

Top-Down Modulation of Lateral Interactions in Early Vision: Does Attention Affect Integration of the Whole or Just Perception of the Parts?

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Summary

Attention can modulate sensitivity to local stimuli in early vision [1–6]. But, can attention also modulate integration of local stimuli into global visual patterns? We recently measured effects of attention [7] on the phenomenon of lateral interactions between collinear elements [8, 9], commonly thought to reflect long-range mechanisms in early visual cortex [10–15] underlying contour integration [16]. We showed improved detection of low-contrast central Gabor targets in the context of collinear flankers, but only when the collinear flankers were attended for a secondary task rather than ignored in favor of an orthogonal flanker pair. Here, we contrast two hypotheses for how attention might modulate flanker influences on the target: by changing just local sensitivity to the flankers themselves (flanker-modulation-only hypothesis), or by weighting integrative connections between flanker and target (connection-weighting hypothesis). Modeled on the known nonlinear dependence of target visibility on collinear flanker contrast [17–21], the first hypothesis predicts that an increase in physical flanker contrast should readily offset any reduction in their effective contrast when ignored, thus eliminating attentional modulation. Conversely, the second hypothesis predicts that attentional modulation should persist even for the highest flanker contrasts. Our results showed the latter outcome and indicated that attention modulates flanker-target integration, rather than just processing of local flanker elements.

Results and Discussion

As in our original design [7], a central target was flanked by two pairs of patches in an “X” configuration. One pair was collinear with the target, and the other was

orthogonal. Observers performed a detection task on the near-threshold central target (indicating in which of two intervals it appeared) and a concurrent Vernier task on just one or the other of the two flanker pairs (Figures 1A and 1B). We manipulated flanker contrast between experimental blocks according to two different contrast regimes (4%–64% in logarithmic steps, or 16%–80% in linear steps) for two separate groups of subjects.

This contrast manipulation allowed us to distinguish two different accounts for how attention might influence lateral interactions. In the *flanker-modulation-only* hypothesis, attention would directly modulate just the local processing of parts, reducing the effective contrast of flankers when ignored. Attention would thus have only an indirect effect on the outcome of global integration [22]. The second possibility is that information coming from the flankers to influence the representation of the central target may be attenuated or enhanced, as if passing through an amplifier with variable gain. Attention would thus weight the influence of the flankers on the target [23–25]. Only in this *connection-weighting* hypothesis would attention directly affect the core mechanisms by which flanker and target signals are integrated.

We were able to decide between these hypotheses by examining how flanker contrast influenced the observed attentional modulation in relation to divergent predictions from two abstract formal models, in which hypothetical units activated by the target stimulus receive lateral input from units activated by the flanker stimuli (e.g., [22]). An important characteristic of observed psychophysical flanker-target interactions is their nonlinearity with respect to flanker contrast. Several prior psychophysical studies have shown that facilitation of central target detection by collinear flankers increases to a maximum as flanker contrast approaches its contrast threshold; but, thereafter, facilitation from the flankers critically remains constant, irrespective of any further suprathreshold increments in flanker contrast [17–21]. This pattern is consistent with a two-stage model in which flankers and target each stimulate, distinct receptive fields that then integrate their output (e.g., [19]), possibly via horizontal connections (e.g., [17]).

In Figure 2, this nonlinearity is modeled by a compressive function, $T \propto f(C_{\text{flank}})$, relating flanker contrast, C_{flank} , to target contrast sensitivity, T . (It is important not to be misled by the superficial resemblance of these curves to the standard contrast response function [CRF], in which activity of a cortical receptive field is often shown increasing to saturation as a function of stimulus contrast, with attention able to modulate the gain of this function; e.g., see [4, 26]). The flanker-modulation-only hypothesis can then be modeled by having attention alter the flanker contrast gain [27] by some constant coefficient, A , such that $T \propto f(C_{\text{flank}} \cdot A)$. In this expression, the physical flanker contrast, C_{flank} , is first multiplied by the attentional gain factor A , thus changing the flankers' effective contrast. This attentional amplification of the flankers logically occurs prior to the flankers' interaction

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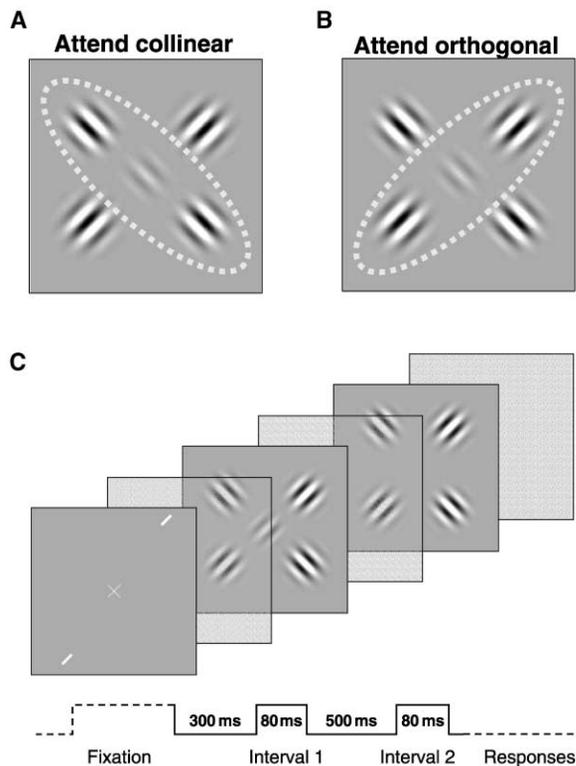


Figure 1. Sample Dual-Axis Stimuli and Trial Sequence

(A and B) Stimuli were composed of two pairs of high-contrast flankers and a low-contrast central target Gabor patch (here shown with higher contrast than usual) that was collinear with one flanker pair. The ellipses are shown here to illustrate schematically the two attentional conditions, in which one or the other flanker pair was attended for a secondary Vernier task: (A) attend collinear flankers, (B) attend orthogonal flankers.

(C) Sequence and timing of events for each trial. A fixation display (not drawn to scale) with peripheral bars indicating the relevant flankers and their relevant direction of Vernier offset was followed by two stimulus intervals, interspersed by blank displays. The target was present in only one interval, while Vernier offsets changed unpredictably for flankers on both axes. The observer then made two responses, indicating first the interval in which the relevant flankers were offset in the relevant direction, then the interval in which (independently) the central target was present. Error feedback was provided for both responses.

with the central target via the nonlinear lateral interactions function. Figure 2A illustrates the resulting hypothetical influence of attended versus ignored collinear flankers on target sensitivity. Notice that target sensitivity with attended flankers (solid line) initially increases more rapidly as flanker contrast increases; then, at higher contrasts, this curve converges on the curve for unattended flankers (broken line) by virtue of their compressive nonlinearity. The implication of this model is therefore that the attentional effect (i.e., the difference between central target detection thresholds with attended versus ignored collinear flankers) should diminish or even disappear at higher flanker contrasts.

In the alternative connection-weighting hypothesis (Figure 2B), attention affects target-flanker integration by directly modulating the lateral interactions mechanism by which the flanker influences the target. Figure

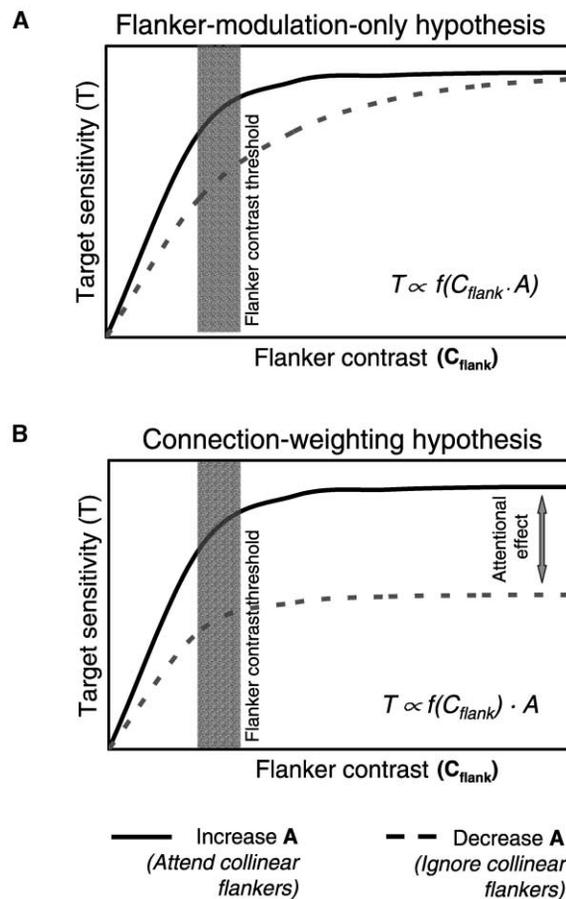


Figure 2. Two Predictions for How Attentional Conditions Should Affect Sensitivity for Detecting the Central Target, as a Function of Flanker Contrast

Hypothetical sensitivity for the central target is plotted as a function of the contrast of its flankers, which may facilitate target visibility via lateral interactions when collinear. The solid curves represent conditions in which collinear flankers are attended for the Vernier task (as in Figure 1A); the dashed curves represent conditions in which collinear flankers are ignored and the orthogonal flankers are attended instead (see Figure 1B).

(A) Flanker-modulation-only hypothesis: note that the attentional effect (vertical distance between the curves) diminishes with increased flanker contrast.

(B) Connection-weighting hypothesis: the attentional effect first increases in magnitude against increased flanker contrast, but it then asymptotes, with further increases in flanker contrast having no effect. See the main text for further details.

2B sketches the function $T \propto f(C_{flank}) \cdot A$, in which the attentional factor, A , affects the gradient of the nonlinear function of flanker contrast rather than modulating the effective flanker contrast itself. With unattended flankers (broken line in Figure 2B), the strength of lateral interactions is attenuated, producing a curve that is flatter than the curve produced with attended flankers (solid line). By virtue of their nonlinearity, these curves continue to diverge rather than converge with increasing flanker contrast; they then finally asymptote so that the benefit from attended flankers is maintained even at very high contrasts. The attentional effect should therefore persist (or even increase) with high flanker contrast (Figure 2B),

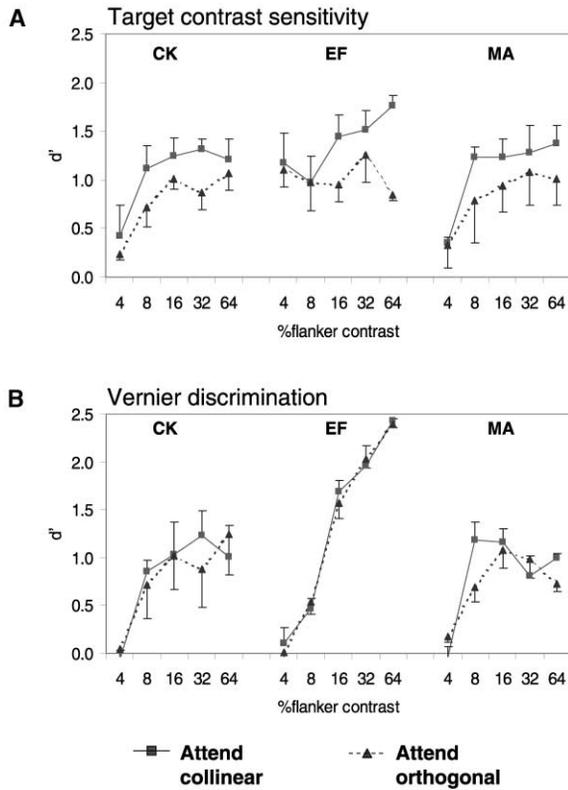


Figure 3. Lower-Contrast Range Results

(A and B) Sensitivity (d') as a function of flanker contrast for three observers; standard error bars are included. The square symbols and solid lines are for the “Attend collinear” condition; the triangles and dotted lines are for the “Attend orthogonal” condition. Note that the x axis is logarithmically scaled. Separate graphs are shown for (A) central target contrast sensitivity and (B) Vernier discrimination on the attended flanker pair.

whereas, in the flanker-modulation hypothesis, the attentional effect should diminish or disappear with higher flanker contrast (Figure 2A).

Our results clearly followed the prediction of the connection-weighting hypothesis: all of our subjects showed attentional effects of roughly constant magnitude, with no sign of any reduction in the magnitude of attentional modulation with increasing flanker contrast. As in our previous study [7], all six subjects showed consistently higher sensitivity (d') for the central target when the secondary Vernier task was performed on the pair of flankers that was collinear with the central target compared to when these were ignored in favor of the orthogonal pair of flankers (Figures 3A and 4A). Critically, this attentional effect was maintained, or even tended to increase, against increasing flanker contrast; this finding is consistent with the prediction from the connection-weighting hypothesis in Figure 2B.

Vernier discrimination showed no consistent differences as a function of whether the attended flankers were collinear or orthogonal to the target. This helps to rule out the possibility that any effects found in the central detection data might simply reflect trade-offs between the two tasks. Vernier discrimination did of course inevitably vary as a function of flanker contrast,

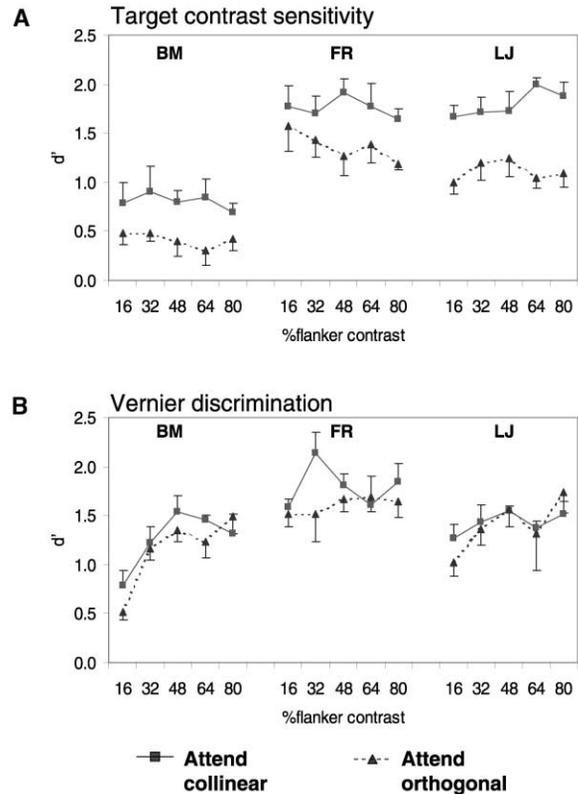


Figure 4. Higher-Contrast Range Results

(A and B) Sensitivity (d') as a function of flanker contrast (linearly scaled) for three observers; standard error bars are included. Separate graphs are shown for (A) central target contrast sensitivity and (B) Vernier discrimination.

with accuracy dropping to near chance at the lowest contrasts (Figure 3B). This variation in secondary task difficulty might account for the overall drop in target detection d' s for very low-contrast flankers (Figure 3A). However, this issue was entirely circumvented when the higher-contrast range was employed (Figure 4A), and those data again showed the persistence of the attentional modulation even for very high-contrast flankers.

For completeness, three subjects were also tested on conventional single-axis stimuli (i.e., a target and just two flankers, so that attention to one or the other flanker pair was no longer manipulated) across the same range of suprathreshold flanker contrasts. Results (not detailed here) confirmed past reports [17–21] that such variations in suprathreshold flanker contrast do not systematically affect target detection.

While the basic attentional effect [7] replicated here is consistent with an effect of attention on early stages of visual processing (i.e., those involved in detection of Gabor signals and in lateral interactions between Gabors), the new results from the flanker contrast manipulations imply that attention can *directly* influence the integrative mechanisms underlying lateral interactions (connection-weighting hypothesis), rather than merely reducing the effective contrast of flankers when ignored.

A defender of the flanker-modulation account might counter that the contrast response to the flankers, even

at the highest contrasts used here, might still be suppressed to a sufficient extent to eliminate their influence on the target when ignored. Because of the nonlinearity of flanker-target interactions, however, such suppression would have to reduce the effective flanker contrast to near-threshold levels before having any appreciable impact on target detection. To calculate the magnitude of the suppression required under this hypothesis (i.e., factor A in the flanker-contrast model), we must first estimate the flanker-contrast threshold. Though not measured directly here, its upper limit is estimated at 8%–12%, which is the flanker contrast at which Vernier discrimination accuracy (Figure 3B) begins to saturate (given that above-threshold Vernier performance should require above-threshold flankers [28]). This value corresponds closely to the flanker contrast at which target detection d' s reliably diverged as a result of attention to the flankers (see Figure 3A); this finding is consistent with the established nonlinear effect of perithreshold flanker contrasts on lateral interactions [17–21]. For the flanker-modulation account to explain our attentional effect, ignored flankers would therefore have to undergo a reduction of their effective contrast from 80% (our maximum value) to around 8%–12% (the threshold estimated above) before ceasing to influence target detection. This implies a flanker-modulation factor A of around 8. Such dramatic modulation of effective contrast would be far stronger than ever reported before [27, 27, 29–31]. Moreover, it is much larger than the corresponding parameter A in the connection-weighting model, estimated at around 1.6 (from the ratio of target-detection thresholds with attended versus ignored collinear flankers across the suprathreshold flanker-contrast range). Note that we do not take our results to imply that there is absolutely no effect of attention on flanker encoding of any kind. Rather, the argument is that any such attentional modulation of high-contrast flankers cannot plausibly be strong enough to affect sensitivity for the central target via lateral interactions in a manner that would be sufficient to produce the observed attentional effects.

There has been some consensus on the likely mechanisms underlying lateral interactions of the kind observed here. For instance, several influential models assume that receptive fields responding to the target integrate information from the flankers via long-range horizontal connections [17, 22, 32–35]. In early visual cortex, such connections have been found to connect cells with similar orientation preference along a collinear axis [36, 37]. This anisotropic connectivity could account for the configuration specificity of target facilitation, found in neurophysiological studies [10–15] as well as in psychophysical studies [8, 9], including the present work.

Importantly, some effects of attention on a similar lateral interactions phenomenon have been directly observed for cell activity within primary visual cortex [24, 38, 39]. The present data appear consistent with the notion, favored by those authors, that attention might function to gate these lateral interconnections [24, 24] (see also [23]). Note that whereas the central target in our study was always attended and task relevant, other paradigms [24, 38, 39] have manipulated whether a particular target was focally attended or not. Such changes

in attentional distribution might affect perceptual processing of *local* elements in a variety of ways; for example, by changing the local spatial resolution or contrast sensitivity within restricted regions [27, 29, 30, 40–42]. An important feature of our paradigm was that we held attention to the target constant and varied only which flankers were attended, rather than comparing focal to diffuse attention or attended to unattended targets.

Our results therefore now allow us to conclude that our observed attentional modulation of target-flanker lateral interactions are unlikely to result solely from local changes in the visibility of the individual parts. Instead, attending to task-relevant parts of a target's surrounding context may serve to integrate this information with the target, while at the same time reducing integration with currently irrelevant context. We propose that top-down attention may directly affect the underlying integrative mechanisms by which the configuration of the parts is represented as a whole in early vision.

Experimental Procedures

Five paid observers plus E.F. participated. All had normal or corrected eyesight. All had prior experience of similar tasks, but were naïve to the purpose of this experiment, with the exception of E.F.

Display parameters approximated conditions used in many previous studies of lateral interactions. Gray level-modulated stimuli were displayed on a 19" CRT (Mitsubishi Diamond Pro 920). Video mode was 1280×1024 , 100 Hz noninterlaced, 8-bit RGB with hardware γ correction. Background luminance was 40.0 cdm^{-2} . The viewing distance was 100 cm in a darkened room. Responses were made via a three-button mouse. Fixation displays comprised a high-contrast central cross, with peripheral bar markers of length 0.28° , and an eccentricity of 1.4° (Figure 1C). Stimulus displays consisted of Gabor patches with carrier wavelength (λ) and Gaussian distribution of the contrast envelope both equal to 0.15° of the visual angle. Spatial frequency of the carrier was therefore 6.7 cycles° . A central Gabor target of either 45° or 135° orientation was surrounded by four flanking patches arranged into two axes with global orientations of 45° and 135° , which bisected each other at right angles (Figures 1A and 1B). Center-to-center separation between the target and each flanker was 4λ . Along each flanking axis, Vernier offsets were introduced by shifting each flanker by the same amount in opposite directions, along a path orthogonal to the global orientation of the axis. Offset magnitude was set for individual subjects on the basis of prior single-task Vernier trials in order to obtain accuracy levels slightly above threshold (values between 0.1λ and 0.3λ). Central target contrast was also set for each subject to the contrast threshold for detecting an isolated Gabor target, again as obtained in prior baseline trials (values between 2.5% and 4% Michelson contrast at maximum signal amplitude). These values remained fixed for each subject throughout all subsequent testing.

Each subject attended at least 2 hour-long experimental sessions containing 20 blocks of 40 trials each. Flanker contrast was varied unpredictably between trials. Orientation of the central target (135° or 45°) changed unpredictably every block, and the attended flanker axis changed every 10 blocks. For each subject, there were at least 160 trials for each flanker contrast by attended-axis cell, from which d' sensitivity scores (for 2AFC designs [43]) were calculated for both the detection and the Vernier tasks.

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