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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.


*Keywords:* Human vision; Spatial summation; Area summation; V1; Contrast detection; Modelfest; Ideal summation; Energy; Contrast sensitivity; Filter shape

## 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 Pythagorian 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 modelfest 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 ($\mathrm{resp}_i$), 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 ($\mathrm{resp}_{\mathrm{total}} = \sum_i (\mathrm{resp}_i^k)^{1/k}$) 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.