

PSYCHOPHYSICAL MEASUREMENT OF ATTENTIONAL MODULATION IN LOW-LEVEL VISION USING THE LATERAL-INTERACTIONS PARADIGM.

Elliot Freeman,¹ Jon Driver,¹ Dov Sagi²

¹ Institute of Cognitive Neuroscience, University College
London, 17 Queen Square, London WC1N 3AR, UK.

² Department of Neurobiology, Brain Research, The
Weizmann Institute of Science, Rehovot 76100, Israel.

Published in *V. Cantoni, M. Marinaro and A. Petrosino (Eds.)
Visual Attention Mechanisms*. Plenum Press, NY (2001).

INTRODUCTION

One of the fundamental functions performed in vision is perceptual grouping. Through grouping we are able to derive, from the relationships between local regions of a scene, a perception of the overall structure and also of the distinctiveness of the separate objects contained within it. A long standing debate in psychology concerns the extent to which perceptual processes are autonomous, operating independently of top-down attentional control¹⁻⁵. According to several influential ‘preattentive’ accounts of grouping⁶⁻¹¹, attention selects between perceptual groups that have already been segmented from each other, but with no direct top-down control over the initial grouping processes themselves.

Recent evidence from neuroscience (see ref. 12 for review) threatens to overturn this simple picture of a preattentive stage of perceptual grouping followed by attentional selection of particular groups, in a strictly feed-forward manner. Data from functional imaging¹³⁻¹⁶ and from single-cell recording¹⁷⁻¹⁹ now indicate that attention can modulate neural activity as early in the processing stream as the primary visual cortex, presumably via top-down influences involving back projections. Such findings may be broadly consistent with psychophysical evidence showing that performance even on elementary visual tasks, such as contrast detection or threshold discrimination of simple attributes such as orientation, can depend to some extent on the allocation of attentional resources (e.g. see refs. 20-25). Given such data, it may seem likely that perceptual grouping could also be subject to attentional modulation²⁶. However, unequivocal psychophysical evidence for a specific effect of attention on low-level perceptual integration of groups has been lacking to date.

We have recently developed a new psychophysical paradigm for probing attentional effects on low-level perceptual integration. Using this paradigm, we have obtained

evidence that ‘lateral interactions’^{27,28} between different parts of a display (neighbouring Gabor patches) can be strongly modulated by attention. Such lateral interactions are thought to reflect low-level grouping mechanisms and have been successfully modelled in terms of the known neurobiology of horizontal connections in early visual cortex. Our results may therefore fit with the emerging neuroscience evidence for low-level attentional modulation. The detailed method and data are presented elsewhere (Freeman, Sagi & Driver, submitted). Here, we examine in more detail the methodological issues involved in experiments of this kind, and how we sought to address those issues. In addition, we present some new data and indicate how future studies could resolve outstanding issues. Finally, we consider some more general implications for understanding the functional role played by attention in low-level vision.

THE ‘LATERAL INTERACTIONS’ PHENOMENON

Our psychophysical methodology is based on the perceptual phenomenon of *lateral interactions*: a central oriented visual target is more detectable in the context of collinear flanking patches. Originally brought to light by one of the present authors (Dov Sagi) together with his coworker Uri Polat^{27,28}, this and related configuration-dependent phenomena²⁹⁻³¹ are thought to reflect fundamental integrative processes within early vision³²⁻³⁴. Typical stimuli in the original lateral-interactions paradigm^{27,28} consisted of three Gabor patches (i.e. 2D Gaussian-modulated sine-wave gratings). Gabor stimuli are optimal for probing the properties of low-level spatial analysers³⁵ whose selectivity for location, orientation and spatial frequency mirrors that of the classical receptive fields found for neurons in early visual cortex³⁶. The central patch in the display (referred to as the *target*) is typically at near threshold contrast, with the other two (the *flankers*) at suprathreshold contrast (see fig. 1a-b). The task is to indicate in which of two successive presentations the barely-visible central target is present, while the highly-visible flankers are always present. Compared to baseline sensitivity for an isolated target, target detection can be significantly better when the three patches are arranged in a *collinear* configuration (see fig. 1a), as if part of a virtual contour. Detection returns to baseline when the target is rotated by 90 degrees, to create a configuration where the target is *orthogonal* rather than collinear with the flankers (fig. 1b). The facilitation by collinear flankers is strongest for target-flanker separations of 3 to 4 Gabor-patch wavelengths (fig. 1c), but persists with larger separations²⁷, even up to 12 wavelengths after practice³⁷. Target detection thus depends on the global pattern it makes in combination with the flankers.

This phenomenon is an attractive platform for studying the possible role of attention in low-level visual grouping, since it appears to reflect low-level processes of contextual integration. A role for attention at this level seems possible, especially given recent evidence of short and long-term memory effects on lateral interactions (e.g. refs. 37-39) which may also involve top-down, task-dependent processes. There are two further attractive features of the lateral interactions paradigm. First, it has a firm grounding in the neurobiology of early vision. Second, contextual integration can be probed indirectly, by measuring target contrast threshold, rather than by requiring subjective judgements of grouping.

Psychophysical testing for effects of flanker configuration, orientation, spatial frequency and separation upon target thresholds^{27,28,40} reveal patterns that are consistent with what is currently known about the architecture of early visual cortex³³. For example, anatomical studies of V1 have revealed long-range horizontal connections between cells, often extending for long distances outside each cell’s classical receptive field along an axis defined by the cell’s orientation preference, to connect with other similarly tuned cells^{41,42}.

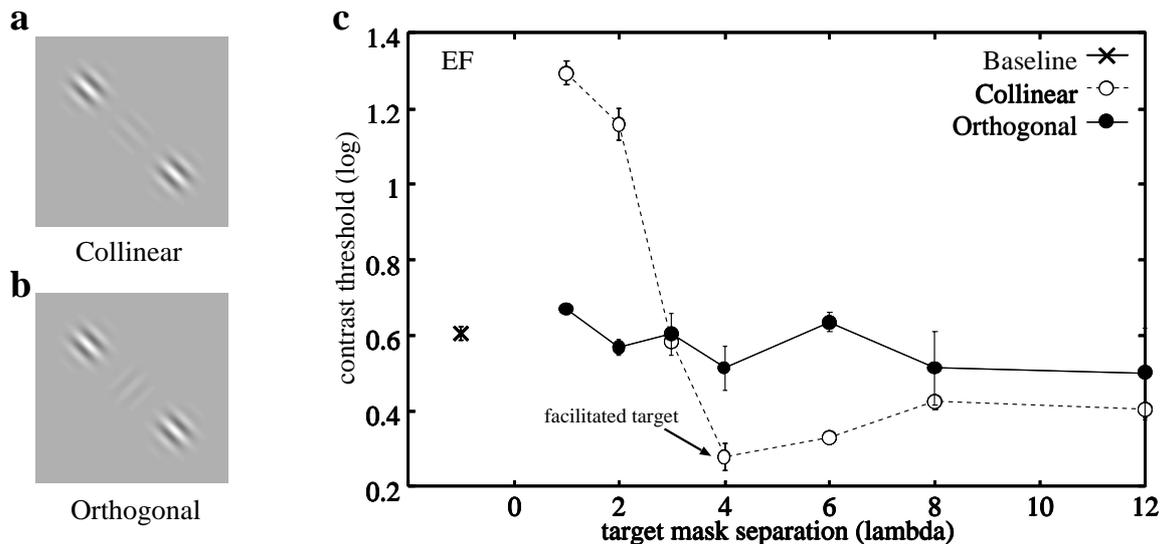


Figure 1. Illustration of the basic Lateral Interactions paradigm (e.g. Polat & Sagi, 1993). (a) Flankers and central target in *collinear* configuration with 4 wavelengths separation; (b) *orthogonal* target-flankers configuration; (c) Typical data (observer EF) showing central target facilitation (lower contrast thresholds) relative to baseline (target without flankers) for collinear configurations with target-mask separation of greater than 3-4 wavelengths, and suppression for smaller separations; neither suppression nor facilitation is observed for orthogonal configurations. Error bars represent one SE.

Physiological data have shown changes in the activity of cells in primary visual cortex depending on the orientation and separation of flanking stimuli⁴³ outside the classical receptive field, in a manner consistent with the anatomical data on horizontal connections and also with human psychophysics. Sharing of contextual information via long-range connections could serve to produce a representation of the extended structure and continuity of a stimulus, by activating several aligned and collinear receptive fields, thus performing a basic grouping function for contour integration^{29,44,45}.

The lateral-interactions phenomenon might thus reflect the earliest cortical mechanisms for contextual integration and grouping³³. Any attentional modulation of this psychophysical phenomenon should therefore have implications for what attention might be doing in low-level vision. Moreover, computational models based on the architecture of early visual cortex^{40,45-48} may be able to generate testable predictions relating to the underlying mechanisms of attention at this level (e.g. see ref. 47).

The lateral-interactions paradigm is an *indirect* measure of context integration, because the effects of the flankers are observed through their influence on the local threshold contrast of the target. In principle, the flankers are irrelevant to the central detection task, and so their effects may thus be probed without necessarily drawing attention to them. Because of this past studies have often assumed (either explicitly or implicitly) that the flankers need not be attended at all in order to affect target perception. An apparently involuntary influence of task-irrelevant flankers on target perception might appear consistent with theories of preattentive vision in which grouping occurs automatically, without requiring focal attention⁵⁻¹¹. In practice, however, it may not be safe to assume that flankers are completely unattended in the lateral-interactions paradigm, merely because they are irrelevant to the central task. In past studies the flankers were always the most salient items in the display; moreover it may have been strategically advantageous to attend to the flankers, especially if doing so could enhance their facilitation of the target and thus improve performance on the relevant central task.

The indirect nature of the lateral interactions paradigm can be turned to our advantage, however. Rather than merely trusting that task-irrelevant flankers will always be passively

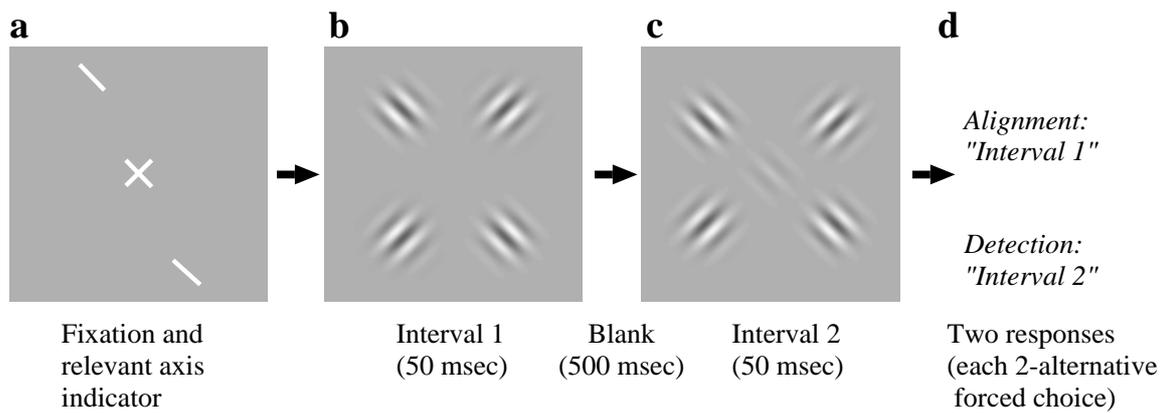


Figure 2. Example sequence of events in the new dual-task paradigm. (a) Fixation display with pre-cues indicating which flanker-pair is relevant to the Vernier task, and the relevant direction of Vernier offset; (b-c) successive displays each with two flanker-pairs (note shifts in Vernier offset) and with a central target present in only one (shown here in c); (d) observer makes two unspeeeded responses: the first indicates the interval (1 or 2) in which Vernier offset of the pre-cued flanker-pair is in the pre-specified direction; the second response indicates the interval in which the central target was present.

ignored, here we impose control over attention to the flankers by requiring a secondary task to be performed on them. This has three benefits: firstly, a relatively ‘clean’ *stimulus effect* can be obtained by comparing collinear with orthogonal target-flanker configurations when these flankers are always task-relevant, thus avoiding uncontrolled variations in attention to the different stimulus components. Secondly, lateral interactions may be measured under conditions in which particular sets of flankers are either actively attended or ignored, while seeking to hold attention to the probed central target constant. This allows us to measure an *attentional effect*, in order to test whether contextual integration specifically depends on attention to one or other set of flankers. Finally, measurement of controlled stimulus and attentional effects is of use for inferring the locus and nature of the interface between stimulus-driven and task-driven processes, as will be explained below.

MANIPULATION AND CONTROL OF ATTENTION TO FLANKERS AND TARGET

In order to measure any attentional effects, we introduced two modifications to the original lateral-interactions paradigm. Firstly, we used novel *dual-axis* stimuli that included a second pair of flankers, differing in orientation by 90 degrees with respect to the first pair, and lying on a virtual axis that intersected the first at right angles. The four flankers thus formed an ‘X’ configuration (see figure 2b,c). The target could be rotated by 90 degrees, so that it was always collinear with one axis (i.e. all elements on that axis had the same orientation), but was orthogonal to the other axis. Secondly, our attentional manipulation was achieved using a *dual-task* methodology, in which the target detection task was performed concurrently with a Vernier offset task on just one pair of flankers. On each axis independently, flankers shifted slightly between successive intervals, in opposite directions to each other, along a path at right angles to their orientation. (Within the range of offsets used, such offsets had little effect on the strength of lateral interactions observed between flankers and central target). The Vernier task was to indicate in which interval the offset between flankers on just one pre-specified axis (fixed throughout an experimental block) was in a pre-specified direction (fixed throughout the experiment). Our hypothesis was that, if lateral interactions are attentionally modulated, then threshold for central target detection should depend on which pair of flankers is attended for the Vernier task. Facilitation should

be found when the collinear flanker-pair is task-relevant, but should be reduced when the orthogonal flanker-pair is relevant and the collinear flankers are ignored.

This method of manipulating attention differs from those used in many previous studies, where the usual approach is to measure how well an observer can judge specific stimulus attributes under conditions in which the test stimulus itself is attended or is ignored to varying degrees. For example, in the typical dual-task paradigm, a visual task is performed on its own or concurrently with an unrelated secondary task (e.g. refs. 20,24,26,49), which is assumed to limit the attentional resources available for the primary task. In spatial cueing experiments, cues direct attention to one or several potentially relevant target locations (e.g. refs. 21-23,25,50). Prior task instructions may also be used to vary the number of locations over which a critical stimulus is expected to appear (eg. See ref. 51).

Such manipulations have been used with much success to test the dependence of different perceptual abilities on general attentional resources. However, they are perhaps less suitable for identifying any more specific effects of attention on low-level processes such as contextual integration. For example, our own goal was to determine whether attention specifically modulates the influence of a flanking context on the perception of a central test stimulus. Measuring the critical changes in target sensitivity caused by any such modulation is likely to be difficult if other variables are also affecting perception at the target location. Such variables might be introduced by typical attentional manipulations of the kinds considered above, which can produce changes in the spatial distribution of attention and/or its likely intensity at the test stimulus location, as well as affecting spatial uncertainty for target location (see ref. 23).

For example, in recent studies by Ito, Gilbert and coworkers^{22,52}, the subjective brightness of a target line was measured under varying conditions of spatial certainty for the location of that line, in the presence or absence of collinear flanking lines. These authors reported that such flanking lines increased the subjective brightness of the target line, but to a greater extent under conditions in which the observer was attending simultaneously to several possible target locations (i.e. diffuse attention), compared to when they were attending one pre-cued target location in particular (focal attention). This was taken as evidence for direct attentional modulation of lateral interactions between the target and flankers. However (as noted by these authors in their 2000 paper, page 1221), focal attention to the target might itself have caused an increase in target salience which masked any additional effect of the flankers on its salience⁵². Furthermore, it is possible that focal attention to a target may cause some shrinkage of corresponding functional receptive fields⁵³, consistent with recent psychophysical evidence from Carrasco and coworkers^{54,55} for an attention-dependent increase in spatial resolution. This could reduce the likelihood of spatial summation of flanker and target luminance. Thus manipulating attention to the target location could affect lateral interactions in several indirect ways, by altering processing of the target itself.

The present method, in contrast to all those considered above, attempts to hold constant the demands on spatial attention with respect to the central target, manipulating only attention to the flankers instead. There is minimal spatial uncertainty in our paradigm, because the target is always in a fixed central location. Moreover, selecting between the two flanking axes (i.e. one or other of the flanker-pairs in the double-axis displays; see figure 2), should not entail any change in the overall area covered by attention, as each pair of flankers is distributed around the fixation point with equal spacing. As we describe later on, we also took care to avoid variations in the difficulty of the Vernier task for one or other pair of flankers that might otherwise have caused a possible trade-off with attention to the central target. Attentional effects on lateral interactions are thus measured in our paradigm under the same task load, in the same central location, and with the same spatial

distribution of attention overall. Gross variations in attention can thus be ironed out, allowing any specific effects of attention on contextual integration to emerge, if they do in fact occur.

DATA AND INTERPRETATION

Here we present results from a total of eight observers. Data from four of these were described in Freeman, Sagi & Driver (submitted), the other four observers having been tested more recently. All observers, except two of the present authors (EF and DS), were naïve to the task and had no previous experience with psychophysical experiments. All were tested with conventional single-axis stimuli (see fig. 3a-b) comprising only one flanker-pair, and also with our novel dual-axis stimuli (see fig. 3c-d and previous section), under dual-task conditions for both types of stimulus (i.e. central target detection, plus offset judgements for one flanker-pair). The four recent observers were also tested on a modified stimulus set (see below). Two-alternative forced choice thresholds were estimated either using an adaptive staircase method (averaged over a minimum of four blocks per condition) or using the Method of Constant Stimuli (data collected over a minimum of 800 trials per condition with thresholds then estimated by Weibull fit of psychometric functions).

Six observers showed strong attentional effects, and a remarkably similar pattern overall, while the remaining two observers showed weaker attentional effects. Thresholds for each condition, averaged across the first four subjects, are graphed in figure 3e,f. In the single-axis condition (figure 3e) thresholds were significantly lower (see 95% confidence interval error bars) by almost 0.2 log units when the flankers were collinear, compared to when they were orthogonal. This *stimulus effect* replicates the basic lateral interactions effect found in previous studies^{27,28} and confirms that the introduction of small flanker offsets and a concurrent Vernier task do not on their own disrupt measurement of this phenomenon. The critical dual-axis *attentional effect* (figure 3f) was also significant and shows a similar pattern, with lower thresholds for the *attend collinear* condition than the *attend orthogonal* condition. Thus, facilitation (relative to the orthogonal single-axis condition) was only apparent when the collinear flankers were attended for the Vernier task, and disappeared when these were ignored with the Vernier task now being performed on the other, orthogonal pair of flankers instead. Note that even though in the dual-axis conditions the stimuli always contained flankers that were collinear to the target, there was no significant target facilitation caused by these collinear flankers when unattended (i.e. compare single vs. dual-axis orthogonal conditions).

As noted previously, these results were obtained under conditions designed to prevent uncontrolled variations in the spatial distribution or intensity of attention with respect to the central target. For example, the target was always task-relevant, and the two pairs of flankers were distributed with equal spacing around it, so that the relevant stimulus area was fixed between conditions. We also checked that Vernier performance did not vary consistently as a function of target contrast and orientation, which were varied only between blocks when using the Method of Constant Stimuli. If, for example, Vernier judgements had been easier with collinear target-flanker configurations, this might have caused attentional trade-offs between the two tasks and thus apparent attentional benefits for target detection. However, Vernier performance did not vary consistently between conditions, ruling out such tradeoffs as an account for the effects we observed. As an additional precaution, two of the observers repeated the experiment with target contrast and orientation randomised within blocks, in order to prevent any strategic reallocation of attentional resources between target and flankers. If, for example, orthogonal targets had

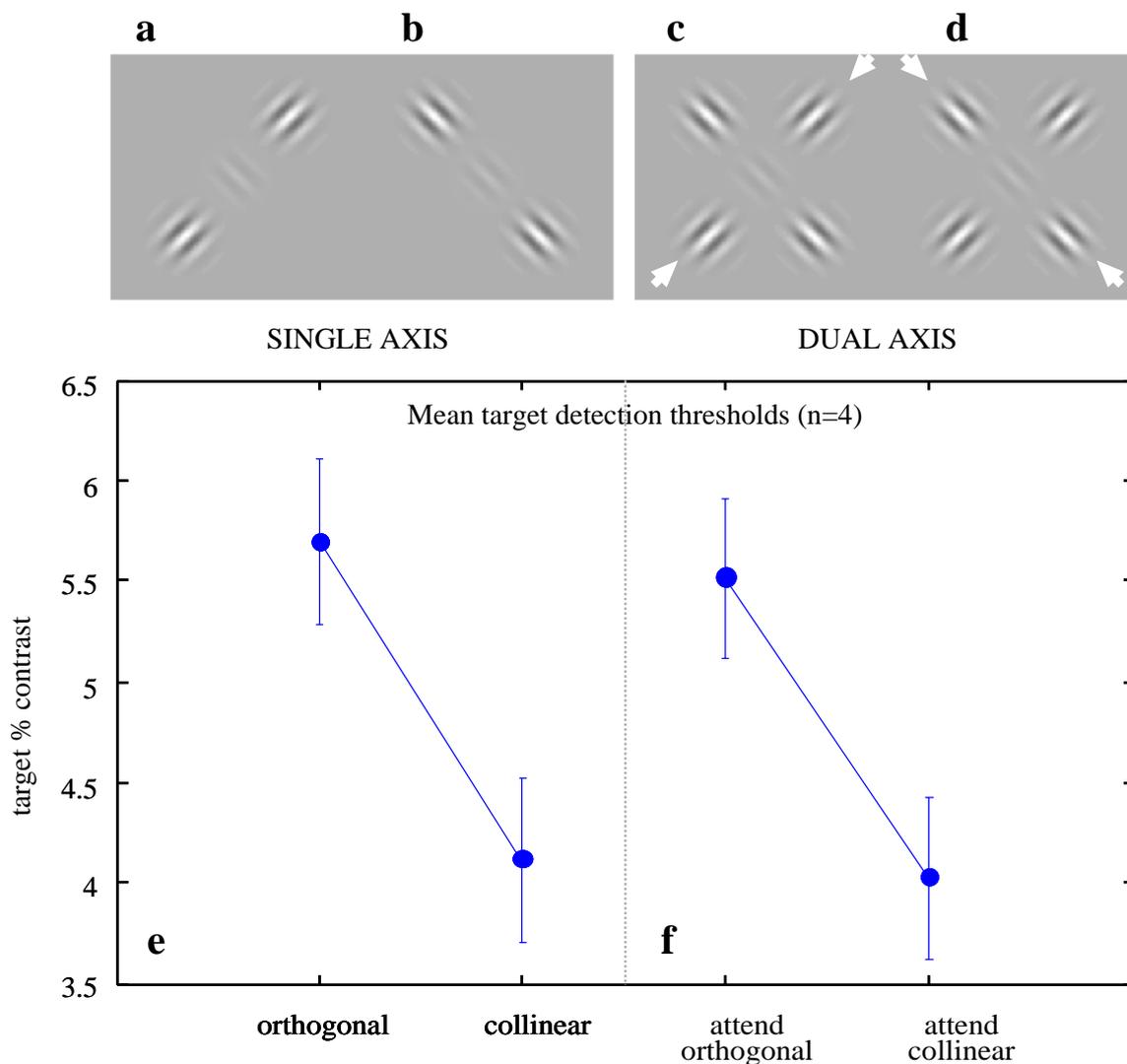


Figure 3. (a-b) Example single-axis stimuli with orthogonal or collinear target-flanker configuration; (c-d) dual-axis stimuli for the two attentional conditions, with arrows illustrating the flanker-pair that is attended for the Vernier task (arrows not shown in actual displays); (e-f) mean thresholds for central target detection: note similarity of single-axis *stimulus effect* (e) and dual-axis *attentional effect* (f). Error bars indicate 95% confidence intervals for stimulus and attentional effects respectively.

made the Vernier task predictably more demanding, then there might have been a strategic shift of limited attentional resources towards the Vernier task, with consequently poorer target detection. Randomisation had no consistent impact on the results, however, thus ruling out such strategic reallocation as an explanation for our results.

Given our efforts to eliminate uncontrolled variations in spatial attention *to the target*, we are able to conclude that the lateral interactions phenomenon appears to be critically dependent on attention being paid *to the flankers*, with no lateral interactions from flankers that are ignored in dual-axis displays. This challenges ‘preattentive’ theories of grouping in early vision⁵⁻¹¹, suggesting that how we integrate the parts of a stimulus together depends on which specific parts (here target plus one or other pairs of flankers) we are attending at a given time.

Comparison of stimulus and attentional effects can help to characterise the role played by attention in greater detail. For example, the magnitude of the attentional effect may be estimated by simply comparing performance, under the same dual-task conditions (i.e. central detection plus flanker Vernier offset judgements), between dual-axis versus more conventional single-axis stimuli (fig. 3a-d). The effect of ignoring the collinear flankers (in

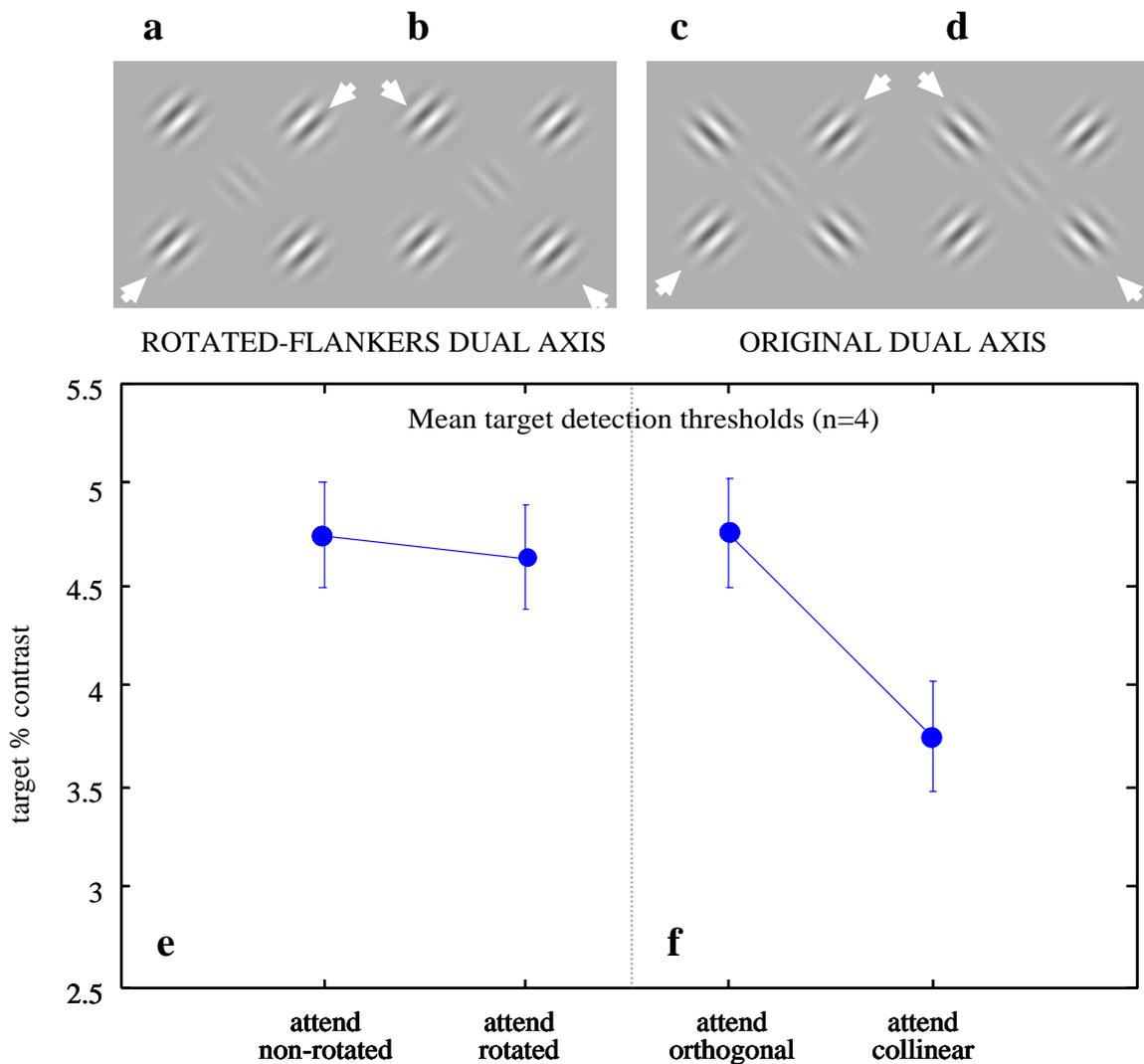


Figure 4. (a-b) Modified dual-axis stimuli, with flankers on one axis *rotated* into a ‘parallel’ configuration; arrows indicate which flankers (a: non-rotated or b: rotated) were relevant to the Vernier task; (c-d) unmodified dual-axis stimuli for comparison; (e-f) mean contrast thresholds for the central target showing replication of the attentional effect (e) and its elimination (f). Error bars indicate 95% confidence intervals for modified and unmodified conditions respectively.

dual-axis displays) may then be compared with the effect of physically removing them altogether (to produce single-axis displays). If the attentional effect were only partial then thresholds with ignored collinear flankers present (i.e. in the attend-orthogonal dual-axis condition) should always be lower, compared to when they are not physically present (as in the orthogonal single-axis condition). This would imply that the stimulus effect is to some extent always automatic, and cannot be completely overridden by attention. However, the similarity of single-axis and dual-axis data that we observed (see figure 3e,f) indicates that the attentional modulation was complete. When the collinear flankers were ignored, performance was equivalent to the single-axis case in which they were not present at all. In terms of their effects on central target detection, ignored flankers were as good as absent, despite having a contrast well above threshold.

Additional *rotated-flankers* stimuli (figure 4a,b) were constructed to investigate further the possible functional locus of the attentional effects we measured. In particular we wished to address the issue of whether attention specifically modulates processes underlying the phenomenon of lateral interactions, or whether it merely rides ‘on top’ of preattentive stimulus-driven effects without affecting them directly. If attention did operate

specifically on lateral interactions, then physically eliminating the possibility of such lateral interactions should also eliminate the attentional effect. In our new stimuli, flankers that were originally collinear with the target were *rotated* by 90 degrees so that they were now orthogonal to the target but parallel to each other in orientation. As before, subjects had to attend either to the old *non-rotated* flankers that were orthogonal to the target (fig. 4a), or to the new *rotated* flankers (arrowed flankers in fig. 4b). Note that accuracy in judging the Vernier offset of the rotated flankers was not appreciably different compared to the non-rotated flankers.

Figure 4e,f shows averaged central target detection thresholds for the four observers recently tested with the modified stimuli. Three of these observers replicated the attentional effects obtained with the unmodified dual-axis stimuli (fig.4f), but none showed any appreciable effects of manipulating attention to orthogonal versus parallel flanker-pairs (see fig. 4e). The absence of attentional effects with the rotated-flankers stimuli allows us to conclude that the attentional modulation observed for the other conditions (e.g. figs. 3f and 4f) is indeed specific to processes depending on the global configuration of target and attended flankers. Note also that the unmodified stimuli containing ignored collinear flankers ('attend-orthogonal' datapoint on fig. 4f) produced no residual target facilitation compared to thresholds obtained with the new stimuli, in which there were no collinear flankers (fig. 4e). This observation adds further weight to the conclusion that lateral interactions between collinear stimuli are completely eliminated when the collinear flankers are unattended in dual-axis displays.

In view of the above results, it seems that theoretical explanations of the lateral interactions phenomenon must now also account for the attentional effects, which depend on similar stimulus parameters and have a similar magnitude. Some might seek to explain away the present data (and all previous data on lateral interactions) as phenomena with no necessary relationship to contextual integration processes. We examine such accounts first, before turning to accounts of lateral interactions as reflecting contextual integration.

One possibility is that attending to a particular flanker-pair improves sensitivity to the global orientation of the virtual axis connecting that pair, perhaps by modulating competition between local orientation-tuned spatial filters²⁰. This might favour targets having the same orientation as the attended axis. This 'global orientation tuning' account might in principle explain the benefit for target detection when the attended flankers are collinear, without requiring attentional modulation of lateral interactions. However, it falsely predicts similar effects when attending to the rotated flankers in the modified stimuli (see fig. 4b and left graph of fig. 4e), because in both cases the target has the same orientation as the attended axis of flankers. A similar account based on tuning to the local flanker orientation could be tested using single-axis stimuli in which target and flankers all have the same orientation but are in a side-by-side configuration. In such a stimulus, the local orientation of the patches is orthogonal to the global orientation of the axis connecting them. Note, however, that in single-task situations²⁸ such permutations never produce facilitation of the same magnitude as collinear configurations, so these tuning accounts fail to explain away the basic lateral-interactions effect.

Another perspective would seek to explain all lateral-interactions phenomena using a single large receptive field that overlaps both target and flankers⁵⁶; but see ref. 57. If the shape of such a large receptive field were modified by attention, this might in principle explain the present attentional modulation effects. However, such accounts usually imply some degree of dependence on the relative phase of target and flankers. Past studies on phase dependence have produced diverse results (often null effects, e.g. refs. 27,40,58; but see ref. 56). Phase dependence was tested in the present work. In one experiment (with two experienced subjects), Vernier offsets displaced the flanker Gabors bodily (i.e. moving both Gaussian envelope and sine-wave carrier components), introducing shifts in target-flanker

relative phase of between 54 and 144 degrees. In other experiments, relative phase remained fixed (i.e. only the Gaussian envelope component was moved, while the position of sine-wave peaks and troughs remained fixed). Large stimulus and attentional effects were still consistently obtained even when the target and flankers were substantially out of phase.

Uncertainty theory assumes that an observer uncertain about the exact location or orientation of the target may sample from a larger number of irrelevant and noisy channels than when more certain about these properties⁵⁹. This might influence lateral interactions if collinear flankers reduce spatial uncertainty by effectively ‘pointing’ to the target location⁶⁰. Attending towards or away from particular flankers might then determine the extent to which those flankers may be used to indicate target location. This is unlikely here, because the location of the flankers themselves was even less predictable than the target, by virtue of the Vernier manipulation. Another uncertainty account is that attention to the collinear flankers might bias the sample in favour of channels with the same orientation as the flankers. Such a mechanism might provide one basis for the ‘orientation tuning’ accounts that we considered (and rejected) earlier. In general, uncertainty models⁵⁹ typically assume that stronger signals are required to combat the extra noise from more irrelevant channels before they can be detected reliably above chance. They therefore predict that uncertainty should lead to a correlation between higher thresholds and steeper psychometric curves. Some correlation of this type was observed in the present data set, but not consistently. Moreover, there was no consistent effect on the slope of psychometric functions of randomising target orientation and contrast, which arguably should introduce the strongest source of uncertainty.

Further experiments in which the contrast of all four flankers is varied may help to distinguish between two remaining accounts, on both of which the observed attentional modulation of lateral interactions would be explained in terms of contextual integration processes. One possibility is that perception of the ignored flankers might be suppressed to such an extent that they no longer affect the target at all⁴⁷. This flanker suppression would have to be very strong if it merely lowered the effective flanker contrast, for previous data suggest that facilitation in the standard lateral-interactions paradigm is unaffected by flanker contrast once suprathreshold contrast is reached^{33,40}. For the high-contrast flankers used here (40%), attentional modulation would thus have to produce more than a fourfold decrease in effective contrast to bring the flankers below threshold. Such large modulations have recently been reported for detecting eccentric target Gabors surrounded by masks under varying dual-task loads⁴⁹, while a recent physiological study showed a comparable range of attentional modulation of cell activity, but only for low- and medium contrast stimuli⁶¹. Much weaker modulations in contrast sensitivity (10% or less) are more typical for unmasked stimuli²⁰. If this ‘flanker suppression’ account is correct, then the attentional effect should get smaller for flankers whose contrast is sufficiently high that they can no longer be suppressed by attention to near threshold.

A second possibility seems to be more plausible, and is based on the physiology and modelling of long-range horizontal interconnections in early visual cortex, as mentioned earlier. The role of attention in this context, as proposed previously^{52,62,63}, might be to control or weight the input to the target receptive field from its context, via top-down feedback to the connections underlying lateral interactions. Because this weighting may have a multiplicative effect on flanker inputs to the central target receptive fields (rather than additive, as in the above ‘flanker-suppression’ account), attentional variations in weighting might then have a greater impact on input from higher contrast flankers. Compared to the flanker-suppression account, this ‘connection-weighting’ account therefore predicts the opposite effect of varying flanker contrast: attentional effects should diminish with reduced flanker contrast, rather than with higher flanker contrast. Note

however, that even if the flanker-suppression account were to be supported by such an experiment, this would still imply that attention may operate at a stage no later than the stage at which lateral interactions start to emerge.

SUMMARY AND CONCLUSIONS

In this chapter we have reviewed our recent experiments using a psychophysical paradigm designed to examine the role of attention in low-level context integration. We observed *lateral interactions* between a target test stimulus (a Gabor patch) and its context (flanking Gabors), a phenomenon thought by several authors to reflect fundamental context integration processes in early vision (e.g. refs. 32-33,45), grounded on the neurobiology of early visual cortex (e.g. refs. 41-43). While measuring central target detection thresholds as an indirect measure of target-context integration, we performed an independent manipulation of attention to different parts of the flanking context. A total of eight observers provided evidence for strong attentional modulation of lateral interactions. Measurement of such effects was made possible by ironing out uncontrolled variations of attention to the central test stimulus itself, that might otherwise have masked or contaminated the more subtle effects of attending to the context. These data suggest several conclusions about the nature of the attentional effect on contextual integration in low-level vision.

Firstly, attention seems to modulate the lateral interactions phenomenon strongly enough to completely override stimulus-driven effects of element configuration. This conclusion is supported by the comparison of stimulus effects (measured under controlled attentional conditions) with attentional effects (measured under controlled stimulus conditions). Attention completely eliminated the influence of actively ignored collinear flankers on thresholds to detect the test stimulus, producing performance indistinguishable from a case in which the same flankers were physically absent (see figs. 3 and 4).

Secondly, the attentional effect seems to be specific, modulating the integration of flanking context with the target. Physically removing any stimulus support for target and flankers forming an integrated contour also eliminated our attentional effects. The general similarity of the observed stimulus effects and attentional effects favours the interpretation that attention may interact directly with the perceptual processes underlying lateral interactions, facilitating or overriding the effects of the flanking stimuli on central thresholds, rather than merely riding on top of purely stimulus-driven processes.

These considerations suggest the following radical conclusion: *There may be no context integration when the context is actively ignored*. As well as narrowing down the possible functional locus of attentional effects, the possible anatomical locus may be further constrained by neurobiologically-grounded models of lateral interactions, based on evidence for long-range horizontal connections in early visual cortex. These constraints already point to a possible mechanism for attentional modulation^{52,62,63}: attention may mediate selective integration of different parts of the surrounding context, by modifying the weighting of the long-range horizontal connections between the population of cells responding to the target and those responding to the flankers.

We close with some speculations on the relation between this apparently specific effect of attention on perceptual grouping, and some more general mechanisms that may underlie attentional modulation in low-level vision. Physiological studies have obtained evidence for attentional mechanisms operating in visual cortex based on the principle of '*biased competition*'^{18,53}. These studies typically probed the effect on classical receptive field activity of a preferred ('good') stimulus and a non-preferred ('poor') stimulus, which on their own produced strong and weak cell firing respectively. When presented

simultaneously within the same classical receptive field, activity was near the average of that produced by the ‘good’ and ‘poor’ stimuli alone. However, activity increased towards full magnitude when the ‘good’ stimulus was attended in the combined display and diminished to the minimum when the ‘poor’ stimulus was attended¹⁸. This was taken to suggest that the two stimuli were competing for dominance of the probed receptive field, and that attention could bias which of the two stimuli won the competition. Such data imply that attention can mediate in cases where averaging the various inputs to a receptive field would otherwise impair the selectivity of a cell’s response.

Our speculation is that the present experimental situation may set up an analogous conflict between alternative perceptual groupings, which attention can intervene to resolve. Instead of presenting two discrete stimuli, as in the above single-cell studies, here we presented two distributed sets of contextual stimuli (i.e. both collinear and orthogonal flanker-pairs), lying along the two axes of the ‘X-shaped’ display (see figure 2b or c). Suppose that both these sets lie within the extra-classical receptive fields⁶⁴ of the population of cells responding to the target, stimulating them via long-range horizontal connections. Analogous to the above example from single-cell studies, the collinear flanker-pair may then be considered a ‘good’ stimulus arrangement, which tends to integrate with the target more readily than the ‘poor’ orthogonal stimulus. Selecting one flanker-pair might then determine the success with which it competes with the other flanker-pair for influence, via horizontal connections, over activity in neurons whose classical receptive field includes the central target. Resolution of such competition might have consequent effects on target sensitivity and perceptual grouping. Thus, if the attentional weighting is in favour of the stimulus context producing good integration (collinear flankers), facilitation of target threshold is observed, but if the poor stimulus context (orthogonal flankers) wins the competition then there is less facilitation or none at all.

With these assumptions, a generalised ‘biased competition’ mechanism, operating not only for classical receptive fields but also for extra-classical receptive field influences, might account for how attention modulates the lateral interactions between target and flankers. Neurophysiological studies have typically reported that attentional competitive interactions are more pronounced for two stimuli that both fall within a classical receptive field^{18,53,65}, than for situations with one stimulus inside and one outside the classical receptive field. However, attentional effects on influences from the extra-classical receptive field might conceivably be more pronounced for stimulus configurations which are optimal for extra-classical influences to be observed (see refs. 52,66,67). Recent data, for example, already suggest a role for delayed feedback from extra-striate visual areas in modulating the influence of surrounding stimulus context on V1 receptive field responses^{63,68}. While these possibilities might fruitfully be explored further using neurophysiology, behavioural studies could usefully examine the effects of manipulations which defuse the putative conflict between alternative perceptual groupings. Stimulus manipulations might involve varying the spatial frequency of one set of flankers, so that they no longer lie within the same target extra-classical receptive fields. Alternatively, we might experiment with tasks such as comparing the relative colour or phase of specific flankers, which, unlike Vernier judgements, should never require selective perception of a global ‘axis’ relating the relevant flankers to each other along a virtual extended contour. An attentional effect that depends on direct competition between alternative perceptual groupings might be diminished in such cases, where such competition is either no longer created by the stimulus, or no longer implicated by the task.

In accord with recent neuroscience evidence of attentional modulation in early visual cortex¹²⁻¹⁹, our data add further weight against the traditional notion of ‘preattentive’ perception, in which fundamental processes such as grouping function entirely

independently of top-down, task-dependent constraints. Our findings suggest instead that attention can interact directly and specifically with low-level contextual integration processes, and may thus influence how local parts of a display are grouped with each other to form a representation of their overall structure. Methods of the kind we have described may further our understanding of the functional consequences of low-level attentional modulation for perception, and help to test hypotheses regarding its possible underlying mechanisms. One possibility we have considered is that attention might modulate competition between populations of extra-classical receptive fields, encoding different spatial relationships between stimulus elements. Attention might thus play the role of mediator in potential conflicts over alternative ways of integrating parts of a stimulus, biasing the competition between these alternative groupings so that only the perception most relevant to the given task emerges to influence later cognitive processes and behaviour.

ACKNOWLEDGEMENTS

This research was funded by a project grant from the Biotechnology and Biological Sciences Research Council (ref. 31/S13736) and a travel grant from the Royal Society (UK). Thanks to Ariella Popple for helpful comments.

REFERENCES

1. D. E. Broadbent, *Perception and Communication*, Pergamon Press, London (1958).
2. H. Pashler, *The Psychology of Attention*, MIT Press, Cambridge, MA (1998).
3. S. Yantis, Goal-directed and stimulus-driven determinants of attentional control, in: *Control of Cognitive Processes*, S. Monsell and J. Driver, eds., MIT Press, Cambridge, MA (2000).
4. J. Driver, G. Davis, C. Russell, M. Turatto, E. Freeman, Segmentation, attention and phenomenal visual objects, *Cognition*, 80, 61-95 (2001).
5. D. Sagi and B. Julesz, "Where" and "what" in vision, *Science*, 228:4704, 1217-1219 (1985).
6. U. Neisser, *Cognitive Psychology*, Appleton, New York (1967).
7. A. Treisman, Perceptual grouping and attention in visual search for features and for objects, *J.Exp.Psychol.Human Perc.Perf.*, 8, 194-214 (1982).
8. A. Treisman, Features and objects in visual processing, *Scientific American*, 255:5, 114-125 (1986).
9. J. Duncan, Selective attention and the organization of visual information, *Journal of Experimental Psychology: General*, 113:4, 501-517 (1984).
10. S. Palmer and I. Rock, Rethinking perceptual organization: the role of uniform connectedness, *Psychonomic Bulletin & Review*, 1:1, 29-55 (1994).
11. J. Driver and G. C. Baylis, Attention and visual object segmentation, in: *The Attentive Brain*, R. Parasuraman, ed., MIT Press, Cambridge (1998).
12. M. L. Posner and C. D. Gilbert, Attention and primary visual cortex, *Proc.Natl.Acad.Sci.USA*, 96, 2585-2587 (1999).
13. S. P. Gandhi, D. J. Heeger, G. M. Boynton, Spatial attention affects brain activity in human primary visual cortex, *Proc.Natl.Acad.Sci.USA*, 96, 3314-3319 (1999).
14. D. C. Somers, D. M. Anders, A. E. Sieffert, R. B. H. Tootell, Functional MRI reveals spatially specific attentional modulation in human primary visual cortex, *Proc.Natl.Acad.Sci.USA*, 96, 1663-1668 (1999).
15. A. T. Smith, K. D. Singh, M. W. Greenlee, Attentional suppression of activity in the human visual cortex, *NeuroReport*, 11, 271-277 (1999).
16. D. Ress, B. T. Backus, D. Heeger, Activity in primary visual cortex predicts performance in a visual detection task, *Nature Neuroscience*, 3:9, 940-945 (2000).
17. B. C. Motter, Focal attention produces spatially selective processing in visual cortical areas V1, V2, and V4 in the presence of competing stimuli, *J.Neurophysiol.*, 70, 909-919 (1993).

18. S. J. Luck, L. Chelazzi, S. A. Hillyard, R. Desimone, Neural mechanisms of spatial attention in areas V1, V2, and V4 of macaque visual cortex, *J.Neurophysiol.*, 24:42 (1997).
19. M. Ito and C. D. Gilbert, Attention modulates contextual influences in the primary visual cortex of alert monkeys, *Neuron*, 22, 593-604 (1999).
20. D. K. Lee, C. Itti, J. Braun, Attention activates winner-takes-all competition among visual filters, *Nature Neuroscience*, 2:4, 375-381 (1999).
21. M. J. Morgan, R. M. Ward, E. Castet, Visual search for a tilted target: tests of spatial uncertainty models, *Q.J.Exp.Psy.*, 51A:2, 347-370 (1998).
22. M. Ito, G. Westheimer, C. D. Gilbert, Attention and perceptual learning modulate contextual influences on visual perception, *Neuron*, 20, 1191-1197 (1998).
23. M. Carrasco, C. Penpeci-Talgar, M. Eckstein, Spatial covert attention increases contrast sensitivity across the CSF: support for signal enhancement, *Vision Research*, 40:10-12, 1203-1216 (2000).
24. J. S. Joseph, M. M. Chun, K. Nakayama, Attention requirements in a 'preattentive' feature search task, *Nature*, 387:9, 805-807 (1997).
25. J. Solomon, N. Lavie, M. J. Morgan, Contrast discrimination function: spatial cueing effects, *J.Opt.Soc.Am.A*, 14:9, 2443-2448 (1997).
26. M. Ben-Av, D. Sagi, J. Braun, Visual attention and perceptual grouping, *Perception & Psychophysics*, 52:3, 277-294 (1992).
27. U. Polat and D. Sagi, Lateral interactions between spatial channels: Suppression and facilitation revealed by lateral masking experiments, *Vision Research*, 33:7, 993-999 (1993).
28. U. Polat and D. Sagi, The architecture of perceptual spatial interactions, *Vision Research*, 34:1, 73-78 (1994).
29. B. Dresch, Bright lines and edges facilitate the detection of small light targets, *Spatial Vision*, 7, 213-225 (1993).
30. D. J. Field, A. Hayes, R. Hess, Contour integration by the human visual system: evidence for a local 'association field', *Vision Research*, 33, 173-193 (1993).
31. I. Kovacs and B. Julesz, Perceptual sensitivity maps within globally defined visual shapes, *Nature*, 370, 644-646 (1994).
32. I. Kovacs, Gestalten of today: early processing of visual contours, *Behavioural Brain Research*, 82, 1-11 (1996).
33. U. Polat, Functional architecture of long-range perceptual interactions, *Spatial Vision*, 12:2, 143-162 (1999).
34. R. Hess and D. Field, Integration of contours: new insights, *Trends in Cognitive Sciences*, 3:12, 480-486 (1999).
35. R. L. DeValois and K. K. DeValois, *Spatial Vision*, New York: Oxford University Press, (1990).
36. D. H. Hubel and T. N. Wiesel, Receptive fields and functional architecture of monkey striate cortex, *Journal Physiology (London)*, 222, 345-356 (1968).
37. U. Polat and D. Sagi, Spatial interactions in human vision: From near to far via experience-dependent cascades of connections, *Proc.Natl.Acad.Sci.USA*, 91, 1206-1209 (1994).
38. Y. Tanaka and D. Sagi, Long-lasting, long-range detection facilitation, *Vision Research*, 38, 2591-2599 (1998).
39. A. Ishai and D. Sagi, Common mechanisms of visual imagery and perception, *Science*, 268, 1772-1774 (1995).
40. B. Zenger and D. Sagi, Isolating excitatory and inhibitory nonlinear spatial interactions involved in contrast detection, *Vision Research*, 36:16, 2497-2513 (1996).
41. C. D. Gilbert and T. N. Wiesel, Columnar specificity of intrinsic horizontal and corticocortical connections in cat visual cortex, *J Neurosci*, 9:7, 2432-2442 (1989).
42. D. Fitzpatrick, The functional organization of local circuits in visual cortex: insight from the study of tree shrew striate cortex, *Cerebral Cortex*, 6, 329-341 (1996).
43. U. Polat, K. Mizobe, M. Pettet, T. Kasamatsu, T. Norcia, Collinear stimuli regulate visual responses depending on cell's contrast threshold, *Nature*, 391, 580-584 (1998).
44. M. K. Kapadia, M. Ito, C. D. Gilbert, G. Westheimer, Improvement in visual sensitivity by changes in local context: Parallel studies in human observers and in V1 of alert monkeys, *Neuron*, 15, 843-856 (1995).
45. M. Pettet, S. McKee, N. M. Grzywacz, Constraints on long range interactions mediating contour detection, *Vision Research*, 38:6, 865-879 (1998).
46. Z. Li, A neural model of contour integration in the primary visual cortex, *Neural Computation*, 10, 903-940 (1998).
47. Z. Li, Visual segmentation by contextual influences via intra-cortical interactions in the primary visual cortex, *Network: Comput.Neural Syst.*, 10, 187-212 (1999).

48. M. Usher, Y. Bonnef, D. Sagi, M. Herrmann, Mechanisms for spatial integration in visual detection: a model based on lateral interactions, *Spatial Vision*, 12:2, 187-210 (1999).
49. B. Zenger, J. Braun, C. Koch, Attentional effects on contrast detection in the presence of salient distractors, *Vision Research*, (2000).
50. B. A. Doshier and Z. Lu, Mechanisms of perceptual attention in precuing of location, *Vision Research*, 40, 1269-1292 (2000).
51. G. W. Balz and H. S. Hock, The effect of attentional spread on spatial resolution, *Vision Research*, 37:11, 1499-1510 (1997).
52. C. Gilbert, M. Ito, M. Kapadia, G. Westheimer, Interactions between attention, context and learning in primary visual cortex, *Vision Research*, 40:10-12, 1217-1226 (2000).
53. R. Desimone and J. Duncan, Neural mechanisms of selective visual attention, *Annual Review of Neuroscience*, 18, 193-222 (1995).
54. Y. Yeshurun and M. Carrasco, The locus of attentional effects in texture segmentation, *Nature Neuroscience*, 3:6, 622-627 (2000).
55. Y. Yeshurun and M. Carrasco, Attention improves or impairs visual performance by enhancing spatial resolution, *Nature*, 396, 72-75 (1998).
56. J. A. Solomon, A. B. Watson, M. J. Morgan, Transducer model produces facilitation from opposite-sign flanks, *Vision Research*, 39, 987-992 (1999).
57. U. Polat and C. W. Tyler, What pattern the eye sees best, *Vision Research*, 39, 887-895 (1999).
58. A. Ishai and D. Sagi, Visual imagery facilitates visual perception: psychophysical evidence, *J.Cog.Neuro.*, 9, 476-489 (1997).
59. D. G. Pelli, Uncertainty explains many aspects of visual contrast detection and discrimination, *J.Opt.Soc.Am.A*, 2:8, 1508-1532 (1985).
60. M. J. Morgan and B. Dresch, Contrast detection facilitation by spatially separated targets and inducers, *Vision Research*, 35:8, 1019-1024 (1995).
61. J. H. Reynolds, T. Pasternak, R. Desimone, Attention increases sensitivity of V4 neurons, *Neuron*, 26, 703-714 (2000).
62. D. Sagi, Early vision: Images, context and memory, in: *Brain Theory: Biological Basis and Computational Theory of Vision*, A. Aertsen and V. Braitenberg, eds., Elsevier Science, Amsterdam (1996).
63. V. A. F. Lamme and P. R. Roelfsema, The distinct modes of vision offered by feedforward and recurrent processing, *Trends.Neurosci.*, 23:11, 571-579 (2000).
64. C. D. Gilbert and T. N. Wiesel, The influence of contextual stimuli on the orientation selectivity of cells in primary visual cortex of the cat, *Vision Research*, 30, 1689-1701 (1990).
65. J. Moran and R. Desimone, Selective attention gates visual processing in the extrastriate cortex, *Science*, 229:782-784 (1985).
66. U. Polat and A. M. Norcia, Neurophysiological evidence for contrast dependent long-range facilitation and suppression in the visual cortex, *Vision Research*, 36:14, 2099-2109 (1996).
67. J. Allman, F. Miezin, E. McGuinness, Direction- and velocity-specific responses from beyond the classical receptive field in the middle temporal visual area (MT), *Perception*, 14:2, 105-126 (1985).
68. H. Supèr, H. Spekreijse, V. A. F. Lamme, Two distinct modes of sensory processing observed in monkey primary visual cortex (V1), *Nature Neuroscience*, 4:3, 304-310 (2001).