

Task-dependent modulation of target-flanker lateral interactions in vision

ELLIOT FREEMAN and JON DRIVER
University College London, London, England

Visibility of a central target Gabor element often improves in the presence of collinear flankers. Such lateral interactions may reflect fundamental mechanisms underlying the perceptual integration of contours in early vision. We recently reported (Freeman, Sagi, & Driver, 2001) attentional modulation of these interactions. Here, we test whether this modulation is task dependent. Subjects had to detect a near-threshold central target while performing a secondary discrimination task on one pair of flankers that could appear with another distractor pair (one pair collinear with the target, the other orthogonal). Central target thresholds were lowered when collinear flankers were judged for the secondary task, but only when this task concerned the global spatial relationship between these flankers (discrimination of their Vernier offset or global orientation). Other secondary tasks involving discriminating the local orientations, contrasts, or colors of the relevant flanker pair produced no such attentional modulation. However, this task-dependent modulation was observed only when two flanker pairs were present, not for displays with only a single flanker pair. Top-down modulation of lateral interactions may function to select between overlapping potential contours whenever the global spatial properties of one are task relevant.

Visual attention can shift between different aspects of our environment, usually depending on their specific relevance to the current task or goal. There is a close relationship between the attentional processes involved in such goal-oriented selection and the grouping and segmentation processes involved in organizing parts of a scene into coherent objects. The nature of this relationship has been the focus of debate for many years (e.g., for historical reviews, see Driver, Davis, Russell, Turatto, & Freeman, 2001; Pashler, 1998). On the one hand, much past data was taken to suggest that fundamental grouping processes may operate “preattentively” to constrain the allocation of attention (e.g., Driver & Baylis, 1998; Treisman, 1982). However, other studies have suggested that perceived grouping can change, depending on task set (e.g., Ben-Av, Sagi, & Braun, 1992; Carrasco & Chang, 1995) or indeed may not be perceived at all without some involvement of attention (Rock, Linnett, Grant, & Mack, 1992). Most recently, studies in psychophysics, neuroscience, and imaging have demonstrated that early visual areas and processes can in fact be subject to some top-down attentional modulation (see, e.g., Carrasco, Penpeci-Talgar, & Eckstein, 2000; Doshier & Lu, 2000; Gilbert, Ito, Kapadia, & Westheimer, 2000; Luck, Chelazzi, Hill-

yard, & Desimone, 1997; Moran & Desimone, 1985; Motter, 1993; Roelfsema, Lamme, & Spekreijse, 1998; Somers, Anders, Sieffert, & Tootell, 1999; Treue, 2001; Watanabe et al., 1998), thus discrediting the notion that early vision is always “cognitively impenetrable.” At the same time, methods for probing the fundamental mechanisms underlying perceptual grouping have become increasingly sophisticated. These advances now provide the necessary tools for a more detailed study of how specific early visual mechanisms of perceptual grouping may be modified under specific task and attentional conditions.

In a recent psychophysical study, we reported that a robust perceptual phenomenon often thought to reflect one of the earliest forms of cortical visual grouping—namely, *lateral interactions* between collinear Gabor patches—can depend on attention (Freeman, Sagi, & Driver, 2001). Here, we seek to determine the stimulus and task-dependent boundary conditions for this attentional modulation in relation to several alternative accounts. In the psychophysical paradigm upon which our approach is based, detection of a low-contrast central Gabor patch depends on the configuration of its surrounding context (Polat, 1999; Polat & Bonneh, 2000; Polat & Sagi, 1993, 1994; Zenger & Sagi, 1996). Thus, target visibility typically improves above baseline when flanked by two high-contrast patches in a collinear arrangement (right of Figure 1A), as if forming parts of a virtual contour, but not when the flankers have orthogonal orientations to the target (left of Figure 1A). It has been suggested that lateral-interaction phenomena of this type may reflect fundamental contour-integration processes operating in early vision, to extract continuous contours from fragmented information (Polat & Bonneh, 2000;

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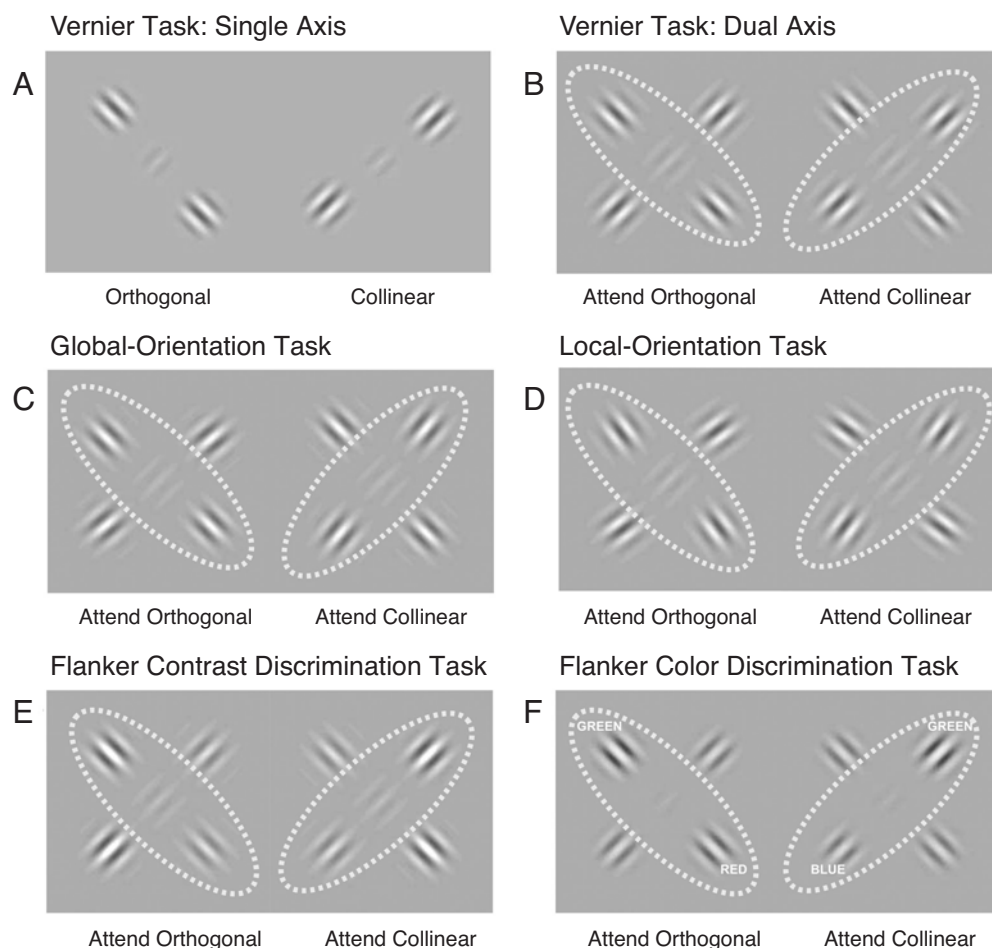


Figure 1. (A) Examples of single-axis stimuli for the Vernier task, with orthogonal (left) and collinear configurations (right), with one pair of high-contrast flankers and a low-contrast central target Gabor patch. (B–F) Sample stimuli used in the different experiments. In each panel, compare left and right images to see how the position, orientation, contrast, or color of flankers differed between trial intervals. In the same figures, ellipses schematically illustrate the flanker pairs that had to be judged for the secondary flanker task, in the attend orthogonal and attend collinear conditions, respectively. (B) Dual-axis stimuli in the Vernier task. (C) Dual-axis stimuli for the global-orientation task (single-axis stimuli not shown). (D) Local orientation. (E) Flanker contrast discrimination. (F) Flanker color discrimination.

Saarinen & Levi, 2001). Moreover, lateral interactions between collinear Gabor patches, together with some other potentially related phenomena (Field, Hayes, & Hess, 1993; Hess & Field, 1999; Kapadia, Ito, Gilbert, & Westheimer, 1995; Kovacs & Julesz, 1994; Lee & Blake, 2001; Morgan & Dresch, 1995; Pettet, McKee, & Grzywacz, 1998; Zenger-Landolt & Koch, 2001), have been considered in relation to the physiology of extraclassical receptive fields in early visual cortex, including area V1. At this level, single cells can show some analogously configuration-dependent activity (Crook, Engelmann, & Lowel, 2002; Kapadia et al., 1995; Kasamatsu, Polat, Pettet, & Norcia, 2001; Mizobe, Polat, Pettet, & Kasamatsu, 2001; Polat, Mizobe, Pettet, Kasamatsu, & Norcia, 1998; Schmidt, Goebel, Löwel, & Singer, 1997), possibly based on long-range horizontal connections between cells with coaxial receptive-field preferences (Fitzpatrick, 1996;

Gilbert & Wiesel, 1990). New electrophysiological evidence from event-related potentials in humans further supports early visual cortex as a primary locus for lateral interactions (Khoe, Freeman, Woldorff, & Mangun, 2004). Thus, lateral-interaction phenomena have some grounding in the neurobiology of early visual cortex and provide a relatively well-understood example of elementary grouping processes.

Some theorists might expect such fundamental visual processes (e.g., lateral interactions affecting detection thresholds for Gabor patches) to operate in a cognitively impenetrable manner (e.g., see Pylyshyn, 1999). However, we recently obtained evidence that psychophysical lateral interactions between collinear Gabor patches can in fact depend strongly on attention to the flankers (Freeman et al., 2001). We observed this using a dual-task procedure with novel “dual-axis” stimuli, in which the

central near-threshold target was now flanked not just by a single flanker pair, but by two pairs, one collinear and the other orthogonal to the target (see Figure 1B). A secondary task required observers to judge the direction of Vernier misalignment between one prespecified pair of flankers, while ignoring the other pair. We found improved thresholds for the central target in the presence of collinear flankers *only* when these collinear flankers were attended for the secondary Vernier task (as indicated schematically by the dotted ellipses on the right of Figure 1B), not when they were ignored with the orthogonal flanker pair being judged instead (left of Figure 1B). Note that our design deliberately avoided inducing shifts in spatial attention toward or away from the central target, which was always attended for the central detection task. We simply manipulated, instead, which of two pairs of equidistant flankers was relevant for the secondary Vernier task. The effects may therefore be attributed to attentional modulation of target-flanker lateral interactions themselves, not to purely local changes in spatial attention toward or away from the target. Thus, we concluded that top-down attention may directly modulate the mechanisms underlying lateral interactions (see also Freeman, Driver, Sagi, & Zhaoping, 2003, for further supporting evidence). This may accord also with recent single-cell neurophysiological data from awake behaving monkeys, indicating that attention can modulate lateral interactions arising for cells in primary visual cortex in response to collinear line elements (Gilbert et al., 2000; Ito & Gilbert, 1999; Ito, Westheimer, & Gilbert, 1998; Roelfsema et al., 1998).

In the present article, we seek to determine whether the attentional modulation effects observed in our new paradigm may depend closely on the *specific task* that is imposed for the relevant pair of flankers. In our previous experiments (Freeman et al., 2003; Freeman et al., 2001; Freeman, Sagi, & Driver, 2004), we had always used Vernier discrimination as a secondary task, with observers having to judge the relative Vernier misalignment of the two task-relevant flankers while ignoring the other pair. This task might potentially have encouraged observers to construct a “virtual contour” connecting the task-relevant elements and then to judge its global orientation (see Mussap & Levi, 1996, for a proposal that some Vernier tasks might provide such global-orientation cues, and Dresch, 2000, for the suggestion that lateral-interaction mechanisms may support Vernier task performance in particular). Such contour formation between discrete elements might specifically tap into lateral interactions between collinear elements of the type measured by the paradigm. If attention can modulate the integration of global orientation via lateral interactions, we might find the strongest attentional modulation of lateral interactions whenever such a *global* spatial property is specifically relevant to the task imposed on the relevant flanker pair, compared with when only *local* properties of the individual flanker elements are relevant. On this

hypothesis, attentional modulation of lateral interactions of the kind we have previously reported (Freeman et al., 2003; Freeman et al., 2001, 2004) might be specific to flanker tasks that require global spatial relationships to be judged along the axis formed between the relevant flanker pair on which the central target also falls. Conversely, attentional modulation effects should be absent for tasks in which only local properties of the individual task-relevant flankers must be judged.

We can also consider an alternative prediction—namely, that *any* sufficiently demanding task for the relevant flanker pair should be capable of producing attentional modulation of lateral interactions, whether or not this task specifically concerns global spatial relationships along the axis formed between the relevant two flankers. Such a task-independent outcome would be expected if it were merely sufficient to direct spatial attention to the flankers collinear with the target in order to obtain the central target benefit. Such a task-independent prediction might also be derived from those “object-based” accounts of attention that posit that attending to one attribute of a selected item (e.g., an attended flanker in the present case) will invariably lead to its other attributes being selected, regardless of the current task (e.g., Duncan, 1984; see Driver et al., 2001, for a discussion). From such a perspective, attending to the flanker pair that is collinear or orthogonal to the central target should presumably have the same impact, regardless of the specific property that is judged for the relevant flankers, provided that the various flanker tasks are similarly demanding. In contrast to the task-dependent hypothesis outlined above, there should therefore be no systematic qualitative difference between the impact of tasks requiring judgment of purely local properties of the relevant pair of flankers, in comparison with tasks requiring judgment of the flankers’ global spatial relationships.

The main purpose of the present study was thus to examine the impact of the specific type of task imposed for the relevant flanker pair on any attentional modulation of lateral interactions with the central target. In addition to addressing this issue using dual-axis stimuli with two concurrent flanker pairs (one pair task relevant, the other to be ignored; see Figure 1B), we examined any impact of varying the flanker task on lateral interactions for more conventional displays, with just a single flanker pair present (see Figure 1A). Some effect of this stimulus manipulation in relation to attentional influences might be expected in view of physiological evidence that attentional modulation is typically intensified when subjects must attend to a relevant stimulus in the context of other competing stimuli (Luck et al., 1997). Task-dependent attentional modulation might be stronger only for dual-axis stimuli, where optimum flanker-task performance may require the observer to select one of two alternative “rival” axes, while ignoring the other. On the other hand, equal attentional modulation (i.e., no task-stimulus interaction) should be found if attention can al-

ways simply “switch on and off” lateral interactions with flankers, whenever their global spatial relationship is task relevant or irrelevant.

As in our previous dual-task experiments (Freeman et al., 2003; Freeman et al., 2001, 2004), the primary task was always two-interval forced-choice (2IFC) detection of a near-threshold low-contrast central Gabor patch. Here, we varied the nature of the secondary task performed on the suprathreshold flanking stimuli. In Experiment 1, we compared two secondary tasks that both required subjects to judge a global spatial relationship along the axis of the relevant flanker pair: either their relative Vernier misalignment (as in all our previously published experiments, so that a replication of results was expected) or instead their global orientation (a new task that might allow us to generalize our results to another global flanker task).

In subsequent experiments, we tested a variety of tasks that required local judgments instead for the relevant flankers: Observers either judged local orientation for these flankers (Experiment 2) compared their different local contrasts (Experiment 3) or colors (Experiment 4). As described later on, care was taken to ensure that any task-specific effects could not be caused by a general shift in the allocation of spatial attention to different parts of the display at different distances away from the central target.

To anticipate the findings, we replicated our previous attentional-modulation results for dual-axis displays (i.e., with two flanker pairs, as in Figure 1B) when using our original global Vernier flanker-task and also extended this replication to the new global task of judging the global orientation of the relevant flanker pair. However, this attentional modulation of lateral interactions was eliminated in similar dual-axis displays when imposing local tasks for the relevant flanker pair. Attentional modulation was therefore strongly task dependent. Finally, for conventional single-axis displays (with only one flanker pair, as in Figure 1A), we found that lateral interactions did not depend at all on the task imposed for the flankers, in sharp contrast to the new results for dual-axis displays.

METHOD

Subjects

Four paid observers and Author E.F. participated. They were between the ages of 21 and 35 and reported normal or corrected-to-normal eyesight. All had prior experience with similar tasks. Except for E.F., all were naive to the purpose of this experiment. The subjects had all shown reliable attentional modulation of lateral interactions in previous sessions using the standard secondary Vernier flanker-task.

Apparatus and Stimuli

Display conditions approximated those used in past studies of lateral interactions (Polat & Sagi, 1993, 1994). Gray-level modulated stimuli were displayed on a 19-in. CRT (Mitsubishi Diamond Pro 920), using an 8-bit RGB mode with hardware gamma correction. The video mode was 1280×1024 pixels, 100 Hz noninterlaced. The background luminance was 40.0 cd m^{-2} . The viewing distance was 125 cm, in a darkened room. The responses were made via a three-button mouse. The fixation displays consisted of a small high-contrast central cross, with two flanking peripheral bar markers 0.28° long and 1.4° in eccentricity. These were used to indicate which aspects of the stimuli were task relevant (see below and Figure 2A). The stimulus displays consisted of Gabor patches with carrier wavelength (λ) and Gaussian distribution (σ^2) of the contrast envelope both equal to 0.15° of visual angle. The spatial frequency of the carrier was therefore 6.7 cycles per degree. In dual-axis stimuli (see Figure 1B), a central target of either 45° or 135° orientation was surrounded by four flanking patches arranged into two oblique axes, which bisected each other at right angles. Along one of these axes, the flankers were collinear with the target (having both similar global and local orientations to the target, although with small differences depending on the secondary task; see below), while the other flanker pair was orthogonal. Similar single-axis stimuli, with only one flanker pair (Figure 1A), were also used in some of the experiments. Center-to-center separation between target and each flanker was 4λ . The target contrast varied over five logarithmically spaced values, with the range approximately centered for each subject on the contrast threshold for detecting an isolated Gabor target, as obtained in prior baseline trials (values between 2% and 7% Michelson contrast at maximum signal amplitude). Except where noted below, flankers were fixed at 31% contrast.

The precise attributes of the flankers (and the preceding fixation display) varied somewhat, depending on the kind of judgment required by the secondary flanker task. For the Vernier flanker task, slight misalignments were introduced by shifting the flankers within a pair by the same distance but in opposite directions to each other,

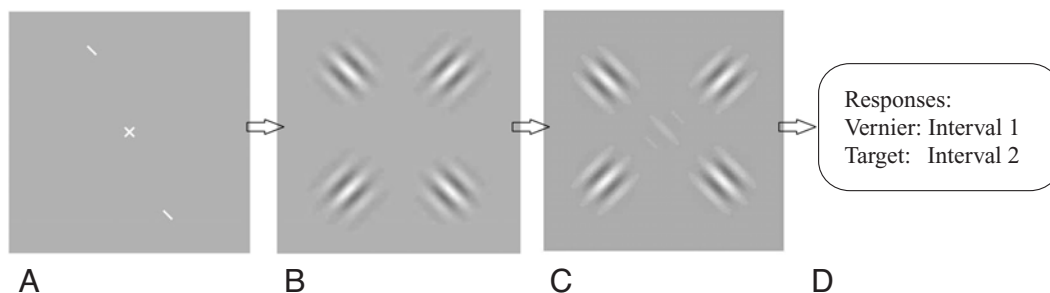


Figure 2. Example of a dual-task trial sequence: (A) initial fixation display indicating the relevant flankers and their relevant properties (in this case, the particular direction of Vernier offset), followed by (B–C) two inter-stimulus intervals and (D) two responses. The cued flanker configuration occurs in Interval 1, and the central target appears in Interval 2. Flanker properties and central target presence varied between trials independently.

Table 1
Magnitudes of Flanker Modulation in Each Task, per Subject

Subject	Vernier Offset (Wavelength, in λ)	Global Orientation		Local Orientation (Rotation)	Contrast Discrimination (Contrast Difference, in %)
		Wavelength, in λ	Rotation		
J.B.	.15	.1	2°	6°	4.7
F.R.	.1	.1	2°	2°	6.3
D.C.	.2	.1	2°	8°	7
E.F.	.15	.15	4°		5.5
L.J.	.2	.1	2°		

along a path orthogonal to the global orientation of the axis (cf. left and right images in Figure 1B for examples of the typical Vernier offsets presented in alternate intervals). Offset magnitude was set for each subject between .1 and .2 λ , to achieve suprathreshold Vernier accuracy (see Table 1). The flanker task was to indicate in which of two stimulus intervals one predesignated pair of flankers had a predesignated configuration of offset. As with all the subsequent experiments, the designated task-relevant configuration (in this case, the particular direction of Vernier offset) remained fixed throughout the experiment and was also indicated by two offset bar markers in the fixation display (see Figure 2A).

In the *global-orientation* task, each pair of flankers rotated slightly around the center of the display, as if connected by a virtual axis with variable orientation (cf. left and right images in Figure 1C for examples of different global rotations). Each flanker-axis could have either of two slightly different global orientations, which alternated unpredictably between display intervals. The subjects had to judge in which interval the relevant flanker-axis had the global orientation indicated in the fixation display by the bar markers (again fixed throughout the experiment for each subject). This global-orientation manipulation was achieved in a similar way to Vernier offset, with flankers moving in opposite directions between two different locations between intervals (but now without changing the distance between flanker centers). In addition, however, there was now a change in flanker local orientation, which eliminated any Vernier offset by realigning the flankers. A global-orientation change of 2° (involving a translation of approximately .1 λ) was used for all subjects except E.F. (4° rotation and approximately .15 λ translation).

The *local-orientation* task used for the flankers in Experiment 3 was similar, except that the flankers now had strictly fixed positions along the 45° and 135° axes. Each flanker of a pair therefore now rotated only about its own local center, by the same amount and in the same direction (cf. left and right images in Figure 1D). Magnitude of rotation was between 2° and 8°, depending on individual subject performance (see Table 1). The subjects had to judge which of the two successive display intervals contained the particular configuration indicated by the bar markers in the fixation display (again fixed throughout).

In the *contrast discrimination* task, flankers were perfectly aligned along the two axes, and subjects now discriminated between displays in which one or the other flanker of a pair had a higher contrast (Figure 1E). The contrast difference was set to between 5% and 7% for individual subjects (see Table 1). One of the bar markers in the initial fixation display was consistently brighter, to indicate the relevant contrast relationship. In the color discrimination task, the upper flanker of a pair could be tinted green and the lower flanker red, or either one of the flankers could be tinted blue (Figure 1F). Subjects judged the interval in which the specific red/green combination consistently indicated by similarly colored bar markers was present.

Design and Procedure

Figure 2 illustrates the trial sequence. Each trial commenced with a fixation display with peripheral bar markers indicating the rele-

vant flanker-axis for that block, and the relevant stimulus attributes to discriminate along the axis, as appropriate for the particular flanker task (illustrated in Figure 2A for the Vernier task, but see above for the alternative possibilities). The relevant axis was switched every 10 blocks (see below), whereas the task-relevant properties (e.g., specific direction of Vernier offset or rotation, etc.) were fixed throughout each experiment. Following a keypress and a 300-msec blank period, there were two interstimulus intervals of 80-msec duration each, separated by a blank period of 500 msec (Figures 2B–2C). The central target was displayed in only one of the intervals, whereas the flankers were present in both. Depending on the experiment, either the position, orientation, contrast, or color of the flankers on both axes changed slightly, with unpredictable and independent ordering of the possible values for the two flanker axes across intervals, according to the attributes relevant to the secondary task. The screen remained blank until responses had been made (Figure 2D). Two 2IFC responses were required, using left and right mouse buttons, with responses emitted first for the flanker task (indicating in which of the two successive intervals the relevant flanker pair had the specific attributes indicated consistently 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.

The subjects were instructed to give greatest priority to the flanker task and not to attend exclusively to the central target. In addition, especially in the local orientation, color, and contrast tasks, the subjects were repeatedly reminded to pay attention to both of the flankers displaying the relevant change, because ignoring one of the flankers would make the flanker task harder.

Each hour-long experimental session contained 20 blocks of 40 trials each. Orientation of the central target (135° or 45°) and its contrast were varied in random order between blocks. The flanker axis that was relevant for the secondary flanker task switched after 10 blocks, in an order that was counterbalanced across subjects and sessions. All the subjects were initially tested with the dual-axis Vernier secondary task, for a minimum of two sessions; one or more of the other secondary tasks with single- and/or dual-axis stimuli were then introduced in separate subsequent sessions, with order of conditions differing between subjects. Thresholds for central target detection were estimated by Weibull fit (using Matlab toolbox PSIGNIFIT, available on line at <http://bootstrap-software.org/psignifit/>), from a minimum of 160 trials per target contrast level per subject. The reliability of threshold estimates was assessed by the bootstrapping method (i.e., from a sample of 1,000 fits through randomly simulated data sets with similar statistical parameters) and is indicated in the figures by error bars representing one standard error of the mean. Confidence limits were computed from the bootstrapping error estimate, on the one-tailed hypothesis that thresholds should be lower with (attended) collinear flankers (as expected, given the previous results of Freeman et al., 2003, and Freeman et al., 2001, 2004). On the basis of this confidence limit, asterisks in the figures indicate statistically significant differences (* $p < .05$, ** $p < .01$) between thresholds in the collinear and orthogonal conditions.

RESULTS

Experiment 1

This experiment examined central target detection, plus any attentional influences upon this, under Vernier and global-orientation secondary tasks, with dual-axis stimuli (i.e., two flanker pairs concurrently present). In these tasks, subjects discriminated, respectively, either the direction of Vernier misalignment for the relevant flanker pair (Figures 1A, 1B) or their direction of rotation around the center of the display (Figure 1C). As in our previous work (Freeman et al., 2003; Freeman et al., 2001, 2004), observers performed the secondary flanker task on a flanker pair that was either collinear or orthogonal to the central target, while ignoring the other flanker pair. Similar central target detection thresholds were obtained for both flanker tasks (see Figure 3). For 4 of the 5 subjects tested, the contrast thresholds for central target detection were significantly lower for each individual when the flankers relevant to the secondary task were collinear with the central target than when they were orthogonal and the collinear flanker pair was ignored instead. (The exceptional subject, J.B., had particularly poor accuracy for global-orientation discriminations, which might explain why this subject alone did not show a consistent attentional effect in that particular task. Accuracy data for secondary tasks are presented later in Figure 7, with diamond symbols for this condition.) Even when including the 1 exceptional subject in a group analysis, a two-factor analysis of variance (attended flankers

by task) revealed a significant main effect of attending to collinear versus orthogonal flankers [$F(1,4) = 15.59$, $p < .017$], whereas the magnitude of the attentional effect did not depend significantly on the task [interaction term: $F(1,4) = 0.225$], and the task itself produced no significant main effect [$F(1,4) = 0.04$].

Overall, the results from the global-orientation flanker task replicate our original finding for the Vernier flanker task. The similarity of the results prompts consideration of the commonalities between the two tasks. Both involved a change in the relative spatial position of flankers between intervals, whereas the global-orientation tasks also included a local rotation of the flankers. For 3 subjects (J.B., D.C., and L.J.), the magnitude of the offset was slightly smaller than for the Vernier task, yet only J.B.'s much poorer performance in the global-orientation condition seems to reflect this, suggesting that the local rotation information could be used to compensate. These observations indicate that rotational and translational information could be used together to discriminate changes in the global orientation of the virtual contour connecting the relevant flankers. Given that the performance of some Vernier discrimination tasks might also be based on global-orientation information (Mussap & Levi, 1996), it may be the common requirement to extract this information, which explains the similar attentional modulation effects observed with the Vernier and global-orientation flanker tasks.

In Experiments 2–4, we examined whether similar attentional modulation of lateral interactions would still be

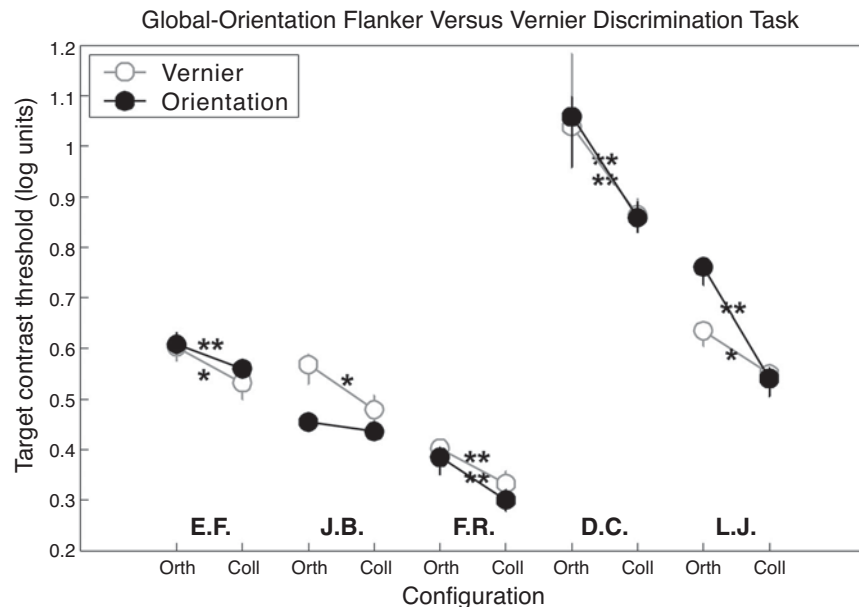


Figure 3. Experiment 1 results. Central target contrast thresholds (log units) under the Vernier or global-orientation flanker tasks. Error bars represent one standard error of the mean. Asterisks in all figures indicate statistical significance on the one-tailed hypothesis of lower thresholds with collinear flankers attended rather than orthogonal. * $p < .05$. ** $p < .01$.

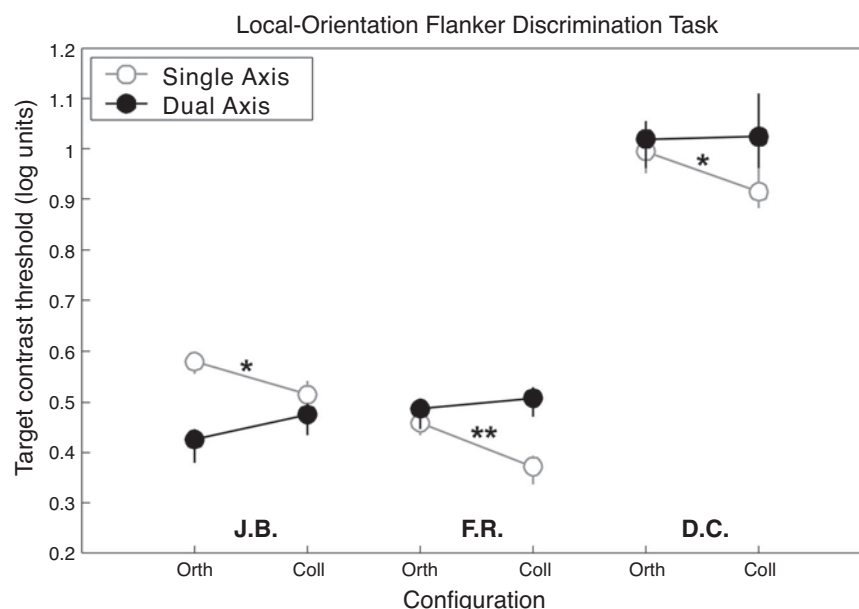


Figure 4. Experiment 2 results. Central target contrast thresholds (log units) for dual-axis and single-axis conditions. The effect of collinear versus orthogonal flankers is significant only for the single-axis displays. * $p < .05$. ** $p < .01$.

found when the flanker task now concerned just local properties of the task-relevant flanker pair, not their global spatial relationship.

Experiment 2

In the local-orientation task, 3 subjects now discriminated the local orientation of the individual flankers in the relevant pair, rather than that of their common global axis. The results of subjects tested with this task were very different from those reported above (cf. Figures 3 and 4). With dual-axis stimuli, there were now no consistent differences in central target sensitivity as a function of attention to collinear versus orthogonal flankers.

This elimination of attentional effects with the local-orientation task might have occurred if there were some general weakening of configuration-specific lateral interactions between target and flankers, as a result of the specific secondary-task demands or the stimulus manipulation. If so, the local orientation task should also eliminate lateral interactions in classical single-axis displays where only one pair of flankers (collinear vs. orthogonal) are presented. However, the results with single-axis stimuli actually indicated a significant advantage for target detection with collinear flankers for all subjects, just as in all previous studies using similar stimulus configurations with a single flanker pair and no secondary flanker task (e.g., Polat & Sagi, 1994). The elimination of attentional modulation observed with dual-axis stimuli with the local-orientation task cannot, therefore, be accounted for by any general weakening of configuration-specific lateral interactions.

Experiment 3

In this experiment, 4 subjects compared the contrasts, rather than orientations, of two predesignated flankers (see sample stimuli in Figure 5). This task does not require construction of any representation of the global spatial relationship between flankers, nor any analysis of their local spatial attributes. However, optimal task performance should still require some perception of a relationship between the two relevant flankers (now their relative local contrasts), albeit a relationship concerning nonspatial local properties. No effect of attention to the collinear versus orthogonal flanker pair was observed in the dual-axis condition (see filled symbols in Figure 5). However, the same flanker task performed on single-axis stimuli still produced strong and significant lateral-interaction effects.

Experiment 4

Our final experiment made use of a nonspatial color-discrimination task for the attended flanker pair (see Figure 6), in which two observers had to indicate the interval containing a specific combination of red and green flankers on the predesignated axis (rather than red and blue or green and blue). Again, optimal performance for this task should require judgment of a relationship (albeit a nonspatial one) between local properties of the relevant two flankers.

Results showed a similar pattern to the previous local flanker tasks (Experiments 2 and 3), in contrast to the previous global spatial tasks (Experiment 1). Thus, for dual-axis stimuli, with two flanker pairs, there was no effect of attention to the collinear versus orthogonal pair of

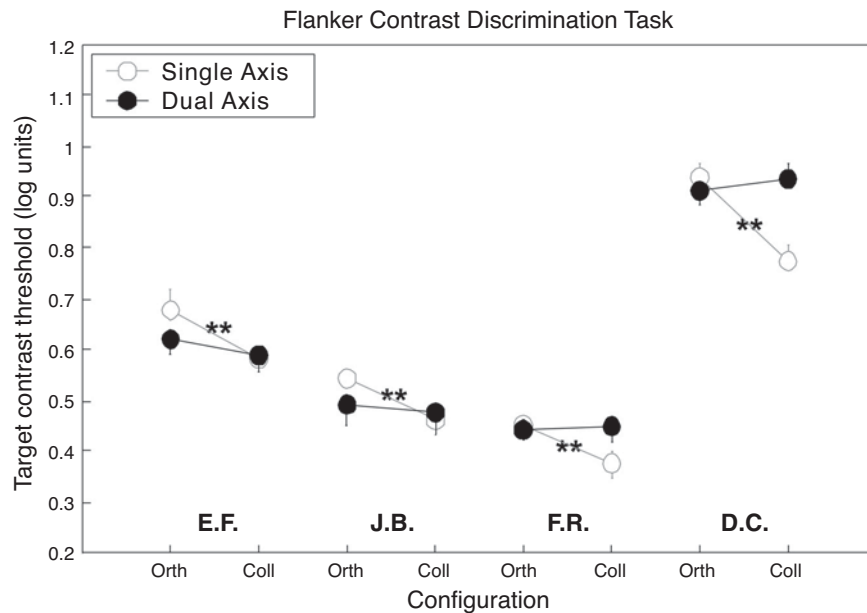


Figure 5. Experiment 3 results. Central target contrast thresholds (log units). The effect of collinear versus orthogonal flankers is significant only for the single-axis displays. $**p < .01$.

flankers for the color task. However, the new flanker task did not change the pattern usually observed for single-axis stimuli: As in the previous experiments and classical lateral-interaction studies, lower thresholds for central target detection for single-axis displays were always found with collinear versus orthogonal flankers, regardless of the task performed on the flankers.

DISCUSSION

The present results show for the first time that attentional modulation of lateral interactions depends strongly on both the specific task that must be performed for the flankers and also on the structure of the display (two axis vs. single axis).

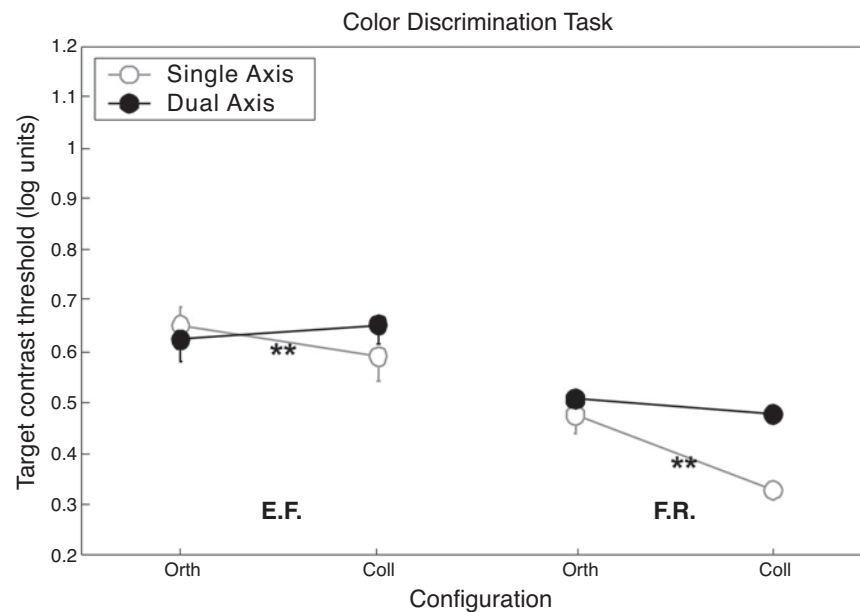


Figure 6. Experiment 4 results. Central target contrast thresholds (log units). The effect of collinear versus orthogonal flankers is significant only for the single-axis displays. $**p < .01$.

A critical question is whether the different flanker tasks produce different effects because of their specific demands on local versus global spatial processing or whether these tasks merely place different loads on general attentional resources. The presence or absence of attentional effects in dual-axis displays could, in principle, depend merely on the difficulty of the secondary flanker task, which might cause some tradeoff in the allocation of attentional resources to the primary central target detection task, versus the secondary flanker task. Thus, if the secondary task were too easy, there might be spare resources for attending both flanker pairs, not just the relevant pair; if it were too difficult, target detection might suffer generally, potentially reducing sensitivity to differences between conditions. When one examines dual-axis secondary-task accuracy across all experiments, it is clear that performance on the flanker tasks did vary between subjects and to some extent within subjects as a function of different flanker tasks (see Figure 7). However, inspection of Figure 7 also clearly shows that any such differences were not consistently associated with the global (Vernier and global-orientation tasks; Experiment 1) versus the more locally based (local orientation, contrast, and color; Experiments 2–4) flanker tasks in particular, thus providing no support for a mere “task-difficulty” account of the systematic presence or absence of attentional modulation in dual-axis displays that we had observed. Furthermore, there was no consistent

evidence of generally higher target-detection thresholds for the locally based tasks, which might otherwise have been expected if accuracy for a harder secondary task was preserved at the cost of primary-task performance.

Another potential objection is that perhaps only the two global tasks required participants to attend to both members of the relevant flanker pair in the dual-axis displays. One might argue that some of the local flanker tasks could be solved by attending to just one member of the relevant pair, since the two relevant flankers were redundant with respect to the local property to be judged for them in Experiments 2 and 3. Such a distorted distribution of attention might, in principle, have consequences for the interactions between flankers and might therefore explain the elimination of attentional effects. Four arguments can be made against this possibility, however. First, logically the same redundancy applies for the two relevant flankers in the global tasks also (i.e., changing the relevant property of one flanker also determined the property of the other member of the pair). Second, the redundancy of the relevant flanker pair should be beneficial to performing all of the flanker tasks, so it would have been suboptimal for observers to base their flanker-task performance on just one flanker in any of the tasks. Third, the color task for the flankers in Experiment 4 (detecting a specific combination of red and green for the relevant flanker pair, where either one could be blue unpredictably) was specifically chosen so that the prop-

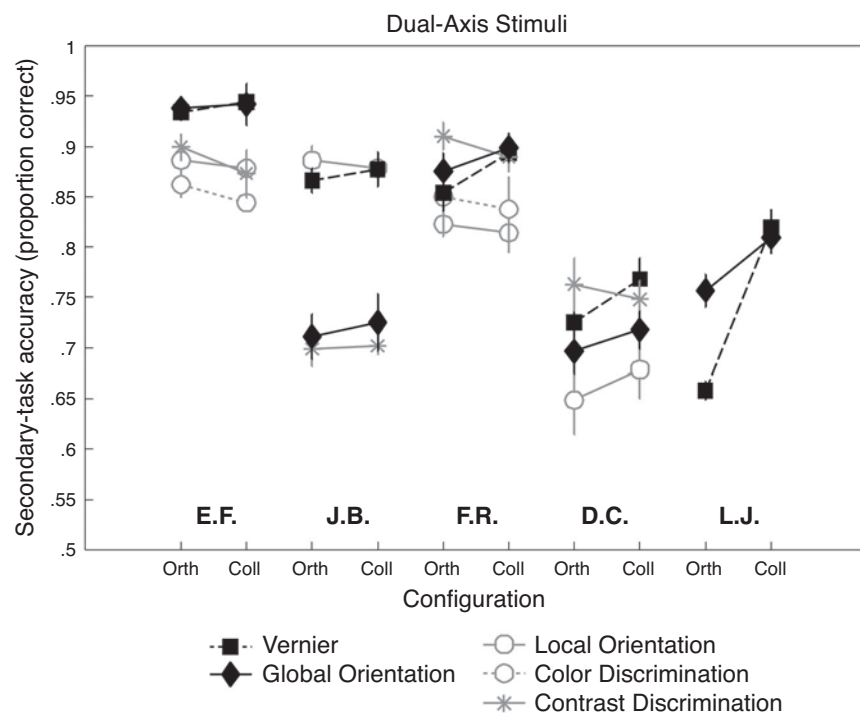


Figure 7. Comparison across experiments of secondary-task accuracy (proportion correct) for dual-axis stimuli. Note that there is no overall systematic difference in the level of performance for the two global spatial tasks (Vernier or global orientation) in comparison with the three local tasks.

erties of both relevant flankers are required to perform the task optimally. If observers had chosen to monitor just one of the relevant flankers for its designated color, their maximum accuracy would be 75% correct (because in half the trials, the other flanker of the pair would be blue). However, percentage correct for the flanker task was significantly above this level for both observers in Experiment 4 (E.F., 87%, SE 1.1%, $p < .01$; F.R., 83%, SE 1.3%, $p < .01$). Finally, perhaps the most compelling argument is based on our single-axis data, where the specific flanker task had absolutely no impact on lateral interactions (see Figure 8 and below for further discussion). If the observed differences in attentional modulation between the global and local flanker tasks were entirely explained by the distribution of attention over the relevant flankers for these different tasks, one should presumably falsely predict a similar global/local task division for the single-axis displays. Note that this argument also generalizes from covert attentional shifts to any suggestions based on eye movements toward one or the other of the flankers.

GENERAL DISCUSSION

As reported in our previous studies, we again showed here that contrast thresholds for detecting a central tar-

get decreased when collinear flankers were attended for a secondary Vernier task, compared with when the same collinear flankers were physically present but ignored in favor of a simultaneously present orthogonal pair. In Experiment 1, we successfully generalized this effect to a different secondary flanker task, which required judgment of the global orientation of the virtual contour connecting the relevant flanker pair. Both Vernier and global-orientation flanker tasks can thus produce reliable attentional modulation of approximately the same magnitude (see Figure 3).

Both of these flanker tasks may involve judging a virtual contour connecting the two task-relevant flankers. Our later experiments tested whether attentional modulation of lateral interactions is specific only to such globally based flanker tasks or whether it is general to all sufficiently demanding flanker tasks. The results of Experiments 2–4 strongly support the former task-dependent hypothesis. Three secondary tasks were chosen so that the global spatial relationship between the attended flanker pair was now irrelevant to performing the flanker task. No attentional modulation was observed in dual-axis displays from secondary tasks performed on just the relevant flanker pair that involved their local orientation (Experiment 2), their relative contrast (Experiment 3), or their colors (Experiment 4), in direct contrast to the ef-

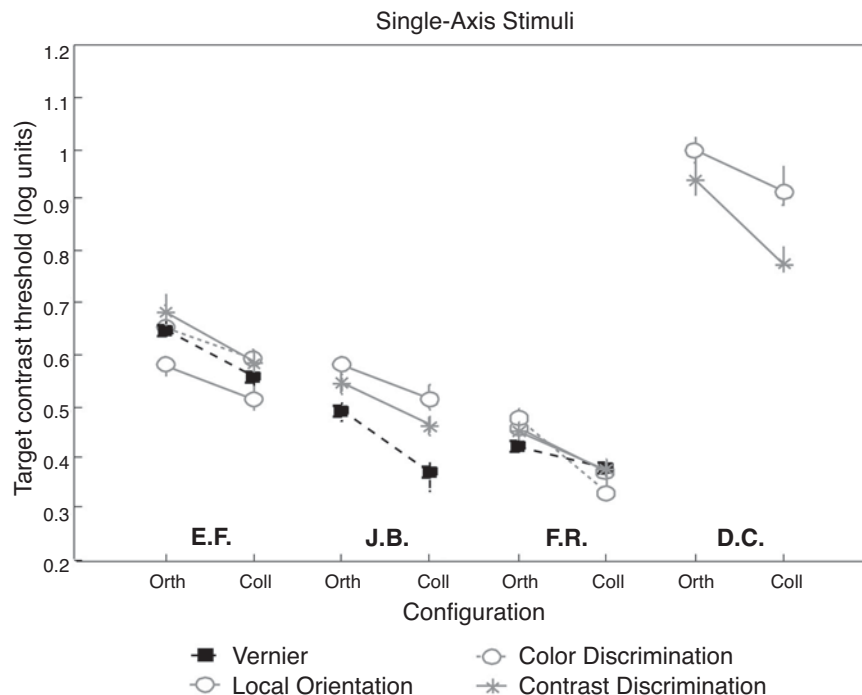


Figure 8. Comparison across experiments of central target contrast thresholds (log units) with single-axis stimuli (data reproduced from previous figures). Note that thresholds were always lower with collinear than with orthogonal flankers, regardless of the flanker task performed. This contrasts with the task-dependent pattern found for effects of attending collinear versus orthogonal flankers in the dual-axis displays (not shown here; see Figures 3–6).

fects of the global spatial tasks in Experiment 1 (and to Freeman and colleagues' previous studies [Freeman et al., 2003; Freeman and colleagues', 2001, 2004], which had all used the Vernier task).

Our new task-dependent results may be hard to reconcile with emerging "feature-based" accounts of attention, in which attention to a given feature effectively increases sensory gain for all stimuli sharing a similar feature elsewhere in the visual field (Martinez-Trujillo & Treue, 2002; McAdams & Maunsell, 2000; Saenz, Buracas, & Boynton, 2002, 2003). This account might predict a limited degree of task-dependency. For example, attending to the orientation of the flankers collinear to the target might enhance target sensitivity merely because the target has a similar local orientation to the attended flankers; on the other hand, attending to the color of the flankers should not benefit the monochrome target because they differ from each other on the task-relevant dimension of color. However, such a feature-similarity account cannot explain the difference in attentional modulation between the global and local flanker tasks, since in all these the central target always shared similar local orientations with collinear flankers, regardless of the task for which the latter were attended (see Freeman et al., 2004, for further data incompatible with such a feature-based attention account).

Our finding of task dependence discounts the simple possibility that it is sufficient merely to attend to the flankers collinear to the target (for any task) in order to obtain target facilitation. The same flankers, when attended for nonglobal tasks, clearly do not produce facilitation. However, the data also appear incompatible with some versions of "object-based" attention theory (e.g., Duncan, 1984; see Driver et al., 2001), according to which attention to any specific property of an item automatically leads to selection of all of its other properties. For example, although, in principle, a specific global attribute of the collinear target-flanker configuration might produce target facilitation only when this is attended, it might be impossible not to process such an attribute when some other local attributes of the same flankers must be attended. Our results suggest that any such processing of global attributes is not obligatory when attending only the local properties of the constituent elements.

Furthermore, even if such obligatory processing of global attributes were not assumed, it remains plausible that a form of object-based attention (spreading of attention to all local object attributes) could work in combination with a feature-based attentional mechanism. According to this idea, attending to the color or contrast of the flankers would lead to obligatory processing of its local orientation, and the latter property in turn would facilitate other elements with the same orientation (as described in the previous paragraph), including the target, if collinear. All of these accounts falsely predict that attentional modulation of lateral interactions should always be found, regardless of the task imposed on the flankers.

On the other hand, the present task-dependent outcome appears to be consistent with the common belief that mechanisms underlying lateral-interaction phenomena may play a role in perceptual integration, integrating outputs of local orientation-selective receptive fields into the representation of more extended contours with global properties, such as orientation, curvature, and continuity (Hess & Field, 1999; Kovacs, 1996; Polat & Bonneh, 2000; Saarinen & Levi, 2001). Until now, there has been limited empirical support for this contour-integration function. Indeed, some authors have suggested that at least some of the psychophysical results under the broad heading of "lateral interactions" might in principle be explained on the basis of local energy summation, without necessarily invoking specialized contour-integration mechanisms (Solomon & Morgan, 2000; Solomon, Watson, & Morgan, 1999). The importance of global spatial tasks for the present results provides new evidence for a close relationship between lateral interactions (at least of the type reported by Polat & Sagi, 1993, 1994) and contour integration. Thus, the present global tasks might have been particularly effective at producing attentional modulation of lateral interactions, because only they involve judging the orientation of a virtual contour connecting the two flankers, and lateral-interaction mechanisms may function precisely to construct just such a contour. The perceptual representation of a contour may thus be modified, depending on its task relevance, via attentional control over the basic integrative mechanisms underlying lateral interactions.

Our results have further implications for the nature of the attentional mechanisms involved in modulating lateral interactions. On the basis of our data from the dual-axis displays alone, it might be supposed that task-based attention can easily switch lateral interactions on or off, depending on whether or not they are helpful for the specific task. Such an extreme conclusion might resonate with proposals that early visual processes such as perceptual grouping and segmentation may be absolutely dependent on attention, not functioning at all when it is withdrawn (Joseph, Chun, & Nakayama, 1997; Mack, Tang, Tuma, Kahn, & Rock, 1992; Rock et al., 1992). However, our single-axis data point to a very different conclusion. As mentioned above, we found a consistent advantage for central target detection with collinear versus orthogonal flankers in single-axis displays, which was completely unaffected by the different attentional demands of the secondary tasks. Figure 8 shows the remarkable similarity of target-detection thresholds across all the single-axis conditions, demonstrating that basic lateral-interaction effects (i.e., collinear vs. orthogonal flankers; cf. Polat & Sagi, 1994), are unaffected by the attentional demands of the different flanker tasks. These single-axis data, when seen in isolation, might have led to the opposite conclusion that early visual processes such as perceptual grouping are quite immune from attentional influences (cf. Driver & Baylis, 1998).

Although seemingly paradoxical to the above traditional accounts, this striking divergence of the task effects for dual-axis and single-axis displays may be readily accounted for by noting that in the present dual-axis displays, there were two "rival" axes along which any grouping may arise, making the stimulus pattern ambiguous and potentially multistable (in the sense that it can be organized along either of two axes, or even be seen as an "X" pattern). Top-down modification of lateral interactions may be needed to resolve such a perceptual ambiguity by reinforcing the grouping of the relevant elements while simultaneously excluding the other, irrelevant elements from the perceived group. However, this intervention may only be necessary in critical task contexts where optimum performance requires achieving a unique and unambiguous representation of the relevant global stimulus properties. In the global tasks, for example, observers must discriminate changes in the global orientation of one axis while similar but uncorrelated global changes occur on the other axis. In other tasks based on local or nonspatial stimulus properties, the perceived global structure is not relevant, and therefore there may be no need for any such top-down intervention. Furthermore, with unambiguous single-axis stimuli, a unique grouping can always be achieved without top-down intervention, whether or not it is task relevant, and so again no top-down intervention is required. Attentional modulation may thus function here to select between different competing global stimulus organizations, whenever such a selection is necessary for optimum performance of the ongoing task.

With respect to the possible neural bases for the effects observed here, it has previously been suggested that lateral interactions may relate to the architecture of horizontal connections between receptive fields that have coaxial-orientation preferences, in early visual cortex (Fitzpatrick, 1996; Gilbert & Wiesel, 1990). Consistent with this, recent physiological studies have demonstrated the activity of cells in primary visual cortex (V1) depend on the presence of collinear flanking stimuli (Kapadia et al., 1995); moreover, the form of this influence can depend on the distribution of spatial attention (Gilbert et al., 2000) and possibly also on the task that is performed on a selected target flanker configuration (Li, Piëch, & Gilbert, 2004). On the basis of such observations, it has been suggested that attention might selectively weight the horizontal connections between V1 receptive fields (Freeman et al., 2003; Freeman et al., 2001; Gilbert et al., 2000; Lamme, Super, & Spekreijse, 1998; Posner & Gilbert, 1999; see also Sagi, 1996). Such models now must be extended to accommodate the present data, which suggest that attention may resolve ambiguities at the level of these integrative mechanisms, in a manner that is constrained by both stimulus and task contexts.

In common with many recent physiological studies (e.g., Luck et al., 1997), we found the strongest attentional effects when there was more than one competing object or perceptual interpretation in the display. This

accords with the emerging notion that attention can select between competing perceptual interpretations by biasing an intrinsic competition between them (Desimone & Duncan, 1995). The general principle of "biased competition" has now been demonstrated in several physiological studies (Desimone, 1998; Desimone & Duncan, 1995; Reynolds, Chelazzi, & Desimone, 1999), showing strong attentional modulation of single-cell activity when the given task requires selection between stimuli for the same or overlapping receptive fields. In such situations, attention may help resolve any potential conflict over the interpretation of information in a particular region of space. Our results suggest that this general approach might now be usefully extended to the case of potential conflicts between different global groupings, rather than just different local interpretations. In the present case, one might consider an intrinsic competition between neural representations of the two flanking axes in dual-axis displays, with attention operating to bias this competition so that the task-relevant representation dominates while others are suppressed. Indeed, Grossberg and Raizada (2000) recently proposed a model of early visual cortex that attempts to account for lateral interactions and attentional modulation thereof, by extending the general principle of biased competition. From the perspective of such a model, the present task- and stimulation-specific attentional effects could represent the psychophysical correlate of biased competition between different subpopulations of horizontally connected receptive fields, each integrating flanker pairs along different axes.

To conclude, we have demonstrated that lateral interactions can be modulated by attention, but in a manner that depends on both the stimulus and the task. We found such modulation only in dual-axis displays with tasks that required judgment of the global properties of the relevant flanker stimuli. This result has implications for understanding the functional role played by lateral interactions and also for the role of attention in modulating the underlying mechanisms in early vision (at stages that can influence objective thresholds for detection of Gabor patches). On the first issue, our results support the common, but until now somewhat uncertain, assumption that lateral interactions may serve the useful function of extracting global properties—such as the overall orientation of a contour—from a set of collinear elements. This could explain why we observed modulations only in global but not in local tasks. On the second issue, our results suggest that a primary role played by attention at the level of lateral interactions may be to resolve conflicts between multiple alternative perceptual groupings, whenever achieving a unique and stable global organization is critical to the current task. Thus, when the display supports only one global organization, lateral interactions operate automatically, regardless of task set. However, when several such organizations are possible, task-directed attention may bias the competition between these organizations in favor of the perception that is most relevant to the task at hand.

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