Vision Research xxx (2010) xxx–xxx

Contents lists available at ScienceDirect

Vision Research

journal homepage: www.elsevier.com/locate/visres

Lateral facilitation – No effect on the target noise level

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ARTICLE INFO

Article history:
Received 11 March 2009
Received in revised form 7 July 2010
Available online xxxx

Keywords:
Signal Detection Theory
Lateral facilitation
Uncertainty
Identification
Scaling
Noise
Transducer
Contrast discrimination

ABSTRACT

The detection threshold of a centrally placed Gabor target is reduced in the presence of aligned high-contrast Gabor patches that are optimally spaced from the target (Polat & Sagi, 1993). Here we determined whether threshold reduction is due to signal enhancement or to decreased signal response variability (internal noise), using a recently developed analysis for a Signal Detection Theory (SDT)-based contrast-identification paradigm (Katkov, Tsodyks, & Sagi, 2007a). We found that flankers did not affect internal noise, but instead caused increased target response when collinear with it, in agreement with the lateral facilitation effect. Based on these results, we concluded that lateral facilitation can be explained by signal enhancement only, and that uncertainty-based models do not provide a satisfactory description of the data.

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1. Introduction

We studied the contextual influence of remote stimuli on the internal representation of a foveal target. This included, in particular, what aspects of the internal representation, the signal magnitude, or the noise variance are affected under experimental conditions that produce lateral facilitation (Polat & Sagi, 1993). Under these conditions, the detection threshold of a centrally located target (Gabor patch) decreases in the presence of laterally placed Gabor patches having a similar orientation, as compared with the threshold of a target flanked by Gabor patches having an orthogonal orientation or that of an isolated target (see Fig. 2). The properties of lateral facilitation in the stimulus domain and how the particular geometrical configuration affects the detection or discrimination threshold are well documented (Adini, Sagi, & Tsodyks, 1997; Bonneh & Sagi, 1998, 1999; Chen & Tyler, 2001; Chen & Tyler, 2008; Huang & Hess, 2007; Freeman & Driver, 2005; Freeman, Sagi, & Driver, 2001; Polat & Tyler, 1999; Solomon & Morgan, 2000; Solomon, Watson, & Morgan, 1999; Woods, Nugent, & Peli, 2002; Zenger & Sagi, 1996), as are the neurophysiological properties of lateral facilitation (Cass & Spehar, 2005; Chen, Kasamatsu, Polat, & Norcia, 2001; Kasamatsu, Polat, Pettet, & Norcia, 2001; Khoe, Freeman, Woldorff, & Mangun, 2004; Meirovithz et al., 2010; Polat & Norcia, 1996, 1998; Polat, Mizobe, Pettet, Kasamatsu, & Norcia, 1998; Sterkin, Yehezkel, Bonneh, Norcia, & Polat, 2008). Although there is no straightforward correspondence, the perceptual lateral-interactions are usually associated with enhanced signals (Polat & Sagi, 2007; Zenger & Sagi, 1996), whereas an alternative account is based on reduced uncertainty regarding target parameters, assuming improved selection of internal responses relevant to the task in the presence of collinear flankers (Petrov, Verghese, & McKee, 2006). A quantitative description of both internal response (signal) and noise parameters related to target detection in the presence and absence of flankers is expected to help in rejecting some models of lateral facilitation (see Section 4). Moreover, to the best of our knowledge, a fast and a reliable method of estimating internal representation for a wide range of contrasts has been proposed only recently (Katkov et al., 2007a). Here we employed this method and investigated whether the presence of flankers increases the signal or decreases its variance.

The theoretical framework used here is Signal Detection Theory (SDT). Accordingly, each sensory stimulus evokes an internal response that varies across presentations. This internal response is used to perform various tasks, such as detection and identification (see below); it is manifested through behavior. SDT relates psychophysical performance to stimulus internal-representation in the form of signal amplitude and its variability. Here we follow a common practice and assume that internal responses are normally distributed across trials, and therefore they can be characterized by two parameters: (1) a mean internal response (signal, μ_i) and (2) a trial-by-trial standard deviation of the internal response (noise amplitude, σ_i), or just "noise" for short. The index i refers to a particular target from a set of targets. Next, we will review how the parameters of the SDT model are linked to performance in the tasks used in the present study.

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doi:10.1016/j.visres.2010.08.030

1.1. Two-alternative forced-choice detection tasks

Two stimuli, separated in time or in space, of different strengths, are presented during a single 2-alternative forced-choice (2AFC) trial. The observer is requested to report which of the two stimuli contains the target. It is commonly assumed that in a given trial, the observer reports as the "target" the stimulus evoking a higher internal response in that trial. The probability of reporting that stimulus j has a higher strength than stimulus i is (Thurstone, 1927)

$$P_{i,j} = \Phi\left(\frac{\mu_j - \mu_i}{\sqrt{\sigma_i^2 + \sigma_j^2}}\right), \tag{1}$$

where

$$\Phi(x) = \frac{1}{\sqrt{2\pi}} \int_{-\infty}^{x} \mathrm{e}^{-\frac{t^2}{2}} dt, \tag{2}$$

is the standard normal cumulative distribution function, and μ_i is the mean internal response associated with stimulus i.

In the context of contrast discrimination experiments, observers are usually instructed to report the interval or position of the stimulus that appears to have the higher contrast. Thus, it is assumed that the apparent contrast is monotonically related to the internal response. The detection experiment can be seen in this framework as discrimination against zero contrast.

1.2. Contrast identification tasks

In a contrast identification task, a single display, with a contrast randomly selected from a predefined set of levels, is presented during a trial, followed by the observer reporting which level (category) was presented. According to SDT, the contrast level of the stimulus is encoded into a decision variable (internal response). At the decision stage, the observer establishes a set of criteria. These criteria define upper and lower category boundaries (see Fig. 1). The observer reports that the presented stimulus belongs to a particular category when the internal response falls between the corresponding category boundaries. Using this model, one can compute the probability $P_{i,n}$ of the internal response R_i to the stimulus contrast s_i, which is smaller than a category boundary κ_n, which corresponds to the probability that an observer reports a category smaller than n. Assuming that criteria are stable across trials, we can write (McNicol, 2005; Torgerson, 1958):

$$P_{i,n} = \Phi\left(\frac{R_i - \kappa_n}{\sigma_i}\right), \tag{3}$$

By increasing the number of stimuli and the number of categories, it is possible to define an over-complete system of Eq. (3), and thus to estimate the parameters in the model (R_i, σ_i, and k_n) from the measured $P_{i,n}$ values. The minimum number of stimuli should be 4 (Katkov et al., 2007a). Fig. 1 illustrates the relationship between the measured values and the SDT model parameters.

1.3. Finger errors/guessing

Usually there is a finite probability that the observers will mistakenly press the wrong key while reporting, or that they are not devoting sufficient attention to the stimulus during a particular trial. Such mistakes will be accounted for in this work by the following mathematical expressions:

$$\widetilde{P}_{i,n} = p_{fe}\frac{1}{N} + (1 - p_{fe})P_{i,n}, \tag{4}$$

for the contrast-identification task, and

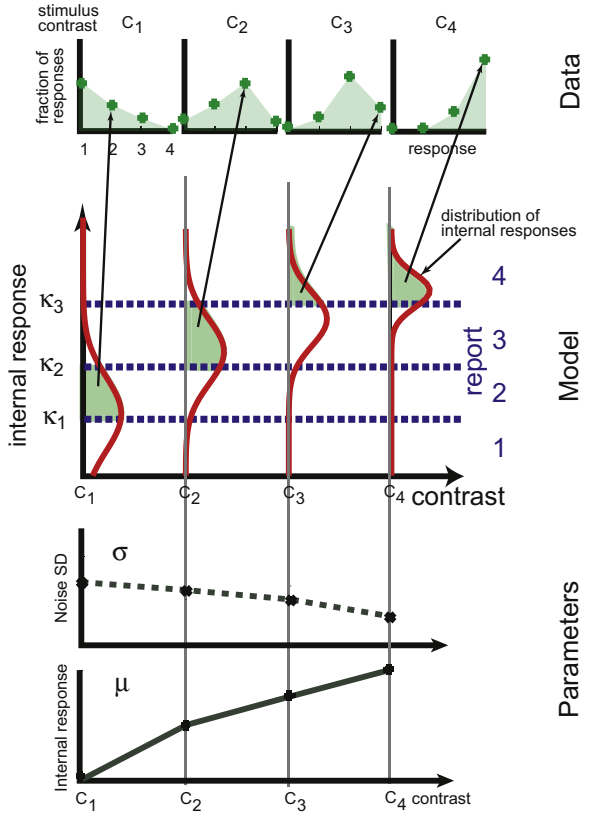

Fig. 1. The relationship between the Signal Detection Theory (SDT) model, parameters, and experimentally measured values. The SDT framework suggests that each stimulus presentation evokes a one-dimensional internal response that changes from trial to trial. For simplification, the distribution of trial responses is assumed to be normal. The "model" panel (middle) shows the four hypothetical distributions (red curves) for four different contrast levels. These four distributions have increasing mean contrast values μ, and a contrast-dependent width σ. The dependence of parameters μ and σ on contrast is summarized in the "Parameters" panel (bottom). At the decision stage, the observer establishes a number of criteria (blue dashed lines on the "Model" panel). The reported contrast corresponds to the region between neighboring criteria where the internal response falls. There are four possible responses for each stimulus. The fraction of a particular response is equal to the area under the corresponding red curve between corresponding criteria. In the plot this relationship is represented by the arrows between the green shaded areas on the "Model" panel and the height of the responses fraction on the "data" panel (top). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

$$\widetilde{P}_{i,j} = p_{fe}\frac{1}{2} + (1 - p_{fe})P_{i,j}, \tag{5}$$

for 2AFC. Here, p_{fe} represents the probability of a stimulus–unrelated response (finger error, unattended response, etc.), and N is the number of categories in the contrast-identification task.

2. Methods

2.1. Stimuli

Gabor patches were used as stimuli.

$$I(x,y) = I_0\left(1 + C\,\mathrm{e}^{-\frac{x^2+y^2}{2\sigma^2}}\cos\left(\frac{2\pi x}{\lambda}\right)\right),$$

where $I(x, y)$ is light intensity at coordinates (x, y), and $(0, 0)$ is a fixation position, I_0 is the mean screen intensity, and C is the contrast. The spatial frequency of the carrier grating was 4 c/deg ($\lambda = 0.25°$) and the width of the Gaussian envelope σ was 0.17°. Fig. 2 shows the stimulus configurations used in the experiments. The distances

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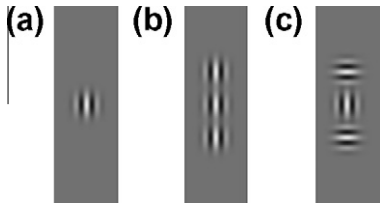

Fig. 2. Stimuli used in the lateral facilitation experiment: (a) target alone; (b) collinear configuration; and (c) orthogonal configuration.

between the centers of Gabor patches in the collinear and orthogonal experiments were 0.75° (3λ). Gabor patches at all locations were identical except for the orientation of the carrier gratings. The contrast of flanking Gabor patches, defined as the amplitude of the carrier grating relative to the background intensity (30 cd/m^2), was fixed at 23%.

A trial started when the observer pressed the "space" bar in the contrast identification task or clicked a mouse button in the 2AFC task. The temporal order of the stimuli was as follows: a fixation point for 200 ms, followed by 300 ms of background intensity, followed by a stimulus presentation for 80 ms. In the 2AFC experiments, the following sequence was added: an empty screen for 500 ms, followed by a second stimulus presentation of 80 ms. Observers reported their decision at the end of the stimulus presentation. In the 2AFC experiment, they pressed the left or right mouse button to indicate whether the target was presented in the first or in the second interval, respectively, and in the contrast identification task, observers reported the contrast level of the presented target, using the numeric keys (1 to N) on the computer keyboard. In some experiments (see details in Section 2.2), auditory feedback was provided. In 2AFC trials, a short tone was played for a wrong response. In contrast identification trials, a low tone was played for an underestimated contrast and a high tone for an overestimated contrast. In both trial types no sound was played for a correct response.

2.2. Sessions

Three types of sessions were used in the experiment. Sessions were separated by a break of at least 30 min, with no more than two sessions a day. On the first day, observers received a brief (~10 min) training on each task before starting the experiment.

The first session consisted of two 2down-1up staircase procedures, and two 3down-1up staircase procedures. Trials corresponding to the different procedures were randomly mixed. In both of them, observers performed a temporal two-alternative forced-choice detection task and reported which of the two intervals contained the target. The target was presented in only one interval. In the case of two or three consecutive correct responses, for the 2-1 and 3-1 procedures, correspondingly, the target contrast was decreased by 0.1 log units. After a wrong response, the target contrast was increased by 0.1 log units. The 2-1 procedure converges to ≈71% correct responses, and the 3-1 procedure converges to ≈80% correct responses. Therefore, during this mixed procedure, most trials were concentrated around the 75% correct discrimination. This procedure was used in an attempt to bound the position of the threshold.

Observers were instructed "to look at the position on the screen, indicated by a fixation point during the whole trial, even when the fixation point disappears, and to report which display, either the first or the second, contained the higher contrast, or in other words, which had a more visible stimulus".

The second session consisted of a contrast identification task under mixed conditions. It started with a training block (~5 min), where observers performed the contrast-identification task with the central target only (no flankers). For each trial the contrast of the target patch was randomly chosen from a set of four contrast levels that, based on the results of Session 1, were selected to provide substantial confusion between neighboring stimuli. More specifically, the four contrast levels were set to (1) 0, (2) threshold, and at the (3) start and (4) end of the fast rising part of the psychometric function.

Observers were instructed that during the trial a stimulus with one out of four different contrast intensities would appear, and that they should report the presented contrast intensity using numeric keys 1–4. They were told that feedback (high tones for overestimated contrast, low tones for underestimated contrast) would be given after the response and that they can and should minimize the number of errors. Observers were told, however, that stimuli were chosen in such a way that errors will occur frequently, and that this is normal, and they should expect it. Our previous experiments show that observers are capable of adjusting their criteria to improve accuracy (Katkov et al., 2007a). During each of the following trials, the observer was presented with either a collinear or an orthogonal configuration. The contrast of the flanking patches was the same and was fixed for both configurations. The set of target contrasts was identical to that in the training block. No feedback was provided.

Observers were instructed that the task is essentially the same – the same four target contrasts will be used in the following experiment, and that they should ignore flankers as much as possible. They were also told that no feedback will be provided.

In the third session, observers performed an identification task with the collinear configuration only. The contrast level of the flankers was fixed and was equal to that under the mixed condition. The contrast of the target patch was randomly chosen from a set of eight contrast levels, with a broader range of contrasts than the range used in the session with mixed conditions. Observers reported the contrast level of the presented target (1–8). High/Low feedback was provided as during training – a high tone for overestimated contrast and a low tone for underestimated contrast.

Observer instructions were identical to those in the training block during session 2.

The fourth session was identical to the third one, but the orthogonal configuration was used instead of the collinear configuration. In the following sessions, observers performed the first four sessions in reverse order – the fifth session was identical to the fourth one, the sixth was identical to the third one, the seventh was identical to the second one, and the last session was identical to the first one.

2.3. Parameter estimation

The SDT model parameters (see Section 1) were estimated by minimizing the chi-square measure between theoretically predicted performances and the experimentally measured ones (see Katkov et al. (2007a)). Here the performance is defined in terms of a confusion matrix. Each cell in the confusion matrix gives the number/proportion of examples from one category (the presented contrast level) classified into another (or the same) category (the reported contrast level).

$$\chi^2 = \sum_{i,n} \frac{\left(\widetilde{P}_{i,n} - \widetilde{P}_{i,n-1} - \widehat{P}_{i,n}\right)^2}{\widetilde{P}_{i,n} - \widetilde{P}_{i,n-1}} N_i, \tag{6}$$

where $\widetilde{P}_{i,n}$ is the model's prediction for the probability of a response smaller than category n for stimulus i (Eq. (4)), $\widehat{P}_{i,n}$ is the measured frequency of responses, and N_i is the number of trials having stimulus i. $\widetilde{P}_{i,n} - \widetilde{P}_{i,n-1}$ represents the value of a confusion matrix cell; it

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is the counterpart of the measured $\widehat{P}_{i,n}$. The number of degrees of freedom is the number of cells in the confusion matrix minus four times the number of stimuli plus two (Katkov et al., 2007a).

Since the performance depends neither on scale nor on the origin of the internal response, during optimization we fixed the internal response and noise for collinear configuration to zero and one, respectively.

Different models were used to initialize the optimization, including a linear transducer with additive noise, the transducer and noise being power functions of contrasts (Kontsevich, Chen, & Tyler, 2002), and a random contrast response function (with monotonic constraint) and random noise amplitudes.

The error bars were computed using parametric bootstrapping. More specifically, new artificial data were simulated based on the best fitted model, and parameters of the model (μ, σ, κ and p_{fe}) were estimated for the simulated data. This process was repeated 1000 times, and the mean and standard deviation were computed for each parameter. During data simulation, normally distributed internal responses were generated for each contrast level, with μ and σ corresponding to the parameters of the estimated model for that contrast. Thereafter, the simulated observer response was generated by comparing the internal response with the best fitted criteria. Some trials, chosen with probability P_{fe}, were assigned uniformly distributed random responses, simulating finger errors. Since the origin and the scale of the axes for each bootstrap iteration are arbitrary, normalization is required before averaging the estimated parameters. Ideally, all estimated parameters have to be aligned to produce minimum variance in the estimated parameters. Nevertheless, to reduce computational load, we rescaled the internal responses, criteria positions, and noise amplitudes and shifted the origin such that the first and the last criterion have the same value for all bootstrapped sets of parameters.

2.4. Observers

Four undergraduate students with normal or corrected-to-normal vision participated in the experiment.

3. Results

First, we replicated the lateral facilitation results (Polat & Sagi, 1993, 1994; Solomon & Morgan, 2000; Solomon et al., 1999; Williams & Hess, 1998; Woods et al., 2002). Fig. 3, Table 1, and Appendix A show the experimental results from the 2AFC task, obtained with the staircase procedure. For illustrative purposes, we also present the maximum likelihood Weibull fit for the data; this optimally weights points according to the number of trials. In the table, we also present the parameters of the fit using the "psignifit" toolbox (Wichmann & Hill, 2001a, 2001b). The results show that the threshold (75% correct discriminations) is two times lower for the collinear configuration than for the orthogonal one, or with the target alone. Note that although the thresholds of the orthogonal configuration and the target alone are similar, the shapes of the psychometric functions differ (see also Shani & Sagi (2006)), suggesting some interaction between the orthogonal flankers and the central patch. However, in this study these possible orthogonal interactions were not further explored. Fig. 3 shows large finger errors under some conditions, most probably an artifact of the staircase method, which results in most contrast levels being sampled around the threshold, consequently undersampling the saturation region of the psychometric function. Therefore, it is impossible to obtain a reliable estimate of finger errors.

We have previously shown that the 2AFC method is not suitable for estimating the internal representation corresponding to the stimuli used here (Katkov, Tsodyks, & Sagi, 2006a, 2006b); therefore, we employed a contrast identification task to estimate the signal and noise values (García-Pérez & Alcalá -Quintana,

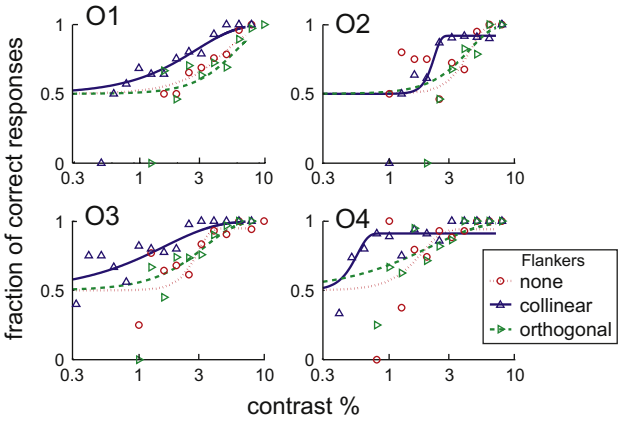

Fig. 3. Two-alternative forced-choice data. Symbols depict the fraction of correct responses computed from data obtained with the staircase procedure; the curves represent the Weibull fit (maximum likelihood) to the measured data. Clearly, the results for the collinear configuration are shifted leftward in comparison with the orthogonal configuration, or with the target alone. From this shift, it can be seen that the threshold is 2–3 times smaller for the collinear configuration - the lateral facilitation effect.

Table 1
Summary of 2AFC results. Threshold contrasts obtained by geometrical averaging of reversals in 2-1 and 3-1 staircases are presented in rows denoted as "2-1", "3-1", respectively. One can see that the threshold contrasts for the collinear configuration are substantially smaller than the thresholds for the orthogonal configuration or target alone. The parameters of the "psignifit" Weibull fit are presented in the rows denoted by "threshold", "power", and "P_{fe}" (probability of finger errors). The values of the "threshold" parameter exhibit a behavior similar to that of thresholds obtained from the geometrical means of reversals (i.e., the threshold for collinear configuration is twofold smaller than that for the orthogonal or target alone). The large finger errors in some fits are probably due to the nonuniform sampling of the staircase method – fewer points (if any) were collected at contrast levels far from the threshold. The 95% confidence interval is presented in parentheses.

	Target	Collinear	Orthogonal
O1			
2-1	4.60	2.34	4.81
3-1	5.80	3.01	7.11
Threshold	4.6 (4.5–5.2)	2.7 (2.6–3.1)	5.4 (5.3–5.8)
Power	2.5 (1.9–3.9)	1.7 (1.3–2.5)	2.5 (1.9–4.9)
P_{fe}	0 (0–0)	0 (0–0)	0 (0–0)
O2			
2-1	4.49	3.48	5.35
3-1	5.95	4.10	6.05
Threshold	4.2 (4.1–4.7)	2.2 (2.1–2.6)	4.4 (4.2–5.2)
Power	4.7 (3.5–9.0)	7.3 (4.4–47.0)	3.0 (2.1–6.2)
P_{fe}	0 (0–0)	15.5% (9.8–31.2%)	0 (0–0)
O3			
2-1	3.12	1.33	2.98
3-1	3.73	1.94	4.14
Threshold	3.0 (2.7–3.5)	1.5 (1.4–1.8)	3.2 (3.1–3.6)
Power	2.6 (2.0–6.6)	1.5 (1.2–2.3)	2.2 (1.8–3.3)
P_{fe}	7.5% (5.1–14.0%)	0 (0–0)	0 (0–0)
O4			
2-1	1.97	0.64	2.10
3-1	3.86	3.31	2.99
Threshold	2.2 (2.1–2.9)	1.0 (0.9–1.5)	2.1 (1.9–2.8)
Power	1.8 (1.2–2.9)	0.9 (0.7–2.0)	1.5 (1.0–2.9)
P_{fe}	0 (0–0)	0 (0–0)	0.0 (0.0–6.4%)

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2009; Katkov et al., 2007a; Katkov, Tsodyks, & Sagi, 2007b). Experimental data for the mixed condition are presented in Fig. 4 (see also Appendix B). It is clear that most of the response distributions for the collinear configuration are shifted rightward – observers rated targets embedded in collinear flankers as having higher contrast than targets embedded in orthogonal flankers. This result shows that target response is enhanced in the presence of collinear flankers.

Although the parameters of the model can be obtained for collinear and orthogonal configurations in separate sessions, it is not possible to directly compare parameters across different conditions, since the origin and scale of the internal response axis are arbitrarily set in the model. That is, the predicted behavioral performance is not affected by the addition of a constant to all internal responses and criteria, or by multiplying all $\mu(c)$, $\sigma(c)$, and κ_i values by a constant (Eq. (3)). Therefore, the experimental conditions should be mixed and special measures should be taken to align the internal response axes. In other words, an experimental paradigm should be used where the common reference for both conditions is a natural choice. In the present work, a training block with no flankers and with feedback was used to allow observers to calibrate their responses. Moreover, they were specifically instructed that targets used under the mixed condition match those from the training block, except that they were positioned between two flankers that should be ignored as much as possible. Therefore, the task and the specific instructions to observers imply common criteria for both tasks. Moreover, no benefit is derived from maintaining separate criteria for the different configurations, since it requires additional effort. The parameters of the models under the mixed condition (assuming common criteria, not shown) are presented in Fig. 5. As shown, the transducer function for the collinear configuration is above the transducer function for the orthogonal configuration, reflecting the fact that the response distributions are shifted rightward

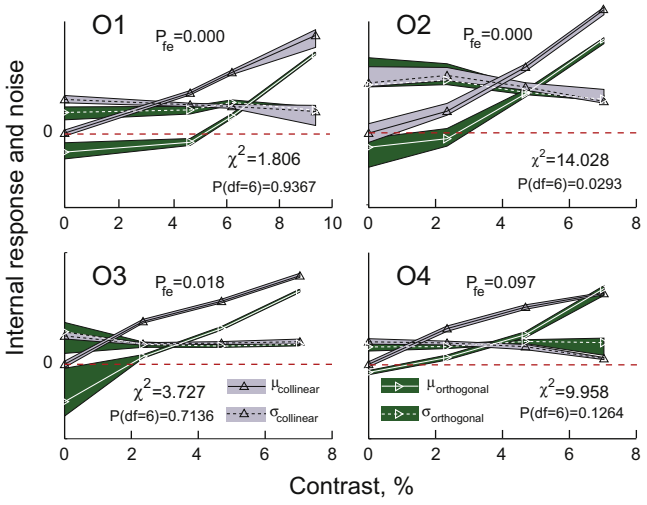

Fig. 5. Parameters of the model, obtained from the mixed conditions experiment. During the parameter estimation only μ and σ for 0 contrast in the collinear configuration were fixed. In addition, it is clear that the estimated contrast response function ($\mu(c)$) for the collinear configuration is shifted upward, and that there is not much difference between the noise levels. Moreover, in the low-contrast region the estimated noise for the collinear configuration is higher than that for the orthogonal one, which opposes the lateral facilitation effect. The intersection of the "μ" and "σ" curves indicate the approximate position of the threshold for the detection task in the "yes–no" paradigm. The width of the shaded region represents one standard deviation of estimated parameters obtained by parametric bootstrapping.

(Fig. 4). On the other hand, the noise parameters obtained are very similar across the stimulus configurations used, with the noise amplitude in the collinear configuration being slightly higher in the region of interest, as compared with the orthogonal

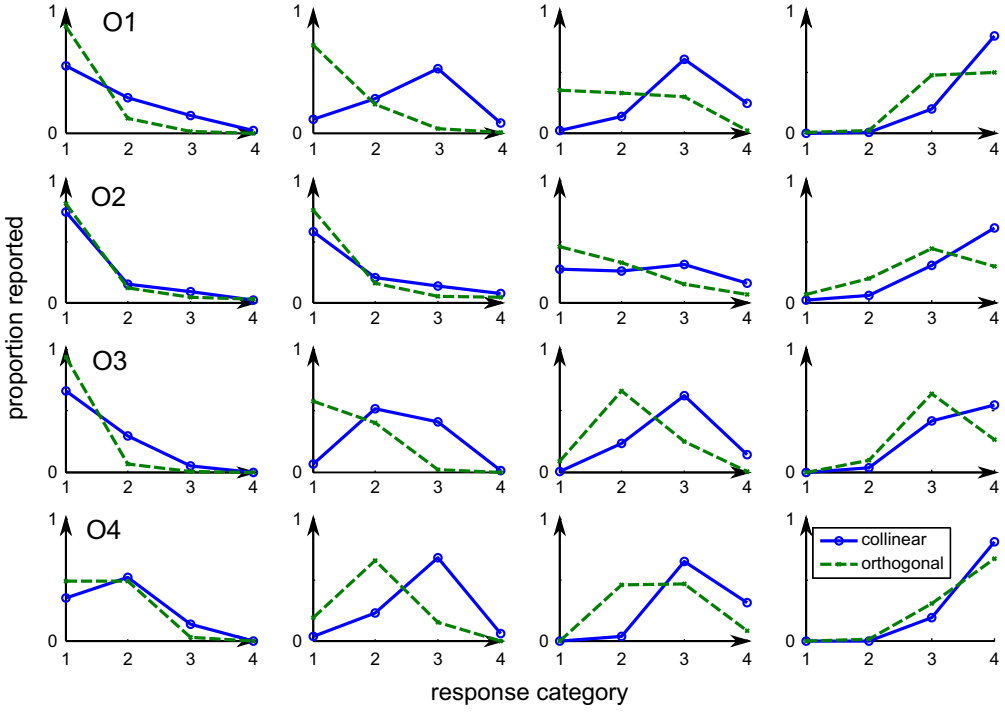

Fig. 4. Fraction of reported contrasts. Each row presents data from a single observer (O1–O4) in format defined in the "Data" panel in Fig. 1. Clearly, most of the response distributions for collinear configurations are shifted rightward – observers perceived targets placed between collinear flankers as having higher contrast than targets placed between orthogonal flankers.

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configuration, having a *negative* effect on lateral facilitation, if any. Looking at the distribution of parameters obtained using parametric bootstrapping, it can also be seen (Fig. 5) that noise amplitudes largely overlap, whereas response amplitudes are well separated.

Next, in sessions 3–6 we measured contrast response functions with flankers. These experiments were identical to those performed in Katkov et al. (2007a), except that two flanking Gabor patches are added here (Fig. 2b and c). The resulting model parameters obtained separately from the 8×8 confusion matrices for collinear and orthogonal configurations are superimposed in Fig. 6. As in previous work, we found that the noise amplitude in both configurations was practically independent of stimulus contrast above some contrast level (7%). In the low-contrast region, in three cases the noise $\sigma(c)$ was somewhat higher than that in the high-contrast region. The transducer function, $\mu(c)$, had a threshold-like shape in two cases, and in two cases the threshold part was cut off.

In addition, since the scale and shift of the internal response axis are arbitrary, the model parameters obtained under the single conditions are superimposed with the corresponding parameters obtained under the mixed conditions to produce least squared differences. Aligned models are shown in Fig. 7. One can see that the model parameters obtained in two independent experiments, with slightly different paradigms, are similar, and that in some cases, they are indistinguishable. This is indirect evidence that the method used here is consistent. It is possible to compare the parameters estimated from the different single-condition experiments using the scale and shift values obtained during the alignment of the two experiments. For instance, plots in Fig. 6 are constructed in such a way. As shown, the initial part of the graph (low-contrast levels) exhibits facilitatory behavior – the two curves diverge, and the collinear transducer has a higher slope. At higher response levels, the two transducers seem to merge and the facilitatory effect diminishes.

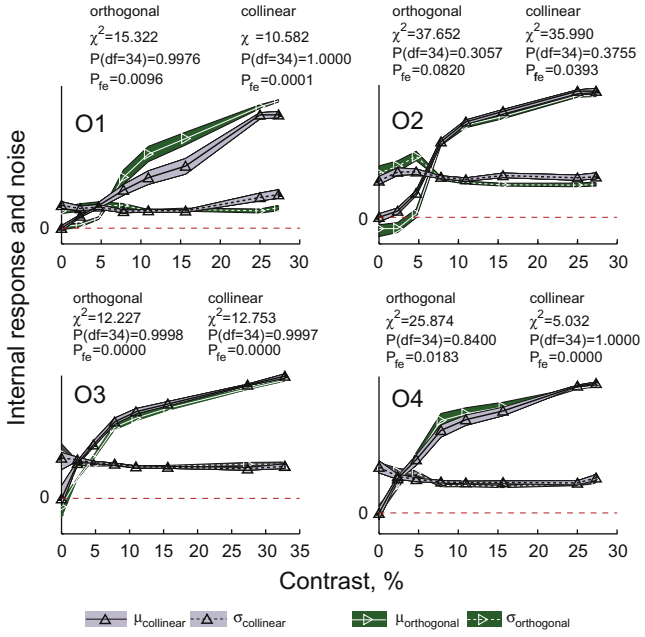

Fig. 6. Model parameters, obtained from the single-condition experiments, superimposed (see details in the text). In the low-contrast region the collinear and orthogonal contrast response functions diverge, a manifestation of lateral facilitation.

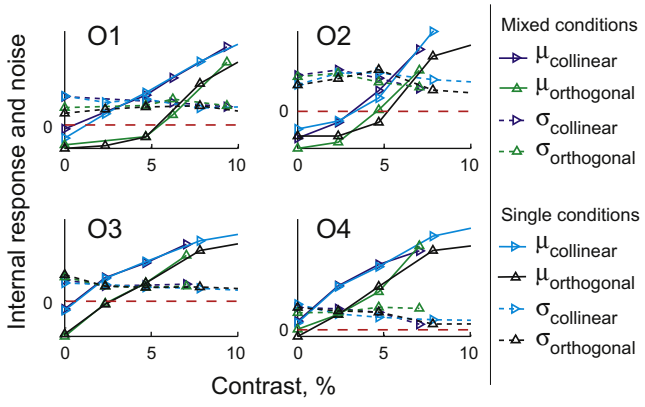

Fig. 7. Superimposed model parameters under the mixed and single conditions. Plots from Figs. 6 and 5. Although the models are obtained in independent experiments, the parameters estimated from these models are similar. Note that there are two curves of each type, derived from the mixed and the corresponding single condition.

4. Discussion

Here we replicated the lateral facilitation effect (Polat & Sagi, 1993) – a twofold decrease in detection threshold in the presence of collinear flankers, and more importantly, following Katkov et al. (2007a), we were able to estimate the internal response and noise amplitude in two spatial configurations: collinear and orthogonal (Fig. 2). Our results show that the noise functions are practically the same in both configurations, and thus the full effect of lateral facilitation should be described as a change in the transducer function (Fig. 7).

Our results reject an alternative account of lateral facilitation based on stimulus uncertainty (Petrov et al., 2006). According to this account, observers do not have the exact stimulus parameters available, in particular, the stimulus location, and thus are forced to integrate neuronal responses within the uncertainty range. The presence of collinear, but not orthogonal, flankers is assumed to reduce uncertainty and, as a consequence, to increase performance relative to the no-flankers conditions. The expected behavior of internal response and noise parameters depends on the

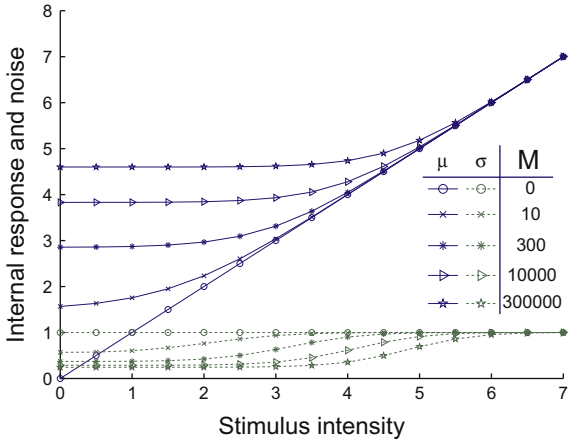

Fig. 8. Estimated mean and variance of internal response based on the Pelli (1985) uncertainty model. Clearly, the greater the uncertainty is (the number of irrelevant channels), the greater is the mean of internal response, and the smaller is the internal noise. The detection threshold depends on the signal-to-noise ratio, and the overall effect leads to higher contrast thresholds with larger uncertainties. See details in the text.

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specific model used to describe neuronal integration under uncertainty. Of particular interest here is a specific uncertainty model, analyzed in detail by Pelli (1985), which successfully predicts much of the available contrast detection data (Pelli, 1985; Solomon, 2007). This model assumes that the decision in each trial is based on the maximal response available within the uncertainty zone regarding that trial. Thus, the noise distribution is expected to follow that of the maximal value across M independent distributions, with M being the number of neuronal responses within the uncertainty zone. Since the variance of a max distribution is smaller than the variance of the single distribution contributing to the max, a somewhat non-intuitive result here is that the noise under uncertain conditions (low stimulus contrast < threshold) is smaller than under certain conditions (high stimulus contrast > threshold). Thus, according to Pelli (1985), and as demonstrated here in Fig. 8, we expect noise amplitude to increase with stimulus contrast. The magnitude of this change in noise level depends on the level of uncertainty, which, at the typical value of $M = 280$ (Solomon, 2007), is expected to be 2.68. Furthermore, we expect such a contrast dependency only in the "uncertain" orthogonal configuration; however, our data show similar flat noise functions for both configurations. Moreover, stimuli of higher uncertainty are expected to evoke larger responses (see Fig. 8), thus predicting a lower internal response with the more certain collinear configuration. Our data, however, show the opposite (Fig. 4). Although uncertainty can be given a variety of theoretical treatments, it is considered to be a threshold effect where effective uncertainty is eliminated with suprathreshold stimuli, thus predicting response-dependent neuronal integration, and as a consequence, response-dependent noise amplitude. Our data support only those models that predict either decreasing noise with contrast or constant noise. Moreover, the contextual effects on the noise functions are small compared with changes in the contrast response function, if they exist at all. Overall, our results do not support uncertainty effects under our experimental conditions.

Previous applications of the uncertainty model to lateral facilitation (Petrov et al., 2006) based their conclusions on a comparison of psychometric functions, but later work demonstrated that such experimental evidence cannot unambiguously distinguish between uncertainty reduction and gain increase-based models (Shani & Sagi, 2006). The results of Petrov et al. (2006) showing threshold reduction in several configurations not related to the collinear configuration (e.g., a faint circle surrounding the target Gabor patch), combined with our results indicating that the noise level is not changed in lateral facilitation due to collinear flankers, may point to the combined effects of configuration and attention, as suggested by the results of Freeman, Driver, Sagi, and Li (2003). Wu and Chen (2010) measured the effects of laterally placed flankers on contrast detection and discrimination in the presence and absence of a spatial cue using different (pedestal) contrast levels. Their results indicate different behaviors for lateral flankers and spatial cues, leading to the conclusions that "collinear flanker facilitation is not due to uncertainty reduction but to lateral interaction through sensitivity modulation", and that "even the cueing effect can be explained by sensitivity modulation" (Wu & Chen, 2010).

The present work shows that the transducer functions and noise amplitudes of targets flanked by two flankers are very similar to those obtained for an isolated target (Katkov et al., 2007a), regardless of the relative orientation of flankers and target. This may suggest that lateral effects are small relative to the full range of available responses, though they are large enough to double the sensitivity at low contrast levels. The large error in the estimated parameters, in some cases both here and in a previous work (Katkov et al., 2007a), can be attributed to the relatively large spacing between the contrast levels of the stimuli used; therefore, the obtained confusion matrix does not provide sufficient constraints on the estimated parameters. For instance, large error bars in the present work and large intersession fluctuations in the previous work are observed when the distribution of responses are concentrated around a single value (see for example, O3 in Fig. 4).

Recent studies using voltage-sensitive dye imaging in monkeys show that a large population of neurons is activated when stimulated with a small Gabor patch (Chen, Geisler, & Seidemann, 2006; Seidemann, Chen, & Geisler, 2009). Apparently, the bulk of neurons respond in the presence of a stimulus, whereas fine contextual details are encoded in the fine structure of interneuron connections (Meirovithz et al., 2010). The trial-to-trial variability of the population activity in area V1 of the behaving monkey is independent of the stimulus contrast (Chen et al., 2006; Seidemann et al., 2009). This pattern of results is similar to our results – the variance of the response is constant above some threshold and the contextual influence of flankers is small.

The method used here critically depends on the assumed stability of decision criteria, and on the assumption that, under the mixed condition, the same criteria are used with both configurations. Nevertheless, criteria variability, if it exists, is absorbed by the model into the sensory noise parameter (by adding a constant level to all estimated noise amplitudes), if this variability is independent of the criteria placement. The good fit of the model to the data suggests that this is the case. Potentially, since the stimuli in the orthogonal configuration are different from those in the collinear, observers can place criteria separately in different configurations. To prevent this, we performed a set of "calibration" trials before sessions with mixed conditions. In the "calibration" trials observers were presented with target stimuli only and feedback was provided. Observers were requested to minimize the number of miscategorizations. During the session the target was kept the same, but it was surrounded with either collinear or orthogonal flankers, and no feedback was provided. Moreover, observers were informed that this was the case, and they were requested to ignore flankers as much as possible. Therefore, a reasonable strategy is to maintain a single set of criteria for both configurations.

The transducer function and noise amplitudes obtained under the mixed and the single conditions appeared to be very similar. This observation suggests that the method used in Katkov et al. (2007a) and in the current work provides stable and consistent results. Moreover, the measurement time required to characterize the internal representation of the stimuli is comparable with the time required for measuring the Threshold vs. Contrast curve using adaptive procedures. Recent research concerning the information available on internal states, when using different psychophysical procedures (Georgeson & Meese, 2006; Katkov et al., 2006a, Katkov, Tsodyks, & Sagi, 2006b, 2007a; Klein, 2006; Yeshurun, Carrasco, & Maloney, 2008), led us to conclude that only limited information is available from 2AFC procedures, whereas identification tasks provide detailed information about internal states.

Acknowledgments

The authors would like to thank Ido Zak and Jeremy Freeman for helpful comments on earlier versions of the text. This research was supported by the Basic Research Foundation, administered by the Israel Academy of Science and by the US-Israel Binational science Foundation.

Please cite this article in press as: Katkov, M., & Sagi, D. Lateral facilitation – No effect on the target noise level. *Vision Research* (2010), doi:10.1016/j.visres.2010.08.030

Appendix A. 2AFC data

Contrast, %	No flanks	Collinear	Orthogonal
0.49	0/0 (0.00)	0/1 (0.00)	0/0 (0.00)
0.62	0/0 (0.00)	3/6 (0.50)	0/0 (0.00)
0.78	0/0 (0.00)	8/14 (0.57)	0/0 (0.00)
0.98	0/0 (0.00)	13/19 (0.68)	0/0 (0.00)
1.23	0/0 (0.00)	18/28 (0.64)	0/1 (0.00)
1.56	1/2 (0.50)	27/42 (0.64)	2/3 (0.67)
1.96	5/10 (0.50)	43/57 (0.75)	6/13 (0.46)
2.47	17/26 (0.65)	49/61 (0.80)	19/27 (0.70)
3.11	31/45 (0.69)	45/57 (0.79)	26/41 (0.63)
3.91	47/62 (0.76)	40/43 (0.93)	42/58 (0.72)
4.93	51/65 (0.78)	21/21 (1.00)	56/81 (0.69)
6.20	48/50 (0.96)	14/14 (1.00)	76/85 (0.89)
7.81	20/20 (1.00)	14/14 (1.00)	35/36 (0.97)
9.84	0/0 (0.00)	0/0 (0.00)	2/2 (1.00)
0.98	2/4 (0.50)	0/1 (0.00)	0/0 (0.00)
1.23	4/5 (0.80)	2/4 (0.50)	0/0 (0.00)
1.56	3/4 (0.75)	7/11 (0.64)	0/0 (0.00)
1.96	3/4 (0.75)	19/31 (0.61)	0/1 (0.00)
2.47	6/13 (0.46)	33/38 (0.87)	6/13 (0.46)
3.11	21/29 (0.72)	19/21 (0.90)	21/31 (0.68)
3.91	25/37 (0.68)	11/12 (0.92)	33/40 (0.82)
4.93	37/39 (0.95)	10/11 (0.91)	22/28 (0.79)
6.20	12/12 (1.00)	9/10 (0.90)	21/21 (1.00)
7.81	8/8 (1.00)	10/10 (1.00)	7/7 (1.00)
0.25	0/0 (0.00)	0/1 (0.00)	0/0 (0.00)
0.31	0/0 (0.00)	2/5 (0.40)	0/0 (0.00)
0.39	0/0 (0.00)	6/8 (0.75)	0/0 (0.00)
0.49	0/0 (0.00)	6/8 (0.75)	0/0 (0.00)
0.62	0/0 (0.00)	6/9 (0.67)	0/0 (0.00)
0.78	0/0 (0.00)	14/25 (0.56)	0/0 (0.00)
0.98	1/4 (0.25)	32/39 (0.82)	0/1 (0.00)
1.23	10/13 (0.77)	24/30 (0.80)	4/6 (0.67)
1.56	9/14 (0.64)	31/40 (0.78)	9/20 (0.45)
1.96	17/25 (0.68)	40/50 (0.80)	34/46 (0.74)
2.47	27/44 (0.61)	41/42 (0.98)	36/49 (0.73)
3.11	55/66 (0.83)	17/17 (1.00)	50/66 (0.76)
3.91	40/43 (0.93)	14/14 (1.00)	54/60 (0.90)
4.93	19/21 (0.90)	14/14 (1.00)	30/31 (0.97)
6.20	18/18 (1.00)	14/14 (1.00)	16/16 (1.00)
7.81	16/17 (0.94)	14/14 (1.00)	14/14 (1.00)
9.84	3/3 (1.00)	0/0 (0.00)	0/0 (0.00)
0.39	0/0 (0.00)	3/9 (0.33)	0/0 (0.00)
0.49	0/0 (0.00)	14/19 (0.74)	0/0 (0.00)
0.62	0/0 (0.00)	12/15 (0.80)	0/0 (0.00)
0.78	0/2 (0.00)	10/11 (0.91)	1/4 (0.25)
0.98	4/4 (1.00)	8/9 (0.89)	6/9 (0.67)
1.23	6/16 (0.38)	9/12 (0.75)	10/16 (0.63)
1.56	27/34 (0.79)	15/16 (0.94)	18/19 (0.95)
1.96	23/31 (0.74)	10/11 (0.91)	10/14 (0.71)
2.47	26/28 (0.93)	12/14 (0.86)	18/22 (0.82)
3.11	15/17 (0.88)	13/13 (1.00)	19/22 (0.86)
3.91	13/14 (0.93)	7/7 (1.00)	14/14 (1.00)
4.93	10/10 (1.00)	7/7 (1.00)	7/7 (1.00)
6.20	7/7 (1.00)	7/7 (1.00)	7/7 (1.00)
7.81	7/7 (1.00)	7/7 (1.00)	7/7 (1.00)

Appendix B. Contrast identification data

	O1, collinear					O1, orthogonal				
	c_1	c_2	c_3	c_4	Total	c_1	c_2	c_3	c_4	Total
R_1	128	26	4	0	158	188	152	80	1	421
R_2	68	67	29	1	165	26	50	75	5	156
R_3	33	124	131	46	334	2	8	68	108	186
R_4	4	20	53	187	264	0	1	4	113	118
Total	233	237	217	234	921	216	211	227	227	881
	O2, collinear					O2, orthogonal				
R_1	158	126	56	5	345	167	172	103	14	456
R_2	32	45	53	13	143	24	36	73	41	174
R_3	19	30	64	66	179	9	11	34	95	149
R_4	4	16	33	134	187	5	9	14	63	91
Total	213	217	206	218	854	205	228	224	213	870
	O3, collinear					O3, orthogonal				
R_1	140	16	1	0	157	212	131	21	0	364
R_2	63	125	52	8	248	14	91	155	22	282
R_3	10	98	138	95	341	1	5	58	141	205
R_4	0	3	32	125	160	0	0	1	59	60
Total	213	242	223	228	906	227	227	235	222	911
	O4, collinear					O4, orthogonal				
R_1	42	4	0	0	46	53	19	0	0	72
R_2	62	27	4	0	93	53	66	53	1	173
R_3	16	81	75	21	193	3	15	54	32	104
R_4	0	7	36	92	135	0	0	9	70	79
Total	120	119	115	113	467	109	100	116	103	428

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