Facilitation of contrast detection by flankers without perceived orientation

Daisuke Hayashi

Ikuya Murakami

To extract meaningful structure from noisy input signals, the human visual-processing system uses elementary structures, such as contours, to extract more complex informative structures. The first step in contour processing involves identifying local orientation. The phenomenon of collinear facilitation is important for understanding how orientation detection is implemented; at the fovea, a stripe near the contrast threshold (target) is easier to detect when it is collinearly flanked by stripes with the same orientation (flankers). This facilitation requires collinear alignment and presumably reflects cortical mechanisms in the early visual cortex. Strong collinear orientation signals are said to help in detecting a feeble signal and in establishing a smooth conscious linkage of orientations. However, contrary to this notion, we show here that relatively small but significant facilitation occurs even when the flankers have no perceived orientation. One such case involves concentric flankers that have unbiased luminance energies in all orientations. When collinearly surrounding an oriented target, these flankers facilitated detection of the target. In another case, oriented flankers that were made invisible through interocular suppression and that were monocularly surrounding an oriented target yielded collinear facilitation even though the flankers themselves were completely masked by random patterns presented to the other eye. These findings indicate that automatic, preconscious processing of orientation information at some early stage can improve the visibility of local linear elements. They also indicate the usefulness of latent visual information in detecting orientation and constructing our visual world.

Introduction

The visual system must extract meaningful structures from registered input signals mixed with noise in order to construct a meaningful visual world. Contours are one such structure. The retinal projection of an object forms a silhouette that constrains possible object shapes, and textured surfaces with various curvatures project informative surface contours. The ability to identify contours within a noisy field depends on the relationship between a global configuration and local orientations of edge components (Field, Hayes, & Hess, 1993). This means that contour processing starts by identifying local orientation elements. The major problem confronting the visual system is how to detect a feeble signal from noisy impoverished retinal inputs, and this applies to local-orientation detection as well. Therefore, understanding how the visual system detects weak orientation signals plays an initial critical role in elucidating the way our visual world is constructed.

A human perceptual effect in this situation is collinear facilitation. A barely visible “target” stimulus with a particular orientation is more readily detected in the presence of two high-contrast “flanker” stimuli with the same orientation (Polat & Sagi, 1993). Collinear alignment is required so that vertical flankers are vertically aligned with a vertical target (Polat & Sagi, 1994a). This effect is tuned to basic visual characteristics such as spatial phase (Solomon, Watson, & Morgan, 1999; Williams & Hess, 1998) and spatial frequency (Polat & Sagi, 1993; Tanaka & Sagi, 1998). Psychophysical proposals for mechanisms of collinear facilitation can be roughly grouped into two hypotheses: interactions within a single elongated spatial filter (Morgan & Dresp, 1995; Solomon et al., 1999; Williams & Hess, 1998; Yu & Levi, 1997) and long-range lateral interactions between filters (Cass & Alais, 2006; Cass & Spehar, 2005a; Polat & Sagi, 2006;
Solomon & Morgan, 2000). There is some physiological indication that this effect may be partly based on orientation-selective mechanisms within the primary visual cortex (V1: Kapadia, Ito, Gilbert, & Westheimer, 1995; Polat, Mizobe, Pettet, Kasamatsu, & Norcia, 1998; Polat & Norcia, 1996). Perceptual-learning effects show the plasticity of such interactions (Polat & Sagi, 1994b). The involvement of higher order processing, such as attentional modulation (Freeman, Driver, Sagi, & Zhaoping, 2003; Freeman, Sagi, & Driver, 2001) and reduction of spatiotemporal uncertainty (Petrov, Verghese, & McKee, 2006), is also indicated. These accumulated findings suggest that higher and lower order processes in the visual system cooperatively help detect a feeble orientation signal.

However, just how low such lower order processes might be is unknown. Some studies have suggested that collinear facilitation occurs because strong collinear-orientation signals help detect feeble signals between them to establish a smooth conscious linkage of orientations (Loffler, 2008; Polat, 1999). However, previous investigations have always used flankers with distinct orientations, making it impossible to assess to what degree our conscious access to orientation-specific information is necessary. In fact, a lot of orientation-specific information is initially contained in cortically registered input signals but is lost in our conscious awareness because such information is gradually reassembled by early nonlinear operation for efficient coding (Schwartz & Simoncelli, 2001). The idea that such orientation-specific signals are never consciously perceived but are nonetheless represented in the early visual cortex has psychophysical support: Orientation-selective adaptation occurs even when the orientation of an adapter is never seen because of binocular rivalry, crowding, or unresolvably high spatial frequency (Blake & Fox, 1974; He, Cavanagh, & Intriligator, 1996; He & MacLeod, 2001). Given the suggested contribution of the early visual cortex (Kapadia et al., 1995; Polat et al., 1998; Polat & Norcia, 1996), it is possible that flankers without perceived orientations can still cause collinear facilitation.

Here, we demonstrated psychophysically that this is indeed the case. We used two types of flankers that did not have perceived orientation but were able to activate the orientation-selective neurons in the early visual cortex. In Experiments 1.1 through 1.5, we showed that facilitation of vertical-target detection also occurred when flankers were not specifically oriented stimuli but rather were concentric patterns. The Fourier components of such flankers had omniorientation luminance energies, so these concentric flankers, which had neither physical nor perceived orientation, could still activate oriented linear luminance filters approximating the behavior of some orientation-selective cortical neurons (Carandini, Heeger, & Movshon, 1997; Heeger, 1992, 1993; Hubel & Wiesel, 1962, 1968). In Experiments 2.1 and 2.2, we more directly investigated whether the visibility of flankers played any role in collinear facilitation by rendering flankers invisible through interocular suppression, and we showed that collinear facilitation still occurred without conscious awareness of the flankers. These findings suggest that the facilitation results from a rather automatic, preconscious operation at some early stage that improves the visibility of local linear elements. Our results also indicate the usefulness of latent visual information in detecting orientation and constructing our visual world.

We investigated whether collinear facilitation occurs when flankers are concentric patterns rather than oriented stripes. We used D2 patterns, which were the second derivative of a two-dimensional isotropic Gaussian distribution (for details, see Methods of Experiment 1.1), as the target and flankers (Motoyoshi & Nishida, 2001). Each pattern looked like a blurry stripe with a specific orientation (Figure 1Aa, Ab), and the linear summation of two mutually orthogonal patterns was equivalent to a concentric luminance modulation that appeared to be a bullseye (Figure 1Ac). Two flankers were presented, one above and one below the target position (Figure 1B). The target was a vertical D2 pattern. Three types of flankers were used: a vertical D2 pattern (V), a horizontal D2 pattern (H), and their linear summation (HV). The HV flanker contained Fourier luminance energies in all orientations equally (Supplementary Figure S1) and thus was expected to yield unbiased activations of all orientation-selective linear filters at an early stage of visual processing. In monkeys and cats, orientation-selective responses first emerge in neurons in the primary visual cortex, whose receptive fields are often modeled as linear filters (Carandini et al., 1997; Heeger, 1992, 1993; Hubel & Wiesel, 1962, 1968). Thus, the concentric HV flankers can activate orientation-selective mechanisms at an early stage but do not result in the conscious perception of any specific orientation.
Experiment 1.1: Concentric flankers yield facilitation

First, we examined whether concentric flankers behave like vertical flankers and facilitate target detection.

Methods

Observers

Participants were nine adult human observers with normal or corrected-to-normal vision. All but the first author were unaware of the purpose of the experiments. In all the experiments described hereafter, all participants provided written informed consent, and all experiments were approved by the ethics committee of the University of Tokyo and conducted in accordance with the Declaration of Helsinki. Each observer viewed visual stimuli in a dark room at a viewing distance of 95 cm, constrained by a chin rest. Stimuli were viewed with both eyes open.

Apparatus

Stimuli were generated by a computer (Apple PowerMac G5) and were displayed on a CRT monitor (Iiyama HM204D). Luminance was gamma corrected with a 10-bit-depth color lookup table on a video card. The monitor’s spatial resolution was $1600 \times 1200$ pixels, and the refresh rate was 60 Hz. The MATLAB programming environment and the Psychophysics Toolbox extensions were used to generate visual stimuli (Brainard, 1997; Kleiner, Brainard, & Pelli, 2007; Pelli, 1997).

Luminance patterns

To render a blurry luminance stripe, we used a D2 pattern (Motoyoshi & Nishida, 2001), namely the second derivative of a two-dimensional isotropic Gaussian distribution ($G$). The luminance modulation ($L$) of the D2 pattern ($D_2$) is formulated as

$$L(x, y|c, \theta, \sigma) = L_{\text{mean}}[1 + c \times D_2(x, y|\theta, \sigma)],$$

$$D_2(x, y|\theta, \sigma) = \frac{(xcos\theta + ysin\theta)^2 - \sigma^2}{\sigma^4} \times \exp \left[ \frac{-(x^2 + y^2)}{2\sigma^2} \right],$$

where $L_{\text{mean}}$ is the mean luminance of the background (40 cd/m²), $c$ is the contrast (set at 9 for the flankers and variable for the target), $\theta$ is the orientation, and $\sigma$ is the space constant (2.7 min). The mean luminance of the D2 pattern was equal to the background luminance.
luminance. Note that the sum of two orthogonal D2 patterns is equivalent to an isotropic Laplacian of Gaussian,

\[
L_{\text{mean}}[1 + c \times [D_2(x, y|0, \sigma) + D_2(x, y|\pi, \sigma)]]
\]

\[
= L_{\text{mean}} \left[ 1 + c \times \left\{ \left[ (\cos x + \sin y)^2 - \sigma^2 \right] + \left[ (\cos \pi x + \sin y^2)^2 - \sigma^2 \right] \right\} / \sigma^4 \right]
\times \exp \left( - \frac{(x^2 + y^2)}{2\sigma^2} \right)
\]

\[
= L_{\text{mean}} \left[ 1 + c \times \left\{ \left[ x^2 + y^2 - 2\sigma^2 \right] \right\} \times \exp \left( - \frac{(x^2 + y^2)}{2\sigma^2} \right) \right],
\]

(2)

which we actually used as a blurry concentric pattern that appeared as a bullseye (Figure 1A). By scrutinizing the Fourier power spectra, we confirmed that this concentric pattern contained luminance energies in all orientations that overlapped those of a D2 pattern, and that the Fourier power did not differ across orientations within spatial frequencies lower than 20 c/° (Supplementary Figure S1). The visible size of each D2 pattern was approximately 0.3° wide, and the wavelength \( \lambda \) of the most dominant spatial frequency was 0.15°. We also used Gaussian blobs as the flankers. Their luminance modulation obeyed the primitive function of the D2 pattern:

\[
G(x, y) = \exp \left( - \frac{(x^2 + y^2)}{2\sigma^2} \right)
\]

(3)

The maximum luminance of the Gaussian blob was set to be equal to that of the D2 patterns.

**Stimulus presentations**

The target was a vertical D2 pattern presented at the fovea. Two flankers of the same type were presented above and below the target position. The separation between the target and each flanker was 0.45° (=32'). The maximum Michelson contrast of the flankers was set at 72%, whereas the target contrast was systematically varied to home in on the detection threshold through an adaptive psychophysical method (see Procedure). The flankers were presented throughout each stimulus interval (i.e., 200 ms = 12 frames), whereas the target, if present, flickered at 30 Hz such that it was shown in only odd-numbered display frames (i.e., the first, third, fifth, seventh, ninth, and 11th frames). In every other frame, the target region of the monitor remained uniformly gray. This manipulation effectively attenuated the target contrast by half.

Four types of flankers were used (Figure 1A): a vertical D2 pattern (V), a horizontal D2 pattern (H), an isotropic (concentric) Laplacian (HV), and a Gaussian blob (G), with positive or negative versions chosen randomly. The Gaussian-shaped flankers provided the same spatial and temporal predictability cues with respect to the target as the other flanker stimuli and had luminance energies within a lower spatial-frequency range in all orientations than those of the HV flankers (Supplementary Figure S1); thus it was sensible to examine whether these flankers could cause collinear facilitation despite its known spatial-frequency tuning (Polat & Sagi, 1993; Tanaka & Sagi, 1998). The condition involving the H flankers was regarded as the baseline condition throughout the experiments described hereafter.

**Procedure**

We determined the target contrast at the detection threshold with a two-interval forced-choice paradigm (Figure 1B). Before each trial, a fixation cross was presented at the center of the monitor on a uniform gray background. When an observer fixated on the cross and pressed a button to initiate each trial, the fixation cross disappeared, and 500 ms later, the first and second stimuli were presented for 200 ms each, with an interstimulus interval of 1000 ms. Each presentation of the target and flankers was temporally blurred by a raised-cosine temporal window:

\[
\frac{1}{2} \left( 1 + \cos \left( \frac{0.6 + 0.8(i - 1) - 5}{5\pi} \right) \right) (i = 1, 2, 3, \ldots, 12).
\]

(4)

The flankers were presented at both stimulus intervals, but the target was presented during only one of the stimulus intervals, which was chosen randomly. The observer was asked to press the computer button corresponding to the target-containing interval in a two-interval forced-choice fashion. When the observer’s response was incorrect, a computer beep was delivered as auditory feedback. To determine the threshold, we used the four-down-one-up staircase method: The target contrast was increased by 0.1 log unit after each incorrect response and decreased by 0.1 log unit after four consecutive correct responses. This staircase algorithm was designed to reach the asymptote at an 84% correct-response level (Levitt, 1971). Each staircase sequence ended at the eighth reversal, and the geometric mean of the contrasts at the last six reversal points was used as a tentative threshold. After approximately every 10 trials of each staircase sequence, a trial with a target whose contrast was well above the threshold was inserted to maintain the observer’s motivation.
Results and discussion

A one-way ANOVA was used to compare differences in sensitivity. Because the main effect of flanker type was significant, $F(3, 24) = 10.65, p = 0.0001$, multiple comparison analyses were performed. As expected, the V flankers increased sensitivity relative to the H flankers (0.086 log units), $t(8) = 4.45, p = 0.013$, indicating conventional collinear facilitation. The Gaussian blobs did not yield a significant difference in sensitivity (0.0053 log units), $t(8) = 0.47, p = 0.65$, indicating that only circular stimuli were not sufficient to cause facilitation. Most importantly, the HV flankers did cause a significant increase in sensitivity (0.047 log units), $t(8) = 3.60, p = 0.021$ (Figure 2). The differences in sensitivity between the V and G flankers and between the HV and G flankers were also significant—$t(8) = 3.70, p = 0.018$, and $t(8) = 4.28, p = 0.013$, respectively—whereas the difference between the V and HV conditions was not significant, $t(8) = 1.68, p = 0.26$. Thus the concentric flankers with no distinct orientation yielded facilitation, indicating that certain orientation-selective and spatial-frequency-selective neural responses to flanker stimuli that occur at an early stage are sufficient for the operation of the underlying mechanism of collinear facilitation. Perception of a specific orientation is not a necessary condition.

The facilitation due to the HV flankers tended to be weaker than that due to the V flankers, although the difference between them was not significant. This may be because the mechanisms tuned to noncollinear, especially orthogonal, orientations activated by the HV flankers suppress the facilitatory effect of the mechanism tuned to the collinear orientation. A previous study on surround suppression raised the possibility that a collinear component of a surrounding stimulus has smaller suppressive influence when there is a simultaneously overlapping orthogonal component (Petrov, Carandini, & McKee, 2005). However, in contrast with the fact that flanker stimuli with the same orientation as the target but a different spatial location result in deterioration of collinear facilitation (Polat, 1999; Solomon & Morgan, 2000), our finding that the HV flankers cause facilitation indicates that the activation of mechanisms tuned to other orientations may weaken but cannot nullify collinear facilitation. That may be because mechanisms with similar rather than different preferred orientations tend to make lateral connections (Stemmler, Usher, & Niebur, 1995), which may underlie collinear facilitation (Kapadia et al., 1995; Polat et al., 1998; Polat & Norcia, 1996).

The smaller facilitation induced by the HV flankers may also be explained by the difference in the physical energy of the vertical “component”: because an HV flanker was the sum of a V flanker and a H flanker, the vertical energy of the HV flanker should be smaller than that of the V flanker. To investigate this possibility, we also compared the detection sensitivity of the V flankers with full luminance contrast and those with halved luminance contrast. Sensitivity did not differ significantly (30.1 ± 1.71 with full contrast and 28.9 ± 1.74 with halved contrast), $t(8) = 1.34, p = 0.22$, which is consistent with previous studies (Polat, 1999; Polat & Sagi, 1993). Thus, an explanation based on a difference in the physical energy of the vertical component seems unlikely.
Experiment 1.2: Horizontal flankers are slightly better than no flankers

The first experiment assumed the H flankers as the baseline, but previous studies typically had no flankers in the baseline condition (Polat & Sagi, 1993, 1994a). To make sure that what we obtained was facilitation from a valid baseline rather than merely a difference relative to a baseline yielding poorer sensitivity, we compared the detection sensitivities with and without the H flankers.

Methods

The methods were identical to those of Experiment 1.1 except for the following. Six adult observers with normal vision participated. Stimuli were generated by a computer (Apple Mac Pro Mid 2012) and were displayed on a CRT monitor (Iiyama HM204D). The target was accompanied by either the H flankers or no flankers. In both cases, we presented two black crosses well above and below the target position (4.5° = 30λ) throughout each stimulus interval as a temporal cue of target presentation (Polat & Sagi, 1993, 1994a).

Results and discussion

The presence of the H flankers increased detection sensitivity compared with trials in which the target was presented alone (0.082 log units), t(5) = −2.38, p = 0.031 (Figure 3).

This result has two implications. First, the importance of the flankers for the baseline condition was confirmed. Early studies of collinear facilitation typically had no flankers in the baseline condition (Polat & Sagi, 1993, 1994a). However, several studies have demonstrated that target detection with no flankers is more difficult than that with flankers because of the spatiotemporal uncertainties of the target presentation (Pelli, 1985; Petrov et al., 2006). Horizontal flankers have been reported to facilitate target detection to some degree (Cass & Spehar, 2005b; Polat & Sagi, 1994a) and to work as a cue for reduction of spatiotemporal uncertainty (Petrov et al., 2006). It has been suggested that the presence of flankers as spatiotemporal markers should be controlled in the baseline condition. Another possibility is that presenting anything with the same spatial frequency as the target leads to a facilitatory effect. Whatever the reason, the H flankers that differed from the V and HV flankers only with respect to orientation information were slightly better than no flankers; hence the most stringent control involves defining facilitation as a further increase in sensitivity relative to trials including H flankers. The H flankers were therefore used as the baseline condition in the remaining experiments as well as in Experiment 1.1.

Second, the quantitative difference in the degree of facilitation between the present and previous studies (e.g., Polat & Sagi, 1993, 1994a) was partly reconciled. The extent of facilitation in Experiment 1.1 was smaller (0.086 log units for the V flankers and 0.047 log units for the HV flankers) than that observed in previous studies (typically 0.1–0.3 log units). This difference may have stemmed from a difference in baseline configuration: The previous studies typically had no flankers in the baseline condition, whereas we presented the H flankers. In Experiment 1.2, the degree of facilitation with the H flankers was 0.082 log units relative to that without flankers. Thus, sensitivity with the V flankers must be 0.17 log units higher than that without flankers if we sum the facilitations in Experiments 1.1 and 1.2. This value is comparable to those in the previous studies.

There may be some other components to the facilitation caused by the H flankers, such as cross-orientation facilitation (Cass & Spehar, 2005b). To clarify whether the facilitation due to the H flankers resulted from uncertainty reduction or from other factors, we also measured detection sensitivity with a stronger spatiotemporal cue for target presentation. To implement such a cue, we presented four diagonal bars around the target region throughout each stimulus interval. The presence of the H flankers had no effect on detection sensitivity compared with trials in which the target was presented alone (30.9 ± 4.73 with the H flankers and 33.4 ± 2.69 without flankers), t(3) = −0.871, p = 0.45, suggesting that observed facilitation...
due to the H flankers did indeed result from reduction of spatiotemporal uncertainty (Petrov et al., 2006).

**Experiment 1.3: Facilitation by concentric flankers is phase dependent**

The facilitation by vertical flankers becomes weaker when the target and the flankers have different spatial phases (Solomon et al., 1999; Williams & Hess, 1998). To examine whether such phase dependence also exists when facilitation is due to concentric flankers, we compared the degree of facilitation between the V flanker and its negative image and between the HV flanker and its negative image.

**Methods**

Eight adult observers with normal vision participated. The negative images of the V and HV flankers were also employed as flankers (Figure 4A). Otherwise, the methods were identical to those of Experiment 1.1.

**Results and discussion**

The presence of the V flankers and the HV flankers increased detection sensitivity compared with the baseline condition with the H flankers (0.090 and 0.063 log units)—$t(7) = -5.71$, $p = 0.0036$, and $t(7) = -3.00$, $p = 0.0099$, respectively—whereas the effects of the negative V flankers and the negative HV flankers were not significant (0.029 and 0.023 log units)—$t(7) = -1.38$, $p = 0.10$, and $t(7) = -1.09$, $p = 0.16$, respectively (Figure 4B). The difference in facilitation between in-phase and antiphase was significant, as revealed by a significant main effect of phase in a two-way ANOVA, $F(1, 7) = 26.98$, $p = 0.0013$. Neither the main effect of flanker type, $F(1, 7) = 1.77$, $p = 0.22$, nor the interaction between phase and flanker type, $F(1, 7) = 1.03$, $p = 0.34$, was significant.

These results indicate that facilitation by concentric flankers involves spatial phase dependency, as does facilitation by collinear flankers (Solomon et al., 1999; Williams & Hess, 1998; but see Zenger & Sagi, 1996), and suggest a single filter as an underlying mechanism. Previous psychophysical studies have suggested two possible mechanisms of collinear facilitation: interactions within a single elongated spatial filter (Morgan & Dresp, 1995; Solomon et al., 1999; Williams & Hess, 1998; Yu & Levi, 1997) and
long-range lateral interactions between small spatial filters (Cass & Alais, 2006; Cass & Spehar, 2005a; Polat & Sagi, 2006; Solomon & Morgan, 2000). The spatial phase dependency of facilitation is thought to support the hypothesis of a single elongated filter (for a review, see Loffler, 2008), because similar phases at different locations would sum in an oriented receptive field and dissimilar phases would cancel. Nonetheless, our results do not necessarily eliminate a modified hypothesis of multiple small filters with phase-sensitive interconnections.

Experiment 1.4: Facilitation by concentric flankers occurs within a short range

Thus far, each flanker was placed at 3λ from the target. Previous studies that manipulated the separation between the target and flankers have shown that flankers at 2λ facilitate target detection to the same degree as flankers at 3λ (Huang, Mullen, & Hess, 2007; Polat & Sagi, 1993; 1994a). Furthermore, flankers at 6λ caused a smaller but significant facilitatory effect (Huang et al., 2007; Polat & Sagi, 1993; 1994a). To examine how the separation between the target and flankers affects facilitation by concentric flankers, we tested V flankers and concentric flankers at separations of 2λ and 6λ.

Figure 5. Results of Experiment 1.4, revealing the spatial range of facilitation by concentric flankers. Facilitation is described with respect to sensitivity (whose absolute value was 33.7 at 2λ and 30.1 at 6λ) in the baseline condition (H flankers at each separation). The column graph shows the mean across observers. Error bars indicate standard errors.

Methods

Ten adult observers with normal vision participated. The separation between the target and each flanker was manipulated. The V flankers and the HV flankers were tested. The H flankers were also tested at each separation, representing baseline performance. Other settings were identical to those of Experiment 1.2.

Results and discussion

Facilitation, namely a sensitivity increase relative to baseline performance at each separation, was observed with the V flankers (0.072 log units), t(9) = -2.47, p = 0.018, and was marginally significant with the HV flankers (0.041 log units), t(9) = -1.62, p = 0.070, at 2λ separation; however, at 6λ, facilitation by the V flankers was marginally significant (0.042 log units), t(9) = -1.76, p = 0.056, whereas the HV flankers did not yield a significant sensitivity change (−0.0056 log units), t(9) = 0.39, p = 0.65 (Figure 5).

The facilitatory effect by the vertical flankers at both 2λ and 6λ is consistent with that found in previous studies (Huang et al., 2007; Polat & Sagi, 1993, 1994a). In contrast, facilitation by the concentric flankers tended to occur marginally at 2λ but not at 6λ. A facilitatory effect by flankers at 6λ may require long-range lateral interactions across small spatial filters (Cass & Spehar, 2005a; Tanaka & Sagi, 1998). In contrast, a facilitatory effect by flankers at 2λ or 3λ may reflect interactions within a single elongated, spatially limited filter (Morgan & Dresp, 1995; Yu & Levi, 1997). Taken together, our findings suggest that a single elongated spatial filter is the best candidate underlying mechanism of facilitation by concentric flankers, whereas both of candidate mechanisms can explain facilitation by vertical flankers.

Experiment 1.5: Facilitation by concentric flankers is monocular

We also examined whether facilitation by concentric flankers is monocularly driven, as is the case for collinear facilitation by vertical flankers (Huang, Hess, & Dakin, 2006; Tanaka & Sagi, 1998).

Methods

The methods were identical to those of Experiment 1.1 with the following exceptions. Six adult observers with normal vision participated. Stimuli were viewed dichoptically through a mirror stereoscope. The domi-

Downloaded from jov.arvojournals.org on 09/24/2019
nant eye of each observer was determined using a hole-in-card test. Stimuli were generated by a computer (Apple PowerMac G5) and displayed on a CRT monitor (Mitsubishi Diamondtron M2 RDF223H). The flankers and target were presented either monocularly or dichoptically via the mirror stereoscope. The monocularly presented H flankers served as the baseline condition. We also provided four diagonal bars, each 0.11 long, as a cue for binocular fusion. These bars were presented around the target region throughout each stimulus interval. Upper left and lower right bars were presented to the dominant eye, and upper right and lower left bars were presented to the nondominant eye. These bars reduced the spatiotemporal uncertainty of the target and were also useful for checking that observers had no perceptual suppression of visual stimuli presented at the target region of either eye. As an additional aid to binocular fusion, we also binocularly provided a 3/8-wide square frame consisting of 0.15-thick lines filled with static random dots. This frame was presented throughout the experiment, and the static random dots were refreshed every trial.

Results and discussion

When the flankers were presented to the same eye together with the target, both the V and HV flankers caused significant increases in sensitivity (0.065 and 0.030 log units)—t(5) = -3.82, p = 0.0062, and t(5) = -2.42, p = 0.030, respectively. In contrast, when the flankers were presented to one eye and the target was presented to the other eye, neither the V nor HV flankers had any effect on detection sensitivity (0.011 and -0.020 log units)—t(5) = -0.24, p = 0.41, and t(5) = 0.81, p = 0.77, respectively (Figure 6).

Therefore, facilitation by concentric flankers shared the characteristic of monocularity with facilitation by vertical flankers (Huang et al., 2006; Tanaka & Sagi, 1998). It is shown that the perceptual collinearity of concentric flankers and the target is not a sufficient condition for facilitation to occur, suggesting that facilitation by concentric flankers is not merely based on higher order processing that relates to perceptual appearance.

Experiments examining collinear facilitation by masked and invisible flankers

Our results thus far suggest that same-eye activation of orientation-selective and spatial-frequency-selective filters in early visual processing is sufficient and that perceived orientation is not necessary for collinear facilitation to occur. However, the concentric flankers themselves were clearly visible, so we cannot conclude that it was implicitly represented collinearity and not conscious access to collinear alignment that was critical for the facilitation. To clarify whether the visibility of flankers plays any role, we next examined whether collinear facilitation occurs when the flankers themselves are subjectively rendered invisible by interocular suppression.

We used the method of continuous flash suppression (CFS; Tsuchiya & Koch, 2005). The stimuli were presented dichoptically, and both the flankers and the target were presented to the dominant eye. We used two types of flankers: a vertical D2 pattern (V) and a horizontal D2 pattern (H). To render them invisible, rapidly refreshed random patterns, which served as masking stimuli, were presented at the locations corresponding to the flankers—but to the nondominant eye. The presence of these masking stimuli made the flankers completely invisible (Figure 7A).

Experiment 2.1: Interoculurally masked and invisible flankers yield facilitation

We examined whether facilitation occurs even when flankers themselves are rendered invisible by interocular suppression.

Methods

The methods were identical to those of Experiment 1.5 except for the following. Nine adult observers with
normal vision participated. As a masking stimulus, we used a square-shaped achromatic pattern, which consisted of rectangles of random sizes, positions, and luminances (black, gray, or white). The extent of the pattern was $0.3$ $\times$ $0.3$. Both the flankers and the target were presented to the dominant eye, whereas the masking stimuli were presented to the nondominant eye at the locations corresponding to the flankers. In the cyclopean view, the flankers went unnoticed due to CFS (Tsuchiya & Koch, 2005).

Results and discussion

The H flankers that were not accompanied by the masking stimuli and were therefore visible were regarded as the baseline condition. When the H flankers were made invisible, we observed neither facilitation nor suppression of target detection ($0.019$ log units), $t(8) = -1.14, p = 0.14$, confirming that the presence per se of the masking stimuli had no effect on target detection. Importantly, the V flankers significantly increased sensitivity regardless whether the flankers were visible or invisible ($0.062$ and $0.044$ log units) — $t(8) = -2.67, p = 0.014$, and $t(8) = -1.94, p = 0.044$, respectively (Figure 7B).

To validate the effectiveness of masking, we further tested the flankers’ visibility. During this validation, the stimulus presentation in each trial was the same as in other experiments except that the target was not presented and that at each stimulus interval, either the V flankers or the H flankers were chosen randomly. The observer was asked to indicate whether the flankers presented in the first stimulus interval and those presented in the second stimulus interval were the same or different. Within each experimental block, trials with and without the masking stimuli were presented in random order. There were 25 trials for each condition within each block, and two blocks were run for each observer. When the masking stimuli were absent, the correct-response rate was much greater than the chance level of $50\%$ ($96.2\% \pm 0.78\%$), $t(8) = 59.43, p <$
7.1×10^{-12}, and almost perfect. In contrast, the correctresponse rate was not different from the chance level (53.6% ± 2.66%), t(8) = 1.34, p = 0.22, when the masking stimuli were present, confirming that CFS made the flankers invisible as we had intended.

**Experiment 2.2: Facilitation by masked and invisible flankers occurs within a short range**

To compare the facilitatory characteristics of invisible flankers with those of visible flankers, we next investigated the effect of separation. We have seen that vertical flankers at 2λ, 3λ, and 6λ were associated with significant facilitation (Huang et al., 2007; Polat & Sagi, 1993; 1994a), whereas concentric flankers caused facilitation only at 2λ or 3λ; we tested whether interocularly masked and invisible flankers exhibit similar spatial characteristics. Additionally, to investigate more directly whether orientation-selective contrast-detection facilitation occurs without the visibility of flankers themselves, Experiment 2.2 involved invisible H flankers at each separation. If the detection sensitivity with invisible V (collinear) flankers was higher than that with invisible H (orthogonal) flankers, it would follow that orientation-selective facilitation could occur without the visibility of the flankers themselves.

**Methods**

Four adult observers with normal vision participated. The separation between the target and each flanker was manipulated. In all trials, masking stimuli were presented to the nondominant eye at locations corresponding to the flankers presented to the dominant eye, so that the separation between the masking stimuli changed with the separation between the target and flankers. This manipulation helped the observers attend to the locations of the invisible flankers, which is important for the occurrence of collinear facilitation (Freeman et al., 2001). Other settings were identical to those of Experiment 2.1.

**Results and discussion**

When the flankers were located at 3λ, presumably the most appropriate separation for collinear facilitation (Polat & Sagi, 1993), the invisible V flankers significantly increased detection sensitivity compared with the invisible H flankers (0.041 log units), t(3) =

![Figure 8. Results of Experiment 2.2, revealing the spatial range of facilitation by invisible flankers. Facilitation is described with respect to sensitivity whose absolute value was 23.9 at 2λ, 29.5 at 3λ, and 32.1 at 6λ in the baseline condition (invisible H flankers at each separation). The column graph shows the mean across observers. Error bars indicate standard errors.](image-url)

-3.49, p = 0.020 (Figure 8); therefore, the collinear flankers facilitated contrast detection even when the flankers were always rendered invisible by the CFS.

At 6λ, however, no difference in detection sensitivity between the invisible V and H flankers was observed (0.0033 log units), t(3) = -0.38, p = 0.37. In Experiment 1.4 and previous studies (Huang et al., 2007; Polat & Sagi, 1993, 1994a), visible collinear flankers at 6λ facilitated target detection; hence, the facilitatory effect of invisible collinear flankers may be limited within a narrower range of separation between the target and flankers. Alternatively, it may be that a modest effect at 6λ was combined with a modest effect of invisible flankers, resulting in no observable facilitation.

At 2λ, no effect was observed (−0.035 log units), t(3) = 0.97, p = 0.80. This may be because the separation was too small to maintain our experimental rationale of local masking. As the separation between the target and the flankers decreased, the mask stimuli also approached the location corresponding to the target. This may have caused a spillover of binocular rivalry or contrast masking into the target location, making the task difficult, reducing sensitivity, and preventing a facilitatory effect by collinear flankers, because collinear facilitation occurs only when the target has a contrast near the absolute threshold (Chen & Tyler, 2002; Huang & Hess, 2007). As supporting evidence for this interpretation, the standard error was much larger and the absolute detection sensitivity much lower (more than 0.2 log units) when the flankers were located at 2λ than when they were located at 3λ or 6λ.

Facilitation by invisible collinear flankers occurred at 3λ but not at 6λ. It is said that a facilitatory effect at 6λ corresponds to long-range lateral interactions across small spatial filters, which can occur with a relatively
large separation (Cass & Spehar, 2005a; Tanaka & Sagi, 1998), whereas a facilitatory effect at 3Δ can be explained by interactions within a single elongated spatial filter, which are relatively spatially limited (Morgan & Dresp, 1995; Yu & Levi, 1997). The present results suggest that a single elongated spatial filter is a plausible candidate for the underlying mechanism causing facilitation by interocularly masked and invisible flankers.

As in Experiment 2.1, we validated the flankers’ invisibility. When the masking stimuli were absent, the correct-response rate was always much higher than the chance level of 50%: 97.0% ± 1.00%, t(3) = 47.00, p = 2.1×10⁻⁵ for 2Δ; 99.0% ± 0.58%, t(3) = 84.87, p = 3.6×10⁻⁶ for 3Δ; and 97.0% ± 1.00%, t(3) = 47.00, p = 2.1×10⁻⁵ for 6Δ. Indeed, it was almost perfect. In contrast, the correct-response rate did not differ from the chance level when they were present—52.0% ± 4.24%, t(3) = 0.47, p = 0.67 for 2Δ; 54.0% ± 3.56%, t(3) = 1.12, p = 0.34 for 3Δ; and 46.5% ± 4.35%, t(3) = −0.80, p = 0.48 for 6Δ—confirming that CFS rendered the flankers invisible as we had intended.

In short, these results indicate that collinear facilitation occurs even when the flankers themselves are subjectively rendered invisible by interocular suppression, and that such a facilitatory effect is limited to the appropriate spatial separation (3Δ) between the target and the flankers. Thus, we can conclude that it is not conscious access to collinear alignment but implicitly represented collinearity that is critical for facilitation, meaning that invisible flankers can help make an invisible target visible.

General discussion

The present results demonstrate that concentric flankers placed above and below a vertical target facilitate detection of the target, and that collinear facilitation also occurs even when the vertical flankers are artificially made invisible.

Relationship to previous psychophysical studies

Some studies partially explain collinear facilitation in terms of reduction in the spatiotemporal uncertainty of the target (Pelli, 1985; Petrov et al., 2006). However, this account fails to explain the present results, which used the flankers or four diagonal bars to provide the same spatial and temporal predictability cues across conditions, including the baseline condition.

Some researchers have argued for the existence of similarities between collinear facilitation and contour integration (Loffler, 2008; Polat, 1999; Polat & Sagi, 1994a), whereas others have suggested that they are distinct (Huang et al., 2006; Huang & Hess, 2007; Williams & Hess, 1998). In the present study, facilitation by the concentric flankers as well as the vertical ones exhibited phase dependency (Experiment 1.3), whereas contour integration between edge components is reportedly phase insensitive (Field et al., 2000). Also, to interpret local features as constituting a unitary global shape may require conscious awareness (Schwarzkopf & Rees, 2011), whereas the facilitation we examined here does not (Experiment 2.1). This suggests that the facilitation results from rather automatic operation at some early stage to improve visibility of local linear elements, which subsequently feed to a stage of contour integration where feedback signals from higher processes related to cognition may play an executive role.

The relationship between visual attention and awareness is also worth mentioning. Experiment 2.1 demonstrates that collinear facilitation does not require conscious awareness of collinear flankers, whereas attention to them may modulate flanker–target integration (Freeman et al., 2001; Freeman et al., 2003). Attention and awareness seem to be strongly related (Posner, 1994) but may be distinct (Koch & Tsuchiya, 2007; Lamme, 2003). Attention could modulate the processing of invisible stimuli (Boxtel, Tsuchiya, & Koch, 2010; Kanai, Tsuchiya, & Verstraten, 2006), suggesting the possibility that an attentional process somehow plays a facilitatory role in the detection of the target sandwiched by the collinear flankers, without conscious awareness of the latter.

Relationship to studies of orientation processing without conscious awareness

It is well known that neural activation to orientation stimuli often contributes to visual functioning even when the stimuli are not consciously visible. For example, invisible orientation can change the apparent contrast of orientation stimuli, either via adaptation or via surround suppression (Blake & Fox, 1974; He & MacLeod, 2001; Motoyoshi & Hayakawa, 2010; Rajimehr, 2004). Also, unconscious orientation can change the appearance of orientation stimuli in the tilt aftereffect and the simultaneous tilt contrast effect (Clifford & Harris, 2005; He & MacLeod, 2001; Kanai et al., 2006; Motoyoshi & Hayakawa, 2010). Additionally, a crowding effect of orientation stimuli can occur with the use of invisible flankers (Ho & Cheung, 2011; Shin & Tjan, 2011, 2013; but see Wallis & Bex, 2011). The present results can also be viewed as another experiment using invisible orientation stimuli. These previous investigations, however, have always used phenomena that can affect suprathreshold orientation.
appearances. In contrast, collinear facilitation occurs only when the target has a near-threshold contrast (Chen & Tyler, 2002; Huang & Hess, 2007; Polat et al., 1998; Williams & Hess, 1998). The processing of near-threshold stimuli is not the same as that of supra-threshold stimuli (Graham, 2011), so the present results make a unique contribution to understanding unconscious orientation processing.

Neurons can be activated by unconscious orientation information; therefore, activation in V1 is not a sufficient condition for conscious awareness (Crick & Koch, 1995), as supported by our findings, among many others. On the other hand, the effects of conscious awareness on V1 responses are still controversial. For example, psychophysically, the degree of adaptation either changes (Blake, Tadin, Sobel, Raisian, & Chong, 2006; Tsuchiya & Koch, 2005) or does not change (Blake & Fox, 1974; He et al., 1996) with an adapter’s visibility. Physiologically, the neural activities in the primary visual cortex are either affected (Maier et al., 2008; Yuval-Greenberg & Heeger, 2013) or not affected (Watanabe et al., 2011) by stimulus visibility. Our finding that orientation information made unconscious through interocular suppression can cause monocularly driven collinear facilitation suggests that interactions between the flankers and the target take place preconsciously at a stage as early as V1, where monocular neurons are still ubiquitous, and they are not affected by flankers’ visibility.

**General significance of collinear facilitation by flankers without perceived orientation**

Orientation processing has been proposed to pass through nonlinear computation, such as rectification and normalization (Carandini et al., 1997; Heeger, 1992, 1993). Such nonlinear processing can remove redundant information and contribute to efficient processing (Schwartz & Simoncelli, 2001). The present results, however, indicate that such eventually neutralized orientation information that is unnecessary for conscious perception can be still useful in orientation detection, one of the most fundamental tasks in visual processing (Loffler, 2008). So the facilitatory effect we found can be viewed as making maximum use of latent information to improve system performance such that task performance can be improved by task-irrelevant information (Eriksen & Eriksen, 1974; Gilbert, 1941; Sakima & Murakami, 2010). Also, our findings can be viewed as demonstrating a contextual effect by invisible stimuli, an effect that is highly related to processes of extracting meaningful structure from registered input signals (Albright & Stoner, 2002). Indeed, the present study offers a clear demonstration of how the visual system constructs our conscious visual world from preconscious contextual visual information.

**Conclusion**

Here, we demonstrated that collinear facilitation occurs with concentric flankers that have no perceptually distinct orientation and with collinear flankers that are artificially rendered invisible through interocular suppression. Orientation detection is automatically facilitated when flankers at a proper separation activate orientation-selective and spatial-frequency-selective mechanisms at an early stage of visual processing regardless of perceived orientation, indicating the usefulness of preconscious latent information in detection performance.

**Keywords:** contrast detection, collinear facilitation, nonlinear orientation processing, interocular suppression, contextual effect

**Acknowledgments**

The authors thank Satoshi Hirata for constructive discussions and Goro Maehara, Masahiko Terao, and Kenji Kobayashi for their comments on earlier versions of the manuscript. DH received funding from the Japan Society for the Promotion of Science (JSPS) Grant-in-Aid for JSPS Fellows (2610958). IM received funding from the JSPS Funding Program for Next Generation World-Leading Researchers (NEXT, LZ004) and from the JSPS KAKENHI Grant Number 25119003.

Commercial relationships: none.

Corresponding author: Daisuke Hayashi.
Email: daisuke@fechner.c.u-tokyo.ac.jp.
Address: Department of Psychology, The University of Tokyo, Tokyo, Japan.

**References**


