



City Research Online

City St George's, University of London

Citation: Freeman, E. D., Sagi, D. & Driver, J. (2004). Configuration-specific attentional modulation of flanker target lateral interactions. *Perception*, 33(2), pp. 181-194. doi: 10.1068/p3481

This is the unspecified version of the paper.

This version of the publication may differ from the final published version. To cite this item please consult the publisher's version.

Permanent repository link: <https://city-ref-test.eprints-hosting.org/id/eprint/2056/>

Link to published version: <https://doi.org/10.1068/p3481>

Copyright and Reuse: Copyright and Moral Rights remain with the author(s) and/or copyright holders. Copies of full items can be used for personal research or study, educational, or not-for-profit purposes without prior permission or charge, unless otherwise indicated, provided that the authors, title and full bibliographic details are credited, a hyperlink and/or URL is given for the original metadata page and the content is not changed in any way. For full details of reuse please refer to [City Research Online policy](#).

Configuration-specific attentional modulation of flanker – target lateral interactions

Elliot Freeman, Dov Sagi¶, Jon Driver

Institute of Cognitive Neuroscience, University College London, 17 Queen Square, London WC1N 3AR, UK; e-mail: elliott.freeman@ucl.ac.uk; ¶ Department of Neurobiology, Brain Research, The Weizmann Institute of Science, Rehovot 76100, Israel

Received 25 October 2002, in revised form 23 June 2003

Abstract. Elements of a contour are often easier to detect when they possess collinearity, with their local orientations matching the global orientation of the contour. We recently reported attentional modulation of such lateral interactions between a central near-threshold target Gabor patch and flanking high-contrast patches (Freeman et al, 2001 *Nature Neuroscience* 4 1032–1036). Here, we examined whether such attentional effects reflect specific modulation of mechanisms sensitive to collinear configurations, or instead more general modulation of sensitivity to either the global or local orientation-components of the stimulus. Thresholds for detecting a central Gabor target were measured, while observers also judged the Vernier alignment between one pair of flankers and ignored a second flanker pair (when present). Target contrast-thresholds were facilitated only when attending collinear flankers. There was no facilitation when attending flankers that shared only local orientation with the target, or flankers that fell on a global axis aligned with target orientation but having orthogonal local orientation. Ignored collinear flankers had no effect on target thresholds. These results demonstrate strong and specific attentional modulation of contour-integration mechanisms in early vision sensitive to collinear configurations.

1 Introduction

The visual system is particularly sensitive to patterns in which the stimulus elements appear to form part of a continuous contour (eg Bonnef and Sagi 1998; Field et al 1993; Lee and Blake 2001; Polat 1999; Polat and Bonnef 2000; Saarinen and Levi 2001; Zenger and Sagi 1996). This is particularly pronounced for patterns with the property of collinearity, where the local orientation of each individual element of a stimulus corresponds with the global orientation of a virtual line drawn through all elements. For example, detection of a low-contrast oriented patch improves markedly in the context of flanking patches when they all form a collinear configuration (Polat and Sagi 1993). Moreover, physiological observations in early visual cortex have now shown that flankers outside the classical receptive field for a target can nevertheless affect activity in that receptive field when collinear with the target (Gilbert et al 1996; Kapadia et al 2000; Polat and Norcia 1996), possibly via horizontal connections in early visual cortex (Kapadia et al 1995; Kasamatsu et al 2001; Mizobe et al 2001; Polat et al 1998; Schmidt et al 1997).

We recently reported psychophysical data suggesting that lateral interactions between a target and collinear flankers might be modified by top–down attention (Freeman et al 2001, 2003). We used displays that comprised four suprathreshold flankers (figures 1c and 1d) surrounding a central near-threshold target (ie two pairs of flankers, rather than the usual single pair; see figures 1a and 1b). One flanker pair was collinear with the target, while the other was orthogonal (figures 1c and 1d). Subjects performed two-interval forced-choice detection of the central target, while also being required to judge Vernier offset for just one of the flanker pairs (with the other pair to be ignored). This manipulation of attention to the flankers was found to affect target sensitivity: when the collinear flanker axis was attended, target detection improved; when the orthogonal axis

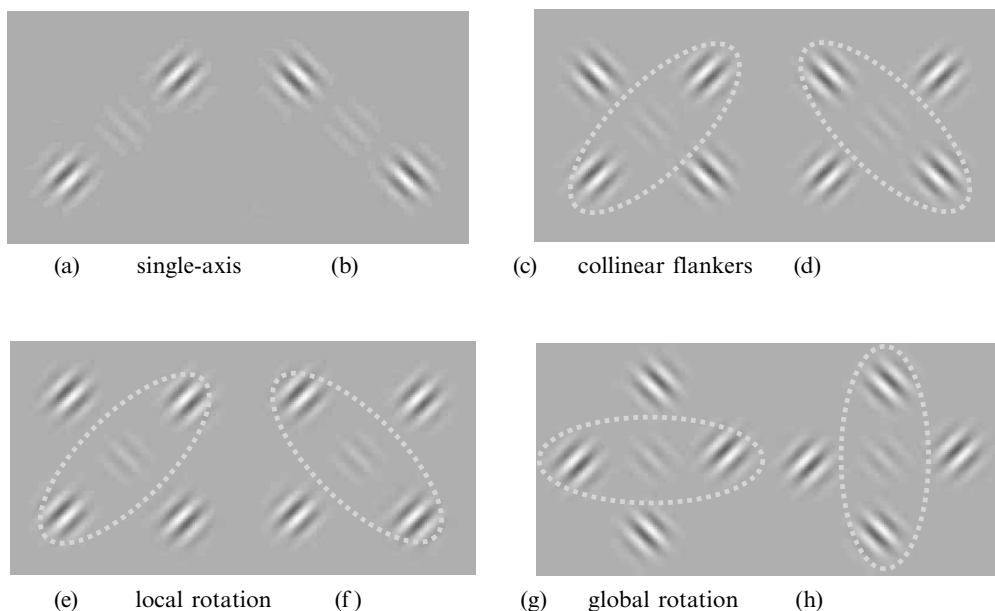


Figure 1. Examples of stimulus displays consisting of a central Gabor target and one or more pairs of Gabor flankers, each pair having a Vernier offset. (a) and (b) Single flanking axis with target orthogonal or collinear to flankers, respectively. (c) and (d) Non-rotated dual-axis stimuli: two pairs of flankers with target orthogonal or collinear to flankers on the attended axis, respectively (attended axis indicated for purpose of illustration by dashed ellipses). (e) and (f) Local-rotation: flankers on one axis rotated, with the global orientation of the attended axis (see ellipse) being orthogonal (e) or similar (f) to the target. (g) and (h) Global-rotation: both axes rotated by 45° , but with the orientation of individual flankers unchanged; target and attended flankers have orthogonal (g) or the same (h) local orientation. Note the absence of collinearity in all of the rotated-flankers displays (e) to (h).

was attended instead, target detection was poorer. Flankers collinear with the target thus appeared to facilitate target detection only when attended for the Vernier task.

This result is consistent with the intriguing possibility that top-down attention can specifically modulate the response of early visual processes to collinearity, thus affecting whether target and flankers get grouped into a contour. This would provide a challenge to traditional accounts of visual attention that have emphasised grouping as a preattentive process (eg Driver and Baylis 1998; Duncan 1984; Moore and Egeth 1997; Neisser 1967; Palmer and Rock 1994; Treisman 1986), but may accord with recent data on attentional modulation in early visual cortex (Gandhi et al 1999; Gilbert et al 2000; Ito and Gilbert 1999; Ito et al 1998; Luck et al 1997; Moran and Desimone 1985; Motter 1993; Roelfsema et al 1998; Somers et al 1999; Watanabe et al 1998).

It remains uncertain, however, whether our attentional effect reflects modulation of lateral interactions between collinear elements in particular, or other more general mechanisms at a different level of processing. One reason for this uncertainty is that the critical 'attend collinear' versus 'attend orthogonal' comparison in our original study (figures 1d versus 1c, respectively) involved a change not only in the collinearity of attended elements but also in two other critical properties. As mentioned earlier, in a collinear configuration the target not only has the same local orientation as the flankers, but is also congruent with the global orientation of the virtual line connecting all patches together. Both these congruencies are disrupted in orthogonal configurations. The different effects of attending collinear versus orthogonal configurations might thus in principle be accounted for by a change in sensitivity to either of these

local or global attributes alone, rather than reflecting specific modulation of sensitivity to collinearity per se (ie the conjunction of these two properties).

For example, attending to a particular pair of flankers might generally improve sensitivity for elements having the same local orientation as these flankers; this could benefit detection of a target in a collinear configuration with the attended flankers, merely because that target has the same local orientation. Such an effect might be predicted by a currently popular theory of feature-specific attention, according to which attention to a given feature can enhance sensitivity for similar features throughout the visual field (eg see Saenz et al 2002; Treue and Martinez Trujillo 1999). Alternatively, observers might attend to the orientation of the global virtual contour connecting the relevant flankers. This might be expected given past data suggesting that such global orientation information is used in the performance of Vernier discrimination tasks (eg Mussap and Levi 1996). Attending to this orientation might again result in enhanced visibility for a central target having a similar orientation to this global axis. In neither of these cases would it be necessary to invoke attentional modulation of mechanisms specific to collinearity.

To distinguish between these possibilities, we modified the stimuli so that collinearity was now disrupted while either just global (experiment 1, see figures 1e and 1f) or just local (experiment 2, see figures 1g and 1h) orientation congruency was selectively preserved. If attention specifically modulates sensitivity to collinearity in our paradigm, no attentional modulation should be measurable in either of these cases when collinearity is disrupted. On the other hand, if attention only modulates sensitivity to just local or just global stimulus orientations, disruption of collinearity should have no influence on our attentional effect provided the relevant (local or global) attributes are preserved.

Even if collinearity-specific attentional modulation were demonstrated, this might still not be sufficient to conclude that attention directly controls the integrative mechanisms underlying target facilitation by collinear flankers. The attentional effect might instead be indirect or accidental. For example, the target might reciprocally influence the appearance of collinear flankers (cf Solomon et al 1999). This might provide an extra cue for detecting the target, which would only be detectable when the flankers are attended. A further possibility is that the secondary Vernier task becomes easier when the attended flankers are collinear with the central target, leading to a redistribution of attentional resources in favour of the target detection task. On such accounts, observations of attentional modulation might be specific to collinear configurations, but they need not imply any direct attentional modulation of the mechanisms underlying flanker–target facilitation. If true, we should find that the attentional effects always ‘ride on top’ of any fundamental effects of flanker collinearity on target visibility, with residual facilitation from collinear flankers even when they are task-irrelevant. Uncertainty over this issue remains because in our previous attentional studies (Freeman et al 2001, 2003) we only manipulated whether collinear flankers were attended for the secondary task or were instead ignored, not whether collinearity was physically present or absent in the dual-axis (ie four-flanker) stimulus. In the present study, our modified (collinearity disrupted) stimuli (see figures 1e–1h) should make it possible to measure directly the impact of ignored collinear versus noncollinear flankers on target detection (see experiment 1 below).

Any conclusion that attention directly modulates lateral interactions should thus rest on two strict criteria: the attentional effect should not only be specific to collinear configurations, but should also be strong enough to completely modulate lateral interactions, with no evidence of residual target facilitation from ignored collinear flankers as compared to cases where all collinearity is physically eliminated.

2 General method

2.1 Subjects

One of the authors (EF) and six paid naïve observers participated. The naïve subjects had undergone at least two practice sessions involving target detection and Vernier discrimination (as single tasks) prior to the experimental sessions. Different sets of three naïve observers participated in our two experiments, while EF participated in both experiments.

2.2 Stimulus displays

Display conditions approximated those used in past studies of lateral interactions (eg Polat and Sagi 1993). Grey-level modulated stimuli were displayed on a 19-inch CRT (Mitsubishi Diamond Pro 920), with an 8-bit RGB mode with gamma correction. Video mode was 1280×1024 , 100 Hz non-interlaced. Background luminance was 40 cd m^{-2} . Viewing distance was 125 cm, in a darkened room.

Stimuli consisted of Gabor patches with wavelength and Gaussian distribution both equal to 0.15 deg of visual angle (ie spatial frequency $6.7 \text{ cycles deg}^{-1}$). A central target of either 45° or 135° orientation was surrounded either by just two flanking patches to form a single axis (figures 1a and 1b), or by four flanking patches arranged into two orthogonally bisecting axes (figures 1c–1h). The central target had Michelson contrast ranging from 2% to 10%, and flankers had a fixed contrast of 40%, with centre-to-centre separation between patches of 4 Gabor wavelengths.

Along each flanking axis, a Vernier offset was introduced by shifting each flanker in opposite directions by the same amount, in a direction orthogonal to the global orientation of the axis. Within and between subjects, Vernier offset magnitude could undergo minor adjustments within the range of 0.1 to 0.3 Gabor wavelengths between sessions, to maintain Vernier task accuracy at an approximately constant level for each subject, below ceiling. A preceding fixation display on each trial comprised a high-contrast central cross, with peripheral bar markers (length 0.28 deg, eccentricity 1.4°) to indicate which flanking axis to judge (in a blocked manner) for the Vernier task, and which direction of offset to detect (fixed throughout).

2.3 General procedure

Each 1 hour experimental session contained 20 blocks of 40 trials each. Target contrast was varied randomly between blocks (method of constant stimuli), sampling from a range of five values (with intervals of approximately 0.1 log contrast). This range was centred on the threshold contrast for target detection when no flankers were present, as measured in earlier sessions for each subject individually. Target orientation (135° or 45°) changed randomly every block, and attended flanker axis changed every 10 blocks. The stimulus conditions (eg dual-axis rotated versus non-rotated, and single-axis displays; see figure 1) changed between sessions. Each condition was repeated a minimum of four times, and contrast thresholds for the central target were estimated at 75% correct by Weibull fit of the obtained psychometric functions.

Each trial commenced with a fixation display (figure 2a), with peripheral bar markers indicating the relevant flanking axis (blocked) to judge for the Vernier task, and which direction of offset to report for it (fixed throughout). Following a keypress and a 300 ms blank period, there were two stimulus intervals (figures 2b and 2c) of 80 ms duration each, separated by a blank period of 500 ms. The screen then remained blank until responses had been made. Two two-interval forced-choice (2IFC) responses were required, by pressing left and right mouse buttons (figures 2d), with responses made first for the Vernier task (indicating in which of the two successive intervals the flankers were offset in the direction specified by the bar markers) and then for the target detection task (indicating the interval in which the target was present). A tone sounded for each incorrect response.

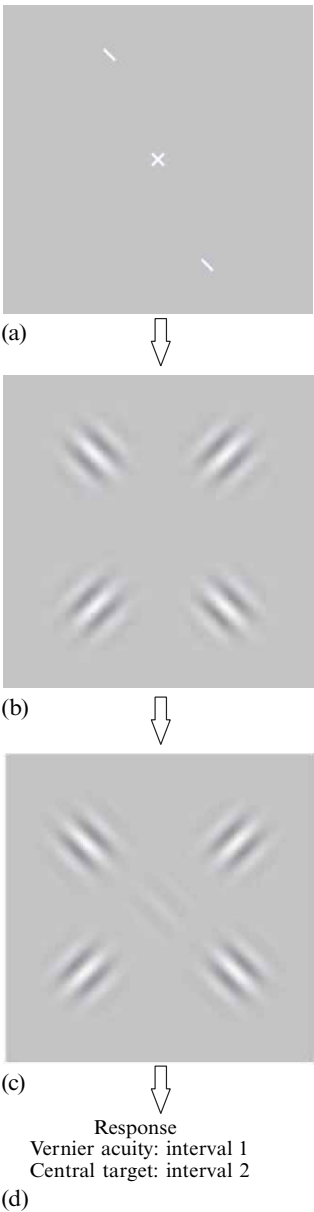


Figure 2. Example trial sequence. (a) Fixation display indicating the relevant flanking axis, and the relevant direction of Vernier offset for the Vernier task. (b) Interval 1, shown here with no target but with flankers on the relevant axis offset in the relevant direction. (c) Interval 2, shown here with target present. (d) The correct pair of responses for this sample trial, with responses for the Vernier task made first. The central target was equally likely to appear in the first or second interval, and the same was true (independently) for the relevant direction of Vernier offset between the relevant flanker pairs. The irrelevant flankers also independently changed their Vernier offset between intervals.

3 Experiment 1

The first experiment was designed to test whether selectively attending to the global orientation of the task-relevant flanking axis might affect target detection. We modified the dual-axis stimuli so that the two flankers that were originally collinear with the target were now each rotated by 90°. In these ‘local rotation’ stimuli (figures 1e and 1f), the global virtual axis formed between the rotated flankers still has a similar orientation to the central target, but collinearity is nevertheless disrupted because each of the relevant flankers now differs in local orientation to the target. Any account based on attention to global orientation would thus predict benefits for target detection when the locally rotated pair of flankers is attended (figure 1f), while an account based on collinearity would not. A control for assessing any such benefits from attention to

global orientation is provided when subjects attend the non-rotated orthogonal pair of flankers in the same stimulus (figure 1e). On this axis, the target is orthogonal to both the local and the global orientation of the attended flankers. We also included the original conditions from Freeman et al (2001), for replication and comparison (see figures 1c and 1d here).

This experiment can also provide a direct test of whether the attentional effect is strong enough to eliminate the influence of collinear flankers when ignored. Two of the above conditions may be compared, in both of which subjects attend a pair of flankers for the Vernier task that are orthogonal to the central target, but where the task-irrelevant flankers are either collinear with that target or orthogonal to it (compare figures 1c and 1e). Any residual advantage in target thresholds with unattended collinear flankers would indicate that attentional modulation of lateral interactions is incomplete. Finally, the effects of this manipulation were also compared with the effect of physically removing the collinear flankers (compare figures 1c and 1a), as in Freeman et al (2001).

3.1 Stimuli and design for experiment 1

For the non-rotated stimuli (figures 1c and 1d), as in the original Freeman et al (2001) study, flankers on one axis were collinear (with small Vernier offsets) with the central target, while the other axis was orthogonal. For the new local-rotation stimuli (figures 1e and 1f), the flankers that had originally been collinear were rotated locally by 90°. Single-axis stimuli (figures 1a and 1b) were also used, based on the non-rotated stimuli but with only one pair of flankers present (collinear or orthogonal with the target).

3.2 Results and discussion

Our attentional effect was replicated with the original unmodified stimuli (see data in figure 3c versus figure 3d), as in Freeman et al (2001). Note that the standard errors plotted in figure 3 allow visual assessment of conventional statistical significance for

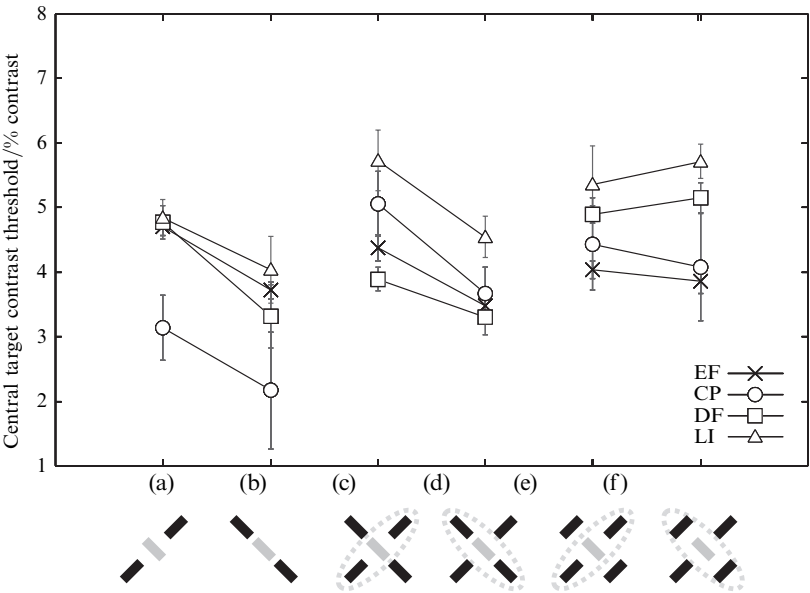


Figure 3. Central target contrast thresholds for experiment 1. (a) and (b) Single-axis, orthogonal and collinear conditions, respectively. (c) and (d) Dual-axis non-rotated stimuli, target orthogonal versus collinear with attended flankers. (e) and (f) Local-rotation stimuli, with the global orientation of the attended axis orthogonal or similar to target, respectively. Different symbols for each subject. Error bars represent 1SE in all graphs. Note cartoons of corresponding stimulus configurations along the *x*-axis, with dotted ellipses indicating the attended flanker axis.

each subject. Contrast thresholds for the central target were reliably lower when this target was collinear with the flankers on the attended axis, as compared with when those flankers were ignored, with flankers orthogonal to the target being attended instead, on the other axis. Also in replication of our previous work, the size of this attentional effect was comparable to the ‘stimulus effect’ of collinear versus orthogonal flanker – target configurations in single-axis displays, measured under identical dual-task conditions (ie central detection plus Vernier judgments), but with just one pair of flankers present (see data for figure 3a versus those for figure 3b).

A critical new finding was that no attentional modulation was observed with the novel local-rotation stimuli, as a function of which axis was attended for the Vernier task (figures 3e and 3f). That is, when collinearity was disrupted by local flanker-rotation, central target detection no longer depended on which flanker axis was attended, even though for one axis (with the rotated flankers, figure 1f) the global orientation of the attended axis and the target’s own orientation were still similar. The attentional effects cannot therefore be explained by just the global relationship between attended axis and target orientation, without also considering local orientation-similarity. This supports the hypothesis that the attentional effect is specific to collinearity (ie local plus global orientation similarity) between attended flankers and central target. Experiment 2, below, was designed to test whether local orientation similarity alone might still explain the results.

A second new finding was that when collinear flankers were ignored in displays with two pairs of flankers (see figure 3c), their presence produced no reliable benefits for target detection, as compared with ignoring flankers on the same axis that had been locally rotated so as to be orthogonal to the target (figure 3e). This suggests that the attentional effect can be strong enough to completely eliminate the impact of flankers that are collinear with the target, when these are ignored in displays with two pairs of flankers.

4 Experiment 2

Having rejected an account based on attention to global orientation alone, we now tested whether our original attentional effect could be explained by feature-specific enhancement of target detection due to attending flankers having similar local orientations only. We introduced new dual-axis displays that preserved just the local orientation-similarity of the target to the critical pair of flankers, while disrupting their overall global relationship (and thus collinearity). This was done by rotating the global axes of both pairs of flankers by 45° (see figures 1g and 1h). In these global-rotation stimuli, the central target and one of the two pairs of flankers still share the same local orientation, but are locally at 45° to the global virtual axis that might be formed between the two members of this flanker pair. Attending to the two flankers that share their local orientation with the central target (figure 1h) might nevertheless still benefit its detection, if local orientation-similarity is sufficient to produce the attentional effect, in the absence of collinearity.

Attending to the other axis (ie the other pair of flankers; see figure 1g) in the same display provides a control condition where neither the local nor the global orientations are similar between target and flankers, so that no benefits should arise. Finally, a fresh replication of the original Freeman et al (2001) design with non-rotated single-axis (figures 1a and 1b) and dual-axis stimuli (figures 1c and 1d) was also included, to allow within-subjects comparisons against the novel conditions introduced in this experiment.

4.1 Stimuli and design for experiment 2

For the new global-rotation stimuli (figures 1g and 1h), the global orientation of both flanking axes was rotated, in the same direction, by 45° , while local flanker orientation remained fixed. Non-rotated dual-axis stimuli (figures 1c and 1d) and single-axis stimuli (figures 1a and 1b) were also used again, just as before. (Note that subject EF only

had already performed the latter two conditions in experiment 1; accordingly the same data are presented again for him here.)

4.2 Results and discussion

The pattern of results was similar to that in experiment 1. As before, the attentional effect found with dual-axis non-rotated stimuli (as in Freeman et al 2001) was replicated with three more naïve subjects (see figure 4c versus figure 4d), and was again comparable to the ‘stimulus effect’ found in displays with only one pair of flankers (see figure 4a versus figure 4b), under the same dual-task conditions (ie central detection plus Vernier judgments). This replicates both the present experiment 1 and Freeman et al (2001). Critically, no such attentional modulation was found with the new global-rotation stimuli (see figure 4e versus figure 4f). This implies that mere similarity in local orientation between target and attended flankers is insufficient to explain the attentional effect. Instead, it seems that the attended pair of flankers in four-flanker displays must be collinear with the central target in order to facilitate its detection.

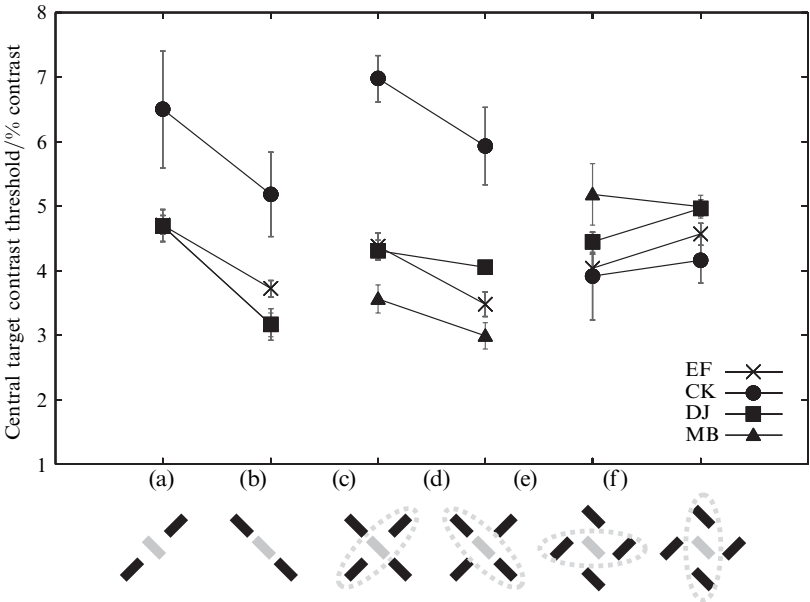


Figure 4. Central target contrast thresholds for experiment 2. (a) and (b) Single-axis controls. (c) and (d) Non-rotated dual-axis stimuli. (e) and (f) Global rotation stimuli, with target having orthogonal or same local orientation as attended flankers.

5 Combined group analysis of experiments 1 and 2

We conducted a further statistical test of the general hypothesis that our attentional effect depends specifically on collinearity between the central target and the attended flankers. Mean target thresholds from the rotated-flanker dual-axes conditions in experiments 1 and 2 (which themselves were statistically indistinguishable) were pooled together, and compared against the thresholds for non-rotated dual-axis conditions (ie the original stimuli with collinear axes), in a repeated-measures two-way ANOVA ($n = 6$, after excluding non-naïve subject EF, since he was unique in performing both experiments). The two factors were stimulus type (rotated versus non-rotated) and attended axis.

Neither factor produced significant main effects, but their interaction was significant ($F_{1,5} = 35.3, p < 0.002$). This arose because facilitation of target thresholds depended on two constraints applying conjointly: the stimulus must contain a set of flankers in

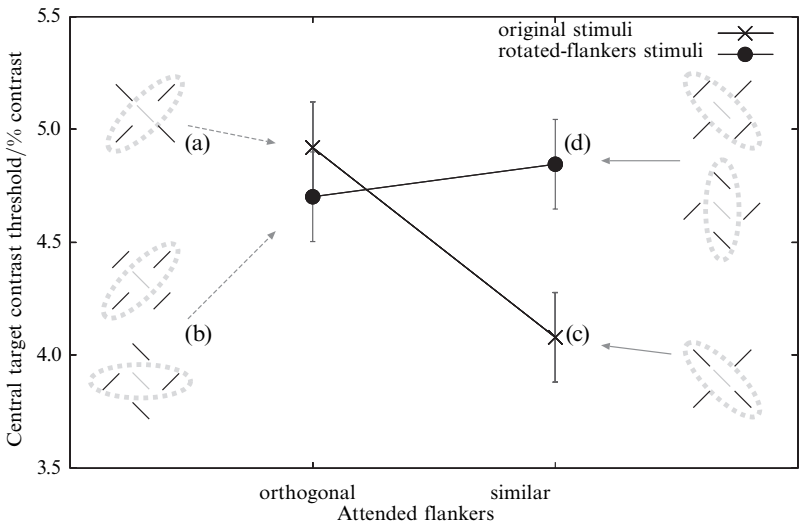


Figure 5. Target contrast thresholds averaged across experiments and subjects (excluding EF). Cross symbols: original unmodified dual-axis stimuli, as in Freeman et al (2001); filled circles: stimuli with rotated flankers (both local and global rotation averaged). Display configurations for each condition are cartooned, with an arrow pointing to the corresponding datapoint: (a) collinear flankers unattended; (b) flankers with global or local orientation-similarity unattended, data pooled across experiments; (c) collinear flankers attended; (d) flankers with global or local orientation-similarity attended.

a collinear configuration with the target, and these collinear flankers must be attended rather than ignored for the Vernier task (see figure 5 for a graph of this interaction, with non-overlap of error bars indicating statistical significance at $p < 0.05$). Analysis of simple effects confirmed that central-target thresholds were significantly lower for attended collinear flankers (compared to attended rotated flankers) ($t_5 = 4.76$, $p < 0.01$), while there was no evidence for any reliable residual benefit from unattended collinear flankers (relative to unattended rotated flankers) ($t_5 = 1.04$, ns). The attentional modulation therefore appears strong enough to completely eliminate lateral interactions from collinear flankers when these are unattended for the Vernier task in the four-flanker displays. This latter conclusion was also supported by comparisons against single-axis stimuli that had only two flankers present (see figures 3a and 3b, and 4a and 4b), which again suggest that in terms of the effect on target detection, ignoring collinear flankers in the four-flanker displays is equivalent to removing them altogether.

5.1 Vernier accuracy

Accuracy in the Vernier task was examined to assess whether any differences in the difficulty of Vernier discrimination for the different flanker-configurations might have caused a trade-off with performance in the central detection task. For example, in experiment 1, if Vernier discrimination for the rotated flanking patches had been harder than for the non-rotated patches, this could in principle have drained attentional resources from the central task, raising target thresholds for that detection task. Accuracy in the Vernier task, averaged over target contrasts for each subject, is displayed in figures 6 and 7 (for experiments 1 and 2, respectively). Despite differences between subjects in overall accuracy, neither graph shows any consistent differences in Vernier performance between the conditions, thus arguing against any trade-off accounts.

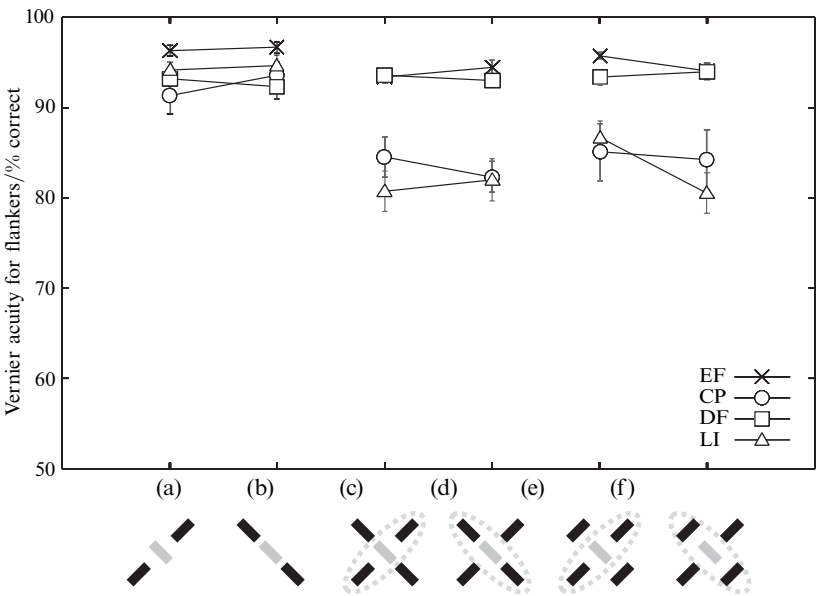


Figure 6. Experiment 1. Vernier acuity, percentage correct for each subject. Corresponding conditions are cartooned along x-axis.

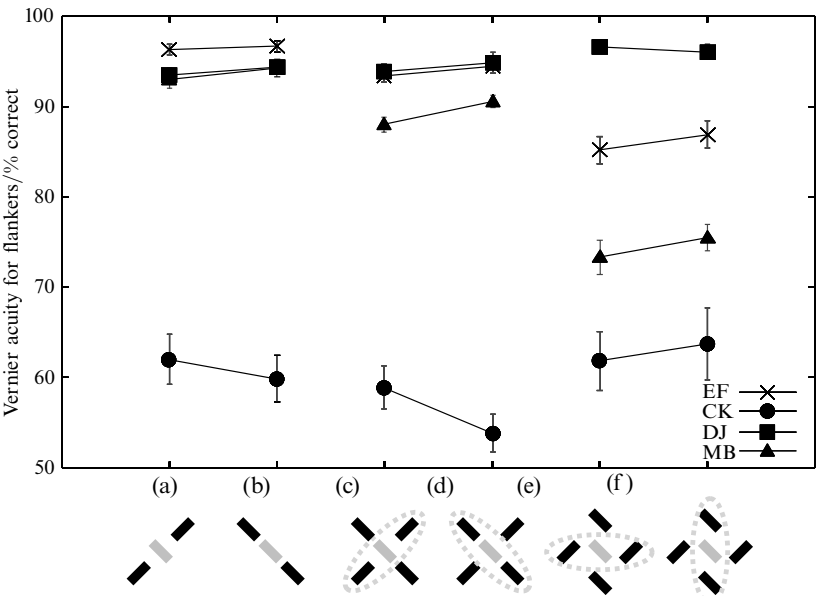


Figure 7. Experiment 2. Vernier acuity, percentage correct for each subject.

6 General discussion

Our two new experiments clarify and extend Freeman et al’s (2001) recent report of attentional modulation for lateral interactions between a near-threshold central Gabor patch and high-contrast flanking patches. The results reveal two characteristics of the attentional modulation. First, the attentional effect is highly specific, depending on the precise spatial configuration of the stimuli. In particular, an attentional effect was only obtained when the target was collinear with one pair of flankers, having both the same global and local orientation. By rotating the critical flankers so that either their

global orientation (experiment 1) or their local orientation (experiment 2) was different from the target, the attentional effect was abolished. Given these results, an interpretation of the attentional effect is clearly required that takes into account the precise spatial configuration of the stimuli, and in particular the dependence on collinearity.

Second, the attentional effect is strong: target facilitation seems to depend entirely on whether the observer is attending a pair of collinear flankers, when present, or ignoring them. New support for this conclusion comes from comparison of the original four-flanker (Freeman et al 2001) stimuli with the new (rotated) four-flanker conditions, revealing that unattended collinear flankers have no more impact than unattended flankers which are not collinear with the target. In addition, we find once again that the effect of ignoring (versus attending) collinear flankers is equivalent in magnitude to the effect of physically removing them altogether (so that only one non-collinear pair is displayed). The attentional effect may thus be strong enough to completely override any facilitatory effect from collinear flankers.

This new evidence for strong and specific attentional modulation argues against any account that would predict relatively weak (incomplete) or non-specific influences from attention. For instance, there have been recent claims that ‘feature-based’ attention can enhance the response to features throughout the visual field that are similar to an attended target (eg Saenz et al 2002; Treue and Martinez Trujillo 1999). Such an improvement could arise in a number of ways, for example via reduction of uncertainty (Morgan et al 1998; Pelli 1985), application of a noise-reducing template (Lu and Doshier 1998), or sharper orientation tuning (Lee et al 1999), but contrary to the present findings any resulting attentional modulation would be neither specific for collinearity nor complete.

A different test of this ‘feature-based’ account was recently reported independently, by Saenz and Boynton (2002) at the meeting of Society for Neuroscience. They used stimuli in which target and flankers on one axis were arranged parallel to each other (ie side-by-side, rather than end-to-end). These elements therefore had the same local orientations but no collinearity. In apparent support for the ‘feature-based’ attention hypothesis, they reported that target detection improved slightly when this non-collinear axis was attended, compared with attention to the other orthogonal axis. However, any such improvement might have been due to the weak facilitation known to be found with such parallel target – flanker arrangements (Polat 1999; Polat and Sagi 1994). Such an explanation would be consistent with the results of the present experiment 2, which used a configuration (45° local rotation; see figures 1g and 1h) for which target facilitation has never previously been found. There was neither a consistent benefit in this experiment from attending flankers whose local orientation matched the target, nor in our first experiment with orientation similarity at the global level. Feature-specific enhancement effects alone cannot therefore explain the attentional modulation observed here when both global and local orientations combine to produce collinear configurations. While these results do not rule out the possibility of feature-specific effects in other paradigms, they converge with past results in suggesting that feature-based attention may not on its own improve perceptual sensitivity (Moore and Egeth 1998; Shih and Sperling 1996; we are grateful to an anonymous reviewer for pointing this out).

Our finding of strong (ie complete) attentional modulation also weighs against such accounts, and indeed any other account on which the mechanism responsible for the observed task-dependent modulation does not directly interact with those responsible for the lateral-interactions phenomenon. On accounts of this type, the modulation should always ‘ride on top’ of the configuration-dependent lateral interactions themselves. However, we found no evidence of residual facilitation from ignored collinear flankers to support this.

Any satisfactory account of the lateral-interactions phenomenon now needs to accommodate the strong attentional modulation that we have demonstrated, and the fact that this is specifically constrained by collinearity. One possibility is that the effective contrast of actively ignored flankers may be suppressed to the extent that they can no longer contribute any activity to the target receptive fields. However, this latter possibility seems unlikely given that the flankers were at high contrast here. Moreover, in another recent study we still found attentional effects with even higher (80%) flanker contrasts (Freeman et al 2003), adding further weight against such a hypothesis. Instead, our results might relate to recent neurobiological evidence for the special sensitivity of neurons in early visual cortex to collinear elements beyond their receptive fields (eg Kapadia et al 1995; Mizobe et al 2001; Polat et al 1998; Polat and Norcia 1996). Our data appear consistent with attention selectively gating the horizontal connections between separate cortical receptive fields that most likely support such interactions (Gilbert et al 2000; Lamme et al 1998; Posner and Gilbert 1999; Sagi 1996), so that contextual integration arises primarily when both the central target and its relevant context are attended together.

Acknowledgments. This research was supported by a project grant to JD and EF from the BBSRC (UK). JD holds a Royal Society–Wolfson Research Merit Award. Thanks to anonymous reviewers for thoughtful comments.

References

- Bonneh Y, Sagi D, 1998 “Effects of spatial configuration on contrast detection” *Vision Research* **38** 3541–3553
- Driver J, Baylis G C, 1998 “Attention and visual object segmentation”, in *The Attentive Brain* Ed. R Parasuraman (Cambridge, MA: MIT Press) pp 299–325
- Duncan J, 1984 “Selective attention and the organization of visual information” *Journal of Experimental Psychology: General* **113** 501–517
- Field D J, Hayes A, Hess R, 1993 “Contour integration by the human visual system: evidence for a local ‘association field’” *Vision Research* **33** 173–193
- Freeman E, Driver J, Sagi D, Zhaoping L, 2003 “Top–down modulation of lateral interactions in early vision: does attention affect integration of the whole or just perception of the parts?” *Current Biology* **13** 985–989
- Freeman E, Sagi D, Driver J, 2001 “Lateral interactions between targets and flankers in low-level vision depend on attention to the flankers” *Nature Neuroscience* **4** 1032–1036
- Gandhi S P, Heeger D J, Boynton G M, 1999 “Spatial attention affects brain activity in human primary visual cortex” *Proceedings of the National Academy of Sciences of the USA* **96** 3314–3319
- Gilbert C D, Das A, Ito M, Kapadia M, Westheimer G, 1996 “Spatial integration and cortical dynamics” *Proceedings of the National Academy of Sciences of the USA* **93** 615–622
- Gilbert C D, Ito M, Kapadia M, Westheimer G, 2000 “Interactions between attention, context and learning in primary visual cortex” *Vision Research* **40** 1217–1226
- Ito M, Gilbert C D, 1999 “Attention modulates contextual influences in the primary visual cortex of alert monkeys” *Neuron* **22** 593–604
- Ito M, Westheimer G, Gilbert C D, 1998 “Attention and perceptual learning modulate contextual influences on visual perception” *Neuron* **20** 1191–1197
- Kapadia M K, Ito M, Gilbert C D, Westheimer G, 1995 “Improvements in visual sensitivity by changes in local context: Parallel studies in human observers and in V1 of alert monkeys” *Neuron* **15** 843–856
- Kapadia M K, Westheimer G, Gilbert C D, 2000 “Spatial distribution of contextual interactions in primary visual cortex and in visual perception” *Journal of Neurophysiology* **84** 2048–2062
- Kasamatsu T, Polat U, Pettet M W, Norcia A M, 2001 “Collinear facilitation promotes reliability of single-cell responses in cat striate cortex” *Experimental Brain Research* **138** 163–172
- Lamme V A, Super H, Spekreijse H, 1998 “Feedforward, horizontal, and feedback processing in the visual cortex” *Current Opinion in Neurobiology* **8** 529–535
- Lee D K, Itti L, Koch C, Braun J, 1999 “Attention activates winner-takes-all competition among visual filters” *Nature Neuroscience* **2** 375–381
- Lee S H, Blake R, 2001 “Neural synergy in visual grouping: when good continuation meets common fate” *Vision Research* **41** 2057–2064

-
- Lu Z L, Doshier B A, 1998 “External noise distinguishes attention mechanisms” *Vision Research* **38** 1183–1198
- Luck S J, Chelazzi L, Hillyard S A, Desimone R, 1997 “Neural mechanisms of spatial selective attention in areas V1, V2, and V4 of macaque visual cortex” *Journal of Neurophysiology* **77** 24–42
- 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” *Visual Neuroscience* **18** 377–391
- Moore C M, Egeth H, 1997 “Perception without attention: evidence of grouping under conditions of inattention” *Journal of Experimental Psychology: Human Perception and Performance* **23** 339–352
- Moore C M, Egeth H, 1998 “How does feature-based attention affect visual processing?” *Journal of Experimental Psychology: Human Perception and Performance* **24** 1296–1310
- Moran J, Desimone R, 1985 “Selective attention gates visual processing in the extrastriate cortex” *Science* **229** 782–784
- Morgan M J, Ward R M, Castet E, 1998 “Visual search for a tilted target: tests of spatial uncertainty models” *Quarterly Journal of Experimental Psychology A* **51** 347–370
- Motter B C, 1993 “Focal attention produces spatially selective processing in visual cortical areas V1, V2, and V4 in the presence of competing stimuli” *Journal of Neurophysiology* **70** 909–919
- Mussap A J, Levi D M, 1996 “Spatial properties of filters underlying Vernier acuity revealed by masking: evidence for collator mechanisms” *Vision Research* **36** 2459–2473
- Neisser U, 1967 *Cognitive Psychology* (New York: Appleton)
- Palmer S, Rock I, 1994 “Rethinking perceptual organization: the role of uniform connectedness” *Psychonomic Bulletin & Review* **1** 29–55
- Pelli D G, 1985 “Uncertainty explains many aspects of visual contrast detection and discrimination” *Journal of the Optical Society of America A* **2** 1508–1532
- Polat U, 1999 “Functional architecture of long-range perceptual interactions” *Spatial Vision* **12** 143–162
- Polat U, Bonneh Y, 2000 “Collinear interactions and contour integration” *Spatial Vision* **13** 393–401
- Polat U, Mizobe K, Pettet M, Kasamatsu T, Norcia T, 1998 “Collinear stimuli regulate visual responses depending on cell’s contrast threshold” *Nature* **391** 580–584
- Polat U, Norcia A M, 1996 “Neurophysiological evidence for contrast dependent long-range facilitation and suppression in the visual cortex” *Vision Research* **36** 2099–2109
- Polat U, Sagi D, 1993 “Lateral interactions between spatial channels: Suppression and facilitation revealed by lateral masking experiments” *Vision Research* **33** 993–999
- Polat U, Sagi D, 1994 “The architecture of perceptual spatial interactions” *Vision Research* **34** 73–78
- Posner M L, Gilbert C D, 1999 “Attention and primary visual cortex” *Proceedings of the National Academy of Sciences of the USA* **96** 2585–2587
- Roelfsema P R, Lamme V A, Spekreijse H, 1998 “Object-based attention in the primary visual cortex of the macaque monkey” *Nature* **395** 376–381
- Saariinen J, Levi D M, 2001 “Integration of local features into a global shape” *Vision Research* **41** 1785–1790
- Saenz M, Boynton G M, 2002 “Feature-based attention modulates lateral interactions in contrast detection” Program No. 457.2 2002 *Abstract Viewer/Itinerary Planner* (Washington, DC: Society for Neuroscience)
- Saenz M, Buracas G T, Boynton G M, 2002 “Global effects of feature-based attention in human visual cortex” *Nature Neuroscience* **5** 631–632
- Sagi D, 1996 “Early vision: Images, context and memory”, in *Brain Theory: Biological Basis and Computational Theory of Vision* Eds A Aertsen, V Braitenberg (Amsterdam: Elsevier Science) pp 1–17
- Schmidt K E, Goebel R, Löwel S, Singer W, 1997 “The perceptual grouping criterion of colinearity is reflected by anisotropies of connections in the primary visual cortex” *European Journal of Neuroscience* **9** 1083–1089
- Shih S I, Sperling G, 1996 “Is there feature-based attentional selection in visual search?” *Journal of Experimental Psychology: Human Perception and Performance* **22** 758–779
- Solomon J A, Watson A B, Morgan M J, 1999 “Transducer model produces facilitation from opposite-sign flanks” *Vision Research* **39** 987–992
- Somers D C, Anders D M, Sieffert A E, Tootell R B H, 1999 “Functional MRI reveals spatially specific attentional modulation in human primary visual cortex” *Proceedings of the National Academy of Sciences of the USA* **96** 1663–1668

-
- Treisman A, 1986 "Features and objects in visual processing" *Scientific American* **255**(11) 114–125
- Treue S, Martinez Trujillo J C, 1999 "Feature-based attention influences motion processing gain in macaque visual cortex" *Nature* **399** 575–579
- Watanabe T, Harner A M, Miyauchi S, Sasaki Y, Nielsen M, Palomo D, Mukai I, 1998 "Task-dependent influences of attention on the activation of human primary visual cortex" *Proceedings of the National Academy of Sciences of the USA* **95** 11489–11492
- Zenger B, Sagi D, 1996 "Isolating excitatory and inhibitory nonlinear spatial interactions involved in contrast detection" *Vision Research* **36** 2497–2513