Spatial and Temporal Integration of Signals in Foveal Line Orientation

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Westheimer, Gerald and Eric J. Ley. Spatial and temporal integration of signals in foveal line orientation. J. Neurophysiol. 77: 2677–2684, 1997. The discrimination of the orientation of a line improves with line length, reaching an optimum when a foveal line is ~0.5° long. We studied the effect of eliminating sections of the line, of displacing them out of alignment, and of delaying them. Orientation discrimination thresholds are only a little elevated when a 25-arcmin line is replaced by three equally spaced collinear 5-arcmin segments. Two collinear 5-arcmin segments show better thresholds than a single one when they are separated by as much as 20 arcmin. But thresholds are impaired by bringing line segments out of collinearity by as little as 1 arcmin. Asynchrony of up to 50 ms can be tolerated, but when the middle segment of a three-line pattern is delayed by ~100 ms there is active inhibition, thresholds being now higher than when the middle segment is absent. It is concluded that for signals to address the orientation discrimination mechanism optimally, they have to be contained inside a narrow spatial corridor and be presented within a time window of ~50 ms, but that some spatial summation can take place over a length of ~0.5° in the fovea. Because short lines made of black and white collinear segments do not have good orientation thresholds, whereas longer and interrupted lines do, it is concluded that what is involved is potentiating interaction between collinearly arranged neurons with identical orientation selectivity rather than summation of signals within the receptive fields of single neurons.

INTRODUCTION

The discrimination of orientation reaches an optimum in the human fovea when a contour has length of ~0.5°. This matches the diameter of the fovea approximately, but probably exceeds the estimated receptive field length of orientation-selective neurons in this part of the primary visual cortex, which are thought to form the basis for the elaboration of the “orientation” attribute of stimuli. Of course, the full population of neurons subserving this area has probably not been charted, and there are indeed, in layer VI, neurons with a direct input from the geniculate that integrate contours over a considerable length (Gibert 1977). Still, it remains likely that the discrimination of border or edge orientation derives its high sensitivity because there is interaction not only within the array of neurons subserving the same area of the visual field, whose orientation tuning encompass the stimulus orientation, but also within an ensemble of neurons of like orientations that are strung out along the length of the stimulus. The primacy of long straight lines in visual perception has been adduced as a fundamental consideration for the value of Listing’s law of eye movements, according to which the eyes always move so as to preserve collinearity of segments of a line passing through the center of the fovea (Westheimer 1981). The conjecture that there might be a basis for it in neuroanatomy (Mitchison and Crick 1982) was followed by experimental documentation of facilitation among cooriented, coaxial simple cells in the cat striate cortex (Nelson and Frost 1985). Here we report a variety of experimental findings bearing on the question of how line segments contribute excitation in time and space to act as a stimulus that optimally addresses the cortical mechanism that processes contour orientation.

METHODS

Psychophysical experiments were performed to test normal observers’ ability to detect the tilt away from the horizontal, clockwise or counterclockwise, of configurations made up of line segments 5 arcmin long and ~0.5 arcmin wide. Each segment could be independently rotated in 0.43° steps and placed on the screen to a precision of a few seconds of arc. It was thus possible to arrange several of these segments as if they were part of a single long line, or to give them specified offsets. In a given presentation, a configuration was shown that was made of one or more of these segments arranged in various ways and subjected to a rotation as a whole around the center. During experimental runs, in a given presentation this orientation had randomly one of seven equipartitioned values in a range from 2.5° counterclockwise to 2.5° clockwise. The observer had to indicate, by pressing a mouse button, whether the pattern appeared tilted clockwise or counterclockwise. Data were accumulated in sessions of 150 presentations, 3 s apart, in which a particular configuration was shown at random in a range of seven orientations spanning the horizontal. Psychometric curves resulting from this constant-stimuli procedure were analyzed by the method of probits, which gave a threshold, measured by half the distance between the 25 and 75% points, and an SE of this measure. All data points in this study are based on ≥300 responses obtained on at least two separate days. To obviate training and other long-term effects, results included in each figure were always obtained as a self-contained series even though sometimes two series included identical patterns. This explains the several occasions in this study where there are differences between threshold values for the same observer and configuration occurring in more than one series.

Stimuli were generated under computer control on HP1345A vector displays, which draw smooth lines. Observation was binocular at a distance of 3.75 m in a dimly lit room. The P31 phosphor of the display units gave a line intensity in the moderately high photopic range with high contrast. To obtain the data in Figs. 8 and 9, stimuli were generated by an antialiasing method on 1,024 × 768-pixel raster scan monitors, refreshed at 60 Hz and controlled by a Matrox Millenium video board on a Pentium computer. The uniform background on which black (2 cd/m²) and white (90 cd/m²) lines were superimposed had a luminance of ~40 cd/m². Lines 10 or 15 arcmin long, observed at 5 m, were drawn with an intensity gradient profile that made them appear smooth and tilted at angles as small as 0.5° from the horizontal.

The two authors as well as two undergraduate students, naive as to the problem, served as observers. All had normal vision, in the case of observer GW with a spectacle correction. Some had extensive practice in orientation discrimination tasks, but even
those who did not had initial thresholds in the vicinity of 0.5° of orientation. Steady head posture was aided by a head and chin rest. The exposure duration generally was 20 ms, but most of the data for observer GW were generated with an exposure duration of 200 ms. It had been shown earlier (Westheimer and Pettet 1990) that exposure duration is not a critical parameter in these tasks.

RESULTS

First of all, we determined, as a baseline, line orientation thresholds as a function of line length for foveal vision. This is shown as the solid line in the graphs of Fig. 1. As had been previously established, the threshold, measured as the minimum detectable change in angle of orientation and expressed in degrees, decreases with increasing line length and begins to asymptote when the line has a length of ~0.5°. (Note that in this and similar studies 2 separate dimensions share the same measure of “degree”: 1 is the meridian of line orientation and the other is the line length in terms of the angle it subtends at the eye.)

We now examine how well our observers can detect changes in tilt of a 25-arcmin line when various segments are removed. In Fig. 2 we show orientation discrimination thresholds for a 25-arcmin line when it is presented (Fig. 2A) as a continuous line, (Fig. 2B) when two 5-arcmin segments are removed, (Fig. 2C) when in addition another inner 5-arcmin segment is removed, leaving only two 5-arcmin terminators, and finally (Fig. 2D) when a middle orthogonal line is introduced, interrupting the “silent” continuity between these two outer segments. The results indicate a steady deterioration of performance from the first of these conditions to the last. In Fig. 1 it is seen that a single 5-arcmin line has an orientation discrimination of nearly 2°. The performance with two collinear segments in Fig. 2C is much better than could be accounted for by probability summation. (The observer knew that both segments always had the same orientation during a given presentation and could therefore identify the direction of tilt from either). Thus we measured the extent over which this potentiation occurs. The dashed lines in Fig. 1 show orientation discrimination thresholds of lines of various lengths when only their outer 5-arcmin terminators are displayed. Although the performance is never as good as for a fully drawn line, the presence of a collinear line segment separated by as much as 35 arcmin confers an approximately threefold improvement over the threshold for a single short line.

There is need, however, to address a separate issue. When a configuration consisting of two collinear lines is rotated, there is a translation of the endpoints. It is important, therefore, to examine the possibility that the observers’ facility in detecting the tilting of two line segments away from the horizontal rests on a true orientation discrimination and not on the detection of the vertical misalignment of the ends of the line segments. To decouple this vernier misalignment detection of the endpoints of the two line segments from true orientation discrimination, thresholds were measured

FIG. 1. Orientation discrimination thresholds as a function of line length in the human fovea (---). Also shown are thresholds for orientation discrimination of 2 collinear 5-arcmin line segments with identical outer end-to-end distances (---). Exposure duration: 20 ms (observers EL and ET), 200 ms (observer GW).
when the two line segments were rotated around their inner endpoints without the concomitant change in position of these endpoints if the whole configuration were part of one straight line. Thresholds are considerably higher now (Fig. 3). In a further experiment, vernier misalignment thresholds of two 5-arcmin-long purely horizontal lines was measured for a range of line separations. The results were expressed not in terms of the vertical linear displacement of the two lines at threshold but in terms of the angle, with respect to the horizontal, made by a hypothetical line joining the two inner endpoints. This mode of graphing the data allowed a direct comparison with the original situation depicted in Fig. 1, where the two line segments formed a part of a straight line whose misorientation with respect to the vertical had to be judged. It is seen in Fig. 4 that when the separation is <20 arcmin, the pure vernier task manifests a higher threshold. Taken together, the results shown in Figs. 3 and 4 constitute abundant evidence that the potentiating effect of a second collinear line segment in establishing the orientation of a straight line rests in the orientation domain and cannot be accounted for by offset detection of the line ends.

Once it is accepted that there is cooperative interaction of orientation signals between collinear line segments, questions concerning the spatial and temporal windows for this interaction can be asked. In the following we describe experiments relating to the width of the zone surrounding the line within which this pooling is effective, and also the time over which it occurs.

Figure 5 illustrates orientation discrimination thresholds for configurations in which parts of a straight line are parallel to but displaced by just 1 arcmin in a direction orthogonal to the other line segments, but all parts of the configuration always share the same orientation. (Here, as well as in the data of Fig. 6, the conditions were run in separate blocks, so that position or orientation ‘noise’ could not be invoked for threshold elevations.) It is seen that even this small displacement elevates thresholds compared with the situation when all the segments are exactly collinear. This phenomenon was studied parametrically in the experiment shown in Fig. 6. Here there were just two lines, 5 arcmin long and with an inner separation of 15 arcmin. Orientation discrimination was measured with an offset of the second line of 0–3 arcmin with respect to strict collinearity; the lines, however, rotated together. Again, even 1-arcmin offset impaired threshold. Thus it appears that the width of the pooling zone surrounding a straight line is exceedingly narrow.

Given such a low tolerance for spatial misalignment, what about temporal synchrony? In an earlier study (Westheimer and Wehrhahn 1994) it was demonstrated that there was an approximate doubling of orientation discrimination threshold when a 30-arcmin line was laid down by sequentially presented dots within a period of ~200 ms. Here we carried out the experiment of delaying the central segment of an aligned configuration made up of three equally spaced 5-arcmin segments for a total length of 25 arcmin. Figure 7 shows the result for a range of asynchronies. Two aspects of the curve are interesting. First, it appears that asynchronies up to 40 or 60 ms do not have much of an effect. This

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**Fig. 3.** Analytic experiments demonstrating that the superiority of orientation discrimination for 2 separated but collinear line segments over a single short line cannot be accounted for by vernier discrimination of the inner ends of the line segments. A: 2 collinear 5-arcmin line segments with 15-arcmin inner separation. B: vernier threshold for 2 lines, 5 arcmin long and separated by 15 arcmin, which remained strictly horizontal throughout. C: 2 5-arcmin line segments with 15-arcmin inner separation that were each rotated around their inner endpoint. D: single 5-arcmin line. Thresholds are expressed in degrees of rotation. In A, values represent angle of rotation of the single straight line on which both line segments are situated. In B, values represent the angle made between the horizontal and the virtual line joining the inner ends of the lines when the latter are in the position of just detectable misalignment. In C, values represent angle through which both line segments are rotated, each being rotated around its inner end. The fact that thresholds are larger in B than in A shows that observers could not use the vernier cue when making the judgment that the straight line in which the 2 segments are situated had experienced a rotation.

**Fig. 2.** Orientation discrimination of configurations composed of collinear 5-arcmin-long segments. A: 5 segments forming a single continuous line 25 arcmin long. B: 3 equally spaced 5-arcmin segments, overall length 25 arcmin. C: 2 5-arcmin lines with a 15-arcmin gap. D: 2 5-arcmin segments with 15-arcmin inner separation and a 5-arcmin orthogonal segment in the middle. Numbers: threshold for discrimination of orientation (°). Three observers; presentation duration 20 ms.
conforms to similar results obtained when the two components of a vernier task are delayed with respect to each other (Westheimer 1990). When there is asynchrony of several hundred milliseconds, thresholds are essentially equivalent to the situation in which the middle segment is absent. But at an intermediate delay in the vicinity of 100 ms, there is active inhibition. Showing the middle segment with this kind of delay now elevates thresholds substantially. A check test in which the middle segment is shown turned through 90° reveals that this inhibition is nonspecific with respect to orientation of the interfering stimulus.

**DISCUSSION**

Our experiments concern the mechanism by which contour orientation is processed in the primate brain. Of relevant interest is the fact that orientation processing reaches hyperacuity values, i.e., that the intact organism’s sensitivity transcends the grain of the available neural components. This applies equally to the mosaic of retinal receptors, whose acceptance zones and spacing are much wider than the few seconds of arc that separate the end positions of two lines with just discriminably different orientations, and the cortical orientation-selective neurons, whose orientation tuning widths are not nearly as narrow as the ≈0.5° line orientation discrimination thresholds routinely manifested by untrained normal observers. It follows that the intact organism’s performance depends on more than the response of a single neuron in the sensory stream whose trigger feature happens to be matched by the presentation of a given line target. The present study is intended to elucidate the neural interaction that must be in play when an observer identifies the orientation of a line target with such high accuracy.

In arriving at the surprising conclusion that summation of orientation signals of lines proceeds optimally only within a very narrow lateral range, one needs to be conscious of the geometry of the layout of the stimuli. The significant thread that runs through the current study is the role of collinearity for short line segments in the detection of orientation differences. The point of departure is a single straight line, whose significant attribute is orientation, defined by the angle it makes with the horizontal meridian passing through the fixation point. The first experiment was to test the dependency of the orientation discrimination on the length of the line. Then various segments of the line were blanked out, but collinearity of the remaining segments was retained (Figs. 1 and 2). Because there is inevitably a vertical offset between the inner ends of two separated near-horizontal but collinear line segments, and because we know that observers have great sensitivity for vernier misalignment detection, it was necessary to demonstrate that vernier acuity does not account for our thresholds. In Fig. 4 we have assurance that this is the case for a separation of ≈25 arcmin. The distinction

![Graph](image)

**FIG. 4.** Orientation discrimination threshold of a collinear line pair for a range of inner separations, and vernier misalignment detection threshold of 2 short horizontal lines with equal separation. For ease of comparison, both sets of data are plotted in terms of the angle of the virtual line joining the lines’ inner ends. Three observers; exposure duration 20 ms for EL and ET, 200 ms for GW. This experiment demonstrates that vernier discrimination cannot account for the superiority of orientation discrimination of 2 collinear line segments separated by up to ≈25 arcmin.
between the detection of vernier misalignment and difference in line orientation, which can be made on experimental grounds, has been examined in greater detail in a recent paper (Westheimer 1996). Once the focus has been established on line orientation and the role of vernier misalignment detection has been effectively discounted, it is possible to examine what happens when failure of collinearity is deliberately introduced. In Figs. 5 and 6 it is seen that parallel line segments no longer fully cooperate to pool their orientation signals when there is as little as 1 arcmin of deviation from collinearity. These results are in accord with recent studies on the orientation sensitivity of illusory contours when the supporting borders are not perfectly aligned (Westheimer and Li 1997). The implication for the pattern of cortical connectivity put forward by Mitchison and Crick (1982) and demonstrated by Nelson and Frost (1985) for simple cells in the cat striate cortex is the need for high precision of positional alignment of fields sharing the same orientation.

Central to the issue is the receptive field length of orientation-selective neurons in V1 subserving the fovea, where our measurements were made. This width can be as low as 4–6 arcmin (Dow et al. 1981; Gur and Snodderly 1987). Data for the aspect ratio are not readily available, and it is not known to what extent endstopped units, whose signal acceptance in the orientation direction is limited, are involved. Moreover, there are neurons in layer VI with much longer receptive fields (Gilbert 1977). However, our orientation discrimination threshold keeps on improving with line lengths (Fig. 1), and the possibility has to be considered that the final elaboration of the orientation attribute depends on the confluence of signals from neurons that are arrayed along the direction of the line. This concept has to be distinguished from the usual one put forward for the high sensitivity for orientation, according to which the latter arises from something like a `vector sum’ from a population of neurons of a range of cognate orientations (Gilbert and Wiesel 1990; Vogels and Orban 1990). But the receptive fields of such neurons would be in more or less the same position and would differ only in the orientation. On the other hand, when studying the line length dependency of human line orientation sensitivity, the significant issue is confluence of signals from neurons whose receptive fields have the same orientation but whose locations are arrayed along the direction of this orientation.

Does the neural substrate of our excellent ability to identify the orientation of long lines reside in orientation-selective neurons with long receptive fields or in the pooling of signals from smaller fields with the same orientation? The consensus among those recording receptive fields in the primary visual cortex is that there is no overlap of fields when the recording site has been shifted through one hypercolumn, i.e., from one site with a given receptive field orientation to the next one over. Distance between hypercolumns in the monkey is ~1.5 mm. Extrapolation of magnification factors into the center of the fovea suggests values of ~0.1°/mm (Hubel and Freeman 1977; Hubel and Wiesel 1974) or perhaps even less (Dow et al. 1981). This means that receptive fields with identical orientation selectivity separated by one hypercolumn would differ in position in the visual field by ~0.15°. It follows that targets separated by 0.5° would be represented by neurons several hypercolumns apart and, therefore, not likely to have overlapping receptive fields. If this view is correct, the interactions characterized by our data would have to be subserved by horizontal connections between neurons, which are known to exist and to extend.

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**FIG. 5.** Orientation discrimination of parallel line segments with and without collinearity. A: single line 25 arcmin long. B: 2 5-arcmin line segments with an intervening 15-arcmin segment displaced upward by 1 arcmin. C: 3 5-arcmin collinear segments, 5 arcmin apart each. D: as in B, but middle line displaced upward by 1 arcmin. E: as in C, but there were 2 middle segments, 1 above and the other below the straight line on which the outer segments lie. All parts of all configurations were rotated together and throughout maintained their relative positions with respect to the straight line defining their orientation.
The data in Fig. 7 show further that the temporal window for such interaction is several tens of milliseconds; beyond that there is an inhibitory interaction that emerges for an onset asynchrony of $\approx 80$ ms.

Although the narrowness of the corridor for spatial summation of orientation signals is somewhat surprising, the confluence of oriented signal along their direction of orientation complements previous findings on improved detection of such stimuli. Polat and Sagi (1994), using Gabor patches, and Kapadia et al. (1995), using line stimuli, found a reduction of detection threshold when a similar suprathreshold target was situated along the direction of orientation. As a confirmation that orientation-selective neurons in V1 are indeed involved, Kapadia et al. were able to demonstrate...
were, therefore, broadly comparable with ours. The longer the rectangles, the lower were Thomas’ thresholds, but the data also fail to show the reciprocity between length and thresholds that would be expected if there were strict summation of light signals. These findings can be regarded as corroboration that simple length summation is not a factor when thinking about the processing of line orientation.

Our results, however, involve not the detection of oriented stimuli but rather the discrimination of their orientation. That there is need to postulate confluence of orientation-selective signals over a range of spatial positions is a view that has been previously advocated by, among others, Wenderoth et al. (1978), Morgan and Hotopf (1989), and Field et al. (1993). The latter study seeks to explain perceptual grouping of a string of oriented targets by an orientation-selective and possibly phase-invariant linking process extending over retinal regions of up to 0.9°. Wenderoth et al. and Morgan and Hotopf, using, respectively, an alignment paradigm and the emergence of virtual contours in lattices, inclined toward the view that the output of local units with preferred orientation was processed by integrator or collector units. There is a fundamental difference between these two models: one may be regarded as hierarchical, in which a further stage fed by first-level orientation-selective units is postulated, whereas we, in accord with the view of Field et al. and more recent notions about dynamic cortical processing (Gilbert et al. 1996), are willing to entertain ideas of potentiating interaction within the first ensemble of orientation-selective neurons. That opposite contrast polarity cannot be accepted for contiguous line segments but does not stop facilitation of separated line segments speaks strongly against the integration or pooling of light signals in single simple neurons. The notion of “collector” units arose in connection with perceptual phenomena such as illusory contours. But recent work on illusory contours (Westheimer and Li 1997) has shown that they do not possess the good orientation sensitivity that is highlighted in the current experiments, and it would therefore be inappropriate to look to such units to account for our present data. Thus it might be parsimonious to seek interpretation in terms of dynamic processing, in which the response properties of early units are modified as a result of interaction within their own ensemble.

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