over much larger areas (Field, Hayes, & Hess, 1993; Wilson & Wilkinson, 1998).

4.4. What processes might underpin the summation results here?

The extent to which physiological summation and probability summation contributed to the results of this study is

not clear. Neither are we lead to firm conclusions regarding the physiological underpinnings of the threshold anisotropies. However, there are several factors that could contribute, and more than one may be involved. We summarise these in Fig. 10, which for simplicity shows only a single pooling mechanism for each tail-type, though we envisage a range of mechanisms pooling over a range of spatial extents. In Fig. 10a, different levels of summation reflect differences in the spatial extent of the pooling. Thus, in this scheme, the asymmetry of the pooling mechanisms is a direct reflection of the asymmetries in the experimental data. This is one of the schemes considered by Polat and Tyler (1999).

A second factor is shown in Fig. 10b. Using patches of horizontal grating, Pointer and Hess (1989) found that sensitivity declines at about 0.3 dB per cycle in the horizontal meridian and about 0.5 dB per cycle in the vertical meridian (see numerical insets, which represent sensitivity for 2-

cycle steps). This asymmetry could contribute to the higher levels of summation seen for horizontal skunk-tails over tiger-tails because the tiger-tails extend into the less sensitive vertical meridian. As detailed comparisons across meridians for vertical gratings have not been performed, no insets are shown for the vertical carrier in Fig. 10b.

A third factor is shown in Fig. 10c. Here the pooling mechanisms are extended to include one suitable for the square stimuli. For vertical carriers, the observer can select between this type of mechanism and those that pool appropriately for the tail stimuli. For the horizontal carriers we show an extreme situation where there are no pooling mechanisms for the tiger-tails. In this case, the square mechanism could be used to sum over an entire tiger-tail, but at the cost of summing additional noise. Thus, the efficiency for horizontal tiger-tails is less than for the other stimuli and sensitivity is lower (Fig. 9).

4.5. Fixation marks

Previous studies have used a variety of different configurations for fixation marks, presumably because the authors had concerns similar to ours about interactions between the fixation marks and the test stimuli. However, we do not know of any previous study that has demonstrated the effects that we found here. We found different thresholds for the smallest patch using (a) a single central fixation point, (b) no fixation points and (c) a quad-cross of fixation points (lowest, intermediate and highest sensitivity, respectively). Uncertainty effects are often attributed to the loss of sensitivity from (c) to (b), though we found no evidence for this from the slope of the psychometric function. It seems unlikely that uncertainty or accommodation cues would change very much from (a) to (c), leaving suppression as a likely contender. Whether this is due to masking or different states of adaptation is not clear. Finally, we cannot rule out the possibility that facilitatory sensory interactions are involved in (c).

It remains unclear how other studies might have been affected by these issues. Foley et al. (2007) used cross-hairs with a central gap as fixation marks Howell and Hess (1978) and Rovamo et al. (1993) used no fixation point, and the modelfest group used a square arrangement of four L-shaped markers that were each 1.5 deg away from the centre of the display. Two of the observers in the Polat and Tyler study used a fixation configuration similar to our central quad of points, and for the other two, a central fixation circle appeared before the onset of the stimulus. It is not clear whether it was removed during stimulus presentation, but in any case, it might have contributed to suppression of the central target region and subsequent overestimation of summation slopes.

5. Summary and conclusions

For foveal stimulation we have demonstrated a clear advantage for skunk-tails over tiger-tails, but only for

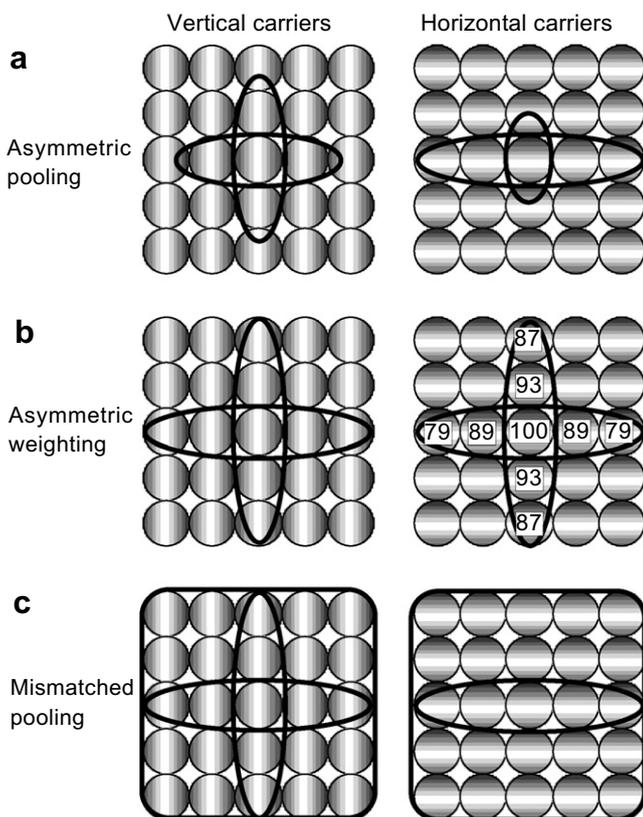


Fig. 10. Three higher-order pooling schemes for noisy first-order filters in spatial vision. Vertical and horizontal first-order filters are shown on the left and right respectively. (a) The spatial extent of pooling for vertical carriers is similar for both tail-types (both meridians), but less than for horizontal skunk-tails and more than for horizontal tiger-tails. (b) The spatial extent of pooling is the same for both carrier orientations and both tail-types. However, for horizontal carriers, sensitivity of the first-order filters declines at a faster rate for tiger-tails than for skunk-tails (numerical insets). Insets are not shown for vertical carriers as these have not been thoroughly investigated across different meridians. (c) Pooling mechanisms are available for both tail-types and both carrier orientations, but are not matched to the horizontal tiger-tails. In this case, pooling results in greater summation of noise than for the three matched cases and performance is compromised.

horizontal carriers. For vertical carriers, summation for the different tail-types was similar. These results are consistent with those of Howell and Hess (1978) and Foley et al. (2007), and modelfest (Carney et al., 2000). Our results are qualitatively consistent with those from the Sagi laboratory in Polat and Tyler (1999) but not those from the Tyler laboratory. We have not been able to resolve this discrepancy.

For parafoveal stimulation, we found substantial summation for both skunk-tails and tiger-tails. These high levels of summation are consistent with those of Mayer and Tyler (1986) and Manahilov et al. (2001), but not Robson and Graham (1981). It remains unclear why the earlier study found different results from the rest.

Overall, the evidence from these studies supports high levels of spatial summation of contrast in the periphery, but much less so in the fovea. However, the spatial restriction in the fovea could be a consequence of the compounding effects of retinal inhomogeneity, size dependent noise, and contrast response nonlinearity (Meese, 2007). Thus, it remains possible that contrast is summed over several cycles in both the fovea and the periphery, but that the process has remained obscured in the fovea.

The asymmetries in our results (across tail-type) could be due to anisotropies in either (i) the sensitivities of lower-order mechanisms that detect small regions of the stimulus (ii) the connectivity between the lower-order mechanisms and higher-order summing units or (iii) mismatched summation mechanisms that pool additional noise in conditions where sensitivity is lowest.

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