



Vernier Acuity with Non-simultaneous Targets: The Cortical Magnification Factor Estimated by Psychophysics

BETTINA L. BEARD,*‡ DENNIS M. LEVI,† STANLEY A. KLEIN*

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The eccentricity at which peripheral thresholds double their foveal value (E_2) may relate to the visual system's anatomical organization. Using a variety of experimental approaches, previous estimates of E_2 for vernier acuity have ranged from less than 0.1 deg to greater than 15.0 deg. This broad range of values seems to challenge the usefulness of E_2 for determining visual topography. We explain that the varying contributions from at least two different regimes, spatial filter and local sign, may explain the broad range of E_2 values found previously. We attempt to limit responses to the local sign regime, where it may be possible to determine the psychophysical analog to the gradient of the cortical spatial grain. In our experiments we measure how vernier task performance falls off with eccentricity. We hypothesize that if the vernier features are adequately separated in time, they will fall outside of the spatial filter's temporal integration span and the local sign regime would then predominate for precise positional processing. Using an interstimulus interval ranging from 20 to 200 msec between the two vernier features, we estimate that vernier thresholds in the local sign regime double at about 0.8 ± 0.2 deg eccentricity, which is similar to anatomical estimates of the eccentricity at which the linear spacing of human cortical units doubles. Copyright © 1996 Elsevier Science Ltd

Vernier acuity Cortical magnification Periphery Temporal Local sign

INTRODUCTION

Visual performance is often better in the central visual field than peripherally. The fall off in performance with eccentricity is nearly linear for many spatial tasks (Weymouth, 1958). To quantify the fall off rate of spatial thresholds, Levi *et al.* (1984, 1985) introduced the E_2 factor. E_2 represents the eccentricity at which peripheral thresholds double the foveal value and is simply the negative of the x -axis intercept of a linear threshold vs eccentricity function. It was thought that the magnitude of the psychophysically based E_2 factor could potentially provide information about visual system functional organization through its connection to spacing of anatomical units. However, the usefulness of E_2 estimates for determining visual topography has been called into question (Whitaker *et al.*, 1992) since estimates

based on various experimental approaches range from less than 0.1 deg to greater than 15.0 deg (see Table 2). The present paper has two aims: (1) to explain this wide range of E_2 estimates as a reflection of the confounding of two regimes; and (2) to present data in which E_2 values for vernier acuity may be connected with the anatomical cortical magnification factor.

Although there may be many mechanisms or sources of noise that limit performance, two distinct regimes appear to be responsible for localization judgments: (1) spatial filter; and (2) local sign (Burbeck & Yap, 1990; Levi & Klein, 1990). For small separations, localization thresholds depend primarily on the stimulus feature separation (rather than eccentricity) and are most likely limited by the responses of spatial filters sensitive to both stimulus features (Watt & Morgan, 1983; Klein & Levi, 1985, 1987; Wilson, 1986; Bradley & Skottun, 1987; Waugh & Levi, 1993a). Figure 1(a) presents a schematic of a spatial filter detecting the spatial offset of two abutting, dark, horizontal lines. When the vernier feature separation is large relative to the eccentricity [see Fig. 1(b)], vernier thresholds depend on stimulus eccentricity (rather than separation). In this regime, thresholds may be based on

*University of California, School of Optometry, Berkeley, CA 94720, U.S.A.

†University of Houston, College of Optometry, Houston, Texas, U.S.A.

‡To whom all correspondence should be addressed [Email: tinab@adage.berkeley.edu].

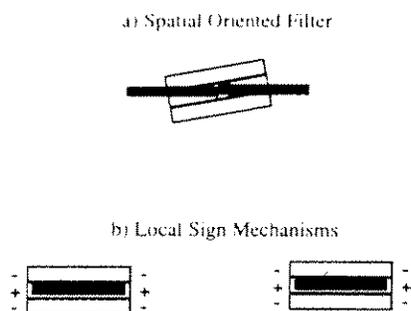


FIGURE 1. Schematic of spatial filter and local sign mechanisms. (a) For abutting stimuli, both the reference and test lines would be processed within a single filter. (b) For widely separated reference and test lines, each feature would be processed independently by local sign mechanisms.

the linear spacing of human cortical functional units. The mechanisms that limit performance in this regime have been referred to as "local signs" since each element is thought to possess a unique position label or "sign" (Lotze, 1884). Local sign mechanisms have been posited to place a separate position label on each stimulus feature. These position labels are thought to be compared at a later stage using something analogous to a cortical ruler. Within the local sign regime, vernier thresholds would be limited not only by the spatial uncertainty within the local position labels (Lotze, 1884; Klein & Levi, 1987; Levi & Klein, 1990; Waugh & Levi, 1993a; Wang & Levi, 1994) but also by higher-order processes (Sterken *et al.*, 1994) in the later comparison stage.

Both the spatial filter and local sign regimes involve filter responses, however, we argue that in the small separation regime the most sensitive mechanism for position is based on the contrast responses of spatial filters, while in the large separation regime, the local sign (position label) of the filters becomes more important. Positing two regimes appears necessary since a single filter mechanism cannot explain data showing that thresholds for widely separated target features are not changed by the addition of distractors (Morgan & Ward, 1985; Levi & Westheimer, 1987). To clarify the difference between the spatial filter and local sign regimes, we will introduce two numbers, S_2 and L_2 , corresponding to the point at which thresholds double in the separation and local sign regimes, respectively.

The factors limiting vernier acuity in the fovea (e.g., stimulus feature characteristics and filter properties) may be qualitatively different from the factors limiting acuity in the periphery (e.g., sampling, uncertainty, attention, masking). Later in the Discussion section, we will provide evidence that some previous estimates of E_2 may have confounded the responses of spatial filter and local sign mechanisms. Our aim in the present study is to reduce the qualitative differences between the fovea and periphery and limit responses to the local sign mechanisms. We attempt to suppress spatial filter responses by temporally separating the reference and test targets. The logic is that the two feature halves should fall outside of

the temporal integration span (≈ 100 msec; Waugh & Levi, 1993b) of a single spatial filter. Localization thresholds within the local sign regime are independent of stimulus feature characteristics because this information is not required to assign the position labels or to compare outputs. Therefore, at long temporal separations, localization thresholds would be expected to be independent of stimulus characteristics. Using same and opposite polarity stimuli (Experiment 1) or different stimulus strengths (Experiment 2) our results are consistent with the idea that local sign mechanisms primarily mediate threshold when the reference and test target features are successively presented. Experiments 3 and 4 estimate L_2 over a range of temporally successive presentations. The use of a temporal asynchrony and opposite polarity features minimize the use of spatial filters for closely spaced stimuli. Under optimal conditions our average estimate of L_2 is 0.8 ± 0.2 deg.

GENERAL METHODS

Experiments 1–3

Portions of these experiments were performed sequentially in two laboratories using similar equipment; one laboratory is located in the College of Optometry in Houston, Texas and the other in the School of Optometry in Berkeley, California. In both laboratories, line stimuli were presented on a Tektronix 608 monitor with a P31 phosphor (decay rate to less than 1% within approximately 250 μ sec) and generated by a Neuroscientific VENUS stimulus generator (frame rate of 270 Hz). Viewing was monocular with best correction using the natural pupil usually from a 2.2 m viewing distance. From this distance, the screen (256 pixels) subtended 4.0 deg visual angle. In the 90 min spatial separation condition, viewing distance was halved (the stimulus width and length were kept at the same angular size). The square display screen had a constant mean luminance of either 132.5 cd/m^2 (Houston lab) or 120 and 114 cd/m^2 (California lab). In the Houston lab, observers were positioned in a chin and forehead rest to minimize head movements. In California, normal room illumination from overhead lighting was prevented from reflecting off the display monitor with a surrounding visor.

Stimuli were horizontally oriented lines with abrupt onset and offset. A 10 min line length was chosen since threshold is independent of line length for lengths above about 5 min arc (Westheimer & McKee, 1977; Watt, 1984). From both the 2.2 and 1.1 m viewing distances, line width was equal to 2.25 min arc (4 and 2 pixels for the 2.2 and 1.1 m distances, respectively) which was always within Ricco's area, as determined in a pilot experiment.

Vernier, or localization, thresholds were measured for simultaneously presented reference and test lines and for temporally asynchronous exposures. Figure 2 shows three possible temporal relationships between the reference and test stimuli: (1) the reference and test stimulus are turned on and off simultaneously (to be called

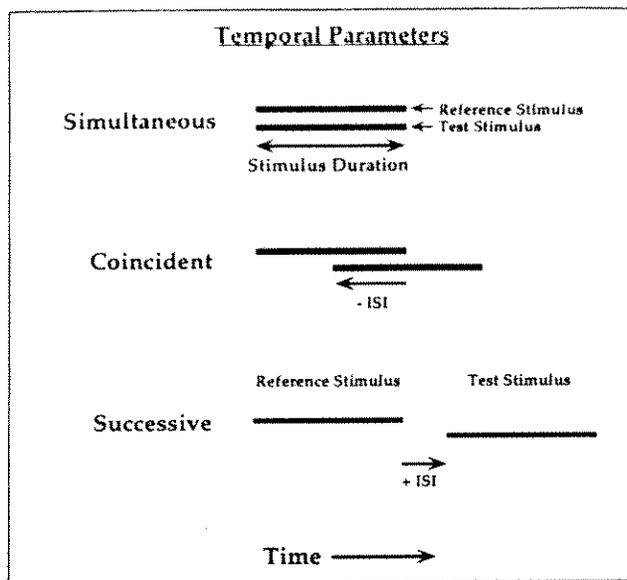


FIGURE 2. The temporal relationships between the reference and test stimuli used in these studies: (1) in the "simultaneous" condition the reference and test stimulus are turned on and off simultaneously; (2) in the "coincident" condition there is some temporal overlap or coincident presentation time; and (3) in the "successive" condition the test target is presented after reference line extinction. Reference and test line durations were always the same except for a few experimental conditions mentioned in the text. The amount of time between reference offset and test onset is the interstimulus interval (ISI). A negative ISI means the targets had some temporal coincidence, whereas positive ISIs represent conditions where the reference and test are successively presented. For the simultaneous condition the ISI is the negative of the stimulus duration.

simultaneous); (2) the reference and test targets have some common presentation time (to be called temporally coincident); and (3) the test target is presented after reference line extinction (to be called successive). Reference line duration was always the same as the test line duration unless otherwise specified. Interstimulus interval (ISI) refers to the amount of time between reference offset and test onset.* A negative ISI means that the targets temporally overlapped (simultaneous and coincident case) for a duration equal to the absolute value of ISI in msec. Observers were instructed to fixate the left "reference" line, while judging the vertical offset direction of the right "test" line.

Experiment 4

For this experiment line stimuli were presented on a SONY monitor (subtending 13×10 deg visual angle from 1 m, with 480 vertical pixels) using David Brainard's MATLAB stimulus presentation programs in conjunction with Denis Pelli's Video Toolbox. The large SONY monitor, with almost twice the number of pixels,

was used to rule out the potential edge effects of the smaller 608 monitor in the wide spatial separation conditions. Viewing was either binocular or monocular (see figure legends) from 2 m for observer BLB and binocular for observers DL and SK. The viewing distance was halved in the 150 min spatial separation condition. The screen had a constant mean luminance of 50 cd/m^2 (with shielded overhead lighting). Horizontally oriented lines (5 min length; 1.2 min height) were used. Localization thresholds were measured for temporally asynchronous (ISI = 125 or 150 msec) test and reference lines. Reference line duration was typically 500 msec, while test line duration was 150 msec.

Psychophysical procedures for Experiments 1-4

Line detection thresholds. Detection thresholds were obtained using a four-choice rating scale method of constant stimuli (Klein & Stromeyer, 1980) with stimuli ranging from not visible to slightly visible. The test stimulus contrast was randomly either 0.0, 1.0, 1.5 or 2.0 times a base level, which was close to each observer's threshold determined from pilot data. The detection stimulus was presented in the same location on the screen on each trial and was located a specified distance from a fixation line. Feedback about the actual contrast level was provided after each response.

Localization thresholds. Localization thresholds were obtained using a five-choice rating scale method of constant stimuli. On a given trial, the test line was randomly presented in one of five offset positions relative to the reference line; horizontally level with the reference line, or displaced one or two levels above or below the reference line. On the Tektronix 608 monitor subpixel offsets were produced by manipulating the pixel contrasts comprising the test line (Morgan & Aiba, 1986; for details see Klein *et al.*, 1990). The psychophysical task was to determine the test line offset direction and magnitude. After each trial, observers were provided with feedback about the correct test line position. Random inter-trial stimulus jitter was used to reduce absolute positional cues.

Data analysis. A minimum of three blocks were run for each condition (one block ≈ 125 trials). We used the ROCFLEX signal detection program to estimate contrast detection and localization thresholds for each block of trials (Levi *et al.*, 1984; Klein, 1985). Thresholds were defined to be at $d' = 1$. For detection, the psychometric function was based on a transducer exponent of $n = 1.5$, where the transducer function is $d' = (s/s_0)^n$, with s being stimulus strength and s_0 being threshold. For localization thresholds, ROCFLEX constrained the transducer exponent to be unity. To verify our choice of n , unconstrained exponents were also determined and were close to 1 for localization and were typically between 1.5 and 2.0 for contrast detection. Plotted thresholds are the geometric mean of three to six estimates that have been weighted by their inverse variance. Standard error bars represent the larger of the within and between run variances (Klein, 1992).

*We use ISI rather than SOA (stimulus onset asynchrony) because the ISI is independent of duration, and because vernier threshold is determined by the temporal overlap of the stimuli, rather than by the SOA.

Six observers participated in different aspects of these experiments: the authors and three naive observers. All were corrected myopes, free of ocular pathology.

EXPERIMENTS 1 AND 2: ARE LOCALIZATION JUDGMENTS FOR TEMPORALLY SUCCESSIVE REFERENCE AND TEST TARGETS INDEPENDENT OF STIMULUS CHARACTERISTICS?

Rationale

We will show later (see Discussion and Table 2 for details) that previous measurements of the fall off in vernier acuity reflect multiple processes. Some estimates of E_2 were actually measures of S_2 , or the separation dependence of vernier acuity because these estimates included spatial filter responses. Since spatial filters provide very precise vernier judgments for closely spaced features, very low values of S_2 would result.

Vernier acuity within the spatial filter regime is dependent on relative polarity (Murphy *et al.*, 1988; O'Shea & Mitchell, 1990; Morgan, 1991; Levi & Waugh, 1994) and contrast (Watt & Morgan, 1983; Bradley & Skottun, 1987; Wilson, 1986; Klein *et al.*, 1990; Wehrhahn & Westheimer, 1990; Waugh & Levi, 1993a). Within the local sign regime, the separate, coarse position labels placed on each stimulus feature are relatively independent of polarity (Burbeck, 1986; Levi & Westheimer, 1987) and contrast (above four times the detection threshold, Waugh & Levi, 1993a). We hypothesized that if the vernier stimulus features are temporally successive, then filter mechanisms will not be used. Rather, local sign mechanisms will mediate threshold, making abutting vernier thresholds polarity and contrast-independent at positive ISIs. We carried out two experiments to test the hypothesis that polarity (Experiment 1) and contrast (Experiment 2) have minimal effects on threshold at larger ISIs.

Methods

Experiment 1: Dependence on polarity. In the first experiment, localization thresholds were determined for reference and test line targets that were either both light, both dark or the reference was light and the test line was dark (opposite polarity). Stimulus duration was different for the two observers (DM = 25 msec and BLB = 50 msec). Detection thresholds (in % min) were determined for the dark (DM = 49.2 ± 2.9 ; BLB = 14.9 ± 1.2) and light (DM = 49.3 ± 4.4 ; BLB = 13.2 ± 1.6) lines for each observer. The light and dark lines were then equated in visibility (DM = 4 times and BLB = 9 times the contrast detection threshold) and localization thresholds were obtained at various ISIs.

Experiment 2: Dependence on contrast. In the second experiment, detection thresholds (in % min) for 50 msec test flash exposures (dark lines) were determined for two observers (SC = 16.1 ± 0.7 ; BLB = 14.9 ± 1.2). Localization thresholds were then determined for different test line contrasts above the detection threshold. In the localization task, the reference line was set to the same physical contrast as the test line and thresholds were

obtained at four ISIs. Experiments 1 and 2 were done in the California lab.

Results

Experiment 1: Dependence on polarity. Figure 3 presents localization thresholds (i.e., vernier thresholds) in arc min for same and opposite polarity reference and test stimuli as a function of ISI for two observers. To see if the change in threshold is a constant factor for all conditions, we use a logarithmic scale for vernier thresholds. The various symbols represent stimulus polarity conditions as shown in the legend. Observer DM collected data for abutting and for spatially separated (90 min separation) reference and test lines, while only abutting thresholds were determined for observer BLB. The leftmost data point (at an ISI of -25 for DM and -50 for BLB) represents localization thresholds for simultaneous exposures. Positive ISIs represent conditions where the reference and test are temporally successive. It is at positive ISIs (indicated with a gray background) that we hypothesize that localization thresholds would be polarity and contrast-independent and therefore limited by local sign responses.

Vernier thresholds were similar when the reference and test stimuli were both light or dark lines, as would be expected since the light and dark line visibilities were equal. The simultaneous thresholds for both observers are higher than typically reported, particularly in observer DM (≈ 0.3 min or 20 sec). These higher thresholds may have resulted from the low stimulus visibility (≈ 4 and 9 times detection threshold for DM and BLB, respectively) along with the $d' = 1$ threshold criterion we used to estimate thresholds (corresponding to 84% correct rather than $d' = 0.675$, corresponding to 75% correct). For both observers, lower thresholds were obtained for the same polarity, simultaneous presentations than for the opposite polarity conditions and this low threshold was maintained as long as there was some temporal overlap (negative ISIs). When the vernier features were temporally successive (ISI > 0), both observers showed threshold elevation. Opposite polarity reference and test targets produced elevated thresholds that were relatively independent of ISI. At negative ISIs there was about a 3- to 4-fold ratio of thresholds between same and opposite polarity conditions. At positive ISIs the ratio of thresholds was about 1.5-fold in both DM and BLB. This 1.5-fold ratio difference between same and opposite polarity conditions was greater than expected, since stimulus polarity should have little differential effect on thresholds if localization thresholds at positive ISIs are limited by local sign mechanisms. Later (Experiment 4) we will show that this ratio approaches unity when anticipatory eye movements are minimized.

Experiment 2: Dependence on contrast. In Fig. 4, localization thresholds are presented for two observers as a function of ISI at three or four contrast levels (specified in contrast threshold units, CTU; shown with different symbols). For both observers, stimulus visibility was important when the reference and test stimuli temporally

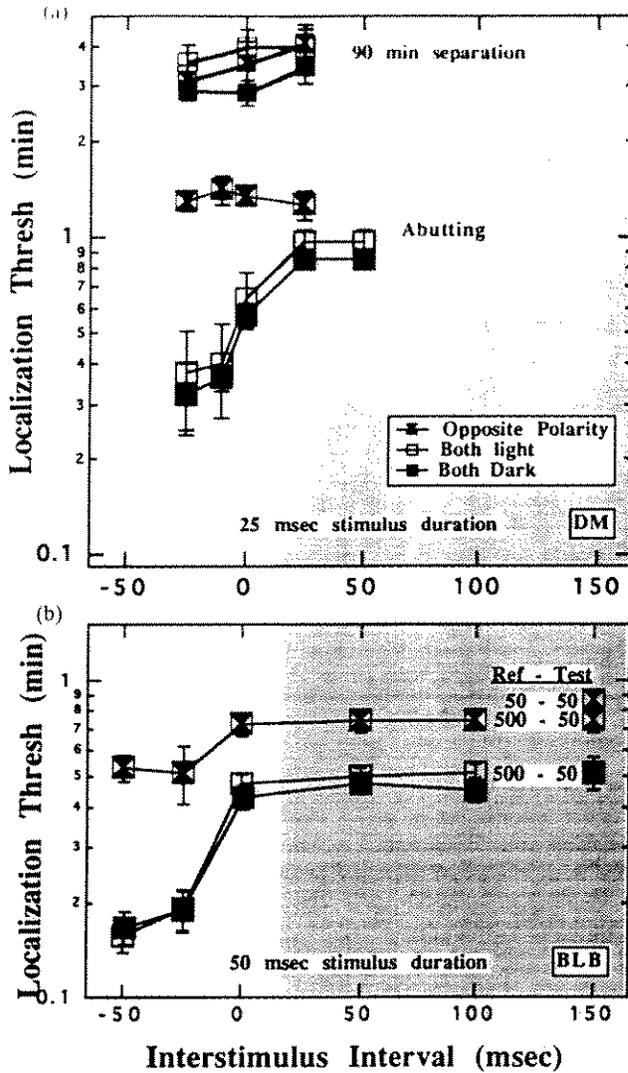


FIGURE 3. Localization thresholds are presented as a function of ISI for same and opposite polarity reference and test stimuli. The leftmost data point represents localization thresholds for simultaneous exposures. Stimulus duration was 25 msec for observer DM (a) and 50 msec for BLB (b). Positive ISIs (successive presentations) have been given a gray background for clarity. On the right-hand side of (b) are three data points representing conditions of different reference line duration. The first number represents the reference line duration in msec, the second number shows the test line duration (always 50 msec). The two upper data points show results for opposite contrast polarity stimuli and the lower data point shows the results for same polarity stimuli (both dark). These data show that although the stimulus exposure was too brief to allow optimal fixation, a longer duration reference line does not alter the 1.5 ratio difference between same and opposite-contrast polarity conditions at positive ISIs. Data for DM at a 90 min spatial separation are also shown.

overlapped (ISI < 0), particularly at the higher contrast levels, but had much less effect when there was no temporal coincidence. A small improvement (50%) in vernier acuity in going from 3 to 11 times threshold is compatible with local sign processing. A much larger improvement would be expected from filter processing. These results are consistent with the hypothesis that filter mechanism responses can be suppressed with temporally successive vernier feature presentation.

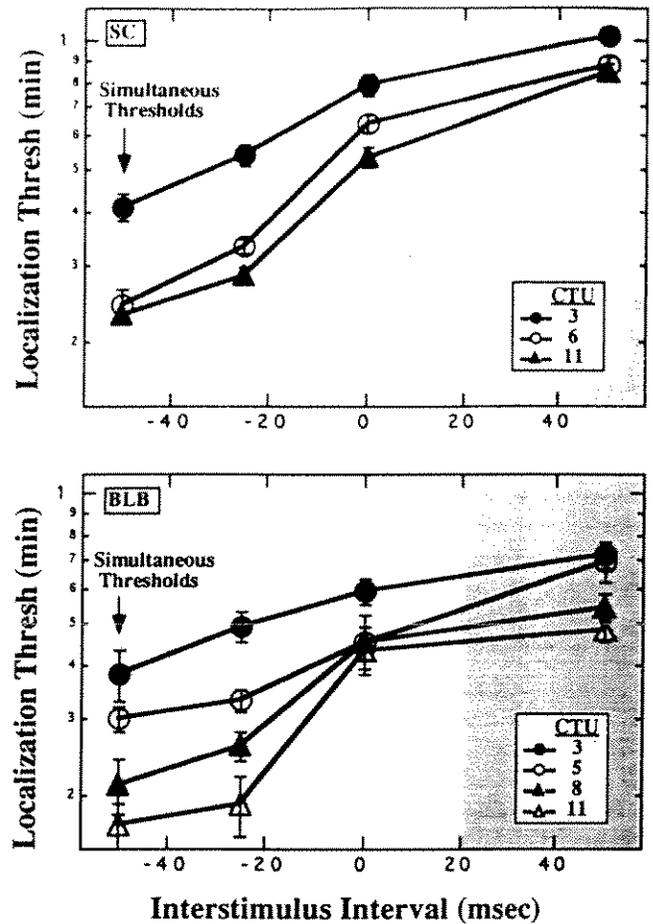


FIGURE 4. Localization thresholds are plotted as a function of ISI. The legend shows the different contrast levels in contrast threshold units (CTU) used for each observer. Stimulus duration was 50 msec.

EXPERIMENT 3: E_2 ESTIMATES FOR SAME POLARITY STIMULUS FEATURES

Rationale

Our first two experiments showed that the isolation of local sign responses is improved by using temporally successive feature presentations. We next hypothesized that the change from spatial filter to local sign mechanisms is gradual across ISI for abutting reference and test features. Conversely, at wide spatial separations, thresholds would be constant across ISI, since at wide separations, thresholds are already mediated by local sign mechanisms. Therefore, at positive ISIs, thresholds for abutting features should approach thresholds for wide feature separations. These thresholds should not completely converge since position uncertainty should increase as eccentricity increases (Levi & Klein, 1990). At long temporal delays (ISI > 200 msec), elevated thresholds would most likely be due not only to local sign mechanism position uncertainty but also eye position uncertainty and memory limitations (Matin *et al.*, 1980; White *et al.*, 1992). The result would be values of E_2 that are inflated. Therefore, in Experiment 3 we measured localization thresholds for various reference

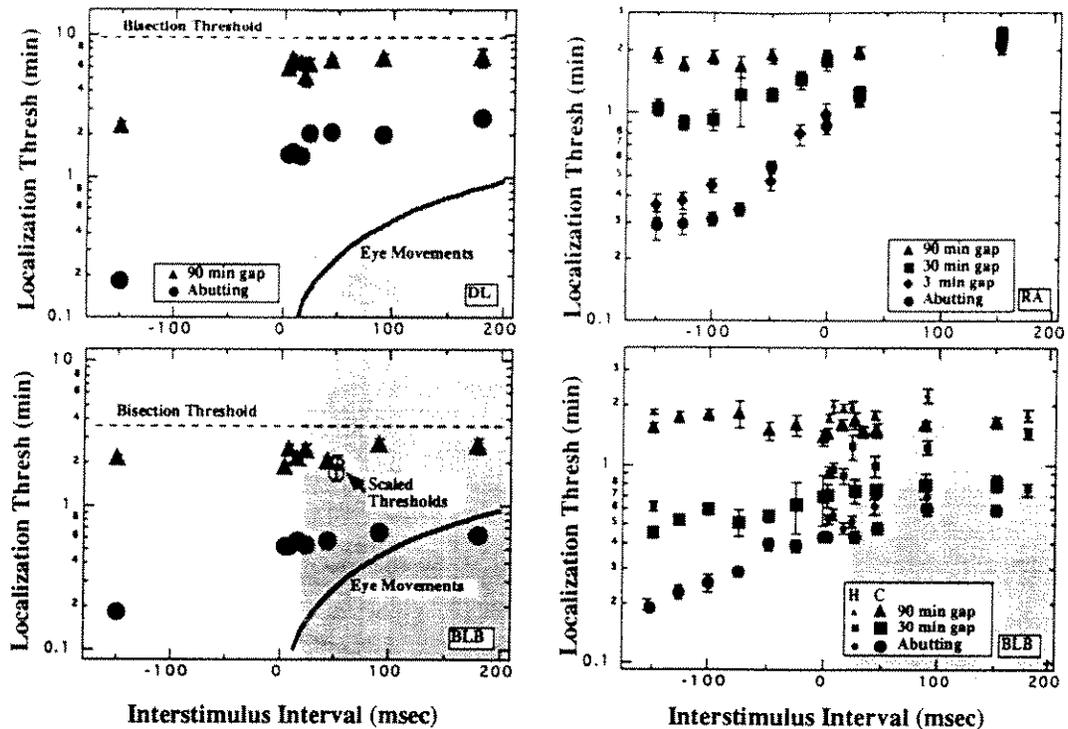


FIGURE 5. Localization thresholds are presented as a function of ISI. On the left-hand side of the figure, the physical contrast was the same (189% min) for both spatial separations. Two spatial separation conditions are shown: abutting (solid circles) and 90 min separation (solid triangles). Bisection thresholds for the test stimulus without the reference are shown by the dashed line. The solid line labeled "Eye movements" is based on data showing that the eye drifts approximately 3 min every second (Riggs *et al.*, 1954). The scaled thresholds (open symbols) are explained in the Discussion. On the right-hand side of the figure, the perceptual contrasts of the stimuli were set to 8 times contrast detection threshold for all separations. Four spatial separation conditions are shown. The 3 min data for BLB were omitted for clarity of presentation. The H and C stand for data collected in Houston and California, respectively.

and test target spatial separations for ISIs ranging from -150 up to 180 msec to obtain S_2 (negative ISIs) and L_2 (positive ISIs) estimates.

Methods

In the third experiment, abutting and 90 min spatial gap conditions were tested for a range of ISIs. Reference and test stimulus duration was 150 msec and line strength (the product of line contrast in % and line width in min arc), was held constant at 189% min (this is about 17 and 8 times detection threshold for abutting and 90 min spatial separations, respectively). Test and reference lines were black.

To determine whether the ability to perform the vernier task was influenced by the visibility differences in abutting and widely separated features, we also obtained measurements when line strength was maintained at 8 times line detection threshold for all feature separations. Two observers were tested in Houston (DL and BLB with simultaneous and successive presentations—see Fig. 1), and two in California over a wide range of ISIs: one psychophysically inexperienced observer who was naive to the purpose of the studies (RA) and one of the authors, who also participated in the earlier experiments (BLB).

Results

In Fig. 5 localization thresholds are plotted as a

function of ISI for reference and test stimuli that were abutting (circles), or spatially separated by 3 min (diamonds), 30 min (squares) or 90 min (triangles). Since reference (and test target) duration was 150 msec, the leftmost data point (-150 ISI) represents localization thresholds for simultaneous exposures as defined in Fig. 2. The conditions where the reference and test are temporally successive and most likely within the local sign regime ($ISI > 20$ msec) have been highlighted in gray.

First examine the results for the two lefthand graphs. Observer DL's threshold for abutting, simultaneously presented targets is similar to BLB's. However, distinct individual differences are evident when an interstimulus interval is introduced. For abutting lines, thresholds increase by a factor of 10 in observer DL and a factor of about 3 for BLB at ISIs near zero. This elevation was not as large at the wider spatial separation. For the 90 min separation, DL demonstrates a 3-fold increase in thresholds when a temporal asynchrony is introduced, followed by thresholds that are relatively constant across positive ISIs. BLB shows localization thresholds that are essentially independent of ISI when the vernier features are spatially separated.

Horizontal lines (10 arc min length) separated by 90 arc min are located close to the Tektronix 608 vertical screen edges. It may be argued that thresholds would be

either helped or hurt by the presence of the edges. To reduce the edge cue, we jittered the stimulus position from trial to trial by an amount greater than the largest vernier offset. This jitter, however, is not a perfect control since the observer could possibly make independent screen bisection judgments for both the test and the reference features and then compare these judgments. For this reason we ran two control experiments to determine if the edge was used for localization judgments. First, we halved the viewing distance, stimulus width and stimulus length (so the width and length remained the same angular size) and found that localization thresholds did not substantially change from the normal viewing conditions. Second, we measured test line position thresholds without a reference target (i.e., the bisection cue) to see if the horizontally oriented screen edges were influencing vernier thresholds. The horizontal dashed line (labeled bisection threshold) presented in both left-hand panels of Fig. 5 represents individual test line localization thresholds obtained without a reference line. Since this screen bisection threshold was higher than the 90 min gap localization thresholds, this edge cue cannot fully account for vernier thresholds at the wide spatial separation. On the basis of these results it is doubtful that the screen edges provide a useful cue in the 90 min spatial separation condition. In a later experiment (see Experiment 4) we wished to investigate localization thresholds for even wider (150 min) spatial separations. Because of our concern about possible bisection cues, we carried out the experiment on a display that was more than three times larger in the relevant dimension, thus placing the screen edges out of harm's way.

In the two right-hand graphs of Fig. 5, simultaneously presented stimulus thresholds ($ISI = -150$) increased sharply with increasing spatial separation, as would be expected if an oriented filter mechanism were operating for the abutting case. As hypothesized, abutting targets (solid circles) show a gradual increase in thresholds with ISI in both observers. This gradual threshold increase levels off at around $ISI = 80$ msec for observer BLB. We found that the slope of this increase is determined by the stimulus duration (i.e., the slope is greater for briefer durations). Targets separated by a 30 min spatial gap demonstrate an almost 2-fold increase in threshold for RA and a 1.5-fold increase for BLB at negative $ISIs$ but level off at positive $ISIs$. Temporal asynchrony had little effect on reference and test stimuli separated by 90 min, most likely because processing is within the local sign regime. BLB had previously made many of the same measurements (i.e., same perceptual contrast) in the Houston lab (smaller symbols). There is considerable consistency in the data collected in the two labs. These results suggest that localization thresholds are limited by at least two factors, one that is temporally dependent (the spatial filter regime) and one that is essentially temporally independent (the local sign regime).

Within the filter regime, vernier thresholds plotted as a function of target separation follow Weber's law, where threshold is proportional to separation (Sullivan *et al.*,

1972; Beck & Schwartz, 1979; Levi & Klein, 1990). Within the local sign regime, vernier thresholds also increase with increasing target separation except that the increase is now explained by the increased target line positional uncertainty as eccentricity increases (Levi & Klein, 1990). This threshold vs eccentricity function can be fit with a straight line that intersects the x -axis at a value defined by (negative) E_2 (Levi *et al.*, 1985). Although a linear function such as:

$$Th = a + bE \quad (1)$$

could be used to estimate E_2 , we used nonlinear regression to obtain standard error estimates of the parameters of interest. This formula took the form:

$$Th = Th_0(1 + E/E_2) \quad (2)$$

where Th_0 is the threshold at the fovea ($E = 0$). The connection between the nonlinear regression parameters Th_0 and E_2 and the linear regression parameters [Eq. (1)] is:

$$Th_0 = a \quad (3)$$

$$E_2 = a/b \quad (4)$$

In Fig. 6 we have plotted localization threshold in min as a function of the spatial separation between the reference and test line features for two data sets taken from the right-hand panels of Fig. 5. The lower function shows data for simultaneously presented reference and test targets ($ISI = -150$ msec; solid circles). The function would intersect the x -axis at a value defined by (negative) S_2 , since this is the regime where spatial filter responses would be involved. This S_2 value is very small (about 15.3 min or 0.26 ± 0.03 deg), much smaller than estimates of the variation of retinal, LGN or cortical magnification with eccentricity. The upper curve shows data for an $ISI = 88$ msec. Here, we renamed the x -axis estimate, L_2 , representing the eccentricity at which thresholds double their foveal value within the local sign regime. L_2 is about 54 min or 0.91 ± 0.09 deg for this brief ISI . This figure shows how fall off estimates in threshold with eccentricity are highly sensitive to the inclusion of spatial filter mechanisms.

Figure 7 presents E_2 estimates as a function of interstimulus interval based on the data presented in Experiments 1-3 and for some additional data collected in the California lab. Within the filter regime (negative $ISIs$), E_2 values are quite low, too small to reflect alterations in known anatomy or physiology with eccentricity. From $ISI \approx -100$ msec to $ISI \approx 20$ msec, the E_2 values gradually increase. For $ISI > 20$ msec the E_2 values are likely to be representative of the local sign regime (see Discussion). This gradual change in E_2 as the processing mechanism shifts from spatial filters at negative $ISIs$ to local sign mechanisms at positive $ISIs$ may explain a portion of the large range of E_2 values previously reported (see Table 2). As shown in Fig. 7(b), these E_2 estimates have some dependence on stimulus contrast (compare the solid circles with the solid square data), in agreement with previous studies (Wesemann &

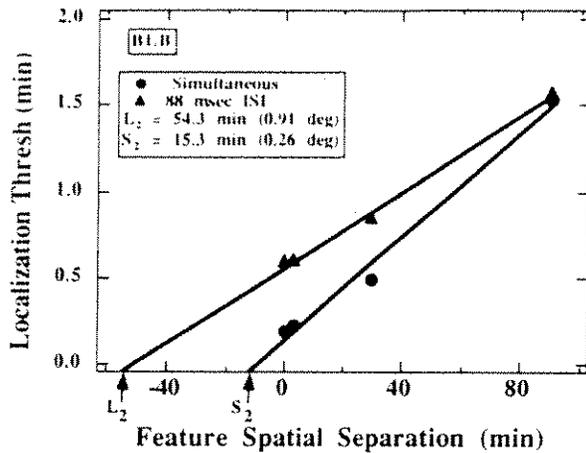


FIGURE 6. Localization thresholds are plotted as a function of the reference and test feature spatial separation. Data are presented for ISI = -150 (simultaneous) and +88 msec and were fit with Eq. (2).

Norcia, 1992; Waugh & Levi, 1993b; Hess & Hayes, 1994). E_2 is larger at lower contrast because the large separation data are less contrast-dependent than the small separation data. This important point will be further discussed in the "Experiment 4" section below.

In our calculation of E_2 (Fig. 7), we assumed that the stimulus eccentricity was the separation between the closest points of the two lines. This assumes that the observer fixated the reference line tip and that when the reference and test line stimuli are physically abutting that the observer is using the point of contact of the two lines to make the localization judgment. This assumption is questionable. It is more likely that observers are averaging over the inner 4–6 min of each line since thresholds improve up to ≈ 5 min lengths and are independent of line length beyond this region (Westheimer & McKee, 1977). We compensated for this offset by subtracting 0.08 deg ($5/60 \sim 0.08$) from each L_2 estimate. This compensation is included in Fig. 8 (open symbols), where we present only those data from Fig. 7 that fall in the temporal regions consistent with the local sign regime (positive ISIs) but brief enough to avoid memory limitations for the first stimulus. Here we plot L_2 (the local sign scaling factor) as a function of ISIs ranging from approximately +25 to +200 msec for the different observers in these experiments (shown with different symbols). Under these constraints the weighted mean (Klein, 1992) after allowing the allowance for integration along the line is 0.71 ± 0.27 deg for the same polarity targets of Experiment 3, where the standard error includes both the within and between sample variability. This L_2 estimate is consistent with human cortical magnification estimates (Horton & Hoyt, 1991; Tolhurst & Ling, 1988). However, since we use same polarity reference and test stimuli there is still the possibility that filter mechanism responses are intruding on our foveal data. To minimize this possibility we conducted Experiment 4.

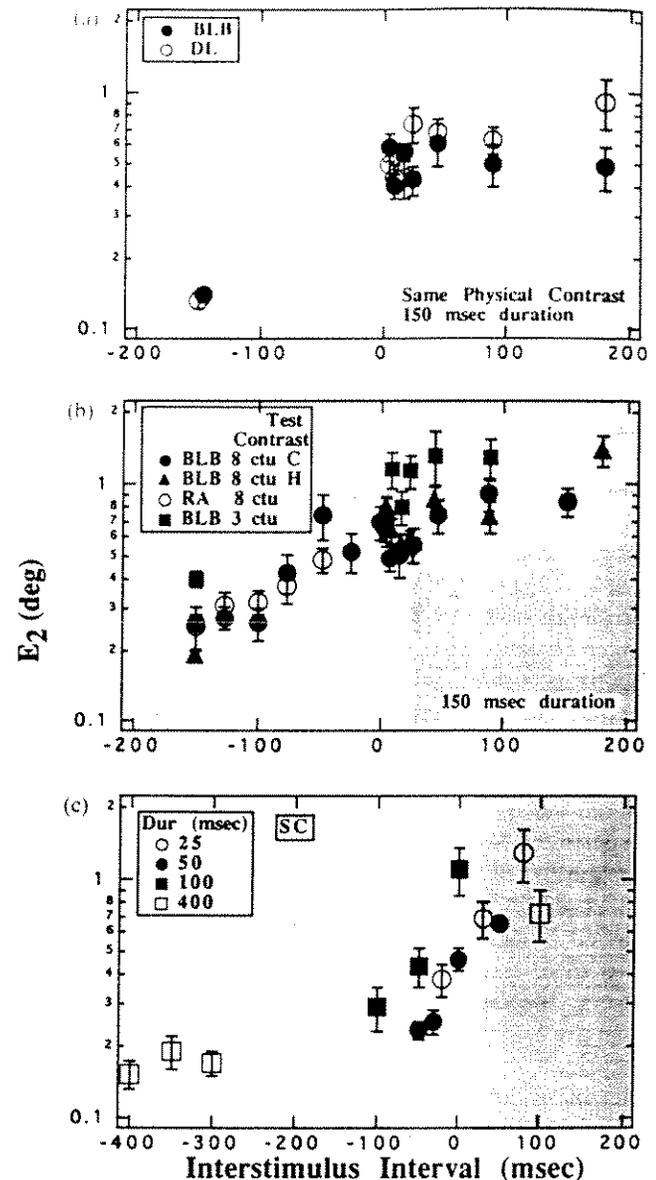


FIGURE 7. X-axis intercepts (E_2) are plotted as a function of ISI. Positive ISI conditions have been given a gray background. (a) Shows intercepts for the data provided in Fig. 5. (b) Contains estimates calculated from the data in Fig. 5. (c) Shows E_2 estimates for another observer in Berkeley.

EXPERIMENT 4: L_2 ESTIMATES FOR OPPOSITE POLARITY STIMULUS FEATURES

Rationale

To see if our average L_2 estimate (≈ 0.71 deg) is primarily reflecting local sign processing, in Experiment 4 we measured vernier thresholds under conditions that optimize local sign responses: (1) vernier stimulus features with *opposite contrast polarity*; (2) a *temporal asynchrony* between the features; (3) *high stimulus contrast*; and (4) a *larger display screen*.

(1) *Opposite contrast polarity.* If localization thresholds at positive ISIs are limited by local sign mechanisms, then stimulus feature polarity should have little

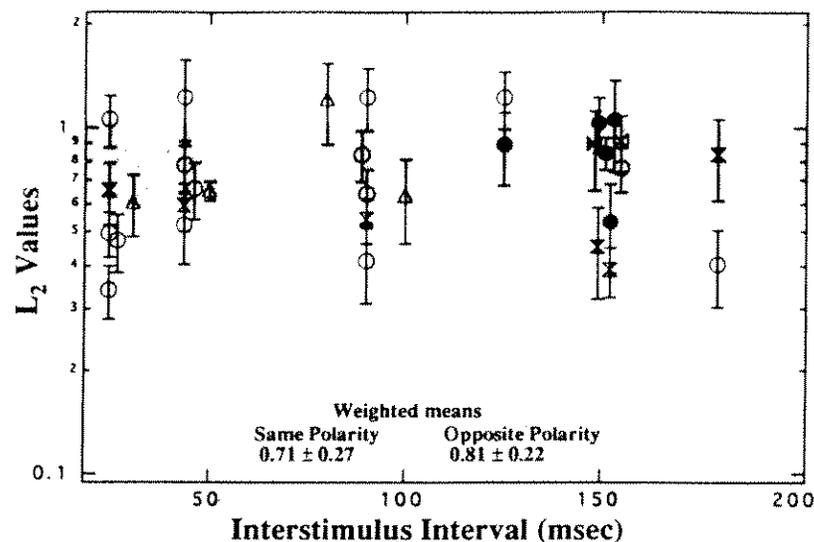


FIGURE 8. Estimates of L_2 for all data in Fig. 7 plotted as a function of ISIs ranging from approximately 25 to 200 msec. After subtracting 0.08 from each estimate to compensate for fixation error (see discussion of Fig. 8 in text) the different symbols refer to different subjects and different conditions. Opposite polarity conditions (Tektronix 608 and SONY monitors) are indicated with the solid symbols. Shading represents the mean and SE for opposite polarity condition.

differential effect on thresholds. However, recall that in Experiment 1 there was a 1.5-fold ratio in threshold between same and opposite polarity stimuli at positive ISIs. This result may be explained in at least three ways: (a) within the local sign regime there may be some dependence on polarity. However, this seems unlikely, since at large gaps, where thresholds are most likely in the local sign regime, thresholds for same and opposite target polarity are virtually identical [see data labeled "90 min separation" in Fig. 3(a)]. (b) At positive ISIs under same polarity conditions there may still be some filter influence, although this dependence would be considerably reduced when compared to the spatial filter responses for negative ISIs. Filter mechanisms may still be used for abutting opposite polarity stimuli because we could still be within the filter's memory for the stimulus at the brief ISIs tested in Experiment 1 (i.e., 50 and 100 msec). (c) A third explanation for the threshold difference in same and opposite polarity conditions at positive ISIs is that our observers may have had difficulty properly fixating due to the brief (e.g., 25 and 50 msec) durations used in these experiments. These brief durations may not have provided enough time for the observer to localize the reference stimulus before it was turned off. If the observer was gazing in the wrong display area when the reference stimulus was presented, then judging the relative position of a simultaneous abutting test stimulus may not be difficult. However, if the test stimulus onset comes after reference cessation, then the observer must rely on memory to fixate in the proper reference location. It is possible that in the positive ISI conditions, where the reference is briefly presented followed by the test stimulus presentation, observers are still searching for the reference line location while the test stimulus is being presented. In an attempt to fixate the brief reference target, the anticipatory eye movements could produce an

artificial directional component (i.e., the test stimulus appears to be located in a position other than its actual location) and this effect may have been stronger for opposite polarity stimuli. To test this latter hypothesis we ran two control conditions. We: (i) increased the reference stimulus duration; and (ii) randomly positioned the test stimulus either to the left or right of the reference stimulus.

(i) Control: Increased stimulus duration

We hypothesized that if more time is provided for the observer to locate and fixate the reference feature, then thresholds would be reduced as compared to the brief reference duration conditions. We presented the reference line for either 50 or 500 msec, while the test line was always presented for 50 msec. The 500 msec presentation was equated in visibility to the 50 msec stimulus (nine times threshold). An ISI = 150 msec was used. We used the 608 monitor with mean screen luminance of 114 cd/m^2 . Thresholds are shown on the right-hand side of Fig. 3(b). The upper data point labeled "50-50" is the control condition where opposite contrast polarity test and reference stimuli were both presented for 50 msec (the same as Experiment 1; observer BLB). The center data point labeled 500-50 shows the localization threshold for opposite polarity reference and test stimuli, where the reference was presented for 500 msec and the test for 50 msec. Thresholds decreased for the 500 msec reference presentation time ($Th = 0.74 \pm 0.06$) in comparison to thresholds for the 50 msec reference presentation ($Th = 0.86 \pm 0.07$). These data suggest that observers may not have been properly fixating at the time of stimulus presentation for brief stimulus presentations. The lowest data point on the righthand side of the bottom panel labeled "500-50" shows that even when the reference stimulus duration was increased, the ≈ 1.5 -fold

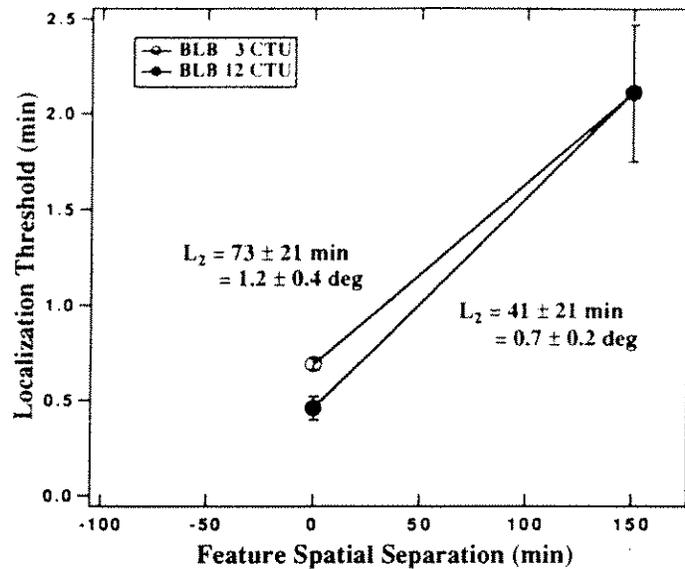


FIGURE 9. Localization thresholds as a function of spatial separation for two stimulus contrast levels (3 and 12 CTU-contrast threshold units). Stimulus features were opposite contrast polarity. Stimulus duration was 500 msec and ISI = +150.

ratio of same (i.e., both dark; $Th = 0.51 \pm 0.06$) vs opposite polarity ($Th = 0.74 \pm 0.06$) conditions remained.

(ii) *Control: Randomize test presentation side*

In the second anticipatory fixation control condition we randomly presented the test stimulus either to the left or right of the reference stimulus. Here it was more advantageous for the observer to maintain fixation than to use anticipatory movements toward the test stimulus. Under these conditions, the ratio of same to opposite polarity thresholds was closer to 1.0 in all three observers.

Since we did not find a continuous deterioration in threshold with ISI, errors in the internal representation of the gaze direction most likely do not contribute much to our threshold measure. We estimated eye drift effects from previous eye movement assessments. It has been reported that the eye drifts about 3 min arc every second (Riggs *et al.*, 1954). To determine the possible effects of eye drift on our thresholds, we have plotted a drift estimate of 3 min arc/sec (see bold line in Fig. 5). Except for the longest ISI for one observer, the eye movements are much smaller than our thresholds, and are therefore unlikely to contribute much to our results (see also Fahle, 1991).

(2) *Temporal asynchrony.* Improper fixation may also partially account for the elevated thresholds found under temporally asynchronous conditions (Fig. 3). However, we chose not to use a fixation point in these experiments for several reasons. First, a fixation mark presented continuously would provide a simultaneous localization cue when the reference and test were shown with a temporal asynchrony. Second, a fixation mark presented just before vernier target presentation could cause temporal interference (Westheimer & Hauske, 1975).

(3) *High stimulus contrast.* Figure 8 (open symbols)

estimates of L_2 predominantly used low visibility conditions because of the short duration of the stimuli. The asymptotic contrast level for abutting, opposite polarity features is not known. For spatially separated targets, contrast will have a small effect at contrasts lower than about 3–6 contrast threshold units, depending on the vernier feature spatial separation (Vaugh & Levi, 1993a). Figure 9 shows the effect of stimulus contrast for abutting and spatially separated opposite polarity stimulus features in observer BLB. Contrast was effective only in the abutting (spatial separation = 0) condition. At the lower contrast of 3 CTU we found an L_2 value that was slightly higher than, but whose range encompassed our average L_2 estimate. The L_2 estimate obtained at 12 CTU approximates our average L_2 estimate. Because of the highly sensitive nature of abutting thresholds to stimulus contrast level (visibility), in Experiment 4 we used the maximum stimulus contrast possible on our apparatus.

(4) *Large display screen.* We were concerned that the screen edges were being used in the 150 min separation condition since the Tektronix 608 oscilloscope screen subtended only a few degrees. To test this, we obtained additional measurements on a Macintosh display using a SONY screen which was more than three times larger in the relevant dimension (see General Methods section above).

Methods

We presented the reference for 500 msec and the test stimulus for 150 (or 125) msec. In addition, line length was shortened from 10 to 5 min arc to compensate for fixation errors. Third, the test stimulus was randomly presented either to the left or right of the reference line to reduce anticipatory eye movements. Three observers participated in this study (DL in the Houston lab; SK and BLB in the California lab).

TABLE 1. Vernier thresholds under conditions that optimize local sign responses

Observer	ISI	Ecc.	Same polarity	Opposite polarity
SK	150	0	0.78 \pm 0.08	0.82 \pm 0.07
		2.5	2.76 \pm 0.18	2.96 \pm 0.44
		L_2	0.98 \pm 0.17	0.95 \pm 0.22
DL	150	0	1.46 \pm 0.10	1.41 \pm 0.16
		2.5	9.20 \pm 0.85	8.02 \pm 1.35
		L_2	0.47 \pm 0.06	0.53 \pm 0.13
BLB	125	0	1.20 \pm 0.15	1.41 \pm 0.09
		2.5	4.31 \pm 0.46	4.58 \pm 0.43
		L_2	0.96 \pm 0.22	1.11 \pm 0.18

To determine if the screen edges were being used in the previous experiments, we obtained additional measurements on a Macintosh display using a Sony screen which had almost twice the number of vertical pixels as compared to the Tektronix 608-Venus display. Here we present the localization thresholds (min) for three observers. Although thresholds were slightly higher in this study because the test stimulus was presented either to the left or right of the reference line, the L_2 values were consistent with those obtained using the smaller screen. Ecc, eccentricity.

Results

Table 1 presents the localization thresholds and L_2 estimates obtained using this experimental apparatus. For these three observers, estimates range from 0.47 to 1.11. The low estimates obtained from observer DL may be explained by his substantially elevated peripheral thresholds. These L_2 estimates have also been plotted in Fig. 8 with solid vertical (DL) and horizontal (SK) hour-glass symbols at 150 msec ISI and by the solid circle (BLB) at 125 msec ISI. The weighted average of all opposite polarity L_2 estimates is 0.81 ± 0.22 , where the standard error includes both the within and between sample variability. Based on these results we conclude that the eccentricity at which local sign thresholds double is around 0.8 deg.

Although thresholds were slightly higher in this study because the test stimulus was presented randomly either to the left or right of the reference line, the L_2 values were consistent with those obtained using the smaller screen. To compare, L_2 estimates (in deg) based on opposite polarity reference and test features using the 608 monitor are included in Fig. 8. We found an average L_2 estimate of about 0.74 ± 0.2 deg using the small screen display for three observers [DL (Houston lab), SK and BLB (California lab)]. To reduce clutter, the L_2 estimates for only one of these observers (BLB) are shown by the solid circles in Fig. 8 at 150 msec ISI. Together, the results of Experiments 3 and 4 suggest that L_2 approximates 0.8 ± 0.2 deg.

DISCUSSION

The goal of this research was to estimate the fall off in precision of the local sign mechanism with eccentricity. To limit our measurements to the local sign regime, the first two experiments defined the temporal response boundaries of the regime within a localization task. Localization thresholds within the local sign regime are

independent of stimulus feature characteristics because this information is not required to assign the position labels or to compare their outputs. The first experiment used same and opposite polarity stimuli. The second experiment used several stimulus strengths. Our results are consistent with the idea that local sign mechanisms primarily mediate threshold with sequentially presented reference and test target features. Experiments 3 and 4 estimated L_2 over a range of temporally successive presentations. Under optimal conditions (opposite polarity and temporal asynchrony) our average estimate of L_2 (the point where vernier thresholds double within the local sign regime) is 0.8 ± 0.2 deg.

The local sign positional assignments could be coded as cortical position. We investigated the vernier threshold fall off with eccentricity in the hope that our psychophysically based estimate would provide information about the rate that the physiologically based cortical magnification factor increases with eccentricity. We will now examine how physiological cortical magnification estimates might correspond to L_2 estimates.

Relationship between psychophysics and physiology

In the local sign regime, a "cortical ruler" could determine position thresholds. To be explicit, suppose we desire to measure the distance between two points. On the cortex these points are at positions x_1 and x_2 , where x_1 and x_2 are two-dimensional vectors that can be represented as complex numbers. One model holds that local sign mechanisms independently assign position labels to the two feature positions. Each label, with some error, or uncertainty, is compared for a match. The cortical distance is $x_1 - x_2$ and the error in cortical units is $\Delta x = (\Delta x_1^2 + \Delta x_2^2)^{1/2}$. We assume that in the local sign regime position uncertainty does not depend upon $x_1 - x_2$, the cortical separation, i.e., there is no Weber fraction for cortical distance. This is the same as measuring distances with a reliable ruler (e.g., a ruler that doesn't expand or contract as temperature fluctuates).

The cortical magnification factor

The eccentricity-dependent cortical magnification factor $M(E)$ provides the connection between a small change in cortical position (Δx) and a small change in retinal angle (ΔE):

$$\Delta x = M(E)\Delta E \quad (5)$$

where $M(E)$ has units of mm/deg.

To a good approximation the inverse magnification, $1/M(E)$, is linearly related to E (Dow *et al.*, 1981; Tootell *et al.*, 1982; Van Essen *et al.*, 1984; Levi *et al.*, 1985):

$$M(E) = A/(E + L_2) \quad (6)$$

so that Eq. (5) becomes:

$$\Delta x = A\Delta E/(E + L_2) \quad (7)$$

The parameter, A , represents the change in cortical position for a given percentage change in retinal distance. Integration of Eq. (7) provides a logarithmic connection

between retinal location, E , and cortical location, x (Schwartz, 1980):

$$x = A \ln((E + L_2)/(E_{ref} + L_2)). \quad (8)$$

E_{ref} , the reference eccentricity, is a constant of integration that defines the origin of the cortical coordinate system so that $x = 0$ when $E = E_{ref}$.

Recently, cortical magnification estimates have been obtained in humans using functional magnetic resonance imaging of fMRI (Engel *et al.*, 1994; Sereno *et al.*, 1994; Sereno *et al.*, 1995). The Appendix presents the MATLAB program we used for re-analyzing the Engel *et al.* and Sereno *et al.* data sets to obtain estimates of A and L_2 . As is typical in cortical measurements, a nonfoveal reference point is taken since the location of the foveal center is difficult to determine. The data were normalized so that the origin of cortical position, x , was taken to be the point corresponding to $E_{ref} = 10$ deg and 4 deg in the periphery for the Engel *et al.* (1994) and Sereno *et al.* (1995) data, respectively. The Appendix (lines 8 and 9) provides the equations used to solve for A and L_2 . For the two observers in Engel *et al.* we found $L_2 = 3.1 \pm 0.9$ and 11.2 ± 2.2 deg, and $A = 17.2 \pm 1.1$ and 20.4 ± 1.9 mm. The large values of L_2 are probably because Engel *et al.* did not include eccentricities less than about 2.5 deg and their data are somewhat noisy. We recalculated the Sereno *et al.* fit using the data from their Fig. 4(C) using their power function with an exponent of -1.26 (see line 8 of the program in the Appendix). The nonlinear regression parameters were $L_2 = 0.4 \pm 0.7$ deg and $A = 19.3 \pm 2.6$ mm. The 0.4 deg value of L_2 is larger than the value of 0.08 deg reported by Sereno *et al.*, but the large uncertainty we found (± 0.7 deg) suggests that L_2 is difficult to determine with this method. The Sereno *et al.* value for A is remarkably close to the value that we found from the Engel *et al.* data. In the periphery, when $E \geq L_2$, a value of $A = 20$ mm means that a 5% change in retinal eccentricity corresponds to a 1 mm shift on the cortex (about 1 hypercolumn). In the fovea, a 2.5 min shift in retinal position corresponds to one cortical mm [see Eq. (7)].

Grusser (1995) recently reported a very different study of cortical magnification based on migraine phosphenes. He plotted scintillating migraine phosphenes as a function of time and made use of the known total size of human area V1 to estimate the cortical velocity of the migraine. For a subject with 11 migraine attacks, averaged along 62 radii, Grusser found $L_2 = 1.24$ deg and $A = 16.9$ mm (the reciprocal of his parameter, b). This value of A is compatible with the fMRI values, ranging from 17.2 to 20.4. One reason why the migraine data might produce a larger value of L_2 (i.e., 1.24 deg) than we found in the present study (0.8 deg) is that the migraine might start slightly away from the fovea. In most of the directions it will not move along a line directly away from the fovea. This would have the effect of decreasing the rate of cortical expansion, thereby increasing the L_2 value.

The methods that we have discussed for calculating L_2 for the human cortical magnification factor suffer from

methodological limitations. Similar uncertainty exists in the animal physiological estimates, since many early physiological studies suffered from difficulties in studying the convoluted cortex regions and from difficulties associated with estimating magnification near the fovea (where there is dense sampling and where it may be difficult to record from small receptive fields). While anatomical methods (2-deoxyglucose—Tootell *et al.*, 1982), techniques for "unfolding" the cortex (Van Essen *et al.*, 1984) and methods for controlling fixation (Dow *et al.*, 1981) have clearly improved these estimates, there remains a degree of uncertainty. Thus, recent estimates of L_2 for cortical magnification in primates range from ≈ 0.3 to about 1.5 deg (Schwartz, 1980; Dow *et al.*, 1981; Tootell *et al.*, 1982, 1988; Van Essen *et al.*, 1984).

Cortical magnification and psychophysical thresholds

The connection between cortical magnification and psychophysical thresholds is made by taking the position threshold, Th , to equal ΔE in Eq. (7) (Klein & Levi, 1987).

$$\Delta x = ATh/(E + L_2) \quad (9)$$

For the data of BLB in Fig. 5 (right-hand side) at an ISI = 88 msec, the curve slope is

$$Th/(E + L_2) \approx 0.01. \quad (10)$$

corresponding to $\Delta x \approx A \cdot 0.01 \approx 0.2$ mm if $A \approx 20$ mm. That is, a position shift of 0.2 mm of cortex is detected independent of the reference and test location (in the local sign regime). This value is similar to the position thresholds in cortical units discussed by Klein & Levi (1987).

Using the data from a range of physiological paradigms, we have shown that A is consistently around 20 mm. While the parameter A can be measured with good confidence, foveal magnification, $M(0)$ is difficult to measure (similar to L_2) because it is difficult to place stimuli in the center of the fovea. In the preceding analysis we focused on the parameters A and L_2 . It is also common to discuss estimates of foveal magnification given by [see Eq. (6)]:

$$M(0) = A/L_2 \quad (11)$$

Our psychophysical estimates of L_2 averaged 0.8 deg so that the foveal magnification would be $M(0) = 25$ mm/deg. For larger values of L_2 (e.g., Engel *et al.*, 1994) the foveal magnification would be correspondingly smaller.

Previous estimates of E_2

Weymouth (1958) was the first to suggest that acuity thresholds have a linear fall off with eccentricity. He tabulated the slope and vertical intercept for a wide variety of spatial tasks. Levi *et al.* (1984, 1985) specified the fall off in terms of the horizontal (x -axis) intercept, E_2 , to have an index that was independent of task difficulty. The original motivation for calculating E_2 was to connect the psychophysical E_2 estimate to eye and brain anatomical structures. However, some E_2 estimates

TABLE 2. A summary of 23 E_2 estimates

No.	Reference	Fig. No.	Stimulus/Task	Orientation	Visual field region	Range (deg)	Details	Obs	E_2 (deg)
A. Abutting (no mask)									
1	Levi <i>et al.</i> (1985)	11	2 line vernier	Vertical (isoeccentric)	Lower	0-10	Reference and test duration = 250 msec; stimulus length = 12 min	JM PA	0.67 0.53
2	Levi <i>et al.</i> (1985)	11	Multiple-line vernier	Vertical (isoeccentric)	Lower	0-10	Reference and test duration = 250 msec; stimulus length = 12 min	JM PA	0.77* 0.62*
3	Whitaker <i>et al.</i> (1992)		2 line vernier	Horizontal (isoeccentric)	Nasal	0-15	Average of all observers		1.55**
4	Wilson (1991)	2	2 line vernier	Horizontal (isoeccentric)	Temporal	0-30			1.38**
5	Wilson (1991)	2	2 line vernier	Vertical (radial)	Temporal	0-30			0.78**
6	Levi <i>et al.</i> (1985)	7	2 line vernier	Horizontal (radial)	Lower	0-10	Ref on continuously; fixate reference; stimulus length = 90 min	JM PA	0.90 0.74
7	Levi & Waugh (1994)	1	2 line vernier	Horizontal (radial)	Lower	0-10	6 times threshold; mean of four observers		0.89**
8	Levi <i>et al.</i> (1994)	12	Edge vernier	Horizontal (radial)	Lower	0-5	High contrast mean		0.82**
			Line vernier				Low contrast mean		1.00**
							High contrast mean		1.08
							Low contrast mean		1.32
B. Abutting (mask)									
1	Toet & Levi (1992)	T-1	Ts	Vertical (radial)	Temporal	0-10	Mean six observers fixation mark		0.18*
2	Toet & Levi (1992)	T-1	Ts	Horizontal (isoeccentric)	Temporal	0-10	Mean six observers fixation mark		0.34*
3	Levi <i>et al.</i> (1985)	7	2 line vernier	Horizontal (radial)	Lower	0-10	Threshold × ecc. (Point of greatest masking)	JM PA	0.34 0.39
							Mask separation × ecc.	JM PA	0.99 0.72
C. Fixed separation									
1	Beck & Halloran (1985)	5	2 dot vernier	Vertical		4-8	3 deg dot separation; fixation before	AA	16
2	Levi & Klein (1990)	16	3 line vernier						>20

Table 2 continued overleaf.

are substantially larger and some smaller than human cortical magnification estimates. The large range of E_2 values has challenged the validity of a single scaling factor for localization thresholds (Whitaker *et al.*, 1992). The following discussion will consolidate the results of many previous psychophysical estimates of E_2 in an attempt to determine the various factors responsible for the large range of estimates reported in the literature. Table 2 presents a summary of 23 E_2 estimates. Each row of the table contains information about a particular investigation. The second column provides the citation information. Some of these estimates were calculated elsewhere as indicated in the legend, in other cases we have calculated the intercept [using Eq. (2)] from the published figures. The third column indicates the figure from the cited article that contained the data used to estimate E_2 . The fourth through eighth columns provide other study parameters. The ninth column shows the

observer's initials and the final column contains the individual estimates of E_2 .

The studies listed in Table 2 are grouped into six categories according to their methodology: (A) Abutting (no mask), (B) Abutting (mask), (C) Fixed separation, (D) Vary eccentricity/separation, (E) Vary separation and (F) Temporal.

(A) Abutting vernier

One common method used to estimate E_2 involves abutting line stimuli that are moved into the periphery [Table 2(A)]. E_2 values for two-line and multiple-line vernier range from 0.53 to 1.55 deg with an average of 0.9 deg. Although this estimate approximates our L_2 estimates, we do not think that the abutting vernier threshold fall off with eccentricity reflects the local sign magnification. Rather, this fall off more likely reflects the combined effects of (1) the response characteristics of spatially oriented filters whose responses are degraded in

TABLE 2. *contd.*

No.	Reference	Fig. No.	Stimulus/Task	Orientation	Visual field region	Range (deg)	Details	Obs	E_2 (deg)
D. Vary eccentricity and separation									
Large separation									
1	Levi & Klein (1990)	6 7	3 line vernier	Horizontal (radial)	Lower	0.6-10	Stimuli on isoeccentric arc	JT KH	0.48 0.23
Optimal separation									
2	Westheimer (1982)	2	2 dot vernier	Horizontal (isoeccentric)	Temporal	2.5-10	For optimal target placement	GW SR	1.05 1.37
3	Levi & Klein (1990)	6	3 line Vernier	Horizontal (radial)	Lower	0.6-10	Fixate center isoeccentric	JT KH	0.69 0.29
E. Vary spatial separation									
1	Westheimer & McKee (1977)	2	2 dot vernier	Vertical (isoeccentric)	Upper and Lower	0-13	Fixate center; estimate from 4-13 deg	LK SM	0.31 0.97
2	Beck & Halloran (1985)	1	2 dot vernier	Vertical	Lower	0.5-8	Observers naive; no fixation	CB KW VW	0.56 0.35 0.19
3	Klein & Levi (1987)	3	3 dot vernier	Horizontal (isoeccentric)	Temporal	0.04-10		SK DL WS	0.27* 0.09* 0.21*
4	Waugh & Levi (1993a)	5	2 line vernier	Horizontal (isoeccentric)	Temporal	0-1.5	Used model to fit	SJW FR	0.44* 0.51*
							Used raw data to fit	SJW FR	0.07# 0.12#
5	Present study		2 line vernier	Horizontal (isoeccentric)	Temporal	0-15	3 times threshold 8 times threshold	BLB BLB	0.40 0.20
F. Temporal									
1	Present study		2 line vernier	Horizontal (isoeccentric)	Temporal	0-1.5	Average same polarity (minus 0.08)		0.64
							Opposite polarity (minus 0.08)	BLB SK DL	1.03 0.87 0.45
2	White <i>et al.</i> (1992)		2 line vernier	Horizontal (isoeccentric)	Temporal		Used model to fit- (average across ISIs)	DL	0.35*
							Used raw data to fit at ISI = 200	DL	8.84

The estimates marked with a # sign were calculated with Eq. (2) rather than the model predictions that were used in the respective studies. Equation (2) uses a single line function to estimate E_2 . The model used in Waugh & Levi (1993a) to determine the estimate was based on double-line fits to the data (the fit for one line modeled the spatial filters and the other modeled local signs). Further details are provided in the text. Ecc, eccentricity; Obs, observer.

* E_2 estimate provided in respective reference.

** E_2 estimate provided in Levi & Waugh (1994).

the periphery; and (2) an extra degradation (jitter and/or undersampling) in peripheral vision. Filter models of vernier acuity normalize the filter sensitivity to the contrast sensitivity function. Contrast sensitivity has an $E_2 \approx 2.5$ deg (Rovamo & Virsu, 1979). Thus, a filter model of vernier acuity would assume a limited range of filter sizes located at each eccentricity, the sizes of which increase with eccentricity according to an E_2 of 2.5. The test-pedestal approach (Klein *et al.*, 1990) also predicts E_2 of around 2.5. However, as seen in Table 2, the actual fall off is steeper. This extra loss may be explained by peripheral undersampling (Levi & Klein, 1986; Levi *et al.*, 1987, 1994) and/or scrambling (irregularity or jitter) of the filter positions (Wilson, 1991; Hess & Field, 1993; Hess & Hayes, 1994; Levi *et al.*, 1994). Therefore, the E_2 values shown in Table 2(A) most likely reflect the fall off in sensitivity of spatial filters with eccentricity and

include the influences of undersampling and jitter in the periphery.

Whitaker *et al.* (1992) obtained the largest average x -intercept estimate in our sample of abutting vernier acuity studies [see Table 2(A.3)]. They presented thin stimuli in the fovea and magnified versions of their stimulus at different eccentricities. They suggested that estimates of E_2 may be inaccurate if the eccentric conditions are not properly scaled. The idea is that if a proper scaling procedure is used, then each stimulus line element would stimulate the same cortical distance for the abutting and 90 min separation conditions. We did not spatially scale our stimuli, therefore to test the Whitaker *et al.* suggestion, in control experiments we retained the viewing distance (1.1 m), but scaled the stimulus size according to E_2 estimates of 0.77 deg. In addition, as a second check, we doubled the 90 min stimulus size, since the viewing distance was half that of the abutting case.

These results are shown in Fig. 5 by the additional data points (open symbols) at +50 ISI. There is little difference between localization thresholds for scaled or unsealed stimuli. Thus, not scaling our eccentric stimuli did not have much effect.

Furthermore, in the filter regime, there are several problems with using a scaling procedure that could account for the Whitaker *et al.* (1992) large E_2 estimates. First, the resulting changes in line width and length could change line visibility. Since the detection threshold fall off with eccentricity differs from the position threshold fall off, changing the line visibility with eccentricity would confound the results if the fovea and periphery showed different dependence on visibility. Another potential difficulty with this scaling procedure is that it assumes a single scale factor. However, if optimal line-length and optimal vernier threshold vary at different rates with eccentricity (as some of our unpublished data suggest), then the estimate of E_2 will be incorrect. For example, if the optimal line length increases at the same rate as the optimal filter size, ($E_2 \approx 2.5$), while the optimal vernier threshold increases at a faster rate, then the result would be an intermediate value of E_2 . The consequences of this procedure are especially apparent by going to a very short line length, where resolution determines the line length at which the vernier thresholds become infinite. Since resolution scales with $E_2 \approx 2.5$, at the short line end of Whitaker's data we expect to find $E_2 \approx 2.5$. Yet another possible explanation for the higher E_2 values found in the Whitaker *et al.* (1992) and the Wilson (1991) [see Table 2(A.4) and 2(A.5)] investigations pertains to the visual field region and stimulus orientation used in these studies (see the "Stimulus orientation and visual field region" section below).

(B) *Abutting vernier with a mask*

A second method used to measure the peripheral fall off of vernier acuity is to determine the interfering effects of spatial flanks on both sides of the target [Table 2(B)]. E_2 values for crowding paradigms average about 0.3 deg. In an attempt to exclude spatial filter responses and limit thresholds to the local sign regime, Morgan & Ward (1985) measured spatial interval and Levi *et al.* (1985) [see Table 2(B.3)] measured two-line vernier acuity in the presence of flanking, or masking, lines. It was hoped that the flanks would isolate a local sign mechanism since the adjacent features would interfere with the signal within a single spatial filter. From the Levi *et al.* data, we estimate $E_2 \approx 0.36$ at the point of greatest masking (i.e., by plotting the threshold at the masking function peak at each eccentricity against eccentricity). We also calculated an average $E_2 \approx 0.86$ for the same data by plotting mask separation for the point of strongest masking as a function of eccentricity.

Toet & Levi (1992) measured resolution thresholds for orientation discrimination of the letter T as a function of eccentricity and found an average $E_2 \approx 2.0$. To investigate spatial interaction effects, they also measured orientation discrimination thresholds for the letter T in

the presence of flanking Ts located on either side of the target T [see Table 2(B.1) and (B.2)]. The presence of the flanks substantially reduced E_2 estimates ($E_2 \approx 0.34$ and 0.18 for horizontal and vertical meridians, respectively) since thresholds were elevated in the periphery. In the Toet & Levi (1992) experiment, the stimuli were complex and large crowding effects occurred where the visual system had difficulty isolating specific features in the display. The Toet & Levi (1992) experiments are the only non-vernier experiments in Table 2 and were included since the T judgment requires a spatial discrimination (similar to a vernier judgment). A second reason for including the Toet & Levi (1992) non-vernier experiment in Table 2 is the scarcity of other vernier experiments combining crowding and peripheral judgments. As noted in Toet & Levi (1992), the crowding extent in abutting vernier ($\approx 0.1 \times \text{ecc}$) is much less extensive than for letter orientation (where crowding extends up to $0.5 \times \text{ecc}$; e.g., the legibility of a target at an eccentricity of 10 deg would be degraded by a mask up to 5 deg away).

These E_2 values, however, probably do not reflect the local sign scaling factor for two reasons: (1) it is unclear if the foveal spatial filter response was totally suppressed in the presence of a spatial flank. The task might still be done with less optimal filters. (2) The effect of masking might be different in peripheral vision than in foveal vision. In the periphery, the subject might have greater difficulty attending to the stimulus dots and ignoring the mask. Even if the stimuli were properly scaled for the vernier fall off with eccentricity, the scaling may have been inaccurate for a task involving the attentional requirements of peripheral masking. These lower intercept values suggest that peripheral spatial interactions need to be separately accounted for when obtaining a peripheral fall off estimate.

(C) *Fixed separation*

Table 2(C) shows E_2 estimates under conditions where the reference and test features have a fixed separation and are moved into the periphery (Beck & Halloran, 1985; Levi & Klein, 1990). These E_2 estimates are quite large. Consider the Beck & Halloran (1985) study measuring two-dot vernier acuity with the dot separation fixed at 3 deg as the dot pair moves into the periphery for the closest condition. Since fixation is somewhere near the two dot midpoint, each dot is ≈ 1.5 deg in the periphery. Levi & Klein (1990) found that, within the local sign regime where thresholds depend only on the stimulus eccentricity, the threshold should be about $\sqrt{2} \times 0.01$ ($E + 0.7$) or about $0.014 \times 2.2 = 0.031$ deg = 1.8 min. The errors of the two dots add independently, accounting for the $\sqrt{2}$ factor. As the stimulus shifts into the periphery by a small amount, there will be no change in threshold, since for a lateral shift the stimulus dots lie on an isoeccentric circle where thresholds do not change (Levi & Klein, 1990). Then, as the two dots are shifted further into the periphery, processing changes from the local sign regime to the filter regime, where thresholds depend only

on the separation. A typical threshold would be about 1/60 of the separation. For the present example, this would give thresholds of about $2/60 = 2$ min, very similar to the starting thresholds. This example shows how very large values of E_2 arise under the Beck & Halloran conditions.

We emphasize the importance of an accurate "abutting" vernier threshold, since any error in this threshold will significantly alter L_2 (see Fig. 6). Many previous E_2 estimates have failed because they do not include an abutting condition, for example, studies using dot stimuli with a small separation (Beck & Halloran, 1985; Burbeck & Yap, 1990; Levi & Klein, 1990) or isoeccentric data (Levi & Klein, 1990). In addition, estimates that have included an abutting case may have been influenced by spatial filter responses (see Table 2; Klein & Levi, 1987). Similarly, accurate measurements in the periphery are important. Peripheral thresholds can be substantially affected by the psychophysical task. For example, as discussed above, there may be increased attentional requirements in the periphery when using visual masks (Levi *et al.*, 1985).

(D) Vary eccentricity and separation

Another method used to isolate local sign responses is to present stimuli on an isoeccentric arc (Levi & Klein, 1990). In this method the different vernier target features are presented on an arc that surrounds fixation. The use of an isoeccentric arc decouples eccentricity and separation by maintaining a constant eccentricity, while permitting the manipulation of the vernier stimulus feature separation. Levi & Klein (1990) measured three-dot vernier thresholds from 0.63 to 10 deg in the periphery. They found a ceiling in the data. At small eccentricities the ceiling was located at smaller separations as compared to data collected at larger eccentricities. At separations past the cusp, thresholds remained relatively constant across separation. Levi & Klein (1990) hypothesized that these "large separation" thresholds reflect responses of local sign mechanisms. Within the local sign regime we estimate that their L_2 averages 0.36 deg.

There are two potential problems with the isoeccentric arc method: (1) as discussed above, foveal thresholds cannot be obtained, so slight errors in the estimated threshold will have a large effect on the E_2 estimate; and (2) it is unclear if observers maintained proper fixation at the smallest eccentricity. An error where the actual eccentricity is less than the intended eccentricity would result in an E_2 value that was lower than the true E_2 .

The large separation estimate of 0.36 should be compared to estimates obtained using the optimal separation (the ceiling location) where $E_2 \approx 0.69$ and 0.29 for two observers (Levi & Klein, 1990). Westheimer (1982) similarly plotted their two-dot vernier data at the optimal separation and we calculate their $E_2 \approx 1.05$ and 1.37. This wide range of E_2 estimates is probably due to the multiple factors involved in the task. Thresholds at the optimal separation are most likely limited by spatially oriented filters rather than the local sign. Similar to the

abutting stimuli paradigm described above [Table 2(A)], there is an extra factor that arises from the difference between the fall off in optimal separation ($E_2 \approx 2.5$) and the optimal threshold ($E_2 \approx 0.9$) that may be accounted for by jitter and undersampling.

(E) Vary separation

Table 2(E) presents research that has varied the separation between the reference and test targets with the reference or centroid at the fovea. Using this stimulus, filter models would assume that different size tuned filters are located at each eccentricity, and the optimal filter size would increase with spatial separation. Based on this assumption, threshold would be estimated to be proportional to eccentricity (so that $E_2 \approx 0$). From Table 2(E) (five investigations), however, the mean E_2 is 0.34 deg. In an attempt to isolate local sign responses, Klein & Levi (1987) and Waugh & Levi (1993b) fit their threshold vs spatial separation data with a double-line function. This double-line function indicates the relative contributions of the spatial filters and local sign mechanism responses, since one portion of the line fits the data within the filter regime and the second portion of the line fits the data within the local sign regime. This double-line function permitted Klein & Levi (1987) to find a crude estimate of E_2 for bisection (average $E_2 = 0.5$). For the Klein & Levi (1987) vernier task, however, the two regimes blended together smoothly so that a clear separation of the local sign regime was not possible. L_2 estimates based on this approach were reported to be about 0.45 deg (averaged across observers and spatial interval/alignment conditions—Levi & Klein, 1990). Our recalculation of L_2 for their alignment data using the nonlinear fit described in Eq. (2) is ≈ 0.36 deg. Waugh & Levi (1993b) also fit their vernier data with a double-line fit but did find a cusp in their vernier threshold vs separation function, allowing an estimate of E_2 for vernier [average $E_2 = 0.3$ at 30 times threshold; see Table 2(E.4)].

One of the investigations shown in Table 2(E) measured E_2 for a range of stimulus contrasts (Waugh & Levi, 1993b). The pattern visibility has a mild effect on the rate at which thresholds fall off with eccentricity. Lower contrasts result in higher E_2 estimates. These estimates reflect the responses of both spatial filter and local sign mechanisms (Waugh & Levi, 1993b). Stimulus contrast would most strongly affect the spatial filters. At lower contrasts, thresholds limited by spatial filters will be elevated compared to thresholds at higher contrasts. This would explain the different E_2 estimates found for different contrast levels under same polarity conditions. Because local signs are simply position tags, contrast has much less effect for opposite polarity, abutting vernier features (see our Fig. 9). Consistent with this finding, thresholds for well separated stimuli show very little effect of contrast once the stimulus features are more than about three times the detection threshold (Morgan & Regan, 1987; Waugh & Levi, 1993b; Wang & Levi, 1994; Hess & Hayes, 1994).

The small E_2 estimates described above may be explained by the combined effects of spatial filter and local sign regimes. At the smallest separations, spatial filters would limit threshold. At wider separations, local signs would be the limiting mechanisms. The low thresholds of the spatial filters in combination with the higher thresholds of the local signs would increase the separation \times eccentricity function slope, resulting in small E_2 estimates.

The same two potential problems mentioned above for the Levi & Klein (1990) isoeccentric arc method are also relevant for non-isoeccentric vernier features that are spatially separated as they move into the periphery. (1) By isolating local sign responses there are no foveal thresholds (separations near zero) to restrain the linear fit for the E_2 estimate; and (2) most likely the observers could not maintain sufficiently accurate fixation in order to restrict the stimuli to very small eccentricities. The observer's fixation would most likely drift toward the stimulus location. Difficulty in maintaining fixation (particularly in the 0.625 deg condition) would reduce thresholds for the closely spaced stimuli compared to accurate peripheral fixation, resulting in a steeper fall off and the small E_2 estimates that were obtained. In other words, poor fixation would reduce foveal thresholds and result in smaller E_2 estimates. A third issue is that for both the bisection (Klein & Levi, 1987) and vernier (Waugh & Levi, 1993b) E_2 estimates, any error in thresholds measured near the cusp in the double-line fit (the closest point to the fovea of the local sign part of the data) could significantly alter the estimated point of transition between the putative mechanisms. For example, if filter mechanism responses are inappropriately included in the local sign equation, then E_2 estimates will be too low.

(F) Temporal

None of the previous methods for measuring E_2 are convincingly related to the anatomical cortical magnification factor. For that reason, in the present paper we attempted to develop a new method for revealing an E_2 value that can be related to topographic mapping of spatial location. We used a simple stimulus to avoid the complexity of masking and our measures included foveal thresholds. To minimize the filter regime contribution for

closely spaced stimuli, we introduced a temporal asynchrony. When the reference and test targets were temporally overlapping, E_2 was unnaturally small, but when there was no temporal overlap, E_2 estimates were close to 0.8 deg. The range of E_2 values we found across temporal delays may be explained by differences in the limiting factors of early spatial filter and later local sign mechanisms. The data are consistent with a gradual change in the responding mechanism across ISI. As shown in Experiments 1 and 2, using opposite polarity and low stimulus contrast, the filter mechanism influence drops out as the temporal overlap decreases. This permits relative local sign regime isolation and also allows abutting vernier measurements.

Factors affecting L_2

We hypothesize that processing is within the local sign regime in situations where stimulus characteristics minimally influence threshold. This assumption, however, should be qualified. Although the stimulus independence may be correct to a first order, there are a number of stimulus manipulations that do affect thresholds in the local sign regime, since a comparison of the test and reference must be made at a second processing stage (Sterken *et al.*, 1994). The second stage efficiency could depend on stimulus properties. The dependence will, however, be weaker than if a single spatial filter were used to measure the relative position in a first stage. In the following sections we will examine several factors that affect L_2 .

Stimulus orientation and visual field region

Foveal vernier thresholds are similar for vertical and horizontal orientations (Fahle, 1991), however, in the periphery spatial acuity shows an anisotropy. This anisotropy has been reported for peripheral grating acuity (Rovamo *et al.*, 1982; Wilson, 1991), T-orientation acuity (Toet & Levi, 1992), vernier acuity (Wilson, 1991; Levi & Waugh, 1994) and bisection (Yap *et al.*, 1987; Klein & Levi, 1987). Specifically, thresholds are lower in the periphery for offsets in the isoeccentric vs the radial direction (Yap *et al.*, 1987). Therefore, in a vernier task, horizontally oriented stimuli will produce lower thresholds than vertically oriented stimuli in the temporal visual field. The reverse will be true in the lower visual field (e.g., vertical will produce lower thresholds). The lower peripheral thresholds for radically oriented stimulus features produce increased E_2 estimates as seen in Table 2 (column headings: orientation and visual field region) compared to estimates obtained for isocentric oriented features.†

Lower thresholds for isoeccentric orientations also appear to hold within the local sign regime (Klein & Levi, 1987; Yap *et al.*, 1987). This implies that local sign mechanisms may also be degraded in the radial direction, perhaps due to the second stage comparison of the local position labels (the cortical ruler). If this is correct, then the ruler's tilt would be a more precise judgment compared to the ruler's length. Indeed, Sterken *et al.*

†At first glance, Levi *et al.* (1985) seem to have found the opposite result (see reference A2 vs A6 of Table 1). These E_2 estimates suggest that the fall off with eccentricity is greater for the isoeccentric direction. However, reference A2 (their Fig. 11) presents E_2 estimates for short-length multiple-lines that were briefly presented and scaled according to an E_2 factor of 0.8. Reference A6 (their Fig. 7) presents estimates for long lines that were scaled to an E_2 factor of 2.5 and the reference was on continuously. Since the lines were longer than necessary for optimal performance at all eccentricities, the differences in temporal presentation probably account for the higher estimates seen in Reference 6. It is also possible that the brief, multiple-lines (used in Reference A2) provide additional data for the fovea that are not used in the periphery, therefore increasing the apparent fall off with eccentricity.

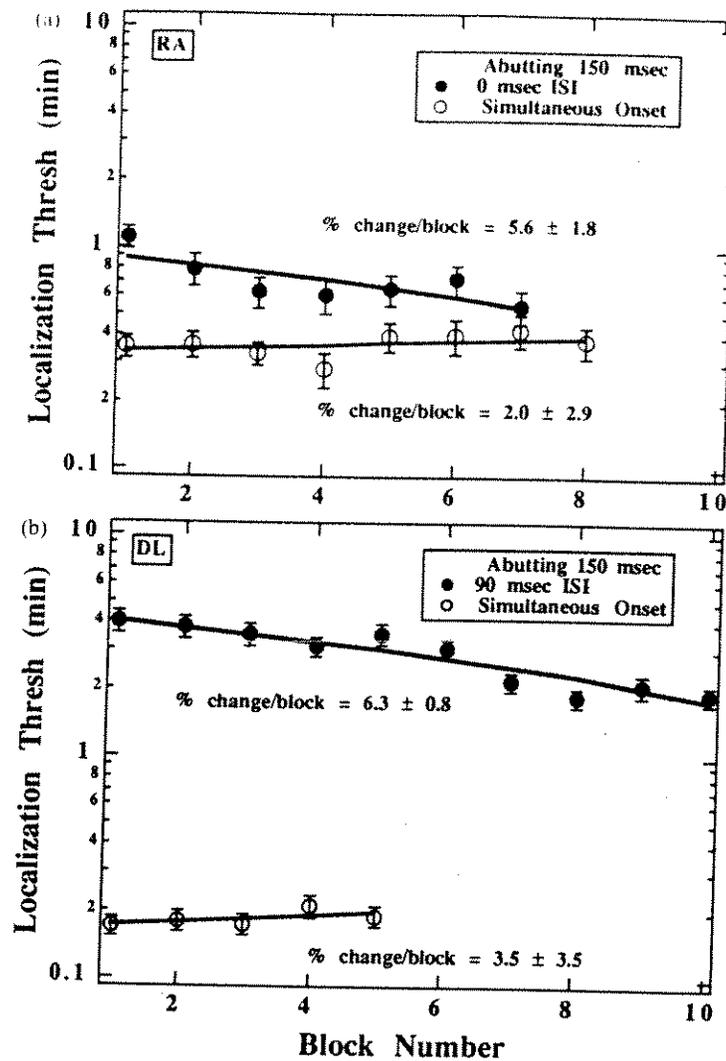


FIGURE 10. To show the effects of practice, localization thresholds are plotted as a function of the block number (125 trials/block). Data for simultaneous (open circles) and positive ISIs (solid circles) are shown for a naive (a) observer and for one of the authors (b).

(1994) have suggested that a second processing stage is needed to explain threshold differences for different stimulus orientations. Our experiments were done in the isoecentric direction. If they had been done in the radial direction (e.g., using a bisection rather than vernier task), then L_2 would be expected to be smaller than those we report.

Referenced vs unreferenced thresholds

It is interesting to compare our data to data gathered under similar conditions except with a dark ISI with no visual references (Foley, 1976; Matin *et al.*, 1980; White *et al.*, 1992). White *et al.* did not find, contrary to our findings, a large difference in thresholds for different reference and test stimuli spatial separations. Our observer DL also participated in their experiment, making it convenient to compare thresholds and the fall off in thresholds with eccentricity for localization done in the dark and in the light. DL's unreferenced thresholds (in Fig. 5 of White *et al.*) at positive ISIs ($\approx +200$ ISI)

were elevated one log unit compared to his referenced vernier thresholds shown in our Fig. 5 (0.1 deg vs 0.01 deg). In the present study, DL showed $L_2 = 0.9$ deg at ISI = 180 msec. To compare, at 200 msec ISI (in Fig. 5 of White *et al.*) observer DL computed $L_2 = 8.8$. Although both data sets represent local sign mechanism responses, the increased noise (i.e., eye position uncertainty) without visual references (in the dark) substantially inflates L_2 estimates. Our data, while not noise-free, are less influenced by factors other than the eccentricity dependence of local sign mechanisms. Having room lights on during the experiment, and thus having stationary references visible to the observer, most likely helps to stabilize the judged eye position.

Training effects

All observers in these experiments showed some increase in localization accuracy after repetitive practice, particularly for the temporally asynchronous conditions. Repetitive training on novel psychophysical tasks is

essential for reliable threshold estimates (McKee & Westheimer, 1978; Poggio *et al.*, 1992; Beard *et al.*, 1995). For this reason, initial measurements for each condition were repeated until stable thresholds were established for at least 4 blocks of 125 trials. Figure 10 shows the effect of practice on localization thresholds for two observers (RA and DL). Localization thresholds (minutes of arc) are plotted as a function of the training block number for two temporal conditions, simultaneous (open circles) and successive (solid circles) presentation. Observer RA had no prior experience making psychophysical observations, whereas DL had extensive past training on localization judgments, including simultaneous and successive stimuli presented in the dark. The simultaneous presentation data over training blocks are shown for both observers. Stimulus features were abutting. Neither observer showed improvement for foveally viewed, abutting, simultaneously presented stimuli over 8 blocks of trials. Also presented are the zero msec (reference offset = test onset; observer RA) and 90 msec (observer DL) ISI data. With a temporal gap, thresholds declined by approximately 6% each block for both observers. This improvement is consistent with other peripheral vernier acuity learning data (Beard *et al.*, 1995).

The underlying reason for this practice-based improvement is not known but may relate to a decrease in the positional uncertainty of local sign mechanisms by a type of peripheral local signs calibration (Maloney & Ahumada, 1989) or to an improvement in the comparison process itself (a more cognitive explanation). Our data do not distinguish between these two possibilities.

ALTERNATIVE EXPLANATIONS FOR OUR L_2 ESTIMATES

Spatial filters

Vernier thresholds are most likely determined by the sum of contributions from various (independent) sources of noise. In the context of the present experiments, this noise may arise from target eccentricity, separation, contrast, polarity and temporal delay. When one of these sources of noise dominate, then threshold will largely be determined by that source, and not by others. Thus, it could be argued that one does not need to invoke separate mechanisms (filters and local signs). Such an argument is based on semantics. We are arguing for separate regimes rather than separate mechanisms, *per se*. Both regimes are based on filter mechanisms; however, when the contrast response of the filters is degraded (by opposite polarity, temporal asynchrony, etc.), we believe that the position labels (local signs) of the filters become more useful. It could be argued that our asynchronous vernier thresholds are limited by large spatial filters with broad temporal integration limits rather than local sign mechanisms. At small spatial separations, the spatial filters may be quite sensitive to temporal asynchrony, while at large spatial separations, spatial filters may be relatively insensitive to temporal asynchrony. This model would predict our finding that thresholds fall off less as a

function of spatial separation with positive ISIs. This model is unlikely, however, because of the results of our Experiments 1 and 2 which showed differential effects of contrast and polarity at small and large separations.

Receptor irregularities

Wilson (1991) has suggested that cone position irregularity can account for the increase of hyperacuity thresholds with eccentricity and separation. He found that the standard deviation of cone spacing in primate (Hirsch & Miller, 1987) and human (Hirsch & Curcio, 1989) can be summarized as:

$$SD(E) = 3.8(\text{sec})(1 + E(\cdot)/E_2) \quad (12)$$

where E_2 for cone randomness was found to be 0.77 deg (Wilson, 1991). That value of E_2 is consistent with our value of L_2 , or the local sign fall off of hyperacuity thresholds in peripheral vision. Wilson further hypothesized that cumulative cone jitter across a string of cones (where the successive cone spacings are assumed to be uncorrelated) may limit foveal thresholds for small separations. From this assumption Wilson (1991) found a good fit for hyperacuity thresholds as a function of spatial separation. Previously, this same data set was thought to require a filter model in order to achieve the rapid degradation of acuity as the feature separation increased (Klein & Levi, 1985; Wilson, 1986). It would be interesting if the filter models could be replaced by a cone jitter model. An argument against the cone jitter model is that thresholds in the closely spaced regime are very sensitive to stimulus manipulations such as stimulus contrast and polarity, as shown in our first two experiments.

Memory limitations

The ability to localize a test target after a reference target has been turned off must require memory of the reference target location. We do not know if these "location" memories are synonymous with the iconic store, or visible persistence, discussed in the literature (Haber & Standing, 1969). Visible persistence typically refers to a continuing physical trace of the first stimulus that endures for some brief time (depending on the stimulus duration) after stimulus offset. The duration of persistence can range from 50 to 200 msec, depending on stimulus characteristics (Coltheart, 1980). It is likely that our observers are using this persisting location trace to help make the vernier judgments, since thresholds are relatively constant over positive ISIs.

Motion mechanisms

For successive presentation, our observers may be using relative motion rather than relative position to perform the localization task. Our stimulus is similar to the stop-go-stop type of movement described by Bonnet (1984) and Levi *et al.* (1984), where a stationary stimulus appears, then jumps, then again becomes stationary. Our task was to discriminate the offset direction of two lines. For abutting vernier features these offsets were well within the 15 min arc displacement limit for the

appearance of motion to occur (Braddick, 1974). To determine if motion mechanisms are responsible for our temporal vernier thresholds, we measured thresholds at 88 and 500 msec ISIs. Since apparent motion is not present at the larger ISIs, if our observers were using motion mechanisms to perform the task, thresholds at 500 msec ISI should be substantially elevated compared to threshold at 88 msec ISI (which is potentially within the motion regime). On the other hand, if the observer is not using a motion mechanism at the shorter ISI then there should be little difference between 88 and 500 msec ISI thresholds. The results of one observer showed that there was little difference (0.76 ± 0.08 min vs 0.80 ± 0.10 min, respectively) between thresholds at the shorter vs longer ISIs, suggesting that our observers were not using relative motion cues to perform the localization task.

CONCLUSIONS

The goal of this paper was to develop a psychophysical method for estimating cortical magnification in humans. We used asynchronous stimuli to obtain thresholds which are relatively independent of polarity and contrast, consistent with the local sign regime in which the two lines are processed by separate filters, and their position labels compared. The temporal asynchrony allowed us to measure vernier thresholds based primarily on local signs for abutting as well as separated stimuli, with minimal contamination from the filter regime. We were thus able to measure L_2 , which represents the rate of fall off for the local sign regime. The broad range of values found for previous estimates of E_2 called into question this number's usefulness in determining visual topography (Whitaker *et al.*, 1992). Our results and analysis suggest that these previous estimates were based on the contribution of several mechanisms and on the absence of, or inaccurate, foveal thresholds. Our estimates of L_2 within the local sign regime are similar to physiological estimates of the cortical magnification factor and may represent a psychophysical analog to these measurements.

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APPENDIX

This Appendix presents the MATLAB program that we used to calculate the cortical magnification parameters from the fMRI data of Engel *et al.* (1994) and Sereno *et al.* (1995). We present the program here because of its simplicity and to facilitate similar calculations by others.

1. load data; % The two columns of the input data are the x positions (mm) and the eccentricity (deg).
2. [params,options,f,j] = leastsq('cmf_fit',[.5, 10],[],[], data);
3. [conf,var] = confint(params,f,j);
4. [params' sqrt(var)] % Print parameters and their standard errors.
5. function dif = cmf_fit(params,data)
6. L₂ = params(1); A = params(2); % The two parameters are named.
7. %Eref = 10; E = (Eref + L₂) * exp(data(:,1)/A) - L₂; % The first column of data gives the cortical location in mm relative to a reference point
8. n = -0.26; Eref = 4; E = (n * data(:,1)/A + (Eref + L₂)^n)^(1/n) - L₂;
9. dif = E - data(:,2);

Explanation of several lines of the MATLAB code.

Line 2. The leastsq program provided by MATLAB carries out a nonlinear regression. There are several inputs to the program: (1) the

name of the function (presented in lines 5–9) that fits the data. (2) Initial guesses for a pair of parameters ($L_2 = 0.5$ and $A = 10$) that we seek to optimize for producing the best match to the data. (3) The third and fourth arguments (presently delimited by `[]`) could have contained information for changing some of the control options for the search (including analytic derivatives) and (4) input data.

Line 3. The variances of the parameter estimates are calculated using a program provided by MATLAB.

Line 5. The function `emf_fit` is used to predict the cortical magnification data.

Line 7. This is the function used for the Engel *et al.* (1994) fit. The initial “%” means to skip this line.

Line 8. This is the function used for the Sereno *et al.* (1995) fit. It could also be used for the Engel data if $k_{ref} = 10$ and $n = 0.0001$. We verified that this choice of parameters gives the same answer (in the limit as n goes to zero) as what is given in line 7.

Line 9. The difference between the expected and the observed data is output.