

Lateral interactions between targets and flankers in low-level vision depend on attention to the flankers

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Published online: 17 September 2001, DOI: 10.1038/nn728

Detection of an oriented visual target can be facilitated by collinear visual flankers. Such lateral interactions are thought to reflect integrative processes in low-level vision. In past studies, the flankers were task-irrelevant, and were typically assumed to be unattended. Here we manipulated attention to the flankers directly, by requiring observers to judge the relative alignment of two flankers while ignoring a second flanker-pair. Under identical stimulus conditions, attended flankers produced typical lateral interactions, but ignored flankers did not. These data show that lateral interactions can depend on attention to the flanking context, revealing the functional consequences of attentional modulation in low-level vision.

A long-standing debate in the study of vision concerns how the attentional state of an observer may modify perception¹. Several influential psychological theories (reviewed elsewhere²) propose that basic perceptual grouping processes (that is, integration of local visual elements into configurations) operate without attentional control. Recent neuroscience data indicate, however, that attentional modulation can arise much earlier than previously thought, affecting even the first area of cortical vision^{3,4}. However, the consequences of this for basic perceptual grouping remain unclear. Here we assessed the involvement of attention in a perceptual phenomenon thought to reflect the earliest form of cortical visual grouping.

A low-contrast, oriented central target (a Gabor patch; Fig. 1) becomes more detectable in the context of collinear flanking patches^{5,6}. Such lateral interactions bear the hallmarks of low-level vision, depending systematically on target-flanker configuration, orientation, spatial frequency and separation^{5–8}, in a manner consistent with the physiological architecture of long-range horizontal connections between units within early visual cortex^{9,10}. Lateral interactions thus provide a testing ground for examining, psychophysically, how attention may affect fundamental grouping processes in low-level vision. Psychophysical studies on lateral interactions affecting contrast thresholds often assume that flankers affect target detection automatically, arising when the specified task involves judgments about just the central target, so that the flankers are presumed to be unattended. However, the flankers may actually be attended even when the specified task only concerns the central target, as they are typically the most salient items in a sparse display¹¹, and can enhance target detection. In the present study, we manipulated attention to the flankers directly. We found that flankers benefited target detection only when attended for a secondary task, not when ignored in that task.

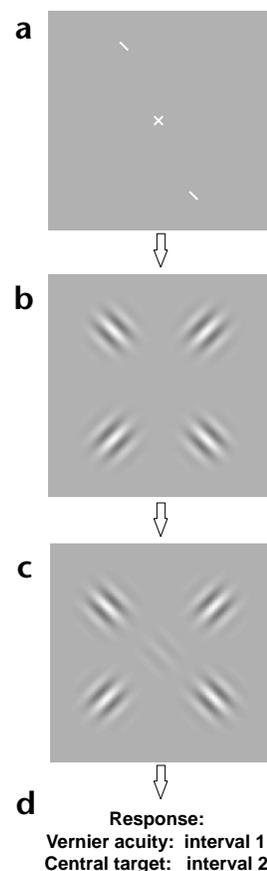
We used a dual-axis stimulus, with four flankers (Fig. 1). The orientation of the central target was collinear with the pair of flankers along one of the axes (albeit with small misalignments, as explained below), but was orthogonal to the orientation of each member of the pair of flankers on the other axis. With only one flanker-pair instead, collinear flankers at the spacing used here enhance central target detection, whereas orthogonal flankers have no effect⁵. As a direct manipulation of attention to one or the other of our two flanker-pairs, we imposed a secondary task for one pair only, to be performed concurrently with the central target detection task. This secondary task required Vernier offset judgments, performed for just the pair of flankers along one pre-specified axis. Subjects judged the relative position of the flankers on this axis, indicating in which of the two intervals they were displaced in a pre-specified direction (Fig. 1). The two flankers on the other axis were to be ignored.

If lateral interactions depend on attention to the flankers, then detection of the central target should be enhanced when flankers collinear to it were attended for the Vernier task, relative to when flankers orthogonal to it were judged for that task instead. The same physical displays were used for these two conditions (Fig. 2c and d), to isolate any attentional modulation of lateral interactions. To compare the size of any such attentional effect against the standard stimulus-driven effect, we also included conventional single-axis stimuli, with only one pair of flankers (Fig. 2a and b). The dual task was performed for these displays also (central target judgments, plus independent Vernier judgments for the single pair of flankers).

RESULTS

Experiment 1 had separate blocks for each of the four dual-task conditions: single-axis orthogonal or collinear conditions

Fig. 1. Dual-task two-interval forced-choice trial sequence, with example dual-axis stimuli. (a) Fixation display with bar markers. (b, c) Two successive stimulus intervals, each composed of four flanking Gabor patches arranged into two orthogonally intersecting axes, with a central target present only in one interval (shown here in c). The central target was always collinear (with small offsets) to the flankers on one axis and orthogonal to those on the other axis. Single-axis stimuli (not shown in this figure) were also used, comprising only one pair of flankers with a collinear or orthogonal target (Fig. 2a and b). Each flanking axis had a Vernier offset (that is, a relative displacement of the two flankers in a direction orthogonal to their common orientation); these offsets independently changed sign (but not magnitude) between intervals, in random order. In experiment 1 only, target-flanker phase varied as a consequence of Vernier offset, as illustrated here. (d) Subjects performed two concurrent tasks. The Vernier task was to judge the relative positional offset of the relevant pair of flankers (this offset varied independently for the two flanker pairs), indicating the interval in which the offset was in a prespecified direction for the relevant pair. The relevant flanker pair and the relevant direction of their offset were indicated by the bar markers at the start of each trial, and remained fixed within blocks. The other task (central detection) was to indicate which interval had a central Gabor target present; this was independent of which interval had the relevant Vernier offset in the attended flankers. Observers made two unspeeded responses, using left or right mouse buttons to indicate the first or second interval respectively. A tone sounded for each incorrect button-press.



(Fig. 2a and b), plus dual-axis orthogonal-attended or collinear-attended conditions (Fig. 2c and d). Two experienced psychophysical observers participated (present authors E.F. and D.S.). Performance for single-axis displays showed the typical lateral-interaction pattern^{5,6}, with detection thresholds for the central target lower in the presence of collinear compared to orthogonal flankers. However, the dual-axis displays showed an attentional effect comparable to the stimulus effect from the single-axis displays (Fig. 2e and f). For a fixed display with four flankers, central detection thresholds were lower when attending the pair of collinear flankers for the Vernier task than when attending the orthogonal pair of flankers instead.

In experiment 2, we sought to replicate and extend these results for six naive observers, plus one experienced observer (E.F.). We used the method of constant stimuli to assess thresholds for the central target, instead of the previous staircases

(see Methods), to allow assessment of whether Vernier performance was influenced by central target contrast. This could address whether any variations in Vernier task difficulty for the relevant flankers produced a confounding trade-off with detection performance for the central target. To test any dependence of the observed lateral interactions on the relative phase of target and flankers, Vernier offsets within flanker pairs were now produced by shifting only the Gaussian envelope of the flankers. Thus, unlike experiment 1, the sinusoidal carrier (and relative target-flanker phase) was now fixed (Fig. 3d and g). Instructions to subjects regarding the Vernier task were unchanged. Three of the subjects also ran single-task conditions (central detection task only), for targets in isolation or with one pair of flankers (single-axis displays), to allow comparison of our new conditions with conventional conditions, that is, with single-task conditions, where a single axis of flankers was present or absent (Fig. 3a–c).

Our critical attentional effect, for the dual-axis displays, was confirmed (group means across all seven subjects, Table 1). A two-way ANOVA on group data ($n = 7$) for the dual-task conditions had factors of single-axis versus dual-axis displays, crossed with collinear versus orthogonal flankers relevant for the Vernier task. This revealed a significant effect of the configuration of attended flankers (when collinear versus orthog-

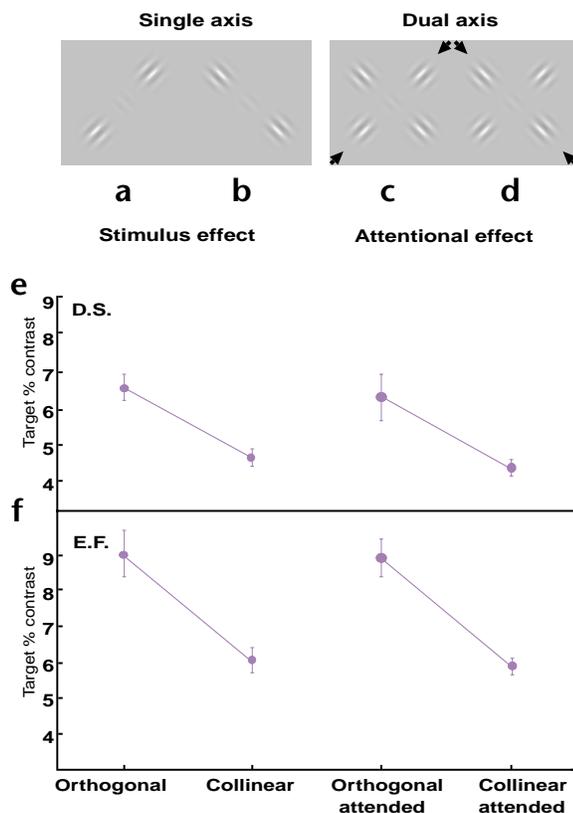


Fig. 2. Example of phase-shifted stimuli, plus staircased contrast-threshold estimates for central target detection in the dual-task conditions of experiment 1. (a) Single-axis stimulus with orthogonal central target, or (b) with collinear target. (c) Dual-axis stimulus in the orthogonal-attended condition, or (d) in the collinear-attended condition (relevant axis indicated here by arrows not present in experiment). (e) Central target detection performance for subject D.S. and (f) for subject E.F. Left two data points show the 'stimulus effect' in single-axis orthogonal versus collinear stimuli, with lower thresholds for collinear configurations. Right two data points show an 'attentional effect,' of comparable magnitude, for dual-axis orthogonal-attended versus collinear-attended conditions. Each data point represents the average of 4–8 staircased threshold estimates, with ± 1 standard error bars.

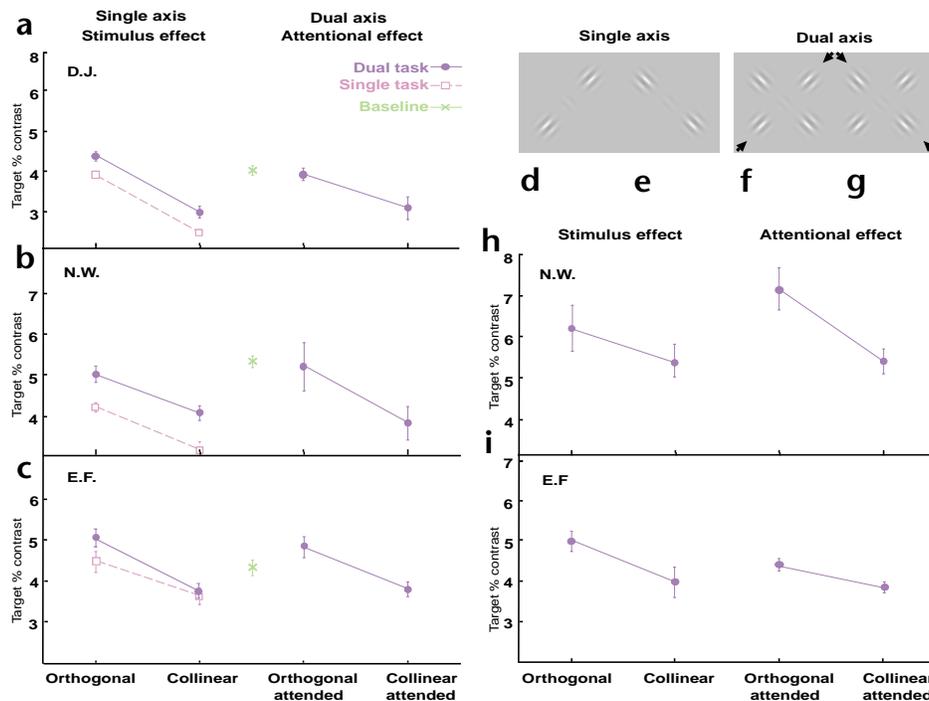


Fig. 3. Example stimuli with no phase shifting, plus central target detection contrast threshold estimates, for experiments 2 and 3. (a–c) Experiment 2 performance for subjects N.W., E.F. and D.J., who all participated in single-task as well as dual-task conditions. Blue circles are for dual-task conditions, white squares are for single-task conditions, and the cross is for single-task detection of an isolated central target, with no flankers. (d–g) Example stimuli for the conditions corresponding to those in the graphs (arrows indicate task-relevant flankers, for illustration only). (h, i) Performance for subjects N.W. and E.F. in experiment 3. Each data point represents thresholds estimated from 800 trials, with ± 1 standard error bars.

onal with the central target; $F_{1,6} = 460.66$, $p < 0.001$). This effect was independent ($F_{1,6} = 1.05$, n.s.) of the presence or absence of task-irrelevant flankers (dual-axis versus single-axis displays, respectively), which itself had no overall impact on performance ($F_{1,6} = 1.65$, n.s.). Target detection therefore seemed to depend entirely on which flankers were relevant to the Vernier task, rather than just on which flankers were physically present in the display. Dual-axis attend-collinear versus attend-orthogonal thresholds differed from each other significantly (Bonferroni, $t_6 = 5.27$, $p < 0.005$), yielding the attentional effect. Moreover, these were each remarkably similar to (statistically indistinguishable from) the corresponding dual-task thresholds for collinear versus orthogonal flankers in single-axis displays (themselves significantly different (Bonferroni, $t_6 = 5.21$, $p < 0.005$), yielding the stimulus effect; Table 1).

Data for the three observers who participated in the conventional single-task condition for the single-axis displays also showed a similar pattern, albeit with better overall performance when comparing single-task to dual-task conditions, as commonly found¹² (Fig. 3a–c). Finally, the target-only baseline confirmed that collinear flankers facilitated detection of the central target, except when unattended in dual-axis displays (Fig. 3a–c).

The final experiment was similar to experiment 2, except that the two possible target orientations (and five possible contrasts for the central target) were now randomized rather than blocked. This ruled out any possibility of anticipating whether the central target would be collinear or orthogonal to the flankers judged in the Vernier task, which might otherwise have led observers to vary their strategy. The attentional effect remained, despite the increase in target uncertainty (Fig. 3h and i).

In experiments 2 and 3, neither the contrast of the central target nor its collinearity with the flankers had a consistent influence on Vernier task difficulty for any of the observers. Moreover, between-subject differences in average Vernier accuracy (for example, experiment 2, mean \pm s.d., E.F., $92 \pm 2\%$; D.J., $87 \pm 3\%$; N.W., $72 \pm 7\%$; group mean \pm s.e.m., $87 \pm 3\%$, $n = 7$) showed no consistent relationship with the magnitude

of stimulus and attentional effects from the flankers on central target detection. Both these findings argue against tradeoffs between the two tasks. The manipulation of relative target-flanker phase, which was fixed in experiments 2 and 3 but varied with Vernier offset in experiment 1 (between 108 – 144° for D.S. and 54 – 108° for E.F.), also had no measurable effect on the lateral interactions observed. This argues against accounts of such lateral interactions based on the spatial summation of target and flanker contrast within hypothetical receptive fields of various sizes¹³, but is consistent with them reflecting non-linear long-range interactions between such receptive fields^{7,8}.

A control study addressed whether our results could be due to the precue (Fig. 1a), which had indicated the relevant flanker-axis for the Vernier task, somehow exerting an effect on central target detection by cueing central target orientation (even though this orientation was either blocked as in experiments 1 and 2, or randomized regardless of the cue as in experiment 3). Targets were now presented in the absence of any flankers, but following precues (Fig. 1a) that were either collinear or orthogonal to the central target in global orientation. Detection thresholds did not differ reliably as a function of precue orientation. For three observers, the nonsignificant differences in thresholds following collinear versus orthogonal precues (in units of percent contrast, with positive values indicating higher thresholds for orthogonal precues) were as follows: 0.00 ± 0.93 (95% confidence interval, E.F.), 0.38 ± 0.52 (G.O.) and 0.23 ± 0.63 (M.L.).

A further issue is whether eye position might have exerted some influence. If subjects had saccaded toward one of the

Table 1. Mean thresholds for 7 observers in experiment 2.

Condition	Percent contrast	Standard error
orthogonal	4.51	0.24
collinear	3.18	0.32
orthogonal attended	4.72	0.25
collinear attended	3.77	0.20

*Significant difference at $p < 0.002$.

flankers relevant to the Vernier task, this might have affected target detection differentially depending on whether the putative eye movement was along the collinear axis, or orthogonal to the axis. The displays were designed to minimize any such influence (see Methods). Nevertheless, we ran a further control study to assess this potential confound. Three observers detected a target among two collinear flankers (with no Vernier offset and no Vernier task), under three randomly intermingled conditions: stimulus centered at the fixation point, so that the target should be foveated, or the whole configuration unpredictably shifted either along or orthogonal to the target-flanker axis, so that subjects should foveate either toward a collinear flanker or a similar distance away from the flanker axis. For the foveal, off-axis and along-axis conditions respectively, thresholds (in units of percent contrast) for subject E.F. were 2.13 (95% confidence intervals of ± 0.28), 2.49 (± 0.35) and 2.66 (± 0.31); for subject M.L., they were 1.47 (± 0.33), 1.91 (± 0.20) and 2.14 (± 0.17); and for subject Z.S., they were 1.64 (± 0.43), 2.29 (± 0.43) and 2.36 (± 0.30). There were no significant differences between conditions. Moreover, any trend for the display-shift conditions is opposed to the possibility that fixating toward a collinear flanker might lower target thresholds.

DISCUSSION

In three main experiments, we investigated effects of attention on a fundamental form of context integration in low-level vision, namely, lateral interactions between a central Gabor patch and flanking patches. Whereas attended collinear flankers in our dual-axis displays produced the usual facilitation of objective thresholds for target detection, the same flankers, when ignored, were prevented from interacting with the target, as if physically removed from the display. These data challenge the view that elementary visual-grouping processes operate regardless of attentional control. Given previous accounts of lateral interactions in terms of the architecture of early visual cortex^{8,10}, our findings reveal attentional modulation of visual grouping that may involve mechanisms at such a fundamental level^{14,15}.

Our study shows that attention to the context (rather than differential attention to the target) can critically determine lateral interactions. Unlike previous studies that used different visual tasks, our method did not compare diffuse versus focused attentional states, nor target detection at cued versus uncued locations^{12,16–18}. Moreover, we did not vary secondary task load, nor rely on an overall cost for dual-task versus single-task conditions^{12,19–21}. Instead, our method manipulated which of two pairs of flankers was relevant for the secondary task, with all flankers being equidistant from the central target, and with a constant secondary task for the critical comparisons. Whereas past studies have typically assumed that the flanking context was always unattended and thus affected target perception involuntarily, our data establish that basic visual processes of context integration are specifically modulated by attention to the surrounding context.

Our findings are distinct from several previously reported results apparently demonstrating effects of memory, imagery, experience or attention to the target on phenomena related to lateral interactions. For example, some previous studies have shown that lateral interactions can be influenced by long-term or short-term memory^{22–24}. They found influences of well-practiced or remembered but physically absent flanker stimuli. The present results, in contrast, show that attention can eliminate lateral influences from physically present, high-contrast stimuli, under the appropriate conditions.

Previous work using subjective brightness judgments^{14,15,17} has suggested that collinear flanker lines (rather than Gabor patches as used here) can increase the reported brightness of target lines. Moreover, early in practice, they can apparently do so more under diffuse than focal attention (manipulated by whether target location was pre-specified). This led to the proposal that an aligned flanker adds no salience to a target that is already attended¹⁵. However, this argument does not apply to the present study, where target location was constant and always attended. Moreover, the similar attentional effects for our experienced and inexperienced subjects indicate that the present effects remain after extensive practice, unlike the subjective brightness findings^{14,15,17}. Here we compared attentional and stimulus effects, using a bias-free measure of objective detection thresholds for Gabors. This comparison revealed that ignoring an irrelevant pair of high-contrast collinear flankers (in four-flanker displays) can be equivalent to physically removing them from these displays, reminiscent of physiological findings on attentional modulation for other classes of stimuli^{25–28}.

Any complete account for lateral interactions now has to explain both the stimulus effect and the comparable attentional effect established here. The basic characteristics of stimulus-driven lateral interactions have been successfully modeled on the neurobiology of early cortical visual areas, such as V1 (refs. 7, 29), where anatomy and electrophysiology reveal the long-range cortical connectivity required^{9,10,30}. In terms of such neurobiological models, at least two alternative accounts arise for how attention could produce the present effects. First, attention could modulate responses to the flankers, as if changing their effective contrast³¹ (either boosting the effective contrast of attended flankers, and/or reducing the effective contrast of irrelevant flankers²⁹). However, target facilitation via lateral interactions is independent of suprathreshold flanker contrast^{7,8}. The 40%-contrast flankers used here would thus need to undergo more than fourfold attenuation to eliminate facilitation from collinear flankers when actively ignored. Such strong modulation exceeds previous psychophysical observations with unmasked stimuli¹² (although masked effects can be larger²¹). Moreover, single cell evidence indicates that attention modulates effective contrast (producing firing-rate changes) only at low or intermediate contrasts³¹, not at high contrasts like those used for the flankers here.

A second possibility is that attention directly modulates the low-level integration processes underlying lateral interactions. The neurobiology of lateral connectivity⁹ suggests early visual cortex as a possible locus for such an influence, where attention might directly modulate the flow of activity between laterally connected units^{15,32}. Applying our design to physiological studies in animals could address this, and might reveal whether the phenomenon reflects modulation of initial neural responses to the stimuli, or later feedback influences from higher areas³³.

The present findings for human vision demonstrate that lateral interactions between a target stimulus and its flanking context, of the kind thought to originate in early visual cortex, can depend upon attention to the context. This reveals a functional role for attentional modulation in low-level vision: to enable the selective, task-dependent grouping of local stimuli by modulating their contextual integration.

METHODS

Stimulus display. Stimuli were displayed on a CRT (Mitsubishi Diamond Pro 920, Itasca, Illinois or Phillips Brilliance 109MP, London, UK), using an 8-bit RGB mode with gamma correction. Mean display

luminance was 39.0 cd/m². Viewing distance was 100 cm, in a darkened room. The fixation display comprised a high-contrast central cross, with peripheral bar markers (length, 0.28°; eccentricity, 1.4°) indicating which flanker axis to judge and which direction of offset to report (Fig. 1a). Gabor stimuli had a wavelength (λ) and Gaussian distribution equal to 0.15° of visual angle (spatial frequency, 6.7 cycles per degree), with center-to-center separation of 4 λ between target and flanker. Within subjects, Vernier offset magnitude underwent minor adjustments between sessions to maintain Vernier task accuracy at an approximately constant level for each subject. These offsets ranged from 0.1 λ (subjects E.F. and D.J.) to 0.4 λ (D.S.).

Procedure. Each trial commenced with a fixation display containing peripheral bar markers (Fig. 1a). These specified the relevant direction of Vernier offset (see below) but provided no information about the central target or its orientation. Following a key press and a 300-ms blank period, there were two stimulus intervals (Fig. 1b and c) of 80 ms duration each, separated by a blank period of 500 ms. The short presentation time was too brief to allow saccades to be generated during displays and, with the long interstimulus interval, should have precluded local adaptation effects. The brief presentations should also have encouraged observers to engage in both the Vernier task and the target-detection task concurrently, rather than sequentially. The near-threshold target for detection was always presented at a known central location, to encourage fixation at this central point. Furthermore, the two flankers to be compared in the Vernier task were in opposite directions from the central target, so that shifting fixation toward one (before a brief display) would be detrimental to the other. The screen remained blank until responses. In dual-task conditions, 2 two-alternative forced choice (2AFC) responses were required (Fig. 1d), with responses emitted 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). In the example shown (Fig. 1), the specified Vernier offset is present in the first interval, and the central target is present in the second interval, but the two events were independent, and so could take any order (and could coincide). In single-task conditions (within experiment 2), only a target detection response was required.

Threshold measurement. In experiment 1, a staircase procedure estimated contrast threshold for the central target. Target contrast incremented following one error, and decremented following three correct responses, by 0.1 log units. Each staircase terminated after eight reversals, with threshold contrast averaged over the final six. Experiments 2 and 3 used the method of constant stimuli, where target contrast varied over 5 levels with 160 measurements per level. Thresholds were then estimated by Weibull fit of psychometric functions.

In the control study assessing any influence of the precue, thresholds were averaged over 8 staircase blocks each composed of a maximum of 60 trials. Given the absence of flankers, auditory signals were used to mark the onset of each of the two intervals, to reduce temporal uncertainty as the flankers had previously done. In the control study assessing any influence of eye position, thresholds for target detection were assessed with a single-interval 'yes/no' procedure (to prevent anticipatory eye movements that might otherwise have arisen for any second interval with shifted stimuli). In along-axis and off-axis conditions, target-flanker displays were shifted from the central position by either 2 λ (observers E.F. and M.L.) or 4 λ (E.F. and Z.S.). The signal-detection parameter d' was estimated twice for each display position at each of 5 target contrast levels, with 40 trials per estimate. Thresholds were then computed by regression at $d' = 1$.

ACKNOWLEDGEMENTS

This research was supported by a project grant (31/S13736) from the Biotechnology and Biological Sciences Research Council (UK) to J.D. and E.F., and by a travel grant from the Royal Society (UK) to E.F. We thank J. Braun, M. Herzog, Z. Li, M. Morgan, M. Posner, R. Perry, G. Rees, T. Shallice, T. Troscianko, J. Wolfe and S. Yantis for comments.

RECEIVED 21 JUNE; ACCEPTED 28 AUGUST 2001

1. Yantis, S. in *Control of Cognitive Processes: Attention and Performance XVIII* (eds. Monsell, S. & Driver, J.) 73–103 (MIT Press, Cambridge, Massachusetts, 2000).
2. Driver, J. & Baylis, G. C. in *The Attentive Brain* (ed. Parasuraman, R.) 299–325 (MIT Press, Cambridge, Massachusetts, 1998).
3. Posner, M. L. & Gilbert, C. D. Attention and primary visual cortex. *Proc. Natl. Acad. Sci. USA* **96**, 2585–2587 (1999).
4. Gandhi, S. P., Heeger, D. J. & Boynton, G. M. Spatial attention affects brain activity in human primary visual cortex. *Proc. Natl. Acad. Sci. USA* **96**, 3314–3319 (1999).
5. Polat, U. & Sagi, D. Lateral interactions between spatial channels: suppression and facilitation revealed by lateral masking experiments. *Vision Res.* **33**, 993–999 (1993).
6. Polat, U. & Sagi, D. The architecture of perceptual spatial interactions. *Vision Res.* **34**, 73–78 (1994).
7. Zenger, B. & Sagi, D. Isolating excitatory and inhibitory nonlinear spatial interactions involved in contrast detection. *Vision Res.* **36**, 2497–2513 (1996).
8. Polat, U. Functional architecture of long-range perceptual interactions. *Spat. Vis.* **12**, 143–162 (1999).
9. Gilbert, C. D. & Wiesel, T. N. Columnar specificity of intrinsic horizontal and corticocortical connections in cat visual cortex. *J. Neurosci.* **9**, 2432–2442 (1989).
10. Polat, U., Mizobe, K., Pettet, M., Kasamatsu, T. & Norcia, T. Collinear stimuli regulate visual responses depending on cell's contrast threshold. *Nature* **391**, 580–584 (1998).
11. Lavie, N. Perceptual load as a necessary condition for selective attention. *J. Exp. Psychol. Hum. Percept. Perform.* **21**, 451–468 (1995).
12. Lee, D. K., Itti, L., Koch, C. & Braun, J. Attention activates winner-takes-all competition among visual filters. *Nat. Neurosci.* **2**, 375–381 (1999).
13. Morgan, M. J. & Dresch, B. Contrast detection facilitation by spatially separated targets and inducers. *Vision Res.* **35**, 1019–1024 (1995).
14. Ito, M. & Gilbert, C. D. Attention modulates contextual influences in the primary visual cortex of alert monkeys. *Neuron* **22**, 593–604 (1999).
15. Gilbert, C., Ito, M., Kapadia, M. & Westheimer, G. Interactions between attention, context and learning in primary visual cortex. *Vision Res.* **40**, 1217–1226 (2000).
16. Morgan, M. J., Ward, R. M. & Castet, E. Visual search for a tilted target: tests of spatial uncertainty models. *Q. J. Exp. Psychol. A* **51**, 347–370 (1998).
17. Ito, M., Westheimer, G. & Gilbert, C. D. Attention and perceptual learning modulate contextual influences on visual perception. *Neuron* **20**, 1191–1197 (1998).
18. Carrasco, M., Penpeci-Talgar, C. & Eckstein, M. Spatial covert attention increases contrast sensitivity across the CSF: support for signal enhancement. *Vision Res.* **40**, 1203–1216 (2000).
19. Joseph, J. S., Chun, M. M. & Nakayama, K. Attention requirements in a 'preattentive' feature search task. *Nature* **387**, 805–807 (1997).
20. Ben-Av, M., Sagi, D. & Braun, J. Visual attention and perceptual grouping. *Percept. Psychophys.* **52**, 277–294 (1992).
21. Zenger, B., Braun, J. & Koch, C. Attentional effects on contrast detection in the presence of salient distractors. *Vision Res.* (2000).
22. Polat, U. & Sagi, D. Spatial interactions in human vision: from near to far via experience-dependent cascades of connections. *Proc. Natl. Acad. Sci. USA* **91**, 1206–1209 (1994).
23. Ishai, A. & Sagi, D. Common mechanisms of visual imagery and perception. *Science* **268**, 1772–1774 (1995).
24. Tanaka, Y. & Sagi, D. Long-lasting, long-range detection facilitation. *Vision Res.* **38**, 2591–2599 (1998).
25. Moran, J. & Desimone, R. Selective attention gates visual processing in the extrastriate cortex. *Science* **229**, 782–784 (1985).
26. Treue, S. & Maunsell, J. Attentional modulation of visual motion processing in cortical areas MT and MST. *Nature* **382**, 539–541 (1996).
27. Recanzone, G. & Wurtz, R. Effects of attention on MT and MST neuronal activity during pursuit initiation. *J. Neurophysiol.* **83**, 777–790 (2001).
28. Reynolds, J. H., Chelazzi, L. & Desimone, R. Competitive mechanisms subserve attention in macaque areas V2 and V4. *J. Neurosci.* **19**, 1736–1753 (1999).
29. Li, Z. Visual segmentation by contextual influences via intra-cortical interactions in the primary visual cortex. *Network Comput. Neural Syst.* **10**, 187–212 (1999).
30. Gilbert, C. D. & Wiesel, T. N. The influence of contextual stimuli on the orientation selectivity of cells in primary visual cortex of the cat. *Vision Res.* **30**, 1689–1701 (1990).
31. Reynolds, J. H., Pasternak, T. & Desimone, R. Attention increases sensitivity of V4 neurons. *Neuron* **26**, 703–714 (2000).
32. Sagi, D. in *Brain Theory: Biological Basis and Computational Theory of Vision* (eds. Aertsen, A. & Braitenberg, V., Elsevier Science, Amsterdam, 1996).
33. Lamme, V. A. F. & Roelfsema, P. R. The distinct modes of vision offered by feedforward and recurrent processing. *Trends Neurosci.* **23**, 571–579 (2000).