Available online at www.sciencedirect.com
ScienceDirect
Vision Research xxx (2007) xxx–xxx
Vision Research
www.elsevier.com/locate/visres

The relationship between the subjective and objective aspects of visual filling-in

Uri Polat [a,*], Dov Sagi [b]

[a] Goldschleger Eye Research Institute, Tel-Aviv University, Sheba Medical Center, 52621 Tel-Hashomer, Israel
[b] Department of Neurobiology/Brain Research, The Weizmann Institute of Science, 76100 Rehovot, Israel

Received 23 April 2007; received in revised form 13 June 2007

Abstract

We explored the relationship between filling-in processes and the known increase in detection sensitivity observed for targets presented between collinear flankers. Filling-in was probed using a Yes/No detection task by measuring the false-positive reports (false-alarm, FA) and hit rate (Hit) for a low-contrast Gabor target with different target-flankers distances. Observers increased the number of reports on the presence of a target (FA and Hit) when the flankers' distance was within the known range of facilitatory lateral interactions. This bias in reporting was reduced with blocked stimulation, when the target-flanker distance was kept fixed across trials. When different distances were mixed by trials the bias followed the pattern of lateral interactions across distance. The effect was maximal when flankers and targets were aligned. These false perceptions are most likely the result of a filling-in process by lateral excitation that produces illusory contours.

Keywords: Filling-in; Illusory contours; Collinear facilitation; Decision; Criterion; Phenomenology

1. Introduction

Filling-in is an important feature of sensory systems; it provides us with the ability to interpolate sensory attributes in the presence of incomplete information by using spatial and temporal contexts. Several perceptual effects are classified as filling-in phenomena (Pessoa, Thompson, & Noe, 1998), including contours (Dresp & Bonnet, 1991) as well as area filling-in (Pillow & Rubin, 2002; Ramachandran, Ruskin, Cobb, Rogers-Ramachandran, & Tyler, 1994). These effects or "illusions" are compulsory, that is, the filled-in regions are seen regardless of our state of mind or regardless of the visual strategy we adopt while looking at these stimuli. The phenomenology of filling-in is remarkably diverse, thus posing an exciting challenge in attempting to map perceptual phenomena on neuronal mechanisms (Komatsu, 2006). Here we examined a typical filling-in process that is involved in contour completion by assessing the subjective quality of visual events occurring in a gap between two contour fragments and then relating these events to objective effects on visual sensitivity. Since the objective measures of visual sensitivity (such as signal-to-noise thresholds ratios, d′) can be reliably converted into an efficiency index of neuronal processing (Sugrue, Corrado, & Newsome, 2005), gauging subjective against objective properties of a visual experience is expected to shed light on the neuronal mechanisms underlying the phenomenal experience.

Detection of a Gabor target is facilitated by the presence of collinear flankers (Polat & Sagi, 1993; Polat & Sagi, 1994a; Polat & Sagi, 1994b). Although this sensory gain (Bonneh & Sagi, 1998; Polat & Sagi, 1993; Polat & Sagi, 1994a; Polat & Sagi, 1994b; Solomon & Morgan, 2000; Woods, Nugent, & Peli, 2002) and its neuronal correlates (Crook, Engelmann, & Lowel, 2002; Kapadia, Ito, Gilbert, & Westheimer, 1995; Mizobe, Polat, Pettet, & Kasamatsu, 2001; Polat, Mizobe, Pettet, Kasamatsu, & Norcia, 1998)

* Corresponding author. Fax: +972 3 5351577.
E-mail address: urip@post.tau.ac.il (U. Polat).

0042-6989/$ - see front matter © 2007 Elsevier Ltd. All rights reserved.
doi:10.1016/j.visres.2007.06.007

are well documented (Series, Lorenceau, & Fregnac, 2003), the perceptual/subjective consequences of such flankers are not known. One intriguing possibility is that the gap between the co-aligned flankers is filled in by neuronal activity as an implementation of a statistical prior that the brain adopts in cases where past experience indicated the presence of continuity in the stimulus despite the incomplete sensory evidence. In the case of lateral facilitation by co-aligned flankers, the relationship between sensory facilitation and filling-in is not clear, nor are the perceptual effects implied by facilitating detection. Aspects of detection are handled by Signal Detection Theory (Green & Swets, 1966) (SDT), the standard framework used to analyze perceptual performance. Here we used both the objective (d′) and the subjective (criterion) descriptors of SDT to establish a link between the objective aspect of lateral facilitation, traditionally documented using d′, and the subjective aspect, documented by the response criterion.

How can we use SDT to probe filling-in processes? At the most basic level of implementation, filling-in is viewed as an increase in activity of neurons which are sensitive to stimuli presented in the visual field between the flankers. Such an activity increase is expected to produce a higher rate of false-alarms (FA) if the absolute response criterion (the neuronal activity level above which a Yes response is produced) is not upward adjusted. It is well known that observers can adjust their decision criteria, and their FA rate, in order to minimize the error-rate, but recent research show that in some conditions the flexibility in criterion setting is lost. For example, in multiple detection tasks, where observers are required to detect one of two targets, presented simultaneously or sequentially, observers adopt the same *absolute* response criterion (C_A, the internal response level used as the decision boundary) for both targets even when the different targets are clearly marked and identified (Gorea, Caetta, & Sagi, 2005; Gorea & Sagi, 2000; Sagi & Gorea, 2004). If filling-in results from an increase in neuronal activity regardless of the target's presence, and if the response criterion is not allowed to increase to compensate for this increased base activity (the mean noise level and/or variance in terms of SDT), then the expected outcome is an increase in FA rate. Thus, if the limitations on criterion setting observed when the presentation of different targets is interleaved within a single block of trials apply to filling-in, then we expect an increase in the FA rate with a filled-in stimulus when its presentation is mixed with a presentation of a standard stimulus where no filling-in is taking place.

In the present study we employed the standard Yes/No experimental paradigm to measure the detection performance of a localized-contrast in the presence of flankers. Sensitivity (d′) and criterion (Cr) were assessed (see Section 2) for different target-flanker distances that were either blocked (Fix) or randomly interleaved (Mix) within an experimental session. As expected, under the Fix procedure, observers were found to have only a moderate bias in criteria weakly dependent on distance, but under the Mix procedure there was a large increase in the FA rate with distances within the range of lateral-facilitation, as expected from filling-in.

2. Methods

Sixteen adult observers with normal or corrected-to-normal vision participated in this study.

The stimuli consisted of localized gray-level gratings (Gabor patches) with a spatial frequency of 9 cycles per degree (cpd) modulated from a background luminance of 40 cd m^{-2} (Fig. 1), with a 80-ms duration. The spread of the Gaussian envelope (σ) was equated with the wavelength (λ) of the carrier (Polat & Sagi, 1993). Stimuli were presented on a gamma corrected Philips multiscan 107P color monitor, using a PC system. The effective size of the monitor screen was 24×32 cm, which at the used viewing distance of 150 cm subtends a visual angle of 9.2×12.2 degrees. Observers viewed the stimuli binocularly in a dark cubicle, where the only ambient light came from the display screen.

Stimuli consisted of a low-contrast Gabor-target and two high-contrast (60%) Gabor-flankers (Fig. 1). Target-flanker distances used were 1, 2, 3, 4, 6, 9, 12, and 15λ (λ being the wavelength of the Gabor carrier), with the exact subset depending on the experiment. Target and flankers orientations varied between experiments (as described in the result section) but were mostly vertical (collinear configuration). Baseline thresholds, against which spatial interactions were compared, were obtained using orthogonal target and flankers with an inter-element distance of 15λ. The contrast of the target was set to the subjects' individual contrast detection threshold, and was kept constant for all target-flanker distances. Using the Yes/No task, the observers were asked to detect the target which was shown in a single presentation, and to report whether the target was present (Yes) or absent (No) by pressing the left and right mouse keys, respectively. They were informed of a wrong answer by auditory feedback after each presentation through out the experiment. A visible fixation circle indicated the location of the target it disappeared when the trial was started. Observers activated the presentation of the trials at their own pace. The false-alarm (FA), Miss, Hit, and correct rejection rates were recorded and analyzed to yield the sensitivity ($d' = z(\text{Hit}) - z(\text{FA})$) and the criterion ($\text{Cr} = (z(\text{Hit}) + z(\text{FA}))/2$) measures, with z defined as the inverse of the cumulative normal distribution function. When the 2AFC task was used, there were two stimulus intervals (80 ms each), presented 800 ms apart, both containing the flankers but with the target presented in only one of the intervals. d′ for the 2AFC task were calculated from the percent correct responses.

There were two main experimental procedures. In the "Mix" procedure, the trials with different target-flanker distances were presented in random order, while in the "Fix" procedure the different target-flankers distances were blocked. In the Fix procedure, target-flanker distance was changed randomly between blocks or was gradually changed from far to near as noted in the result section where the specific experiments are described. In both procedures, each distance was presented 50 or 20 (depending on the experiment) times in a session with target present on about half of the trials (probability of 0.5).

3. Results

In the experiments, observers detected the presence of a foveal low-contrast Gabor target located in-between two high-contrast Gabor flankers (Fig. 1a, see Section 2). In the first experiment target and flankers were vertical with their distance being 3, 4, 6, 9, and 12λ. There was also a baseline condition with horizontal flankers at a distance of 15λ from the target, expecting minimal spatial interactions. Performances were compared between the Mix and

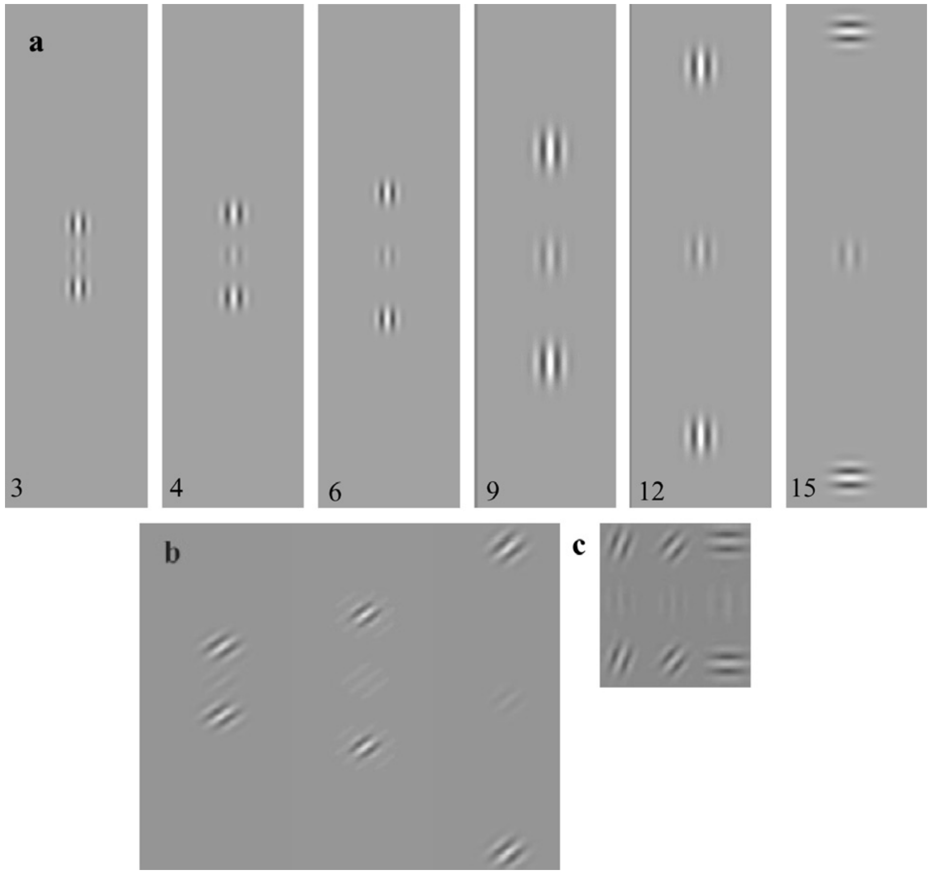

Fig. 1. Example of stimuli used in this study. (a) Collinear configurations with different target-flankers distances (numbers in the left corner indicate the distances in λ units); (b) non-collinear configuration; (c) stimuli with varying target-flanker orientations (3λ only).

the Fix (but with distance varied randomly between blocks) procedures, using sessions with 50 trials per distance. Fig. 2a–d presents data from one observer (L.P.). The results show a high rate of false-alarms (FA) in the Mix procedure, especially with small distances between target and flankers (Mix: $\mathrm{pFA}(3\lambda) = 0.8$). In the Fix procedure, FA is more stable though still somewhat higher at small distances ($\mathrm{Fix{:}pFA}(3\lambda) = 0.3$). Correspondingly, the hit rate was found to increase with small distances and even more so under the Mix procedure ($\mathrm{Mix{:}pHit}(3\lambda) = 0.97$, $\mathrm{Fix{:}pHit}(3\lambda) = 0.9$). This dependence of pFA and pHit on distance implies a strong shift of the relative criterion (Cr) between smaller distances and larger distances, in particular under the Mix procedure. Cr (Fig. 2c) is low and negative (−1.2) at 3λ, whereas it is high and positive (0.5) at 9–15λ under the Mix procedure. Under the Fix procedure Cr is positive and stable at most distances (∼0.3) but is lower (−0.4) at 3λ. On the other hand, sensitivity, as measured by d′, does not vary considerably with distance, though it does depend on the procedure, being higher under the Fix procedure for this subject. Also, d′ measurements are not very stable, as seen from the error bars in Fig. 2d. The means across distance *SE* (across sessions) of d′ for observer L.P. are 0.4 and 0.19 for the Mix and Fix procedures, respectively. We compared these values with the expected *SE* of d′, assuming binomial distribution of the Yes and No responses, and found a highly significant difference with the Mix procedure ($p < .0003$, paired *t*-test) but no significant difference with the Fix procedure ($p = .14$). Overall, when considering all observers (see below), the *SE* on both procedure is significantly larger than the expected *SE* for d′. Note that d′ estimations here are not very reliable, in particular at short distances where pHit approaches 1 (Fig. 2a) since at this level of performance single errors (due to lapses of attention or finger errors) may significantly affect the estimation of d′. This technicality can explain the absence of an increase in d′ at a distance of 3λ, which is expected according to previous studies using the 2AFC method (Polat & Sagi, 1993) or the Yes/No method (Shani & Sagi, 2005). This issue is further explored below.

Fig. 3 presents group data for the Mix ($n = 7$ observers, >>400 trials per observer at each distance) and for the Fix ($n = 4$ observers, >>400 trials) procedures. At 3–4λ the average pFA is larger under the Mix procedure than the Fix procedure (*t*-test, $p < .05$) by a factor of two, whereas pHit is about equal (and high) at these smaller distances. At larger distances, there is a higher pHit under the Fix procedure but this difference does not reach statistical significance at any point (*t*-test, $p > .05$). The resulting effect on the relative criterion is a low negative Cr at 3–4λ. Moreover, Cr is lower for the short distances (3–4λ)

Please cite this article in press as: Polat, U., & Sagi, D., The relationship between the subjective and ..., *Vision Research* (2007), doi:10.1016/j.visres.2007.06.007

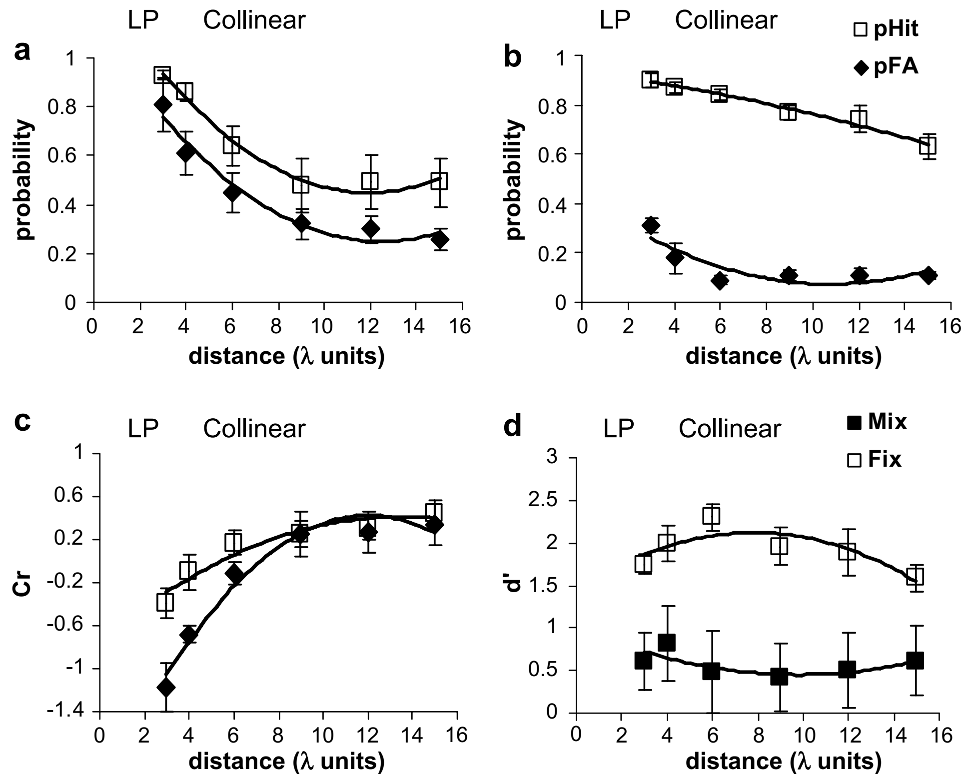

Fig. 2. Experimental results from one observer, obtained with the Fix procedure (400 trials per distance) and with the Mix procedure (420 trials per distance). Results are shown of false-alarm and hit rates for the Mix procedure in (a) and for the Fix procedure in (b). Cr and d′ are shown in (c) and (d), respectively, as a function of the target-flanker distance. The main effect to notice is the increase in target-present reports (pHit and pFA) with shorter distances and the corresponding decrease in criterion. Error bars represent $\pm 1SE$ across sessions.

than for the long distances ($>9\lambda$) under both procedures, but the difference is much more pronounced in the Mix procedure, with Cr varying between -0.4, at short distances, and 0.5 at large distances. (Statistics: we compared the Cr increase between each distance, and 15λ, in the Fix procedure with that of the Mix procedure, a difference which was highly significant at distances of 3 and 4λ; *t*-test, $p < .001$, but not at distances of 6, 9, and 12λ.) d′ was not affected by traget-flankers distance, perhaps showing some higher levels at 3–4λ, as expected from the previous results with the 2AFC methods (Polat & Sagi, 1993). Here again, *SE* (across sessions at each distance for each observer) of d′ were high on the average: 0.25 and 0.37 for the Mix and Fix procedures, respectively, significantly higher ($p < .0009$ and $p < .0002$, respectively) than the expected average *SE* when assuming binomial distribution of the Yes and No responses (which depends on d′ but is ~ 0.15 for most of our measurements when using 400 trials).

The high FA rate found at short distances clearly shows that observers cannot adjust their response criterion in the present experimental conditions, where different target-flankers distances are mixed in a single experimental block (Mix) or session (Fix). In particular, the effect with the Fix procedure, though smaller, is surprising. It seems that the 50 trials/block given in the Fix procedure are not sufficient to achieve a new stable criterion when stimulus parameters are changed randomly between block of trials. We suspect that the strongly biased decision at small distances produce lower d′ estimates. Such an effect can be either due to high values of pHit (as noted above) or due to deviations from the standard SDT assumptions of the noise being constant and normally distributed. Such deviations, even if small, may strongly bias d′ estimates when extreme criteria are used.

The present experiments, using the Y/N task, showed that the measurement of lateral facilitation is sensitive to the experimental procedure used. Such an effect may arise due to instability of the decision strategy or due to effects on sensitivity. While the latter possibility predicts similar effects on sensitivity with the 2AFC task, the former does not. To resolve this issue, the experiment was repeated using the 2AFC task with the Mix procedure. Experiments differed only in the presence of a second target interval which was identical to the first. The target was presented in one of the two intervals with equal probability and observers reported the interval which contained the target. The results presented in Fig. 4 (averaged across 5 observers) clearly show the standard d′ facilitation (×2). These results support the hypothesis that the d′ estimates in the Y/N procedure are strongly affected by decision factors.

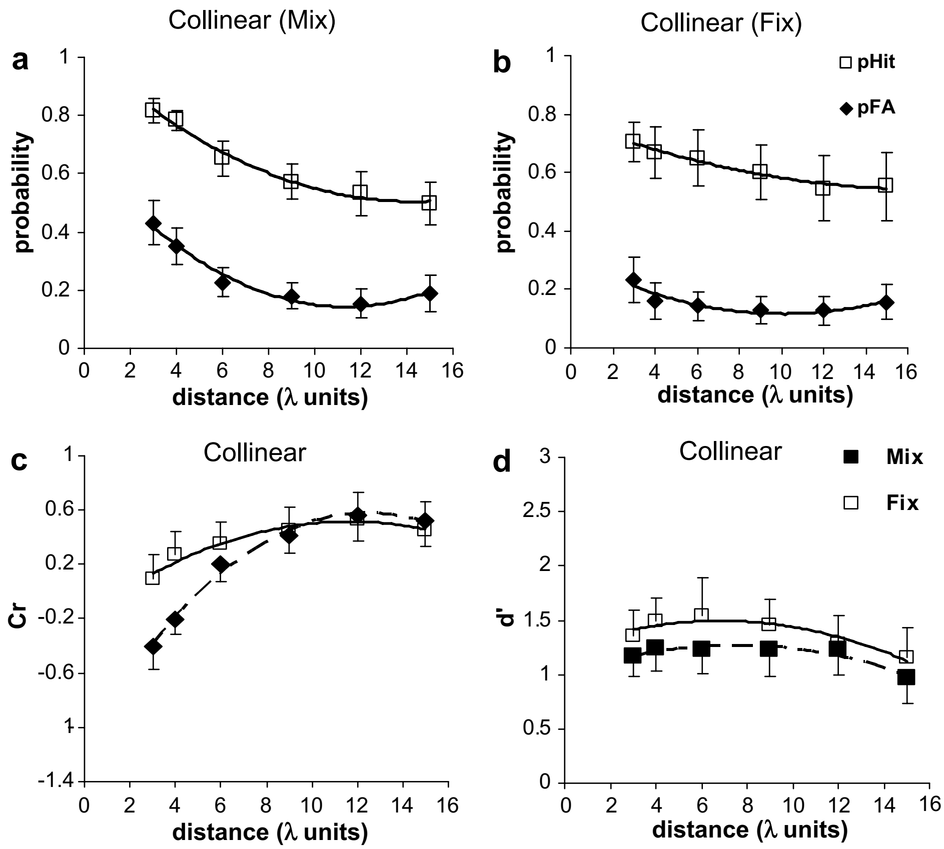

Fig. 3. As in Fig. 2, presenting group data ($N = 7$ observers), with each datum point based on at least 400 trials/observer. Error bars represent $\pm 1SE$ across observers.

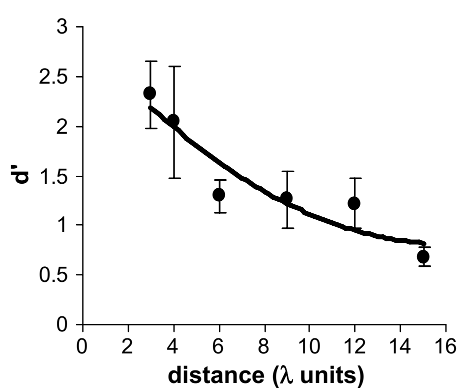

Fig. 4. 2AFC with Mix procedure. Group data ($N = 5$ observers) are presented showing d′ dependence on target-flankers distance using a 2AFC Mixed procedure. Error bars represent $\pm 1SE$ across observers.

3.1. Effects of gradual changes in target-flanker distance

The results above have established (1) that observers were able to partially adjust their response criterion under the Fix procedure and (2) that the inability to adjust the decision criteria affects the sensitivity estimates. Next, we tested whether criterion adjustment can be further improved by using a more stable procedure and whether such an adjustment will yield the expected effects on sensitivity (d′). In the Fix procedure, described above, the different target-flankers distances were blocked but their order was randomized, thus, possibly, requiring a change in decision strategy every 50 trials. In the experiment described next, the Fix procedure was modified to have a fixed order of blocks, gradually changing from far to short distances, thus allowing for a gradual change in the decision strategy. Target and flankers were vertical with their distance being 1, 2, 3, 4, and 6λ. A stimulus without flankers was used as a baseline stimulus, with 4 high contrast crosses marking the stimulus interval as in Polat and Sagi (1993). All other experimental parameters were kept as in the previous experiment. Results are presented in Fig. 5a and b for two observers. The results shown are the average of 10 sessions. As Fig. 5b shows, the decision criterion Cr still varies with distance. This effect is relatively small, in particular for observer A.R. which shows the stronger d′ facilitation, somewhat smaller than for the Fix procedure (Fig. 3) and is much reduced relative to the Mix procedure (Fig. 3). However, as shown in Fig. 5a, d′ increases with the short distances. The d′ facilitation, by a factor of 2 and 1.5 for observers A.R. and E.V., respectively, observed here at a distance of 3λ is similar in magnitude to that observed with the 2AFC method (Polat & Sagi, 1993). The average, across observers and distances, SE of d′ in the present experiment was found to be 0.148, not significantly different from the expected.

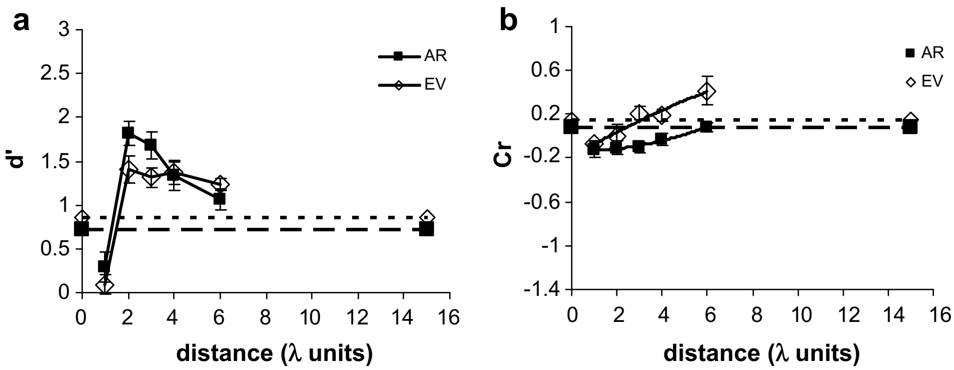

Fig. 5. Effect of stable decision strategy. d′ and Cr are presented (in a and b, respectively) for two observers, using the Fix procedure with target-flankers distance gradually changing between blocks of 50 trials. Error bars represent ±1*SE* across sessions. Dashed horizontal lines mark the contrast threshold of the target alone for each observer.

3.2. Effects of reduced familiarity with the task

The results described above suggest that in some experimental situations, given a sufficient number of trials, observers can correct for bias, as in the case where stimulus parameters are gradually varied across the testing session (Fig. 5). If so, it is possible that observers are able to perform some adjustments when practicing the Mix procedure. To test this possibility, experiments were carried out with 10 novice observers using the Mix procedure with 20 trials per target-flanker distance, totaling 120 trials per session. Each observer repeated the session twice. The results, presented in Fig. 6a–d, show a trend similar to that seen in Figs. 2 and 3. However, when comparing the group averages in Figs. 6 and 3, the effects seen are more perceptible in Fig. 6, i.e. Cr is much lower at 3λ (-0.8 vs. -0.4) and the change from 3 to 12λ is more pronounced. The difference in Cr between 3 and 6λ and the baseline condition (15λ) is significantly higher in Fig. 6 than in Fig. 3 (*t*-test, $p < .05$). The results therefore indicate that the effect of the target-flanker distance on FA and the criterion is stronger with inexperienced observers. Control experiments ($n = 8$ observers) using the same protocol (Mix with 20 trials/distance) but with a non-collinear stimulus configuration (Gabors of 45° orientation, arranged vertically; Fig. 6c) showed stable Cr. More specifically, with the diagonal configuration, the FA rate was almost constant across all distances, as was the Hit rate. As a result, Cr was also stable and did not depend on target-flanker distance. This specificity for the stimulus configuration of the FA dependence on distance supports the notion that the FA effect is a result of a filling-in process operating along extended contours.

3.3. Effects of variation in target-flanker orientation

Next we asked whether the criterion shifts observed for randomization of distance holds also for other stimulus parameters that affect lateral facilitation. The results of the previous experiments indicate that the criterion effect is configuration-dependent, as expected from the architecture of the collinear facilitation (Polat & Sagi, 1994a). It is also known that lateral facilitation diminishes as the orientation between the target and flankers is increased (Polat & Sagi, 1993), thus expecting criterion dependence on orientation difference, very much the same as on distance. Thus, in the present experiment we kept the target-flanker distance constant at 3λ and changed the flankers' orientation, while keeping the target orientation vertical (the orientation between the target and flankers was 0, 5.5, 11, 22.5, 45, and 90°; see examples in Fig. 1c). Flankers orientation was randomized between trials (Mix procedure), with each orientation presented 20 times in an experimental session. The results, presented in Fig. 7, show a high FA rate when target and flankers are of the same orientation (Fig. 7a filled diamonds), with a rapid decline to a steady level which is reached with a target-flankers orientation difference of 22.5°. This FA effect translates into a change in criterion, Cr, from -0.67 (0 orientation difference) to 0.45 (22.5° orientation difference). d′ is not significantly affected by the orientation difference between the target and the flankers. Overall, these results, obtained by mixing different target-flanker orientations, are very similar to those obtained with mixing distances. The present results show that the criterion effect has a narrow orientation tuning, similar to that found by Polat and Sagi (1993) for the orientation tuning of contrast facilitation.

4. Discussion

We were interested in determining whether collinear Gabor stimuli produce illusory percepts in the gap between them. To address this issue, we measured false-positive (false-alarms) responses in a detection task where observers were expecting the presence of real targets between two high-contrast Gabor patches (flankers). The results showed an overall increase in the false-positive responses with flanker distances that were within the excitatory range of interactions previously observed for collinear stimuli (Polat & Sagi, 1993). Importantly, we found that observers could

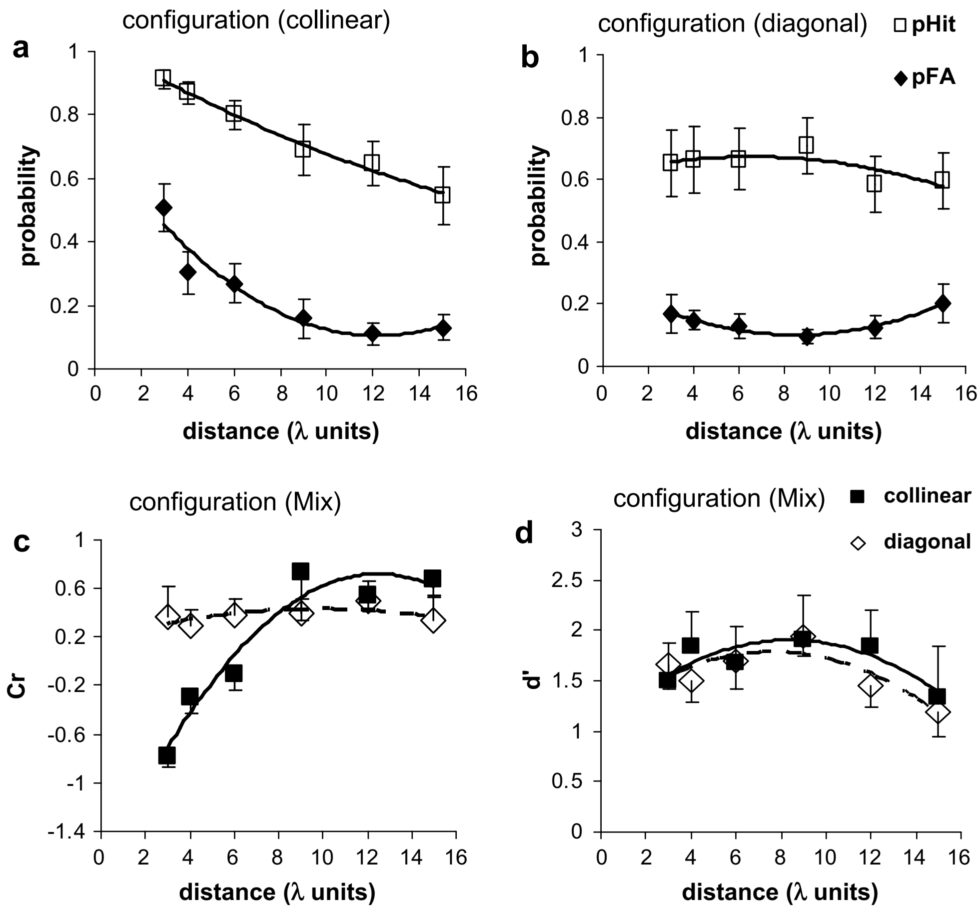

Fig. 6. Reduced familiarity with the task. Novice observers, using only sessions with 20 trials per target-flanker distance, totaling 120 trials per session. Each observer repeated the session twice. A strong dependency of target-present reports on distance is seen with the collinear configuration (10 observers) in (a) but not with the diagonal configuration (stimulus shown in Fig. 1b, 8 observers) in (b). The corresponding Cr and d′ estimates are presented in (c) and (d). Error bars represent ±1*SE* across observers.

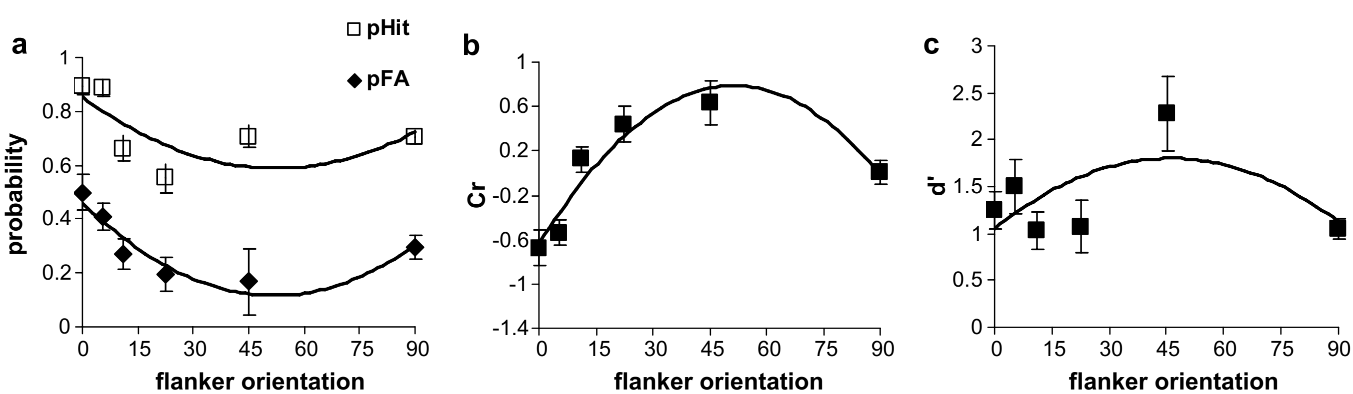

Fig. 7. Effects of orientation randomization. The target-flanker distance was kept constant at 3λ while the flanker orientation was changed. (a) FA rate and pHit; (b) d′, and (c) Cr. The results show that pFA and Cr are tuned to orientation. Error bars represent ±1*SE* across observers ($N = 8$).

correct for false-positive responses by adjusting their response criterion, when the testing conditions were fixed, with the target-flanker distance and orientation difference being constant, but the observers failed to make corrections when different distances or orientations were mixed during the testing. The latter result reflects an inability to employ independent response criteria when different stimuli are mixed, even under conditions where the different stimuli are clearly identifiable (Gorea & Sagi, 2000), as in the present case where the clearly visible Gabor flankers provided a clear indication of their distance from the target within each trial. We contend that this insuppressible increase in the false-positive responses reflects a genuine increase of neuronal activity in the neuronal network that processes the stimuli at locations not directly stimulated by the input but rather by lateral interactions within the network. The increase in the false-positive responses is a direct result of the inability, in some experimental conditions, to increase the criterion level as required by the increase of internal activity.

Recording with fMRI methods has shown that hit and false-alarm responses in a simple contrast-detection task (Yes/No, as used in the present study) are correlated with neuronal activity in the primary visual cortex (Ress, Backus, & Heeger, 2000; Ress & Heeger, 2003). Thus, it seems that contrast detection in humans is limited by neuronal activity already present within the visual cortex or at some earlier processing stage in the visual pathways. Single-unit recordings from the visual cortex of a cat show both increased activity (Polat et al., 1998) and sensitivity (Kasamatsu, Polat, Pettet, & Norcia, 2001) owing to flankers positioned outside of the classical receptive field. Our present psychophysical results are consistent with these electrophysiological measurements in showing that collinear flankers induce more reports of the presence of targets at locations corresponding to the target's location if presented within the range of the lateral interactions shown before to increase visual sensitivity (Polat & Sagi, 1993). The correlation between FA and the architecture (global and local) of collinear interactions supports the proposal that FA occurs because of excitatory input from the flankers to the target, and it supports earlier studies suggesting that collinear interactions promote illusory contours (Dresp & Bonnet, 1991; Dresp & Bonnet, 1993; Pillow & Rubin, 2002; Ramachandran et al., 1994).

A salient result of the present work is the absence of lateral facilitation when randomizing stimulus parameters (such as target-flankers distance and orientation) with the Yes–No task. The standard lateral facilitation is found with the Yes–No task when stimulus parameters are fixed (here with gradually changing distance with the Fix procedure, and in Shani & Sagi, 2005). Lateral facilitation is also observed with parameter randomization when using the 2AFC task. Thus it is reasonable to attribute the lack of lateral facilitation to an inability to adopt an efficient decision strategy when the Mixed Yes–No task is used. In the Fixed Yes–No task observers can adopt a stable decision strategy, different for each stimulus parameter, while in the 2AFC task there is no need to store separate decision rules for each parameter value presented in the randomized condition (Mix) as optimal decision can be reached by comparing the two stimuli shown on each trial. It is evident from the results obtained here that observers have strong decision biases when performing on the Mixed Yes–No task. In these conditions, both FA and Hit rates increase dramatically when stimulus parameters match those that cause facilitation when the 2AFC and the Fixed Yes–No tasks are used. Since we do not have direct evidence to link the criterion effects with the absence of sensitivity effects, we considered some technical issues that allow such a link. One such an issue concerns the observed high Hit rates, often very close to 100%, in the Mixed Yes–No conditions which makes the estimation of d' unreliable, being highly sensitive to response errors which are not directly related to the task, such as finger errors and lapses of attention. Furthermore, extreme Hit rates imply that criteria are set at the tail of the internal-response distribution which may not conform to the standard assumptions used to compute d' within the framework of SDT, such as constant Gaussian noise. Finally, d' was found to be unstable in conditions where facilitation was not observed, as shown by the high *SE* across sessions. This could be a result of an unstable decision strategy which, in addition, may lead increased noise due to uncertaincies regarding the separation of signal and noise.

One important result of this study is the direct evidence showing the inability of observers to adjust their decision-making criteria in a changing environment. Under the Fix procedure, where stimuli of only one type (distance) were presented, the observers were quite successful in balancing their responses and in having an unbiased response after some practice. However, under the Mix procedure, where different stimulus types were mixed by trial, the criteria varied between distances relative to the Fix procedure in a systematic way. The results showed low relative criteria (increased FA rates) for proximal flankers and high criteria (reduced FA rates) for distant flankers. Such a result is the hallmark of the "unique-criterion" principle put forth by Gorea and Sagi (2001) and refute the constant-FA principle (Kontsevich, Chen, Verghese, & Tyler, 2002) according to which observers equate their FA rates across the mixed experimental conditions. In applying the unique-criterion principle to the present results, we propose that the variations in the FA rates observed here are a consequence of (1) observers applying the same absolute response criterion to all stimuli and (2) differences in neuronal activity at the target's location, produced by differences in the flanker's distance.

The inability of observers to apply an optimal decision criterion to each of the stimulus configurations used here under the Mix procedures is probably the result of their inability to independently trace the different statistical distributions associated with each of the stimuli. Instead, observers seem to assume a single distribution, which is the average of all distributions involved in the task (Gorea & Sagi, 2000). It is possible that the inability to adjust the response criterion under the Mix procedure reflects a failure of learning. Under the Fix procedure the desired criterion may be set by a learning process that operates across a number of consecutive trials while under the Mix procedure, such a learning process will fail. Recent studies, using the 2AFC method, show that learning in some contrast discrimination tasks fail under the mixed procedures though they apparently succeed under the fixed procedure (Adini, Wilkonsky, Haspel, Tsodyks, & Sagi, 2004).

The present results strongly support an account of lateral facilitation that posits horizontal excitatory interactions between cortical detectors responding to the target and flankers. An alternative account suggests that the effect of facilitation by collinear flankers is due to uncertainty reduction (Levi, Hariharan, & Klein, 2002; Petrov, Verghese, & McKee, 2006; Shani & Sagi, 2006). Such an account of facilitation is based on the assumption that the flankers allow the observer to better select the neuronal population relevant for the task. A frequently used detection model posits that observers use the maximal sensory response among all detectors considered for the task, many of which are irrelevant for the task in case of uncertainty regarding stimulus parameters (Pelli, 1985). This model predicts higher values of the decision variable in the case of uncertainty (here corresponding to larger target-flanker distances), with a smaller scatter (*SD*). To account for our results of the Mix procedure with this uncertainty based model, it is necessary to assume a response criterion which is decreased at small target-flankers distances and is increased at large target-flankers distances relative to the gradual Fix condition. Such a behavior is not consistent with previous studies of criterion setting with the Mix procedure (Gorea & Sagi, 2000) and with common sense.

Acknowledgments

Part of this study was supported by grants from the National Institute for Psychobiology in Israel and the Israel Science Foundation (U.P.). We thank Andrei Gorea for comments made on an earlier version of this paper.

References

Adini, Y., Wilkonsky, A., Haspel, R., Tsodyks, M., & Sagi, D. (2004). Perceptual learning in contrast discrimination: The effect of contrast uncertainty. *Journal of Vision, 4*(12), 993–1005.

Bonneh, Y., & Sagi, D. (1998). Effects of spatial configuration on contrast detection. *Vision Research, 38*(22), 3541–3553.

Crook, J. M., Engelmann, R., & Lowel, S. (2002). GABA-inactivation attenuates colinear facilitation in cat primary visual cortex. *Experimental Brain Research, 143*(3), 295–302.

Dresp, B., & Bonnet, C. (1991). Psychophysical evidence for low-level processing of illusory contours and surfaces in the Kanizsa square. *Vision Research, 31*(10), 1813–1817.

Dresp, B., & Bonnet, C. (1993). Psychophysical measures of illusory form perception: Further evidence for local mechanisms. *Vision Research, 33*(5-6), 759–766.

Gorea, A., Caetta, F., & Sagi, D. (2005). Criteria interactions across visual attributes. *Vision Research, 45*(19), 2523–2532.

Gorea, A., & Sagi, D. (2000). Failure to handle more than one internal representation in visual detection tasks. *Proceedings of the National Academy of Sciences USA, 97*(22), 12380–12384.

Green, D. M., & Swets, J. A. (1966). *Signal detection theory*. New York: Wiley.

Kapadia, M. K., Ito, M., Gilbert, C. D., & Westheimer, G. (1995). Improvement in visual sensitivity by changes in local context: Parallel studies in human observers and in V1 of alert monkeys. *Neuron, 15*(4), 843–856.

Kasamatsu, T., Polat, U., Pettet, M. W., & Norcia, A. M. (2001). Colinear facilitation promotes reliability of single-cell responses in cat striate cortex. *Experimental Brain Research, 138*(2), 163–172.

Komatsu, H. (2006). The neural mechanisms of perceptual filling-in. *Nature Reviews Neuroscience, 7*(3), 220–231.

Kontsevich, L. L., Chen, C. C., Verghese, P., & Tyler, C. W. (2002). The unique criterion constraint: A false alarm? *Nature Neuroscience, 5*(8), 707, author reply 707–708.

Levi, D. M., Hariharan, S., & Klein, S. A. (2002). Suppressive and facilitatory spatial interactions in amblyopic vision. *Vision Research, 42*(11), 1379–1394.

Mizobe, K., Polat, U., Pettet, M. W., & Kasamatsu, T. (2001). Facilitation and suppression of single striate-cell activity by spatially discrete pattern stimuli presented beyond the receptive field. *Vision Neuroscience, 18*(3), 377–391.

Pessoa, L., Thompson, E., & Noe, A. (1998). Finding out about filling-in: A guide to perceptual completion for visual science and the philosophy of perception. *Behavioral and Brain Sciences, 21*(6), 723–748, discussion 748–802.

Petrov, Y., Verghese, P., & McKee, S. P. (2006). Collinear facilitation is largely uncertainty reduction. *Journal of Vision, 6*(2), 170–178.

Pelli, D. G. (1985). Uncertainty explains many aspects of visual contrast detection and discrimination. *Journal of The Optical Society of America A, 2*(9), 1508–1532.

Pillow, J., & Rubin, N. (2002). Perceptual completion across the vertical meridian and the role of early visual cortex. *Neuron, 33*(5), 805–813.

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. *Proceedings of the National Academy of Sciences USA, 91*(4), 1206–1209.

Ramachandran, V. S., Ruskin, D., Cobb, S., Rogers-Ramachandran, D., & Tyler, C. W. (1994). On the perception of illusory contours. *Vision Research, 34*(23), 3145–3152.

Ress, D., Backus, B. T., & Heeger, D. J. (2000). Activity in primary visual cortex predicts performance in a visual detection task. *Nature Neuroscience, 3*(9), 940–945.

Ress, D., & Heeger, D. J. (2003). Neuronal correlates of perception in early visual cortex. *Nature Neuroscience, 6*(4), 414–420.

Sagi, D., & Gorea, A. (2004). The Unique decision criterion: Constant internal response or false-alarm rate. Vision Sciences Society, abstracts, (p. 454). Sarasota, FL.

Series, P., Lorenceau, J., & Fregnac, Y. (2003). The "silent" surround of V1 receptive fields: Theory and experiments. *Journal of Physiology Paris, 97*(4–6), 453–474.

Shani, R., & Sagi, D. (2005). Eccentricity effects on lateral interactions. *Vision Research, 45*(15), 2009–2024.

Shani, R., & Sagi, D. (2006). Psychometric curves of lateral facilitation. *Spatial Vision, 19*(5), 413–426.

Solomon, J. A., & Morgan, M. J. (2000). Facilitation from collinear flanks is cancelled by non-collinear flanks. *Vision Research, 40*(3), 279–286.

Sugrue, L. P., Corrado, G. S., & Newsome, W. T. (2005). Choosing the greater of two goods: Neural currencies for valuation and decision making. *Nature Reviews Neuroscience, 6*(5), 363–375.

Woods, R. L., Nugent, A. K., & Peli, E. (2002). Lateral interactions: Size does matter. *Vision Research, 42*(6), 733–745.

Please cite this article in press as: Polat, U., & Sagi, D., The relationship between the subjective and ..., *Vision Research* (2007), doi:10.1016/j.visres.2007.06.007