Integration of Foveal Orientation Signals: Distinct Local and Long-Range Spatial Domains

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BrinCAT, Scott L. and Gerald Westheimer. Integration of foveal orientation signals: distinct local and long-range spatial domains. J. Neurophysiol. 83: 1900–1911, 2000. Human observers can discriminate the orientation of a stimulus configuration composed of a pair of collinear visual patterns much better than that of a single component pattern alone. Previous investigations of this type of orientation signal integration and of other similar visual integrative functions have shown that, for closely spaced elements, there is integration only for stimuli with the same contrast polarity (i.e., both lighter or both darker than the background) but, at greater separations, integration is independent of contrast polarity. Is this effect specific to differences in contrast polarity, which is known to be an important parameter in the organization of the visual system, or might there be a cluster of other stimulus dimensions that show similar effects, indicating a more widespread distinction between the processes limiting integration at local and long-range spatial scales? Here, we report a similar distance dependence for orientation signal integration across stimulus differences in binocular disparity, direction of motion, and direction of figure-ground assignment. We also demonstrate that the selectivity found at short separations cannot be explained only by “end-cuts,” the small borders created at the juncture of abutting contrasting patterns. These findings imply the existence of two distinct spatial domains for the integration of foveal orientation information: a local zone in which integration is highly selective for a number of salient stimulus parameters and a long-range domain in which integration is relatively unselective and only requires that patterns be roughly collinear.

INTRODUCTION

The performance of human observers in discriminating the orientation of a visual stimulus improves greatly with increasing length of the stimulus. For a foveally presented line, discrimination thresholds reach an optimum (often <1/2 of a degree of orientation) at line length of 20–30 min of arc. This may be related to the fact that orientation tuning in primary visual cortex neurons is narrower for long lines than for short ones (Gilbert 1977; Henry et al. 1974), since the output of these cells is thought to underlie our ability to make fine judgments of orientation. Besides the obvious benefit of heightened acuity, the sharpening of the neural representation of long contours afforded by this sort of integrative mechanism is probably also important in the detection and processing of extended smooth contours in the visual scene.

A previous investigation of the spatial properties of this phenomenon suggested that the pooling zone for the integration of orientation signals, as measured by this sort of discrimination threshold enhancement, is quite narrow (Westheimer and Ley 1997). Orientation thresholds for a configuration of two short, collinear line segments that are separated collinearly by as much as 30 arcmin in the fovea are significantly better than thresholds for their component lines alone. Performance at these relatively large separations is similar to that found with zero separation (i.e., when the 2 line segments are abutting), and is not greatly different from thresholds obtained when the gap is filled in to create a single long line. In contrast, when one of these line segments is displaced laterally by as little as 1 arcmin (so they remain parallel, but are misaligned), they cannot be integrated to yield enhanced performance (Westheimer and Ley 1997).

These results might suggest that the orientation signals produced by separated collinear lines address, although somewhat less effectively, the same integration mechanisms as a single long line. However, the effects of contrast polarity on orientation integration point toward a more complex picture. When two short line segments have little or no separation, their orientation signals can be pooled only when they have the same sign of contrast polarity (both black or both white on a gray background); thresholds for an opposite polarity configuration (one black line and one white) are no better than those for the individual component lines. However, when the gap between the line segments is larger, performance is independent of contrast polarity. Similar results have been obtained in studies of other types of visual integrative functions (recently reviewed by Dresp 1999; Polat 1999). This implies the existence of two somewhat distinct spatial domains of integration: a short-range zone selective for contrast polarity and a longer-range zone that is robust to differences in contrast polarity.

Is this effect specific to the domain of contrast polarity, or might there be a cluster of other stimulus parameters that show similar effects, indicating a more widespread distinction between the processes limiting integration at local and longer-range spatial scales? In the current work, we seek to answer this question by delineating and comparing the rules of selectivity of orientation integration at short and long-range stimulus separations. We employ the method used by Westheimer and Ley (1997): orientation discrimination thresholds are measured for configurations composed of a pair of collinear, co-oriented stimuli. These two stimuli are either identical, or differ along a single dimension, such as contrast polarity, and are either closely or more distantly spaced. To measure the magnitude and selectivity of threshold improvement for the various stimulus configurations, these thresholds are then compared with those of a single component stimulus alone. We find that, indeed, several other stimulus parameters reveal a similar distinction between local and longer-range integration.
METHODS

For all experiments, the observers’ task was to discriminate whether the orientation of a foveal visual stimulus (e.g., a line or an edge), or a pair of collinear stimuli, was tilted slightly clockwise or counter-clockwise relative to an implicit vertical standard. All data were obtained using the method of constant stimuli: on each presentation, observers were shown a stimulus orientation randomly selected from an array of seven equally spaced orientations, the middle of which was exactly vertical. No error feedback was provided, but thresholds in the hyperacuity range can easily be achieved in the absence of feedback for this type of discrimination.

Each data point presented herein is derived from at least 300 responses collected over at least 2 days. Data were accumulated in blocks of 150 presentations, and, at the end of an experiment, the data for all repetitions of a particular condition were summed and subjected to probit analysis. This procedure fits a cumulative Gaussian curve to the psychometric function, yielding a threshold value that corresponds to one-half the difference between its 25 and 75% points, and a standard error of this measure. To obviate differences between conditions, results for each experiment were always collected as a self-contained series, even though two different experiments sometimes involved identical conditions. Therefore slightly different values may appear in different graphs for the same stimulus condition.

Stimuli were generated by a Matrox Millenium video board on a Pentium computer and displayed on a 15-in. monitor with a resolution of 1,024 × 768 pixels and a refresh rate of 60 Hz. Stimuli were presented on a disk-shaped uniform gray background (~19 cd/m², measured by a Minolta LS110 photometer) 1.75° diam, which remained on at the same lumiance between stimulus presentations. Stimuli were drawn using an anti-aliasing algorithm to ensure their smoothness. For experiment 2, NuVision LCD goggles were used to alternate presentation of two different pages of the video memory to the two eyes. Binocular disparity was introduced by displacing the images presented to each eye by equal amounts in opposite directions. Observation was binocular at a distance of 6.38 m in a dimly lit room, and a chin rest was used for most experiments to keep head position steady. Stimulus duration was 300 ms, unless otherwise noted, and a blank background was shown for 2 s between stimulus presentations. For experiment 4, stimuli were displayed on an HP1345 vector scope, which was utilized because its superior spatial resolution was critical for this experiment. Observation distance for this experiment was 3.71 m.

The two authors and three undergraduate students were observers. All had normal, or corrected to normal, visual acuity. For each experiment, at least one observer was naive as to the experimental problem and expected results.

It is important to point out that, for some of the stimulus configurations employed in the experiments described below, biases in the perceived position of a stimulus caused physically collinear stimuli to appear misaligned. An example can be found in the configuration of collinearly paired white and black luminance edge stimuli depicted in Fig. 5D. Because of the well-known phenomenon of “irradiation” [the apparent displacement of the location of a luminance border toward the darker side (Helmholtz 1911)], the white edge is perceived by most observers to extend farther into the gray background than the black edge, causing them to appear misaligned. A similar situation exists for nominally collinear stimuli that are moving in opposite directions (Fig. 3) or that have different binocular disparities (Fig. 2). We found that the positional bias could be nullled, restoring the perception of collinearity, by a lateral shift of one of the stimuli in the configuration by a distance equal to that of the positional bias, but in the opposite direction. Pilot experiments revealed that these subjectively collinear stimulus configurations yielded as good or better orientation thresholds than physically collinear ones. Therefore each observer’s subjective location of collinearity was carefully measured for each stimulus configuration by an adjustment method, and this lateral displacement (in the opposite direction) was introduced into the stimulus configurations in the main experiments described below.

RESULTS

Experiment 1: selectivity for contrast polarity

Because we are attempting, in this study, to compare the selectivity of short- and long-range integration of orientation signals, we decided to ensure that our observers showed the same basic effect that prompted us to embark on this investigation. We therefore started by replicating the experiment described in Fig. 9 of Westheimer and Ley (1997) on our observers.

Orientation discrimination thresholds were measured for stimulus configurations composed of pairs of short collinear line segments, and compared with thresholds for each of the component segments alone. The line segments were 10 arcmin long and 0.4 arcmin wide, and were either black (0.5 cd/m²) or white (120 cd/m²) on a gray background (19 cd/m²). These were then paired into configurations where the two lines had either the same (2 black or 2 white lines) or opposite (a black and a white line) contrast polarity, and a variable collinear separation (see Fig. 1, top left, for a depiction of these stimuli).

The results for three representative individual observers, and the mean of five observers, are shown in Fig. 1. We calculated a simple index of the threshold improvement for each stimulus arrangement: each observer’s orientation threshold for each stimulus configuration was divided by the mean of the orientation thresholds for its component line segments. This yields values <1 if there is an improvement over the component lines, >1 for impairment, and 1 for no change. We then pooled these values across the two same-contrast polarity conditions, because same versus opposite polarity was the comparison of interest, and calculated the mean of this index for five observers. Thresholds for same-polarity line pairs are ~50% better than their component line segments for all separations tested (0–20 arcmin; Fig. 1, bottom and top left). Pairs of abutting opposite-polarity lines show no such integration; their thresholds are no better than those of their component lines alone. However, when these same lines are separated by 10 arcmin, there is significant integration, although not quite as much as for same-polarity lines. At a separation of 20 arcmin, integration is completely nonselective for contrast polarity; same-polarity and opposite-polarity pairs show identical improvements over their component lines.

Experiment 2: selectivity for binocular disparity

Having replicated the previously reported interaction between contrast polarity and line separation, we looked for a similar effect with other stimulus parameters, which would indicate a more deep-rooted distinction between the putative local and longer-range zones of integration. Orientation integration has been shown to be highly selective for stimulus collinearity. Although summation occurs for a wide range of collinear separations between line segments, if one of them is laterally displaced by as little as 1 min (so they remain parallel, but are misaligned, as in each monocular half of Fig. 2, top), they cannot be integrated (Westheimer and Ley 1997). We were curious to see whether orientation integration exhibited
similarly narrow tuning for binocular disparity, which can be thought of as collinearity in depth.

Orientation discrimination thresholds were again measured for pairs of short lines that were either abutting or separated by 20 arcmin. These separations were chosen to be well within the empirically defined limits of our proposed local and long-range integration domains, respectively. Whereas the upper of the two lines always remained in the plane of the monitor, the bottom line was given a crossed (near) binocular disparity that had values of 2.5, 5, or 10 arcmin in different blocks. Our observers noted that the nearer of the two lines appeared slightly displaced toward the monocular location in the dominant eye, especially at larger disparities. Therefore the lateral displacement necessary to achieve perceptual collinearity was carefully measured separately for each stimulus condition, and, during the actual experiments, the lower line was shifted in both eyes by this amount. Because stereoacuity thresholds have been shown to be suboptimal for short presentation times, stimulus duration was increased to 1 s for this experiment, to allow for full maturation of the disparity signals.

The results in Fig. 2 show that integration of orientation signals is selective for binocular disparity, and that this selec-
activity is much more narrowly tuned for abutting than for separated lines. Abutting lines exhibit summation only when there is little to no difference in disparity between them, whereas thresholds for separated lines are unaffected by 2.5 min of disparity, and, at least for observer SB, significant, but weak, integration can be seen for disparities up to 10 arcmin. Interestingly, observer LG’s results are suggestive of active inhibition, rather than simply a lack of summation, although a firm conclusion cannot be based on a single observer.

Experiment 3: selectivity for direction of motion

Many orientation-tuned neurons in visual cortex are also directionally selective, showing a clear preference for motion of an optimally oriented contour in one direction over the opposite direction. Perceptually, common motion is a strong cue for grouping, whereas the motion of contours in opposite directions usually indicates their belonging to separate objects, or to figure and ground. We, therefore suspected that the integration of orientation signals, as measured by our task, would also be selective for direction of motion.

Testing this hypothesis required an oriented stimulus that gives the appearance of motion, but does not actually shift its mean position, which would disrupt collinearity. We therefore resorted to configurations of square-wave grating patches that drifted orthogonally to their main axis, moving either in the same or opposite direction relative to each other (see Fig. 3, top left, for a highly schematized depiction). Motion was produced by shifting the phase of each grating by 90° every third video frame (50 ms). This ensured that, even for the opposite direction condition, the two gratings’ bars would always be aligned, either in phase, or 180° out of phase. The percept, however, was usually of fairly smooth motion. Each patch was win-
dowed by a circular Gaussian function to force observers to base their judgments on the grating bars, rather than on their edges. It has been demonstrated that very similar, but stationary, patterns (Gabor patches) yield orientation thresholds not significantly different from those found for lines (Westheimer 1998).

We found that, locally, orientation integration was indeed selective for direction of motion (Fig. 3, top right). It could be argued, however, that this may be attributed to the fact that the two gratings had opposite signs of contrast polarity (i.e., 180° phase difference) during half of the presentation. If this effect is indeed only secondary to a contrast polarity difference, then thresholds for the opposite motion direction condition would be expected to be equivalent to or better than those for a pair of opposite contrast polarity gratings drifting in the same direction. We found that the opposite motion condition yielded marginally worse performance of 1.04 ± 0.08 versus 0.94 ± 0.08 for observer SB, and 2.76 ± 0.28 versus 2.35 ± 0.35 for GW (data not shown in figure), suggesting that relative motion has a negative effect on orientation discrimination that cannot entirely be explained by contrast polarity. Summation at long-range separations, at least for the two observers that demonstrated any integration at these separations, was unselective for motion direction.

Experiment 4: selectivity for orientation

Several psychophysical studies of visual contour integration have demonstrated effects that are maximal when the elements to be integrated have similar orientations, and decrease smoothly with increasing angle between adjacent elements, obeying the Gestalt law of good continuity (Field et al. 1993; Kapadia et al. 1995; Polat and Sagi 1993; Yu and Levi 1998). Investigations of the presumed neural substrates of these functions have produced similar results (Bosking et al. 1997; Kapadia et al. 1995). It is not immediately obvious that these...
results would generalize to a task whose dependent variable is itself orientation. One might expect, for example, that an improvement in orientation discrimination might be specific to precisely cooriented stimuli.

We investigated the orientation dependency of orientation integration using the stimulus depicted in Fig. 4 (top right). The central line in this configuration of three segments was given a variable orientation as in previously described experiments, whereas the flanking lines were given orientations equal to the center line’s plus a clockwise (top line) or counterclockwise (bottom line) orientation difference, which was held constant throughout a block of trials. The configuration rotated rigidly about the middle of the center line, and observers were instructed to discriminate the orientation of the entire configuration. The 3 component lines were either abutting or separated by twice their length, and the length of all 3 lines was the same (5 arcmin for LG, 7.5 arcmin for SB). Left: results from 2 observers for a range of orientation differences. Orientation thresholds ± SE for a single component line are marked by the horizontal dotted line and shaded area. Dashed lines represent thresholds for the separated condition; solid lines, the abutting condition. Orientation integration decreases smoothly with increasing angle between component lines, and no integration is found at angles greater than ~45–50°. No clear difference is evident between the separated and abutting conditions.

Orientation integration was found to gradually decrease with increasing relative orientation difference of the component lines (Fig. 4, left). No integration was observed at differences greater than ~45–50°. Unlike all of the other parameters we investigated, there were no consistent differences between abutting and separated stimulus conditions; observer LG shows a trend toward broader selectivity for abutting stimuli, but SB demonstrates, if anything, the opposite. This may be attributed to interobserver differences, or perhaps it reflects a genuine invariance of orientation selectivity with respect to stimulus separation.

Experiment 5: selectivity for figure-ground assignment

It has been cogently argued, based on psychophysical results, that each contour in a visual image is necessarily perceptually assigned to, or “owned by,” only one of the two regions it separates; this region is then perceived as the figure, whereas the other side is perceived as the background (Baylis and Driver 1995). Might such higher-level properties as the perceived assignment of figure and ground influence the integration of orientation signals in a manner similar to that which we have demonstrated for various lower-level stimulus attributes? To answer this question, we created stimuli in which
the direction of figural assignment of an edge could be manipulated independently of its lower-level luminance contrast attributes.

Orientation thresholds were measured for configurations of collinear step luminance edges (see Fig. 5, top, for a depiction). Because these edge stimuli were placed in a large, homogeneous background, they were unambiguously perceived as figural. The region defining this figure could be extending outward from either the right or left side of the centrally located target edge, and therefore we could vary the edge’s direction of figural assignment. Independently, the stimuli could be either lighter or darker than the background. Therefore in pairing these edge segments, we could dissociate the effects of luminance step polarity [the sign of the change in luminance at the step edge (lighter-to-darker or vice versa; the edge equivalent of contrast polarity)] and edge direction polarity (the side on which the figural component of an edge extends). For example, the paired edges in condition C (Fig. 5, top) have opposite signs of edge direction polarity, but the same luminance step polarity—they are both darker on the left side and brighter on the right. Because the local contrast information is the same for both edge segments, a mechanism sensitive to the direction of an edge’s luminance gradient would, theoretically, not differentiate between them, unless its response was modulated by perceived figure-ground direction.

The effect of luminance step polarity on integration of edges (condition D) is very similar to that of contrast polarity for lines; locally, only same polarity segments can be integrated to yield threshold improvements, whereas integration is more or less independent of polarity at larger separations (Fig. 5, bottom). The fact that this effect can be demonstrated for several different types of stimuli attests to its robustness. Edge direction polarity has a similar effect (condition C), suggesting that the direction of edge figure-ground assignment is indeed important in the local elaboration of contours, but less important for longer-range integration. Also, the effects appear additive. Performance with stimulus configurations that are of opposite polarity for both edge direction and luminance step (conditions E and F) are, on average, worse than either C or D, even for the largest separation tested. This suggests that stimulus presentations that are of opposite polarity for both edge direction and luminance step are less effective than the same polarity line. This implies that, whereas they had only a very small detrimental effect on the discrimination of a same contrast polarity stimulus, they received no benefit from opposite polarity.

In all of our experiments, abutting stimuli that differ along some parameter contain a small border, roughly orthogonal to the main stimulus axis, at the junction between the two component stimuli (see Fig. 6, condition C). Grossberg and co-workers (Dresp and Grossberg 1997) have proposed that these borders, which they refer to as endcuts, may weakly excite units tuned to orientations roughly orthogonal to the stimulus axis. These cells, in turn, suppress the mechanisms of integration, preventing significant integration between abutting lines of opposite contrast polarity.1 If endcuts can be generated by other feature contrasts along an edge, besides luminance contrast, then endcut formation might provide a somewhat trivial explanation of the short-range selectivity we have found for a number of stimulus parameters.

We tested this proposition by creating a stimulus that mimics the endcut in opposite contrast polarity stimuli, without actually containing opposite contrast polarity target lines. This was achieved by superimposing a central short horizontal (constant orientation) black-and-white line on a purely white vertical test line (Fig. 6, condition B). If endcuts are responsible for the poor discrimination of opposite contrast stimuli, then our condition B would be expected to impede orientation thresholds relative to the same contrast polarity stimulus (Fig. 6, condition A).

The results suggest that this is not the case. Endcuts alone had only a very small detrimental effect on the discrimination of a same contrast polarity line. This implies that, whereas they may play a minor role, endcuts are not a sufficient explanation of the poor orientation thresholds for opposite contrast polarity stimuli. Because luminance contrast would be expected to generate stronger endcuts than other feature contrasts, we suggest that our results obtained with other stimulus parameters are also unlikely to be explained by endcuts. Rather, some factor intrinsic to closely spaced sharp changes in polarity, other than the border they create, must be responsible. We should point out, however, that our results are generally quite consistent with both the empirical and theoretical work produced by Grossberg’s group (e.g., Dresp and Grossberg 1997), in that both suggest a clear functional distinction between short- and long-range domains in the processing of visual contours.

**DISCUSSION**

In Table 1, we present a summary of the rules of selectivity for the integration of orientation signals that we have described.

1 Note that endcuts are only one of many factors (others include stimulus size and spacing) suggested by Dresp and Grossberg’s model to be important in the dynamics of contour processing. This experiment should not therefore be viewed as an empirical test of their entire model.
above. Strikingly, for all but one of the parameters we tested, selectivity depends greatly on stimulus separation. When two visual patterns are separated by a short collinear distance, the requirements for efficient integration of their orientation signals are stringent. Orientation discrimination thresholds for a pair of identical, closely spaced patterns exhibit a large improvement over those found for the component patterns alone, but this enhancement is eliminated by a significant difference between the patterns along any one of a number of stimulus dimensions. On the other hand, when stimuli are separated by a larger coaxial distance (a minimum of $15\text{ arcmin}$ at the fovea), integration becomes relatively unselective. At these separations, the orientation signals of patterns with opposite signs of contrast polarity, moving in opposite directions, or "owned" by opposite sides of a border, can be integrated to yield threshold enhancements quite similar to those found for their same-sign counterparts. However, long-range integration is limited by a requirement that stimuli be approximately collinear—large differences in depth, orientation, or lateral position eliminate integration. The widespread, qualitative differences between the rules of selectivity for short and long separations can be regarded as strong evidence for the existence and generality of two distinct spatial domains for the integration of orientation signals.

In the case of contrast polarity, this distinction between short- and long-range processing has been documented many times for several other types of visual functions: vernier acuity (Levi and Waugh 1996; O’Shea and Mitchell 1990), facilitation of contrast detection (Wehrhahn and Dresp 1998), sensitization of contrast discrimination (Yu and Levi 1997), illusory contour detection (Dresp and Grossberg 1997), separation discrimination (Levi and Westheimer 1987), and positional attraction/repulsion (Badcock and Westheimer 1985), suggesting that the underlying neural mechanism that restricts fine local processing to same-polarity stimuli is at a fairly low level common to all these tasks (see Dresp 1999 and Polat 1999 for recent reviews of these and other relevant results). Interestingly, the data from all of the visual functions listed above that involve coaxial separations of features in the fovea, converge on $15–20\text{ arcmin}$ as the approximate location of the transition from the short- to long-range zones (Levi and Waugh 1996; O’Shea and Mitchell 1990; Wehrhahn and Dresp 1998; Yu and Levi 1997). Separation discrimination and positional integrations, however, both involve displacement along the axis orthogonal to stimulus orientation, and both yield a transition point of $3–5\text{ arcmin}$ (Badcock and Westheimer 1985; Levi and Westheimer 1987), suggesting the existence of an elongated local integration domain with an aspect ratio on the order of 3:1 to 6:1 (cf. Polat and Tyler 1999). To our knowledge, differences between short-range and longer-range processing have not previously been described for any of the other parameters investigated here.

One might wonder why thresholds for abutting opposite polarity configurations are often approximately the same as those for their component stimuli alone. For example, performance for abutting pairs of opposite contrast polarity lines is very similar to that for the isolated component lines (Fig. 1, top right), and a roughly similar situation exists in the results from...
the disparity (Fig. 2), motion direction (Fig. 3), and figure-ground (Fig. 5) experiments. This is intriguing because, if opposite polarity stimuli were processed by independent mechanisms, with no potentiating interactions between them, one would still expect some threshold improvement over the component lines, simply because of probability summation. One possible explanation is that observers attended to only one-half of the opposite polarity stimuli. This seems unlikely because observers were instructed to discriminate the orientation of the entire configuration and reported that they attempted to do so, and because this account is difficult to reconcile with the gradual transition from no integration to complete integration across contrast polarity with increasing separation (Fig. 1). A more likely explanation is that any potential benefits from probability summation were counteracted by active interference. This explanation is supported by the fact that opposite contrast polarity stimuli have been shown to elicit very poor neuronal responses and orientation selectivity in striate cortex. It is also important to note that probability summation is not a sufficient explanation of the threshold enhancement found in the other conditions. If the component lines were processed completely independently, an improvement based on probability summation alone would allow for thresholds that are, at best, ~70% (i.e., 1/\sqrt{2}) of the component thresholds, whereas we often find enhancements that are significantly greater (e.g., 50–55% for same contrast polarity conditions; Fig. 1). Also, because the mechanisms processing the component lines almost certainly overlap or interact in some way, the actual benefit afforded by probability summation is probably much less than the theoretical 1/\sqrt{2}. Because statistical summation alone cannot explain our results, some type of physiological interactions must be involved. It is widely believed that our exquisite ability to discriminate the orientation of contours relies on the signals of an ensemble of orientation-selective neurons in primary visual cortex. The improvement of orientation discrimination with increasing stimulus length that we have investigated seems quite likely to be related to the narrowing of orientation tuning of V1 cells for longer stimuli (Gilbert 1977; Henry et al. 1974). Recently, there has been some debate about whether a neuronal population’s accuracy in encoding a sensory dimension would, as it is often assumed, be enhanced by a sharpening of the tuning functions of its elements (e.g., Zhang and Sejnowski 1998). The correlation between psychophysical threshold enhancement and narrowing of neuronal tuning for the orientation of long contours suggests (although certainly does not prove) that this may indeed be true in some circumstances. Because the response of virtually all V1 cells (both simple and complex) is strongly suppressed (Hammond and MacKay 1983, 1985), and their orientation tuning function greatly widened (Swindale 1995) by opposite contrast polarity configurations of bars, it should, perhaps, not be too surprising that this type of stimulus would not share the discrimination enhancement conferred by increasing the length of same contrast polarity stimuli. Similarly, we expect that stimuli with increasingly large step changes in orientation or binocular disparity would engender decreasing response in striate cortical cells, because they would encroach more and more into the inhibitory sidebands of first-order simple cells. That short-range selectivity is also found for the direction of figure-ground assignment hints that neurons at the lower levels of the cortical hierarchy may also be sensitive to such higher-order stimulus attributes, as was recently demonstrated neurophysiologically in areas V1 and V2 (Zhou et al. 1998). The short-range integration domain may therefore be identified with interactions within the classical receptive fields of single cells, or the aggregate receptive field of a small ensemble of cells. As opposite polarity stimuli are moved farther apart, they would overlap less in the same receptive fields, and consequently their orientation signals would be less suppressed. The critical separation of ~15 arcmin, beyond which discrimination becomes completely independent of stimulus polarity, might correspond to the length of the foveal receptive fields used for fine orientation discrimination. The threshold improvement found for widely separated, opposite-contrast stimuli cannot be attributed to the properties of single striate cortical cells alone, because no known cell type can summate across contrast polarity for collinear contours. The long-range integration domain must then correspond to either interactions between neurons or to second-order, elongated mechanisms that may reside in higher cortical areas. One candidate mechanism is iso-orientation potentiation via long-range horizontal connections in primary visual cortex, which are known to extend for ≥6 mm (Gilbert and Wiesel 1983), to preferentially link neurons with cooriented, coaxially aligned receptive fields (Bosking et al. 1997), and to give off predominately excitatory connections (McGuire et al. 1991). Further, the layers in which these connections are found in striate cortex (layers 2/3 and 5) contain predominately complex cells, which are insensitive to the sign of contrast polarity and tend to be broadly tuned for binocular disparity, consistent with our long-range results. Another possibility is a vertical feedback loop within V1 that sharpens neuronal orientation selectivity. Reversible inactivation of layer 6 of V1 often results in broadening of orientation tuning in upper layer V1 neurons (Allison et al. 1995), and this layer also contains a population of cells that have very long, narrow receptive fields (Gilbert 1977). Therefore a layer 6 → upper layer feedback circuit could have both the property of integrating inputs over long distances along an axis, and of enhancing orientation selectivity of neurons with receptive fields lying along this axis. Similar models, in which the output of units with collinear receptive fields is summed by “collector units,” have been proposed to explain the appearance of illusory diagonal lines in plaid patterns (Morgan and Hotopf 1989) and results similar to our contrast polarity experiment (Levi and Waugh 1996). Finally, it is quite possible that both of these putative integration mechanisms may be involved. What might be the normal perceptual function of the interactions characterized in the current work? It is quite suggestive that the rules of selectivity derived from our experiments parallel the rules proposed in Gestalt Theory that constrain whether features are grouped to form descriptions of objects (Wertheimer 1923). Collinearity, similarity, common motion, and consistent figure-ground relationships, among the most important of the Gestalt grouping criteria, are all here shown to facilitate orientation integration. Conversely, sharp changes in contrast polarity, depth, direction of motion, orientation, position, or figure-ground relationships between adjacent line or edge elements are generally strong cues that these elements belong to different objects. Therefore the requirements for orientation integration are well-suited to integrate only line and
edge elements are quantitatively similar to the properties of those studied in terms of contrast polarity, depth, and orientation selectivity. We have described for long-range orientation integration in the visual scene. Similar interpretations have been offered for results from other paradigms that involve integrative functions in spatial vision (e.g., Field et al. 1993; Kapadia et al. 1995; Polat and Sagi 1994).

The rules we have described for the integration of separated stimuli would seem to violate both Gestalt grouping principles and our intuitive notions about the nature of object contours. Why would the visual system want to integrate elements moving in opposite directions, at different depths, etc.? A careful consideration of the properties of contours in real visual scenes can reconcile this apparent paradox. Because of the effects of lighting and shadows, a contour can vary in contrast polarity across its length. A contour receding in depth could have sections with quite different disparities. An object rotating around its midpoint would have contour segments moving in opposite directions. And, at least to a localized detector, the side of the contour that seems to belong to the “figure” may vary along its length. Because none of these attributes are reliable indicators of whether separated edge elements lie along the same contour, it makes sense for the visual system to employ a long-range integration mechanism that is relatively insensitive to differences along these dimensions.

A mechanism that is coarsely selective for collinearity of line or edge elements, however, is likely to fare better, because most smooth contours are roughly collinear over the distances used in our study. Conversely, collinear elements at such separations would seem to occur rarely by chance (that is, by the precisely aligned edges of two nearby, but distinct, objects), and therefore it would greatly benefit a contour-detecting mechanism to be sensitive to such correlations in the visual scene. It is worth reiterating that, even at our long-range separations, we find little integration in the fovea at disparities greater than ~5–10 arcmin or angles greater than ~4°. Thus an integration mechanism with tuning properties similar to the selectivity we have described for long-range orientation integration may be well-suited to the type of correlations likely to be present over longer distances along object contours.

The hypothesized role of orientation signal integration in object contour integration is supported by the similarity between our results and those of more direct studies of contour integration. The detection of coherent chains of visual elements within a field of noise elements has been employed to investigate the properties of contour integration (Field et al. 1993; Hess and Field 1995). The properties enumerated in these studies—in terms of contrast polarity, depth, and orientation selectivity—are quantitatively quite similar to the properties we have characterized for long-range orientation integration.

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