Available online at www.sciencedirect.com

ScienceDirect

Vision Research 47 (2007) 3108–3119

Vision Research

www.elsevier.com/locate/visres

Collinear facilitation: Effect of additive and multiplicative external noise

Pi-Chun Huang *, Robert F. Hess

McGill Vision Research Unit, Department of Ophthalmology, McGill University, Montreal, Que., Canada H3A 1A1

Received 23 February 2007; received in revised form 24 May 2007

Abstract

The detectability of a Gabor patch is improved by the presence of collinear flanking Gabors, this phenomenon is termed collinear facilitation. In experiment 1, we investigate the effects of adding 2D spatial luminance noise as a means of investigating different transects through the suprathreshold contrast space to see whether facilitation is ubiquitous throughout the contrast domain or whether it is confined to absolute contrast threshold. The results show that adding luminance noise abolishes the facilitation, showing it is confined to absolute threshold. In experiment 2, we assess whether 2nd order stimuli exhibit collinear facilitation and whether 1st order flanks can induce facilitation in 2nd order stimuli and vice versa. Our results suggest that collinear facilitation, albeit weaker, does occur for some 2nd order stimuli but we did not find any 1st/2nd order interactions, suggesting separate 1st/2nd order cortical processing streams, at least at the level at which this phenomenon occurs. Our two main findings, namely the lack of facilitation at suprathreshold contrasts and its presence for 2nd order processing argue against it playing a pivotal role in contour integration which does occur at all contrasts but not for these 2nd order stimuli.

Keywords: Collinear facilitation; First order; Second order; Additive noise; Multiplicative noise; Contour integration

1. Introduction

The detectability of a spatially bandpass target-element is dependent on the spatial properties of elements in its local neighbourhood. Neighbouring elements that form a common global alignment can facilitate its detection; this is termed collinear (or flank) facilitation (Polat, 1999; Polat, Mizobe, Pettet, Kasamatsu, & Norcia, 1998; Polat & Sagi, 1993, 1994a,b; Polat, Sagi, & Norcia, 1997; Woods, Nugent, & Peli, 2002). A typical stimulus configuration is where the detectability of a central target Gabor element is measured in the presence and absence of two high-contrast flanking Gabor elements of the same orientation and phase. The key determinants of this facilitation are the suprathreshold contrast of the flanks, the flank-to-target distance (i.e. 3–6 × spatial period of the target), the global orientation alignment of the target and flank ensemble (Polat, 1999; Polat & Sagi, 1993, 1994a,b; Polat et al., 1997, 1998; Woods et al., 2002), the phase (Solomon, Watson, & Morgan, 1999; Williams & Hess, 1998) and chromaticity (Chen & Tyler, 2002; Huang, Mullen, & Hess, 2007) of the flank and target. Although the response of cells in V1 has been shown to be modulated by the presence of spatially aligned stimuli falling outside the classical receptive field (Kasamatsu, Polat, Pettet, & Norcia, 2001; Mizobe, Polat, Pettet, & Kasamatsu, 2001; Polat et al., 1998), it is as yet unresolved what mechanism underlies this lateral spatial interaction. One possibility is that detection is mediated by neurons with elongated receptive fields, a notion supported by the finding that flank facilitation is phase and contrast dependent (Solomon et al., 1999; Williams & Hess, 1998; Woods et al., 2002). Another explanation involves multiple neurons at different locations in the visual field interacting via the long-range lateral connections known to exist between V1 cells of similar orientation preference (Hirsch & Gilbert, 1991; Ts'o, Gilbert, & Wiesel, 1986; Weliky, Kandler, Fitzpatrick, & Katz, 1995) or by way of feedback from extra-striate sites (Gilbert & Wiesel, 1989; Girard, Hupe, & Bullier, 2001).

* Corresponding author. Fax: +1 514 843 1692.
E-mail address: pi-chun.huang@mcgill.ca (P.-C. Huang).

0042-6989/$ - see front matter © 2007 Elsevier Ltd. All rights reserved.
doi:10.1016/j.visres.2007.08.007

Here, we ask two questions that are relevant to a better understanding of collinear facilitation and of the cortical cells that may underlie it. Both questions involve the use of 2D visual noise either added or multiplied to the typical stimuli (e.g. 1D Gabors) used to demonstrate collinear facilitation. Since collinear facilitation has only been demonstrated to occur at absolute threshold (i.e. facilitation relative to absolute threshold, see Williams & Hess, 1998), we wonder if this represented a fundamental constraint or whether it could, by a suitable manipulation (i.e. the use of additive noise), be shown to be ubiquitous through the contrast domain (i.e. facilitation relative to any noise-elevated threshold). The threshold elevation provided by additive noise being used to provide different transects through the suprathreshold contrast space. Our second question relates to noise-modulated Gabor stimuli (i.e. multiplicative noise). Since there is good evidence that cells in the visual cortex of primates and cats respond to both luminance- and contrast-defined features (e.g. noise-modulated Gabors) of the retinal image (Sutter, Sperling, & Chubb, 1995), we wondered whether collinear facilitation is as much a property of 2nd order processing as it is for 1st order processing.

An answer to these questions is important for two reasons, the first regards the cellular basis of collinear facilitation and the second, its functional role in perception. If collinear facilitation is a general property of cortical cells then one would expect it to occur throughout the contrast range as well as for second order stimuli, as there is good evidence that cortical cells not only have different absolute contrast thresholds but also they respond to both luminance and contrast-modulated stimuli. If, on the other hand, collinear facilitation is restricted to the processing of 1st order information at absolute threshold then its cellular basis must be likewise confined to only a sub-set of cells with these defining properties. Functionally, a case has been made for collinear facilitation providing the building blocks of contour linking and feature integration (Polat, 1999; Polat & Bonneh, 2000). Contour linking is unaffected by contrast (Hess, Dakin, & Field, 1998) and if collinear facilitation represents its fundamental building block, it too should operate throughout the contrast range. Although it was originally thought that 1st and 2nd order information was always integrated at higher stages in the visual pathway (Cavanagh, Arguin, & von Grunau, 1989; Ferrera & Wilson, 1991), it is now clear that there are specific rules when this does and does not happen. For example, 2nd order information appears not to be used at all for some tasks, for example form-from-motion (Hess & Ziegler, 2000; Landy, Dosher, Sperling, & Perkins, 1991; Mather, 1989) and form-from-stereo tasks (Ziegler & Hess, 1999) as well as contour integration (Hess, Ledgeway, & Dakin, 2000). Second order stimuli do not cohere across space (Hess & Ziegler, 2000) and if collinear facilitation is necessary for such linking operations then one would expect it to be entirely absent for all kinds of 2nd order stimuli.

Here, we use both additive and multiplicative 2D visual noise to create 1st and 2nd order stimuli of comparable spatial composition to explore two issues, namely (1) whether collinear facilitation occurs throughout the contrasts range (utilizing the threshold raising effects of additive noise) and (2) whether collinear facilitation also occurs for 2nd order stimuli (utilizing multiplicative noise to construct contrast-modulated 2nd order stimuli). Our results show that collinear facilitation occurs only at absolute threshold being absent for contrasts above absolute threshold. Secondly, 2nd order stimuli with 1D carriers do exhibit collinear facilitation but there is no evidence for luminance-defined flanks producing collinear facilitation in contrast-defined target stimuli and vice versa.

2. General methods

2.1. Observers

Five observers, PCH, BCH, XFL, LHY, and ATO (only 1D noise experiment) with normal or corrected-to-normal vision participated in the experiments. Two of the subjects (XFL and LHY) were naïve to the purpose of the experiments and had no prior experience in measures of contrast sensitivity. Several practice runs were undertaken by these two participants.

2.2. Apparatus

The stimuli were presented on an Electrohome (Retro III) back-projection CRT system (127.5 cm by 98 cm) and generated by a Pentium PC by using the VSG2/5 graphics card (Cambridge Research Systems Ltd, UK), which had pseudo 15 bits contrast resolution. Frame interlacing was used so that the contrast range could be individually optimized for target and flanks. The screen resolution was 928×732 pixels with frame rate of 120 Hz and the screen mean luminance was 67 cd/m^2. The monitor's gamma value was determined by measuring the relationship between input luminance and measured screen luminance with a photometer (UTD instrument, with a V_λ filter), and the monitor's gamma non-linearity was corrected by means of a software look-up table in the VSG.

2.3. Stimuli

Five types of stimuli were used and are illustrated in Fig. 1a and c. The first stimulus (exp. 1—leftmost in Fig. 1a) is a luminance Gabor (L) and it can be described by the following equation:

$$I(x,y) = I_0 + g\cos(2\pi x/T - \rho) \times \exp[-(x^2+y^2)/2\sigma^2] \quad (1)$$

where I_0 is mean luminance, g is grating contrast, T is the period of the sinusoid, ρ is the phase of the stimulus with respect to the center of a Gaussian window, and σ is the standard deviation of the Gaussian envelope.

The second stimulus (exp. 1—middle in Fig. 1a) is a luminance modulated stimulus (L + N), which consisted of a luminance Gabor to which is added 2D binary noise, all windowed by a 2D Gaussian spatial envelope. The stimuli can be described by the following equation:

$$I(x,y) = I_0[1 + nN(x,y) + g\cos(2\pi x/T - \rho)] \times \exp[-(x^2+y^2)/2\sigma^2] \quad (2)$$

where $N(x,y)$ is the binary noise sample, n is the noise contrast, and g, I_0, T, ρ, σ are the same as Eq. (1). L + N stimuli were constructed by presenting a noise and a grating image, both of which were multiplied by Gaussian window individually, in alternate frames. The noise contrast was kept 0.6 in order to prevent any adjacent pixel non-linearity before interlaced (see Section 2.5 for details). The final contrast of the stimuli was defined by g value.

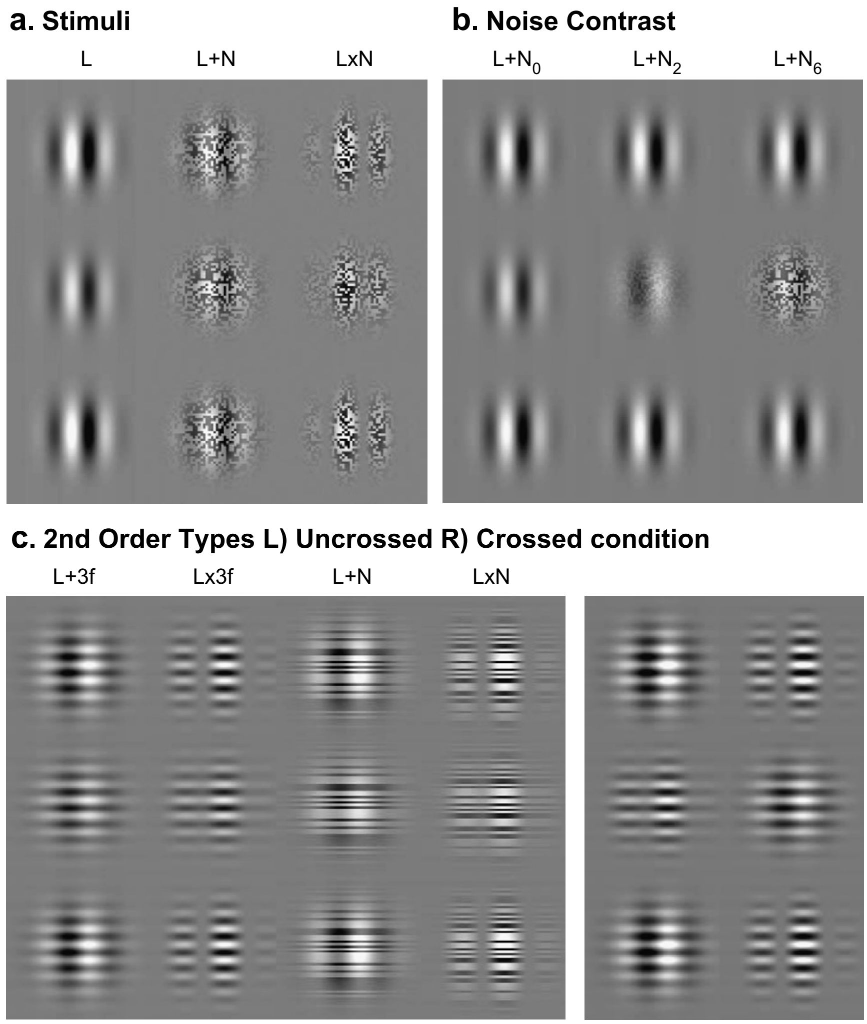

Fig. 1. Examples of stimulus configuration used in each experiment. (a) "L" represents target and flanks are Gabor patches; "L + N" represents target and flanks are Gabor patches to which is added 2D binary noise. "L × N" represents target and flanks are Gabor patches multiplied by 2D binary noise. (b) The stimuli used to measure the TvN function. Flanks are luminance Gabors and the target is a luminance Gabor to which is added to variable contrast of 2D noise (from left to right columns: rms noise contrast goes from 0 to 0.3). (c) Stimulus configuration used in experiment 3. Left box shows the uncrossed condition, in which target and flanks are all L + N or L × N stimuli. "L + 3f" represents the target and flanks are luminance Gabors to which is added a horizontal gratings with a spatial frequency of 3 times that of the target. "L × 3f" represents the target and flanks are luminance Gabors multiplied by horizontal gratings. "L + N" and "L × N" are the same as L + 3f and L × 3f, respectively, except that the carrier is now 1D horizontal noise. Right lower box shows the stimulus configuration for the crossed condition in which the target and flanks are of different order. First column is L + 3f flanks with L × 3f target and the second column is L × 3f flanks with L + 3f target.

The third stimuli (exp. 2—rightmost in Fig. 1a) was a contrast-modulated stimulus (L × N) which comprised the modulation of the contrast of 2D binary noise by a Gabor function, and the equation can be described as

$$I(x,y) = I_0[1 + nN(x,y) \times (1 + g\cos(2\pi x/T - \rho))] \times \exp[-(x^2 + y^2)/2\sigma^2]. \quad (3)$$

And this equation can be rewritten as

$$I(x,y) = I_0[1 + nN(x,y) + ng \times N(x,y) \times \cos(2\pi x/T - \rho)] \times \exp[-(x^2 + y^2)/2\sigma^2]. \quad (4)$$

Parameter values are the same as Eq. (2). The advantage of Eq. (4) is that it separates the noise image from its sideband image ($N(x,y) \times \cos(2\pi x/T - \rho)$). The stimulus is constructed by presenting noise and sideband in alternative frames. The modulation depth of L × N stimuli was defined as the contrast ratio between sideband images to noise image. Thus the modulation depth of the L × N and the contrast of the L + N can be varied by simply changing the look-up tables for the sideband or the luminance image, ensuring that each contrast/modulation depth had the same number of step sizes.

Each image patch was displayed within a rectangle that is 4.75σ by 4.75σ to prevent an edge artifact. Each image is 76 × 76 pixels and the noise element size was 2 × 2 pixels which means each cycle has 19 noise samplings. With a viewing distance of 200 cm, the spatial frequency is 0.75 cycle/degree, space constant (σ) was 0.53 degree (16 pixels) which makes the bandwidth of the Gabor about 1.39 octaves. The noise element was 4.2 × 4.2 arc min. The absolute phase of the grating was sine phase and randomized between trials but not between intervals within a trial. Both the noise and the modulation were static during the presentation interval.

In experiment 2, two additional versions of 2nd order stimuli were used, both with horizontally oriented carriers. The first version consisted of a 1D sinusoid carrier of 3 times the frequency whereas the second version consisted of a 1D noise carrier (see Fig. 1c, leftmost frame; L × 3f and L × N). In each case there is a 1st order control involving the same spatial components added, not multiplied together (see Fig. 1c, leftmost frame: L + 3f and L + N). The crossed condition involved 1st order flanks and a 2nd order target or vice versa (see Fig. 1c, rightmost frame).

2.4. Procedure

Detection thresholds for the three stimulus types were measured using a two interval forced choice paradigm. Interleaved noise (or just background) and sideband (or luminances) were presented in both intervals but in the non-target interval, the contrast of the sideband (or luminance) was set to zero. The subject had to indicate which interval contained the central target. A double staircase method was used to determine the threshold for the target alone as well as for the target in the presence of the flanks within each block. The 2-down and 1-up double staircase method, in which target contrast was increased 0.25 times the contrast following the incorrect response, decreased 0.125 times the contrast following two correct responses, was used in the experiment. The threshold was the average of the last five reversal points, equivalent to 81.6% correct level. During the double staircase, if one experimental condition had six reversal points, that condition ended but the other condition continued. The order of the conditions was random. The temporal presentation of the stimulus was 1000 ms with a Gaussian envelope of sigma 125 ms. The inter-stimulus interval was 1000 ms. The detection threshold was an average for four staircase measures. The *Threshold Elevation* (TE) was defined by the following equation for each run:

$$TE = \log_{10}\left(\frac{TH_{withFlanks}}{TH_{withoutFlanks}}\right). \quad (5)$$

The standard errors for TE were calculated, which was derived from four staircase estimates. If the value of TE was less than zero, it indicates facilitation. A Student *t*-test was used to evaluate if the TE was significantly different from zero for each subject. Group means for each experimental condition were also calculated and reflected between-subject variance.

The amount of facilitation was compared for L, L + N (exp. 1), and L × N (exp. 2) stimuli. Three different target-flank separations (2, 3, 6 λ, which is equal to 2.67, 4, 8 degree visual angle) and two phase conditions (target and flanks were either in the same phase or were 180 degree out of phase) were compared in experiments 1 and 2.

To ensure that L, L + N (exp. 1), and L × N (exp. 2) flanks were of comparable visibility, the detection thresholds of the flanks for each target-flanks separation were measured first. A 2AFC procedure with staircase method was used to make four determinations of the threshold of each of these types of flanks. The contrast of the flanks in both experiments was set to 4 times the threshold in L, L + N (exp. 1), and L × N (exp. 2) conditions. In another control experiment the contrast of the flanks was set to zero so that only noise patches (contrast of 0.3) were presented for three different target-flank distances (2, 3, 6 λ). In the noise contrast experiment, the procedure was the same as for experiment 1, except that the flank stimulus type was L. The noise was added just to the central target Gabor (Fig. 1b) and its rms contrast was varied.

2.5. Calibration

Careful calibration is necessary when using L × N stimuli as a non-linearity in either the display equipment or the visual system could result in luminance artifacts being generated and aiding detection. To ensure that this did not happen we did the following. The projector was gamma corrected and its calibration checked every month. The adjacent pixel non-linearity (APNL) was also checked. The APNL causes a reduction in the mean luminance of the high-contrast image when the luminance change between two adjacent pixels is large in the same video scan line. In turn this results in a luminance artifact that cannot be measured using a standard gamma correction procedure. To assess the influence of this type of non-linearity as well as any biological non-linearity within the early visual pathway, we used a psychophysical motion task adapted from Ledgeway and Smith (1994): four images are sequentially presented for 100 ms. The 1st and 2nd order stimuli were alternatively presented and the phase of the stimulus was 90 degree shifted for each image. The subject was asked to indicate the motion direction of the stimulus. The logic of the task was that if the 2nd order stimulus contained any luminance information, the direction of motion will be biased to one direction. If there is no luminance artifact in our 2nd order stimulus, the motion direction will be ambiguous. The noise contrast and noise size were varied to null out any artifact. PCH participated in this control experiment. If the noise contrast was not higher than 0.6 and the noise element not smaller than 2 by 2 pixels, no luminance artifact was present. So we used these values for our stimulus parameters.

3. Results

3.1. Experiment 1—additive noise

3.1.1. Comparison of collinear facilitation for stimuli without and with additive 2D noise

The detection thresholds of the flanks alone were measured and a within-subject ANOVA test showed that the detection thresholds did not vary with separation (i.e. eccentricity) for stimuli without (i.e. L) and with (i.e. L + N) luminance noise ($F_{(2,6)} = 5.54$, 1.58 for L and L + N, respectively). A control experiment involving three subjects also showed that if the flanks comprised only noise, there was no facilitation effect for an L + N target stimulus (within-subject two ANOVA test, $F_{(2,4)} = 0.87$), indicating flanks comprising just noise did not facilitate the detection of a target Gabor containing additive noise. Therefore any facilitation found for the L + N stimulus must be induced by the spatial periodicity (i.e. L component) within the flanks.

The results for L and L + N stimuli are shown in Figs. 2 and 3, respectively. Here for each of the four subjects, the threshold elevation is plotted against the flank-to-target separation (in units of wavelengths of the target's spatial periodicity). The averaged result is displayed below. Table 1 gives the statistical results. As expected (Polat & Sagi, 1993), for L stimuli (Fig. 2), there is significant collinear facilitation and its magnitude reduces as the separation between target and flanks increases beyond 3 λ. The facilitation disappears when the separation is 6 λ. Also as expected (Williams & Hess, 1998), there is no strong facilitation effect when the target and flanks are 180 degree out of phase. The results for L + N stimuli (Fig. 3) showed a facilitatory effect only for PCH in 2 and 3 λ separations, and XFL in 3 λ separation in the in-phase conditions. The other two subjects did not showed collinear facilitation. LHY and XFL showed an inhibitory effect at 2 λ separation in the out-of-phase conditions. In the averaged data, no significant collinear facilitatory effect was found when luminance noise (rms contrast of 0.3 which is about 15 times its contrast threshold) was added to the stimulus. Although L + N stimuli showed a pronounced decrease in collinear facilitation, the pattern for in-phase versus out-of-phase configuration remains similar to that with L stimuli, namely a phase dependent effect. It is possible that some residual facilitation is present due to template uncertainty for the in-phase configuration. The inhibitory effect found

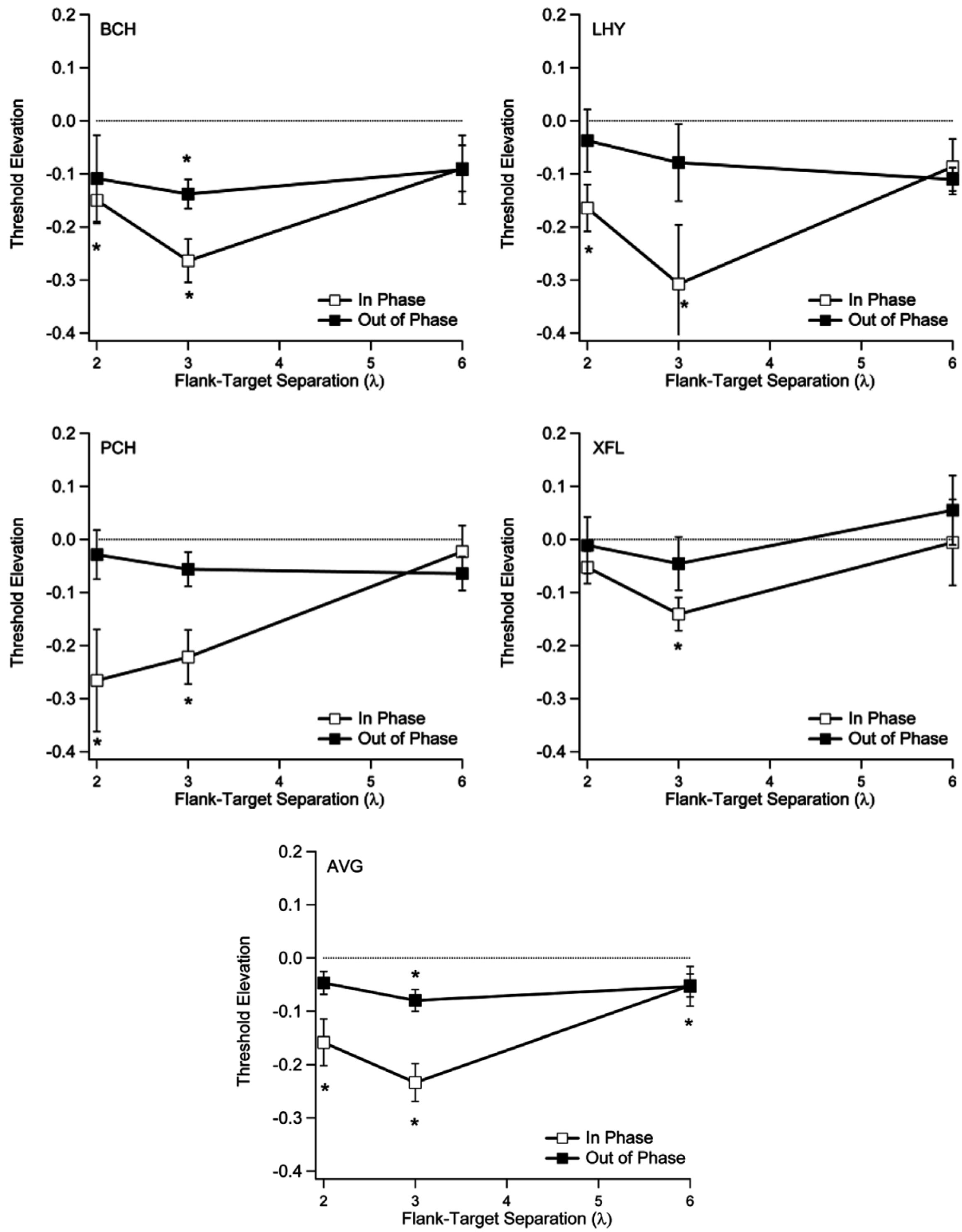

Fig. 2. The assessment of collinear facilitation for "L" stimuli. Threshold elevation index is plotted as a function of target and flank separation expressed in stimulus periods (λ). The white squares represent the condition where target and flanks are in-phase alignment and the black squares represent the condition where target and flanks are 180 degree out-of-phase alignment. Results are for four subjects with the average data shown at the bottom. The symbol "*" indicates where the facilitation is significantly different from zero ($p \leqslant 0.05$). The error bars represent the ±1 *SE*.

in the out-of-phase configuration at 2 λ separation may be due to masking.

These results, averaged across our four subjects, suggest that adding luminance noise of rms contrast 0.3 abolishes the facilitatory effect due to collinear flanks. To explore this further we measured the function relating noise contrast (see Fig. 1b for illustration) and detectability for stimuli with and without collinear flanks (Fig. 4). The rms contrast of the noise is plotted in units of its detectability, the highest being an rms contrast of 0.3. In three out of our four

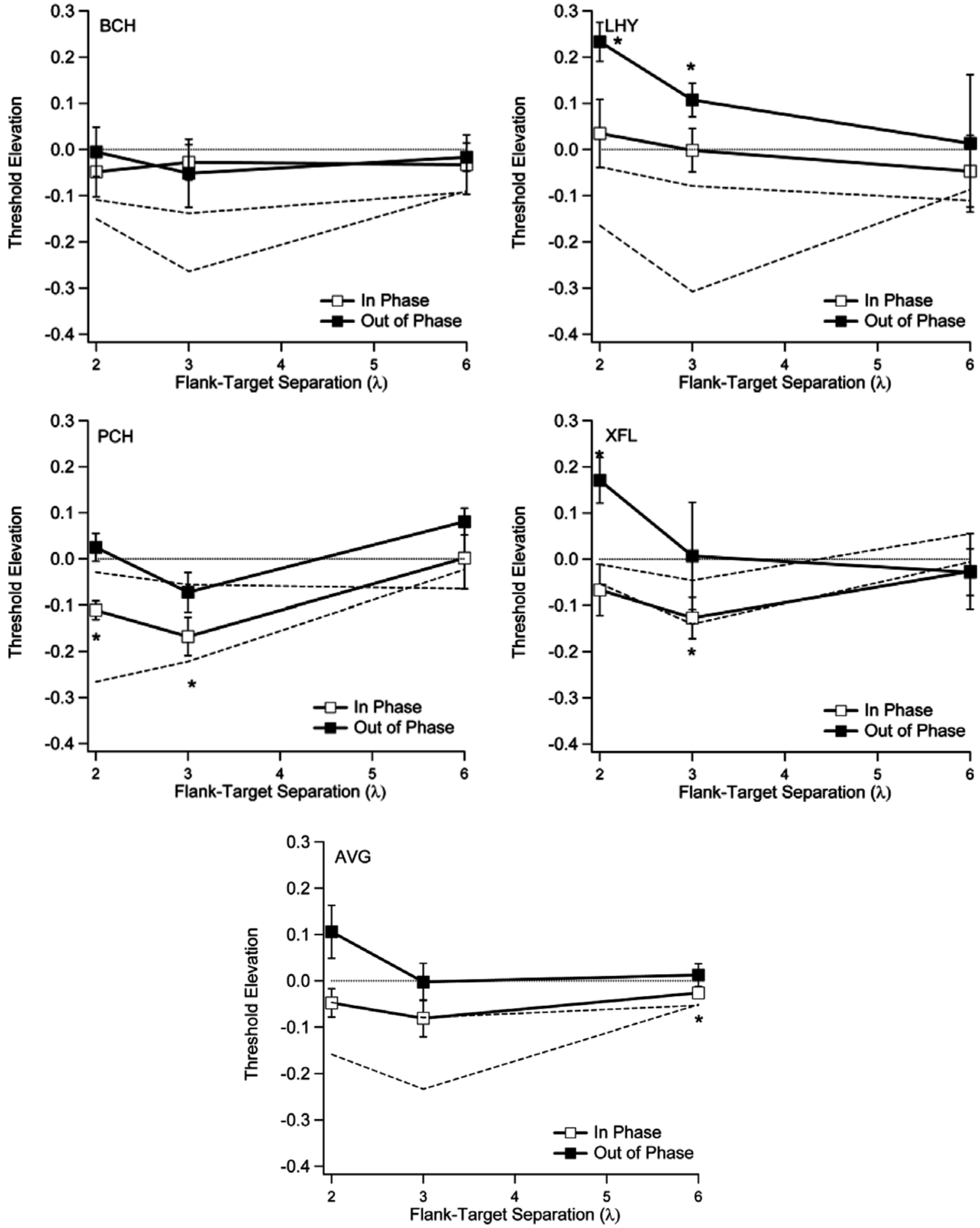

Fig. 3. The assessment of collinear facilitation for "L + N" stimuli. Threshold elevation index plotted as a function of target and flank separation expressed in stimulus periods (λ). The white squares represent the condition where target and flanks are in-phase alignment and the black squares represent the condition where target and flanks are 180 degree out-of-phase alignment. Results are for four subjects with the average data shown at the bottom. The symbol "*" indicates where the facilitation is significantly different from zero ($p \leqslant 0.05$). The error bars represent the ±1 *SE*.

subjects, the effect of adding 2D noise was to abolish the magnitude of collinear facilitation. The one subject (XFL) who exhibited a significant degree of collinear facilitation for stimuli without added noise in Fig. 3 also displayed a collinear facilitation that was noise invariant in Fig. 4.

3.2. Experiment 2—multiplicative noise

The detection thresholds of the flanks were measured and a within-subject ANOVA test showed that the detection thresholds varied with separation (i.e. eccentricity) for L × N stimuli ($F_{(2,6)} = 16.19$). A control experiment

Table 1
Statistics table for L and L + N stimuli

Separation	BCH	LHY	PCH	XFL	AVG
L stimuli: In-phase condition					
2	$t_{(3)} = -3.46^{*}$	$t_{(3)} = -3.72^{*}$	$t_{(3)} = -2.76^{*}$	$t_{(3)} = -1.73$	$t_{(3)} = -3.63^{*}$
3	$t_{(3)} = -6.45^{**}$	$t_{(3)} = -2.76^{*}$	$t_{(3)} = -4.36^{*}$	$t_{(3)} = -4.51^{*}$	$t_{(3)} = -6.57^{*}$
6	$t_{(3)} = -2.07$	$t_{(3)} = -1.66$	$t_{(3)} = -0.47$	$t_{(3)} = -0.07$	$t_{(3)} = -2.38^{*}$
L stimuli: Out-of-phase condition					
2	$t_{(3)} = -1.34$	$t_{(3)} = -0.64$	$t_{(3)} = -0.63$	$t_{(3)} = -0.45$	$t_{(3)} = -2.17$
3	$t_{(3)} = -5.01^{**}$	$t_{(3)} = -1.09$	$t_{(3)} = -1.74$	$t_{(3)} = -0.91$	$t_{(3)} = -3.87^{*}$
6	$t_{(3)} = -1.43$	$t_{(3)} = -5.08^{**}$	$t_{(3)} = -2.03$	$t_{(3)} = 0.98$	$t_{(3)} = -1.43$
L + N stimuli: In-phase condition					
2	$t_{(3)} = -0.89$	$t_{(3)} = 0.47$	$t_{(5)} = -3.45^{**}$	$t_{(3)} = -1.20$	$t_{(3)} = -1.57$
3	$t_{(3)} = -0.72$	$t_{(3)} = -0.04$	$t_{(5)} = -4.96^{**}$	$t_{(3)} = -2.84^{*}$	$t_{(3)} = -2.05$
6	$t_{(3)} = -0.51$	$t_{(3)} = -0.61$	$t_{(3)} = 0.02$	$t_{(3)} = -0.32$	$t_{(3)} = -2.57^{*}$
L + N stimuli: Out-of-phase condition					
2	$t_{(3)} = -0.10$	$t_{(3)} = 5.53^{**}$	$t_{(3)} = 2.06$	$t_{(3)} = 3.46^{*}$	$t_{(3)} = 1.85$
3	$t_{(3)} = -0.70$	$t_{(3)} = 2.97^{*}$	$t_{(3)} = 0.31$	$t_{(3)} = 0.06$	$t_{(3)} = -0.06$
6	$t_{(3)} = -0.55$	$t_{(3)} = 0.09$	$t_{(3)} = 1.45$	$t_{(3)} = -0.55$	$t_{(3)} = 0.50$

Shading area: significant facilitation effect ($p < .05$).
* $p < .05$.
** $p < .01$.

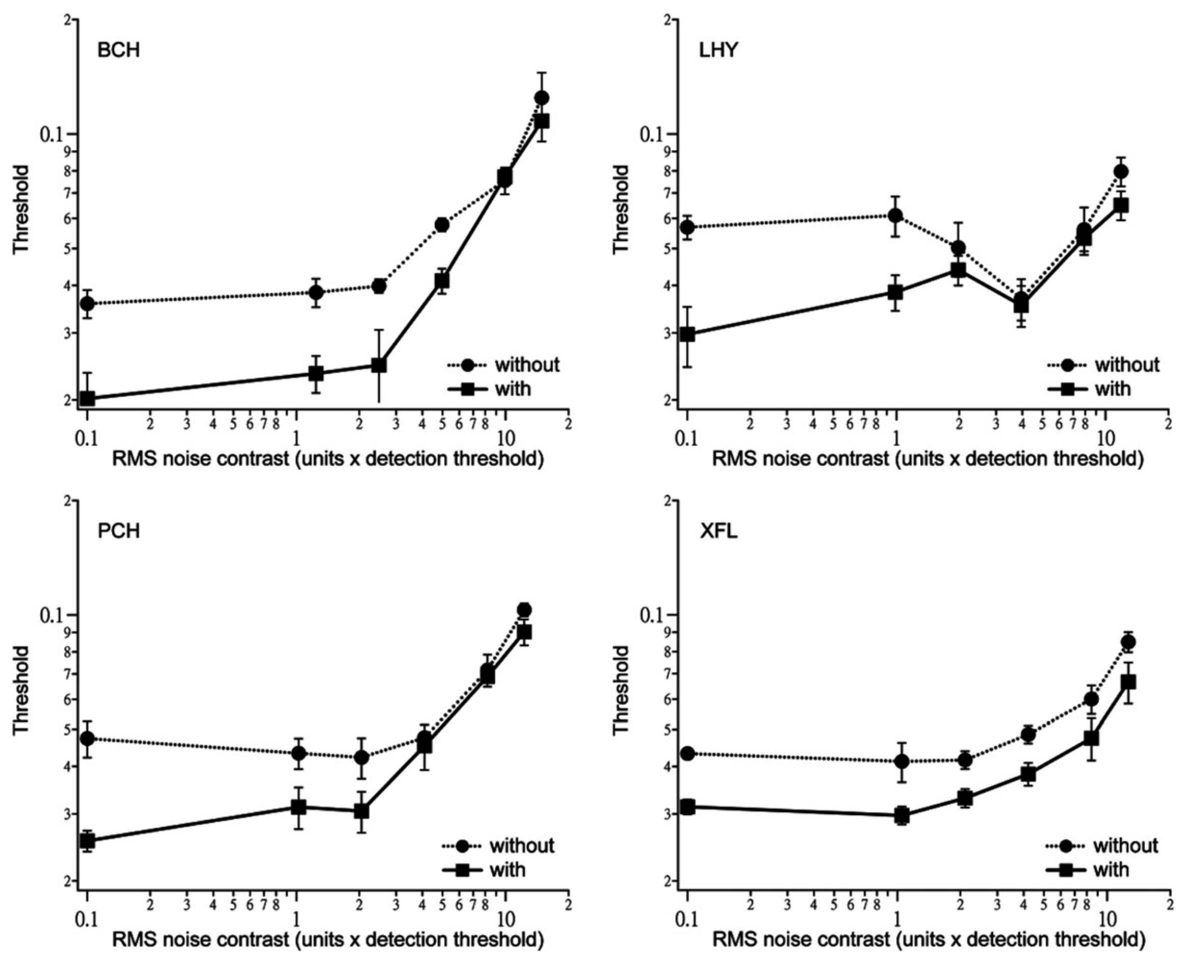

Fig. 4. Threshold versus Noise contrast function (TvN). The detection threshold of the target is plotted as a function of the contrast of added 2D noise. The rms contrast of the noise is plotted in units of its detectability. The filled circles represent measurements in the absence of flanks (baseline condition) and filled square represents measurements in the presence of the flanks (collinear facilitation condition).

on three subjects showed that when the flanks were noise patches, there was no facilitation effect for the L × N stimuli (within-subject two way ANOVA test, $F_{(2,4)} = 0.29$), indicating flanks comprising just noise did not facilitate a target also containing noise as a carrier. Therefore any facilitation found for the L × N stimuli must be induced by the spatial modulation of the carrier.

The results for the L × N stimulus are shown in Fig. 5 and statistical analysis in Table 2. Here for each of the four subjects, the threshold elevation is plotted against the

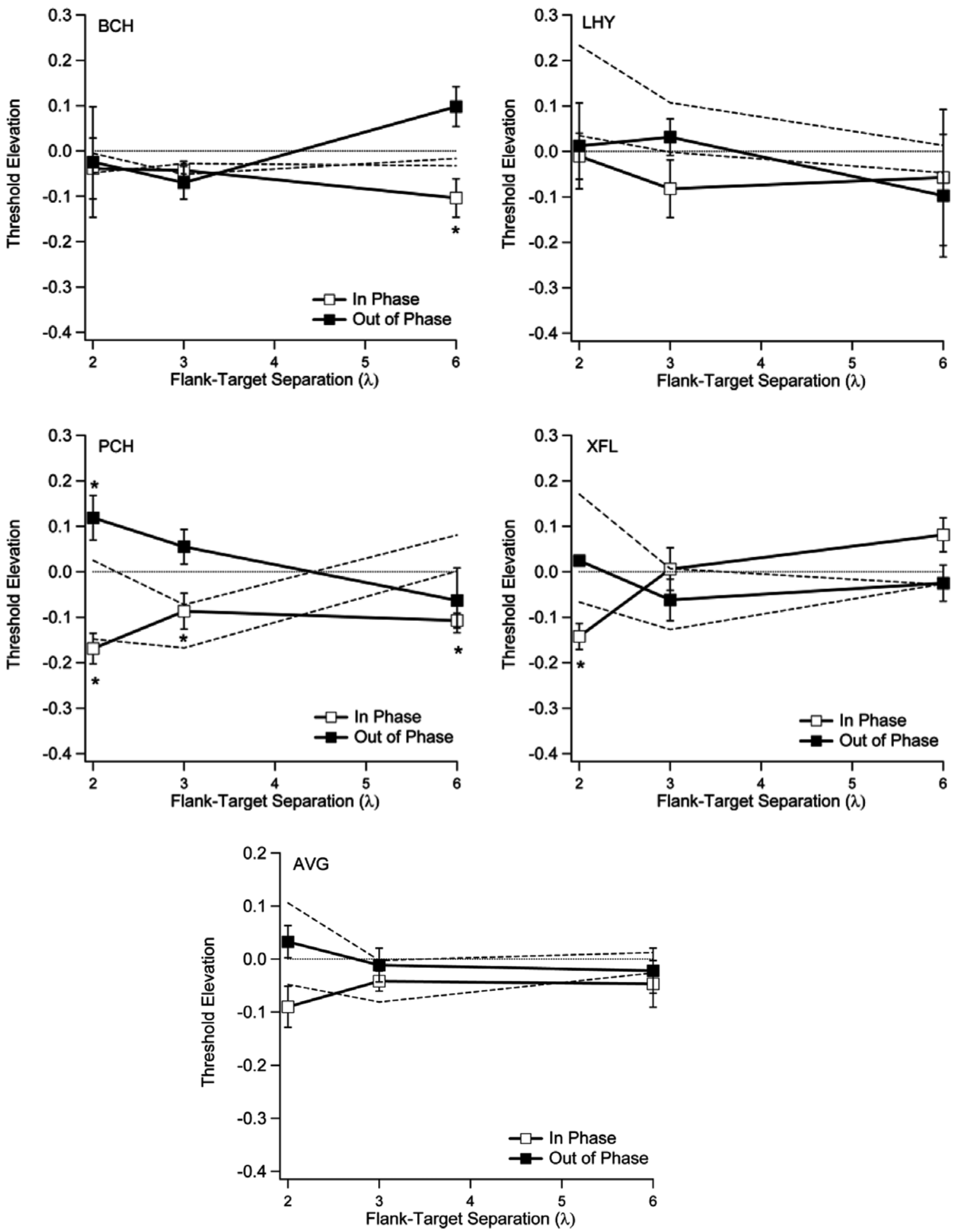

Fig. 5. The assessment of collinear facilitation for "L × N" stimuli. Threshold elevation index is plotted as a function of target and flank separation expressed in stimulus periods (λ). The white squares represent the condition where target and flanks are in-phase alignment and the black squares represent the condition where target and flanks are 180 degree out-of-phase alignment. Results are for four subjects with the average data shown at the bottom. The symbol "*" indicates where the facilitation is significantly different from zero ($p \leqslant 0.05$). The error bars represent the ±1 *SE*.

Table 2
Statistics table for L × N stimuli

Separation	BCH	LHY	PCH	XFL	AVG
L × N stimuli: In-phase condition					
2	$t_{(3)} = -0.57$	$t_{(3)} = -0.21$	$t_{(3)} = -5.02^{**}$	$t_{(3)} = -4.97^{**}$	$t_{(3)} = -2.33$
3	$t_{(3)} = -2.18$	$t_{(3)} = -1.29$	$t_{(8)} = -2.20^{*}$	$t_{(5)} = 0.12$	$t_{(3)} = -2.20$
6	$t_{(3)} = -2.45^{*}$	$t_{(3)} = -0.38$	$t_{(3)} = -6.65^{**}$	$t_{(3)} = 2.16$	$t_{(3)} = -1.06$
L × N stimuli: Out-of-phase condition					
2	$t_{(3)} = -0.20$	$t_{(3)} = 0.13$	$t_{(3)} = 2.41^{*}$	$t_{(3)} = 2.47^{*}$	$t_{(3)} = 1.07$
3	$t_{(3)} = -1.92$	$t_{(3)} = 0.784$	$t_{(3)} = 1.45$	$t_{(3)} = -1.35$	$t_{(3)} = -0.36$
6	$t_{(3)} = 2.22$	$t_{(3)} = -0.72$	$t_{(3)} = -0.89$	$t_{(3)} = -0.63$	$t_{(3)} = -0.52$

Shading area: significant facilitation effect ($p < .05$).
* $p < .05$.
** $p < .01$.

flank-to-target separation (in units of wavelengths of the target's spatial periodicity). The averaged result is displayed below. For L × N stimuli (Fig. 5), although PCH showed a facilitation effect when the target-flank separation was 2 and 3 λ and XFL showed a facilitation effect in the in 2 λ in-phase conditions, the bulk of the data did not show either a facilitatory or inhibitory effect.

For the average data, none of the condition showed significant collinear facilitation. In summary, only L (exp. 1) stimuli showed significant collinear facilitation, L + N (exp. 1) and L × N (exp. 2) stimuli showed neither a facilitatory nor inhibitory effect.

We wondered whether the absence of a facilitatory effect for the 2D noise-modulated stimuli (i.e. L × N) was due to an absence of a facilitatory effect for 2nd order stimuli in general or just for this particular type of 2nd order stimulus (i.e. with a 2D noise carrier). To answer this we compared collinear facilitation for two other types of 2nd order stimuli; one having a 1D horizontal sinusoidal carrier of 3 times the frequency (see Fig. 1c for stimuli, Fig. 6a for results and Table 3 for statistical analyses) and another having a horizontal 1D spatial noise carrier (see Fig. 1c for stimuli, Fig. 6b for results and Table 3 for statistical analyses). The results for four subjects are shown in Fig. 6a and b, where the data for these 2nd order stimuli are compared with their 1st order controls (i.e. L + 3f and L + N). The first comparison is between the 1st (bars with plaid hatching) and 2nd order (bars with vertical hatching) versions of the 1D sinusoidal carrier stimulus (Fig. 6a). The averaged results show that both 1st and 2nd order versions exhibit significant facilitation, but with a significantly reduced facilitation for the 2nd order stimulus. For the stimulus with the 1D noise carrier (Fig. 6b), a similar comparison shows (averaged data) only the 1st order stimulus exhibited significant facilitation. We also tested whether facilitation occurred in the crossed conditions, that is where there are 1st order (L + N) flanks and a 2nd order (L × N) central target stimulus or vice versa (see Fig. 1c rightmost frame for illustration). In the crossed condition where the flanks and target stimuli are of different order (i.e. 1st order flanks with 2nd order target and vice versa), only two subjects (LHY and PCH) could be used for the stimulus with a 1D sinusoid carrier and only two subjects (PCH and XFL) could be used for the stimulus with a 1D noise carrier. This was because only these subjects exhibited significant facilitation on both the 1st and 2nd order stimuli in the uncrossed condition (Fig. 6a and b; plaid and vertically hatched bars). The averaged data from these two subjects for each stimulus version suggest that there is no significant facilitation in the crossed condition (see Fig. 6a and b).

4. Discussion

4.1. Is collinear facilitation confined to absolute threshold?

Our results suggest that collinear facilitation is mainly limited to absolute threshold. Adding luminance noise to a stimulus is one means of artificially exploring visual function above threshold, a region not usually amenable to investigation using the standard detection paradigm. Neurons with elevated thresholds that make their contribution at higher contrasts can contribute to the detection of such a stimulus. On average we could not demonstrate significant collinear facilitation for our luminance modulated stimulus when 2D noise of rms contrast 0.3 was added to it (Fig. 3). Furthermore, when we varied the rms contrast of luminance noise added just to the central target stimulus (see Fig. 1b), collinear facilitation gradually reduced in three out of our four subjects and was no longer present at an rms contrast of 0.3 (equivalent to 15× threshold, the maximum we could use). This suggests to us that the optimum conditions for demonstrating collinear facilitation are at absolute threshold where the internal neural noise is presumably at its lowest. A similar result was reported by Chen and Tyler (2001) using a pedestal masking paradigm, namely an abolition of facilitation when a pedestal was present. This may suggest that the facilitation reflects a signal to noise property of the visual detection process that is unlikely to be relevant under suprathreshold viewing conditions, a conclusion originally proposed by Williams and Hess (1998) using a contrast matching paradigm. The available physiology in fact supports this (Mizobe et al.,

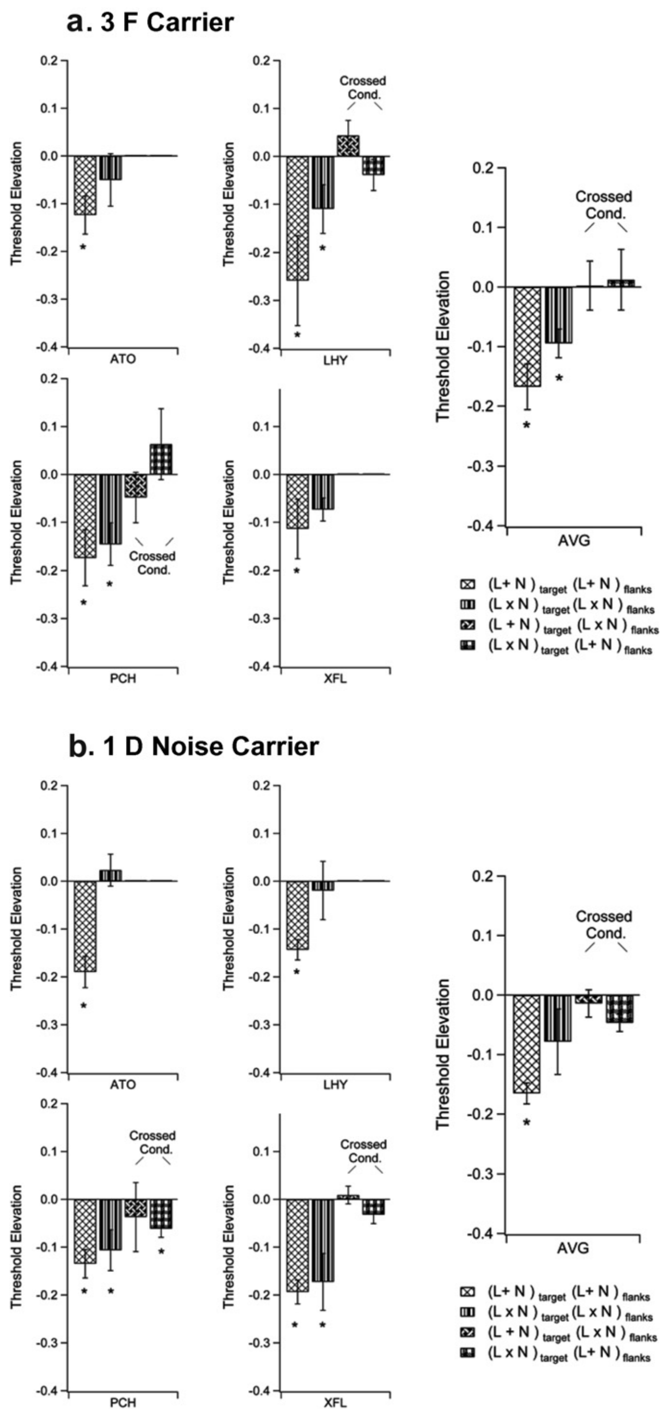

Fig. 6. Assessment of collinear facilitation for two additional 2nd order stimuli. (a) 3f horizontal grating was used as the carrier. The first two bars represent results for the uncrossed condition, in which the target and flanks are of the same order. The bars with oblique plaid hatching represents f + 3f and the bars with vertical hatching represent L × 3f. The final two bars for each subject represent results for the crossed conditions, bars with an oblique weave represents L + 3f target with L × 3f flanks and bars with horizontal/vertical checks represents L × 3f target with L + 3f flanks. The symbol "*" indicates where the facilitation effect becomes significant significantly different from zero ($p \leqslant 0.05$). The error bars represent the ±1 *SE*. The AVG is the average data derived from subjects and the error bar indicated the *SE* among subjects. (b) same as (a) except the carrier is now 1D horizontal noise.

2001; Polat et al., 1998) and may suggest that flanks decrease the neural noise rather than enhance the neural signal.

4.2. Does collinear facilitation occur for 2nd order stimuli?

We find that comparable collinear facilitation does not occur for 1st and 2nd order stimuli, although there is inter-subject variability. We found a smaller magnitude of facilitation across our subjects for two 2nd order stimuli (i.e. 1D 3f carrier and 1D noise carrier) compared with their 1st order counterparts. The 1D carrier of these 2nd order stimuli were not co-aligned with that of the flanks and should not have produced any 1st order artifact. We also found no significant facilitation in the 1st/2nd order crossed conditions (i.e. 1st order flanks and 2nd order target and vice versa), suggesting that the neural processes that mediate the detection of these two stimulus types (i.e. 1st and 2nd order stimuli) are independent.

4.3. Alternate explanations

Three different explanations have been advanced for collinear facilitation: uncertainty, within-channel masking and between-channel interactions. Uncertainty could be reduced as a consequence of the flanks in not only a general positional sense but also temporally and in terms of local stimulus template features such as spatial frequency, orientation, and phase. It is hard to imagine how the addition of luminance noise at a much finer scale to that of the spatial structure that normally produces collinear facilitation could abolish facilitation if it was due solely to the effects of uncertainty of any of the above factors. Any temporal or spatial cueing provided by the flanks is still present in noise. Furthermore, we have previously shown (Huang, Hess, & Dakin, 2006) that collinear facilitation is not present under conditions of dichoptic viewing, a situation that does not affect stimulus uncertainty. We therefore do not feel that stimulus uncertainty is the sole determinant of collinear facilitation, though it may play a role. Our finding regarding noise is not at odds with a within-channel masking explanation, assuming that the noise raises the channel activity out of its normal facilitatory range. However, a within-channel explanation (Bird, Henning, & Wichmann, 2002) would predict large changes (e.g. Betas from around 2.6 without pedestal to 0.8 with pedestal) to the slope of the psychometric function for collinear facilitation. While it is true that the psychometric function is shallower during collinear facilitation (Petrov, Verghese, & McKee, 2006), it is much less than expected from predictions based on within-channel facilitation. For example, Petrov et al. (2006) found betas of 2.4 without flanks and 1.5 with flanks. We do not replicate this. An analysis of the data obtained by Huang et al. (2006), using the method of constant stimuli, found betas of around 3 without flanks and around 2 with flanks. We also collected additional psychometric data (seven subjects) using the method constant stimuli (at least

Table 3
Statistics table for two other types of 1st and 2nd order stimuli

Conditions	ATO	LHY	PCH	XFL	AVG
3F carrier					
$(L+N)_t(L+N)_f$	$t_{(3)}=3.10^{*}$	$t_{(4)}=-2.75^{*}$	$t_{(7)}=-2.99^{*}$	$t_{(3)}=-1.84$	$t_{(3)}=-5.06^{**}$
$(L\times N)_t(L\times N)_f$	$t_{(3)}=-0.82$	$t_{(4)}=-2.18^{*}$	$t_{(7)}=-3.30^{*}$	$t_{(3)}=-2.71^{*}$	$t_{(3)}=-4.54^{**}$
$(L+N)_t(L\times N)_f$		$t_{(3)}=0.98$	$t_{(4)}=-0.83$		$t_{(1)}=0.05$
$(L\times N)_t(L+N)_f$		$t_{(3)}=-0.04$	$t_{(4)}=0.85$		$t_{(1)}=0.24$
1D noise					
$(L+N)_t(L+N)_f$	$t_{(3)}=-5.78^{**}$	$t_{(4)}=-6.69^{**}$	$t_{(7)}=-4.53^{*}$	$t_{(3)}=-7.77^{**}$	$t_{(3)}=-10.77^{**}$
$(L\times N)_t(L\times N)_f$	$t_{(3)}=0.62$	$t_{(4)}=-0.32$	$t_{(7)}=-2.50^{*}$	$t_{(3)}=-2.60^{*}$	$t_{(3)}=-1.65$
$(L+N)_t(L\times N)_f$			$t_{(4)}=-0.39$	$t_{(3)}=0.09$	$t_{(1)}=-0.62$
$(L\times N)_t(L+N)_f$			$t_{(4)}=-3.43^{*}$	$t_{(3)}=-1.22$	$t_{(1)}=-3.20$

Shading area: significant facilitation effect ($p < .05$).
* $p < .05$.
** $p < .01$.

300 trials; 50 trials per condition) and find slopes changing from around 4 (without flanks) to around 2.8 (with flanks). A second reason to reject the within-channel masking model is that the dynamics of collinear facilitation (Cass & Spehar, 2005; Polat & Sagi, 2006) are slow and that of within-channel masking are fast (Georgeson & Georgeson, 1987). An across-channel interaction model involving long-range lateral interactions and or feedback from higher visual areas seems the most likely.

4.4. Perceptual significance

It has often been proposed that collinear facilitation represents the underpinning of a range of more global supra-threshold contour linking. However, the results here suggest otherwise because collinear facilitation only occurs at absolute threshold. Most everyday images contain information at a range of different spatial scales and supra-threshold contrasts and these are not conditions in which the effects of collinear facilitation are found. However, contour integration has been shown to be unaffected by either the absolute or relative feature contrast (Hess et al., 1998). For example, Hess et al. (1998) showed that the supra-threshold appearance of elements comprising a contour is no different from that of elements not comprising a contour (i.e. background noise). Also, they showed that contour linking is not a contrast-dependent phenomenon, being unaffected by both the relative and absolute element contrast, suggesting an underlying code that is different from that used for contrast. Furthermore, although some 2nd stimuli do exhibit collinear facilitation (e.g. 1D 3f carriers) but such stimuli have been shown not to provide support for contour integration (Hess et al., 2000). For example, Hess et al. (2000) used 2nd order stimuli with either 1D or 2D noise and grating carriers in a contour integration paradigm and yet did not find any evidence for above chance performance, even for straight paths. The equivalent 1st order stimuli (with added components) produced ceiling levels of performance for straight paths. On these two counts (absolute contrast threshold dependence and its presence for 2nd order stimuli) as well as others (Huang et al., 2006; Meese, Hess, & Williams, 2001; Williams & Hess, 1998), it seems unlikely that collinear facilitation provides the fundamental underpinning of contour integration.

Acknowledgment

This work was supported by a CIHR grant (#MT108-18) to R.F.H.

References

Bird, C. M., Henning, G. B., & Wichmann, F. A. (2002). Contrast discrimination with sinusoidal gratings of different spatial frequency. *Journal of the Optical Society of America. A, Optics, Image Science, and Vision, 19*(7), 1267–1273.

Cass, J. R., & Spehar, B. (2005). Dynamics of collinear contrast facilitation are consistent with long-range horizontal striate transmission. *Vision Research, 45*(21), 2728–2739.

Cavanagh, P., Arguin, M., & von Grunau, M. (1989). Interattribute apparent motion. *Vision Research, 29*(9), 1197–1204.

Chen, C. C., & Tyler, C. W. (2001). Lateral sensitivity modulation explains the flanker effect in contrast discrimination. *The Proceedings of Biological Sciences, 268*(1466), 509–516.

Ferrera, V. P., & Wilson, H. R. (1991). Perceived speed of moving two-dimensional patterns. *Vision Research, 31*, 877–893.

Georgeson, M. A., & Georgeson, J. M. (1987). Facilitation and masking of briefly presented gratings: Time-course and contrast dependence. *Vision Research, 27*(3), 369–379.

Gilbert, C. D., & Wiesel, T. N. (1989). Columnar specificity of intrinsic horizontal and corticocortical connections in cat visual cortex. *The Journal of Neuroscience, 9*, 2432–2442.

Girard, P., Hupe, J. M., & Bullier, J. (2001). Feedforward and feedback connections between V1 and V2 of the monkey have similar rapid conduction velocities. *The Journal of Neuroscience, 85*, 1328–1331.

Hess, R. F., Dakin, S. C., & Field, D. J. (1998). The role of contrast enhancement in the detection and appearance of visual contours. *Vision Research, 38*(6), 783–787.

Hess, R. F., Ledgeway, T., & Dakin, S. C. (2000). Improvished second-order input to global linking in human vision. *Vision Research, 40*, 3309–3318.

Hess, R. F., & Ziegler, L. R. (2000). What limits the contribution of second-order motion to the perception of surface shape? *Vision Research, 40*(16), 2125–2133.

Hirsch, J. A., & Gilbert, C. D. (1991). Synaptic physiology of horizontal connections in cat's cortex. *The Journal of Neuroscience, 11*, 1800–1809.

Huang, P.-C., Hess, R. F., & Dakin, S. C. (2006). Flank facilitation and contour integration: Different sites. *Vision Research, 46*(21), 3699–3706.

Kasamatsu, T., Polat, U., Pettet, M. W., & Norcia, A. M. (2001). Collinear facilitation promotes reliability of single-cell responses in cat striate cortex. *Experimental Brain Research, 138*, 163–172.

Landy, M. S., Dosher, B. A., Sperling, G., & Perkins, M. E. (1991). The kinetic depth effect and optic flow: II. First- and second-order motion. *Vision Research, 31*, 859–876.

Mather, G. (1989). Early motion processes and the kinetic depth effect. *Quarterly Journal Experimental Psychology A, 41*(1), 199–210.

Meese, T. S., Hess, R. F., & Williams, C. B. (2001). Spatial coherence does not affect contrast discrimination for multiple Gabor stimuli. *Perception, 30*(12), 1411–1422.

Mizobe, K., Polat, U., Pettet, M. W., & Kasamatsu, T. (2001). Facilitation of single striate-cell activity by spatially discrete pattern stimuli presented beyond the receptive field. *Visual Neuroscience, 18*, 377–391.

Petrov, Y., Verghese, P., & McKee, S. P. (2006). Collinear facilitation is largely uncertainty reduction. *Journal of Vision, 6*, 170–178.

Polat, U. (1999). Functional architecture of long-range perceptual interactions. *Spatial Vision, 12*(2), 143–162.

Polat, U., & Bonneh, Y. (2000). Collinear interactions and contour integration. *Spatial Vision, 13*, 393–401.

Polat, U., Mizobe, K., Pettet, M. W., Kasamatsu, T., & Norcia, A. M. (1998). Collinear stimuli regulate visual responses depending on cell's contrast threshold. *Nature, 391*(6667), 580–584.

Polat, U., & Sagi, D. (1993). Lateral interactions between spatial channels: Suppression and facilitation revealed by lateral masking experiments. *Vision Research, 33*(7), 993–999.

Polat, U., & Sagi, D. (1994a). The architecture of perceptual spatial interactions. *Vision Research, 34*(1), 73–78.

Polat, U., & Sagi, D. (1994b). Spatial interactions in human vision: From near to far via experience-dependent cascades of connections [see comments]. *Proceedings of the National Academy of Sciences of the United States of America, 91*(4), 1206–1209.

Polat, U., & Sagi, D. (2006). Temporal asymmetry of collinear facilitation. *Vision Research, 46*, 953–960.

Polat, U., Sagi, D., & Norcia, A. M. (1997). Abnormal long-range spatial interactions in amblyopia. *Vision Research, 37*, 737–744.

Solomon, J. A., Watson, A. B., & Morgan, M. J. (1999). Transducer model produces facilitation from opposite-sign flanks. *Vision Research, 39*, 987–992.

Sutter, A., Sperling, G., & Chubb, C. (1995). Measuring the spatial frequency selectivity of second-order texture mechanisms. *Vision Research, 35*, 915–924.

Ts'o, D. Y., Gilbert, C. D., & Wiesel, T. N. (1986). Relationship between horizontal interactions and functional architecture in cat striate cortex as revealed by cross-correlation analysis. *The Journal of Neuroscience, 6*, 1160–1170.

Weliky, G. A., Kandler, K., Fitzpatrick, D., & Katz, L. C. (1995). Patterns of excitation and inhibition evoked by horizontal connections in visual cortex share a common relationship to orientation columns. *Neuron, 15*, 541–552.

Williams, C. B., & Hess, R. F. (1998). The relationship between facilitation at threshold and suprathreshold contour integration. *Journal of the Optical Society of America, A, 15*(8), 2046–2051.

Woods, R. L., Nugent, A. K., & Peli, E. (2002). Lateral interactions: Size does matter. *Vision Research, 42*, 733–745.

Ziegler, L., & Hess, R. F. (1999). Stereoscopic depth but not shape from second-order stimuli. *Vision Research, 39*, 1491–1508.