The upper disparity limit increases gradually with eccentricity

Saeideh Ghahghaei

The Smith–Kettlewell Eye Research Institute, San Francisco, CA, USA

Suzanne McKee

The Smith–Kettlewell Eye Research Institute, San Francisco, CA, USA

Preeti Verghese

The Smith–Kettlewell Eye Research Institute, San Francisco, CA, USA

Stereopsis is important for tasks of daily living such as eye-hand coordination. It is best in central vision but is also mediated by the periphery. Previously we have shown that individuals with central-field loss who have residual stereopsis in the periphery perform better at an eye-hand-coordination task when they perform the task binocularly rather than monocularly. Here we seek to determine what sets the limit of stereopsis, defined as the largest disparity that supports the sustained appearance of depth, in the near periphery in healthy individuals. While stereoacuity thresholds increase sharply with eccentricity, Panum's area increases much more slowly. We used a rigorous method to determine the uppermost limit of disparity. At long durations, the two half-images that define a large disparity appear as two isolated targets in the same flat plane; small incremental changes in disparity produce changes in the separation between the half-images, and disparity magnitude can be judged on the basis of separation, like a monocular width judgment. The disparity limit is the point at which the threshold for judging dichoptic separation between the half-images is equal to the monocular width-discrimination threshold. The disparity limit at 10° was a factor of 2–4 times larger than the fovea, regardless of the meridian tested. The increase in the disparity limit with eccentricity was shallow, similar to that of Panum's area. Within this disparity limit, disparity increment thresholds were comparable for foveal and peripheral targets, illustrating the significance and utility of peripheral stereopsis, especially in the absence of foveal stereopsis.

Introduction

Our eyes are separated laterally by a small distance, so each eye sees a slightly different view of the physical world. The small differences in feature positions between the two retinal images—the horizontal disparities—are generated by the relative z-axis distances separating the features. Stereopsis refers to the sense of depth generated by horizontal disparity (Julesz, 1971; Wheatstone, 1838); stereoacuity is the measure of the smallest detectable difference in disparity. The median stereoacuity threshold in young adults is about 12 arcsec (Coutant & Westheimer, 1993), although in practiced observers it can be half that value or less (Howard, 1919). Stereoacuity is best in the fovea and declines steeply with increasing eccentricity, reaching a threshold 8–10 times greater than the foveal value at an eccentricity of 10° (Blakemore, 1970; Fendick & Westheimer, 1983; Ghahghaei, McKee, & Verghese, 2016; McKee, Welch, Taylor, & Bowne, 1990; Ogle, 1952a, 1952b; Weymouth, 1958).

The reduced sensitivity to fine disparities with eccentricity does not mean that stereopsis is useless in the peripheral visual field. Perhaps the most compelling demonstration of its utility comes from a study on eye-hand coordination in individuals with central-field loss (Verghese, Tyson, Ghahghaei & Fletcher, 2016). This study showed that people with binocular macular degeneration who had remaining peripheral stereopsis were able to utilize stereopsis to perform a manual task requiring visual guidance: picking up a peg (one of various shapes) from the middle of a pegboard and placing it in its correctly shaped opening. Participants with both healthy and affected vision made fewer errors and took less time when the task was performed binocularly than monocularly. For the healthy age-matched control group, peg-placement time was significantly correlated with stereoacuity—the better their stereoacuity, the shorter their placement time. Importantly, for those affected individuals who had residual stereopsis, peg-placement time fell along the same function of stereoacuity as for the healthy control group.

Not all people with central visual loss have residual stereopsis in their periphery, which raises the question of what sets the limit on stereopsis in these people. Presumably, there has to be functional retina at corresponding, or nearly corresponding, regions in the periphery. Studies on disparity-sensitive neurons in primate V1 show substantial positional overlap of the monocular receptive fields that are combined cortically to generate the disparity tuning of these neurons (Prince, Cumming, & Parker, 2002). However, these physiological studies do not specify what is the largest separation between corresponding loci that will support stereopsis, nor how this upper disparity limit varies with eccentricity. Our primary objective was to determine this upper limit as a function of eccentricity.

Traditionally, the upper fusional limit, called Panum's limit, is determined by increasing a target's disparity until the its binocular image no longer appears fused—that is, the image looks blurred or diplopic ("double"). In the fovea, this limit for a fine-line target is reached when the target's disparity is 8–12 arcmin. However, Schor, Wood, and Ogawa (1984) showed that the diplopia limit depends on the characteristics of the stimulus. Using band-limited difference-of-Gaussians targets, they showed that low-spatial-frequency targets have a much larger fusional range than high-spatial-frequency targets. Their approach, using band-limited stimuli, is unwieldy for measuring stereoscopic fusion in the periphery for two reasons. First, to estimate the fusion limit, they asked their observers to increase target disparity until they perceived a slight doubling or increase in the width of the stimuli, a perceptual criterion that may be difficult to judge at peripheral loci. Second, the lowest frequency targets used in their study were very large (central bright section = ~6°, or ~12° overall), thus confounding eccentricity with target size. Our stimuli represent a compromise between scaling size with eccentricity and confining the target to a particular eccentric locus; we used a large rectangular patch (0.33° vertical × 1° horizontal in the fovea) that was scaled vertically according to cortical magnification (*m*-scaled) and filled with bright, dynamic random dots to minimize the Troxler effect.

Diplopia is a useful criterion for determining the fusional limit, but it does not correspond to the largest disparity that conveys a sense of depth, because diplopic targets may still appear to lie at a nonzero depth. Recognizing this, Schor et al. (1984) used a different criterion to estimate the upper depth limit—the disparity beyond which the two diplopic half-images appeared to lose depth and return to the same plane as the fixation target. Using bright-line targets presented in the fovea, McKee, Levi, and Bowne (1990) measured disparity increment thresholds—that is, incremental changes in a pedestal disparity. In agree-ment with Schor et al., they found that at large pedestal disparities the two half-images appeared to lie in the fixation plane. At this large pedestal, any small change in disparity appeared as a small change in the lateral separation between the two half-images, much like a dichoptic width judgment between the image in the right eye and the image in the left. Indeed, McKee et al. found that the increment threshold for disparity at this point was identical to the increment width threshold for monocular line targets separated laterally by a distance equal to the disparity.

The agreement between dichoptic width thresholds and monocular width thresholds indicates that there are no disparity mechanisms available to process the disparate stimulus. Only information about retinal position remains. Thus, the disparity value where dichoptic and monocular thresholds are equal is a rigorous measure of the upper depth limit. In our first experiment we determined this upper depth limit at three eccentricities (fovea and near periphery) in the lower visual field, using measures of disparity increment thresholds and monocular width thresholds. For comparison, in our second experiment we asked subjects to increase the disparity until the two diplopic images appeared to lie in the fixation plane, following the procedure used by Schor et al. (1984).

Methods

Participants

Two participants (S1: SG and S2: SM; authors) participated in Experiment 1. One author and an additional seven participants participated in Experiment 2; two of them were not able to perform the task, leaving one author and an additional five participants performing the task (S1, S3, S4, S5, S6, and S7). For direct comparison between Experiments 1 and 2, we also collected data from S2 in Experiment 2 along the lower meridian. All participants had previous experience with psychophysical studies and had normal or corrected-to-normal visual acuity and no history of oculomotor abnormality. Ethics approval was granted by the Institutional Review Board of the Smith–Kettlewell Eye Research Institute. Informed consent was obtained from all participants at the beginning of their first session. The study was conducted in accordance with the Declaration of Helsinki.

Apparatus

Shutter glasses (NVIDIA 3D glasses 2) were used to present stereoscopic stimuli. NVIDIA glasses have been

used in previous studies of stereopsis (Wardle, Bex, Cass, & Alais, 2012). The 120-Hz ASUS 3D-ready HDMI monitor alternated between each eye's view, updating at 60 Hz per eye. We used the MATLAB PsychToolbox library (Brainard, 1997; Pelli, 1997) to program the experiment. Subpixel resolution via the graphics card provided a spatial-positioning accuracy much higher than our tasks required.

Experiment 1: Increment thresholds as a function of pedestal disparity

Stimuli

Viewing distance was 1 m. The fixation point was presented at eye level in all experiments. In Experiments 1 and 2, stimuli were composed of patches (reference and test) of bright, dynamic random dots on a gray background. The luminance of the dots and background were 145 and 35 cd/m^2, respectively. The reference patch was displayed above the test patch with a vertical separation of 0.5° at the fovea. The patch subtended 1° (horizontally) × 0.33° (vertically) at the fovea. The stimuli were presented along the lower meridian at 0°, 5°, or 10° (visual) eccentricity, such that the vertical midpoint between these stimuli was placed at these distances from the fixation point (see Figure 1).

Note that we are *not* measuring stereoacuity; stereoacuity is a measure of the signed disparity relationship between two targets—that is, which target is in front of the other. We are instead measuring the ability to discriminate the *z*-axis distance separating two targets. In our stimulus arrangement, one target is always presented in the fixation plane and the other at a pedestal disparity—for example, 10 arcmin—plus or minus an incremental change—for example, ±1 min. The observer judges whether the pair of targets is separated by a *z*-axis distance that is larger or smaller than the pedestal distance, much like an *x*-axis width judgment.

The vertical gap and vertical dimension of the patches were *m*-scaled by a factor of 0.33 with eccentricity (Rovamo & Virsu, 1979; Strasburger, Rentschler, & Jüttner, 2011), so that at 10° eccentricity the patch subtended 1° (horizontally) × 1.44° (vertically). The horizontal dimension was not scaled, because we were looking for the disparity (dichoptic width) where thresholds were equivalent to the monocular width judgments, and that point would have been obscured if the dichoptic targets overlapped horizontally (see Figure 1). Dot density was 200 dots/°^{2}. Dot diameter was 3.5 arcmin. To prevent stimuli from
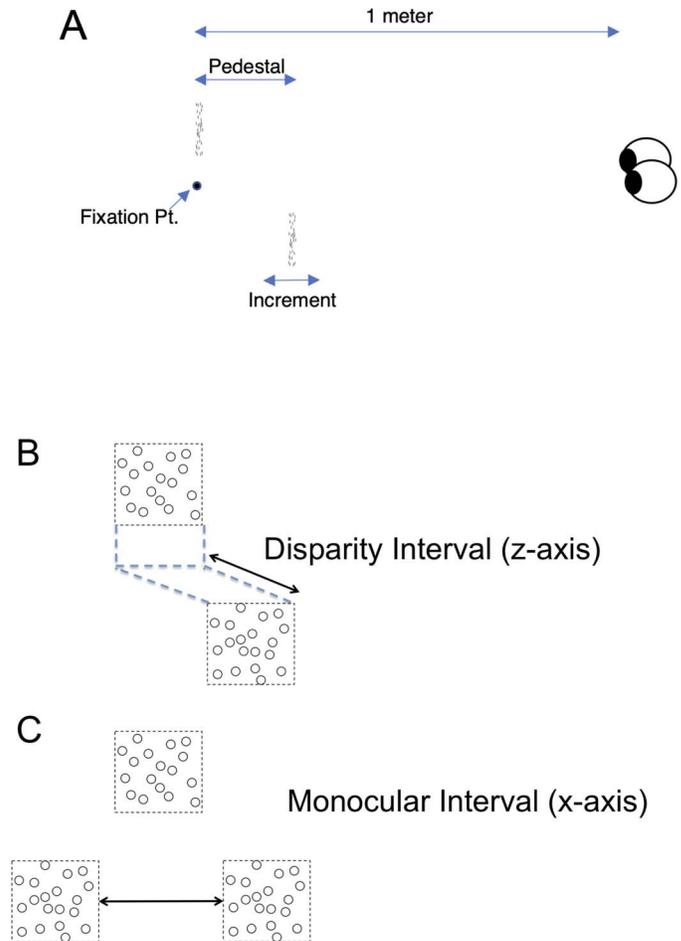

Figure 1. (A) Stimuli in Experiments 1 and 2. The reference patch, fixation point, and nonius lines were shown to both eyes with zero disparity. In Experiment 1a the test patch was shown with crossed disparity; in Experiment 1b, the reference and both eyes' test-patch rectangles were shown to the left eye only. (B) At small pedestal disparities the test patch appears to be in depth and the disparity increment judgment is a depth judgment (z-axis); but (C) at large pedestals, the test patch appears diplopic and the disparity increment judgment becomes equivalent to a monocular incremental judgment of width.

fading in the periphery, the screen was updated every 100 ms with a new set of random dots.

Design

In Experiments 1a and 1b, we used the method of single stimuli (McKee et al., 1990; Morgan, Watamaniuk, & McKee, 2000; Pratt, 1933). Experiment 1a measured disparity increment thresholds. The reference patch was always presented in the fixation plane with zero disparity. In each block, the test patch was presented at a crossed pedestal disparity (PD) with respect to the reference patch. On each trial we

manipulated test disparity around this pedestal, so that the test disparity came from the set of {PD ± 2D, PD ± D, PD}, where D was chosen by the experimenter to achieve a performance level between chance and 100% correct for PD ± D and (close to) 100% correct for PD ± 2D. Twenty trials for each disparity increment level were presented in a random order in each block.

In Experiment 1b we measured thresholds for monocular width judgment. The stimuli were similar to those in Experiment 1a, except that the reference and test patches were shown to the left eye only (the dominant eye for both participants who performed this task).

The eccentricity (0°, 5°, or 10° visual along the lower meridian) and particular pedestal disparity were all presented in separate blocks in each of Experiments 1a (dichoptic) and 1b (monocular). We did not compensate for the vertical tilt of the horopter. Assuming an interpupillary distance of 6 cm and a vertical tilt between 2° and 5° at a viewing distance of 1 m (Schreiber, Hillis, Filippini, Schor, & Banks, 2008; Siderov, Harwerth, & Bedell, 1999), the disparity that corresponds to the distance between the horopter and the fixation plane is between 1.3 and 3.25 arcmin, respectively, at 10° eccentricity along the lower vertical meridian. The pedestal disparities in our study were much larger than these values for the test patch shown at 10° eccentricity.

Procedure

For each condition, before running the main blocks we ran a pilot experiment to find a disparity step (D) that would yield a reasonable probit fit for the set of {PD ± 2D, PD ± D, PD}. Note that all PDs were crossed disparities. Once the disparity step (D) was chosen, the main block was run. Each block consisted of 120 trials. The first 20 trials included four samples of each disparity from the set of {PD ± 2D, PD ± D, PD} in random order, to allow the observer to learn the mean and range of the block; 20 trials are more than sufficient for this purpose (Morgan et al., 2000). The remaining 100 trials included 20 samples of each disparity from the set in random order. Only the last 100 trials were used for probit analysis. The probit fit gave us the estimated increment threshold for a given block; our criterion for threshold was half the disparity or distance corresponding to the 16% and 84% values on the probit function, equivalent to a d' of 1. The mean incremental threshold and the standard error for each pedestal were estimated from repeated blocks for the same condition; a minimum of three blocks were used to estimate thresholds. For large PDs, data for Experiments 1a and 1b for a given condition were collected on the same day and in counterbalanced

order. The task was time consuming, and no more than four blocks of data were collected on the same day.

In each trial, the observer was asked to maintain fixation at the fixation point. In the dichoptic condition they were asked to judge whether the disparity of the test patches in that trial was larger or smaller than the average disparity in the block by pressing the right or left arrow key, respectively, for a larger or smaller response. In the monocular condition, they judged whether the separation between the inner edges of the rectangular patches on a given trial was larger or smaller than the average separation. The patches were presented until the observer responded; audio feedback was presented to indicate incorrect responses. The next trial started 2 s after the response.

Results

In Figure 2, the incremental disparity thresholds (in blue) are plotted versus standing PD separately for each observer (upper and lower panels) and for each tested eccentricity. The red data points are the monocular width judgments for separations between the inner edges of the rectangular regions at the tested pedestal disparities. This separation is equal to pedestal disparity minus 60 arcmin, which is the horizontal extent of the half-image. Blue and red lines corresponding to Weber's law were added for ease of comparison; increment thresholds for both disparity and width are known to obey Weber's law over some portion of their range (Levi & Klein, 1990; McKee et al., 1990; Volkmann, 1863). Beyond a certain PD, the disparity thresholds are roughly equal to the width thresholds. We assume that this indicates that depth information is no longer available. Black arrows in Figure 2 show the point at which the disparity threshold becomes equivalent to the monocular width threshold. We chose the break point as the PD at which dichoptic and monocular thresholds are indistinguishable. The positioning of the black arrow is approximate because we did not measure all possible PDs. Figure 5A (blue lines) plots the position of these break points (the upper disparity limit) as a function of eccentricity for each observer. Note the shallow increase of the upper depth limit with eccentricity.

Although our paradigm may resemble many studies of stereoacuity in which *both* test and reference targets are presented together at a variable distance from the fixation plane (Blakemore, 1970; Ogle, 1953; Siderov & Harwerth, 1993), our disparity increment measurements follow a different function. In the stereoacuity studies, thresholds rise exponentially with the distance of both targets from the horopter. However, the disparity increment function, which we are measuring, rises proportionally to the PD separating the test and
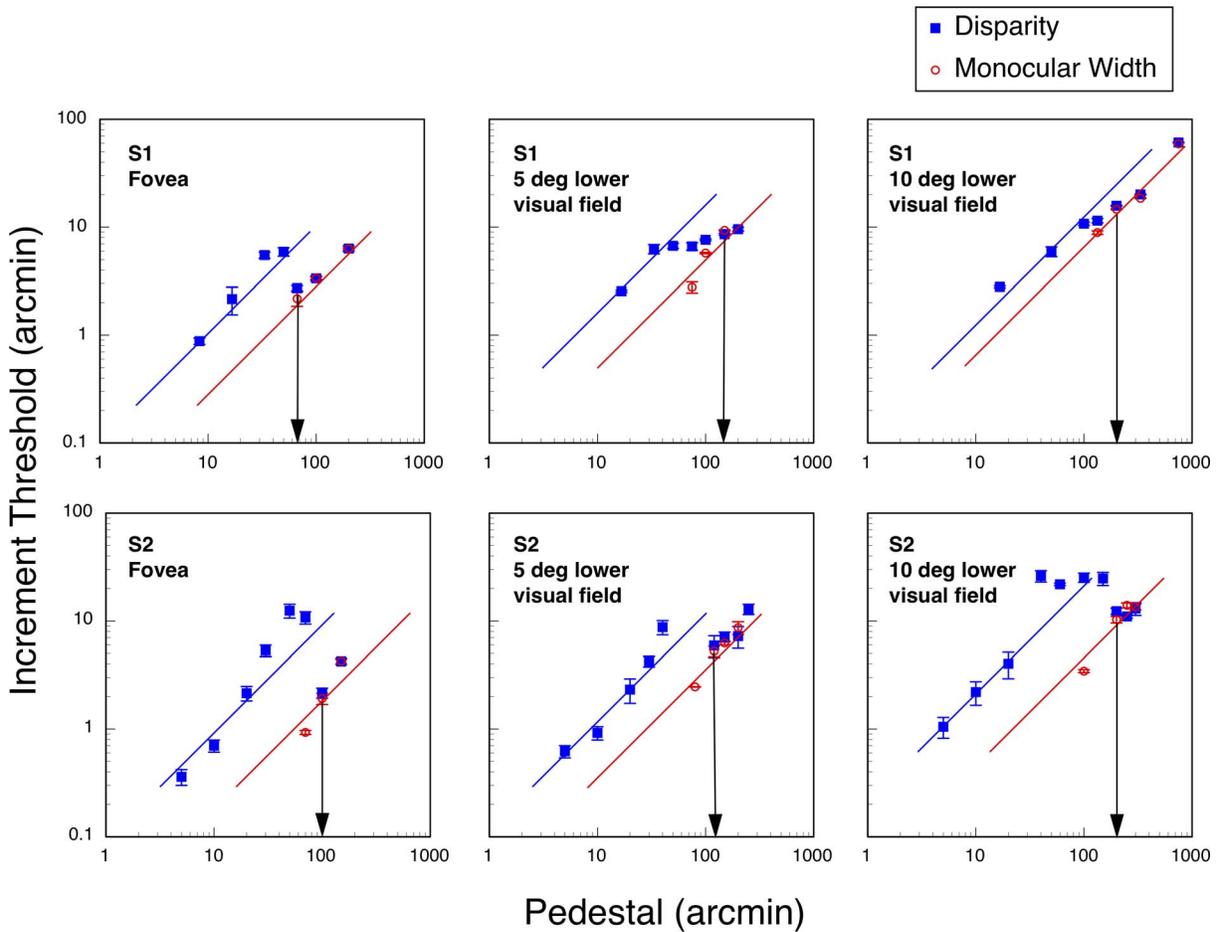
Figure 2. Incremental thresholds for a range of pedestal disparities (separations) in Experiment 1, when the target was viewed dichoptically (Experiment 1a; in blue) or monocularly (Experiment 1b; in red). Each row illustrates data for one participant. Thresholds for 0°, 5°, and 10° eccentricity are in the left, middle, and right columns, respectively.
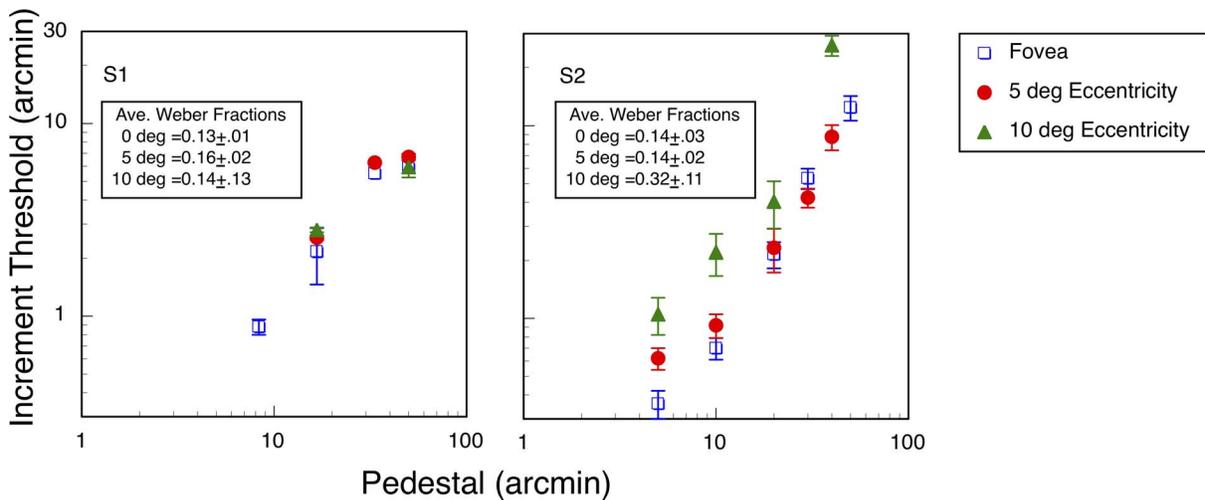

Figure 3. Increment thresholds as a function of pedestal disparity replotted from Figure 2 (Experiment 1a). The blue, red, and green symbols represent eccentricities of 0°, 5°, and 10°, respectively.
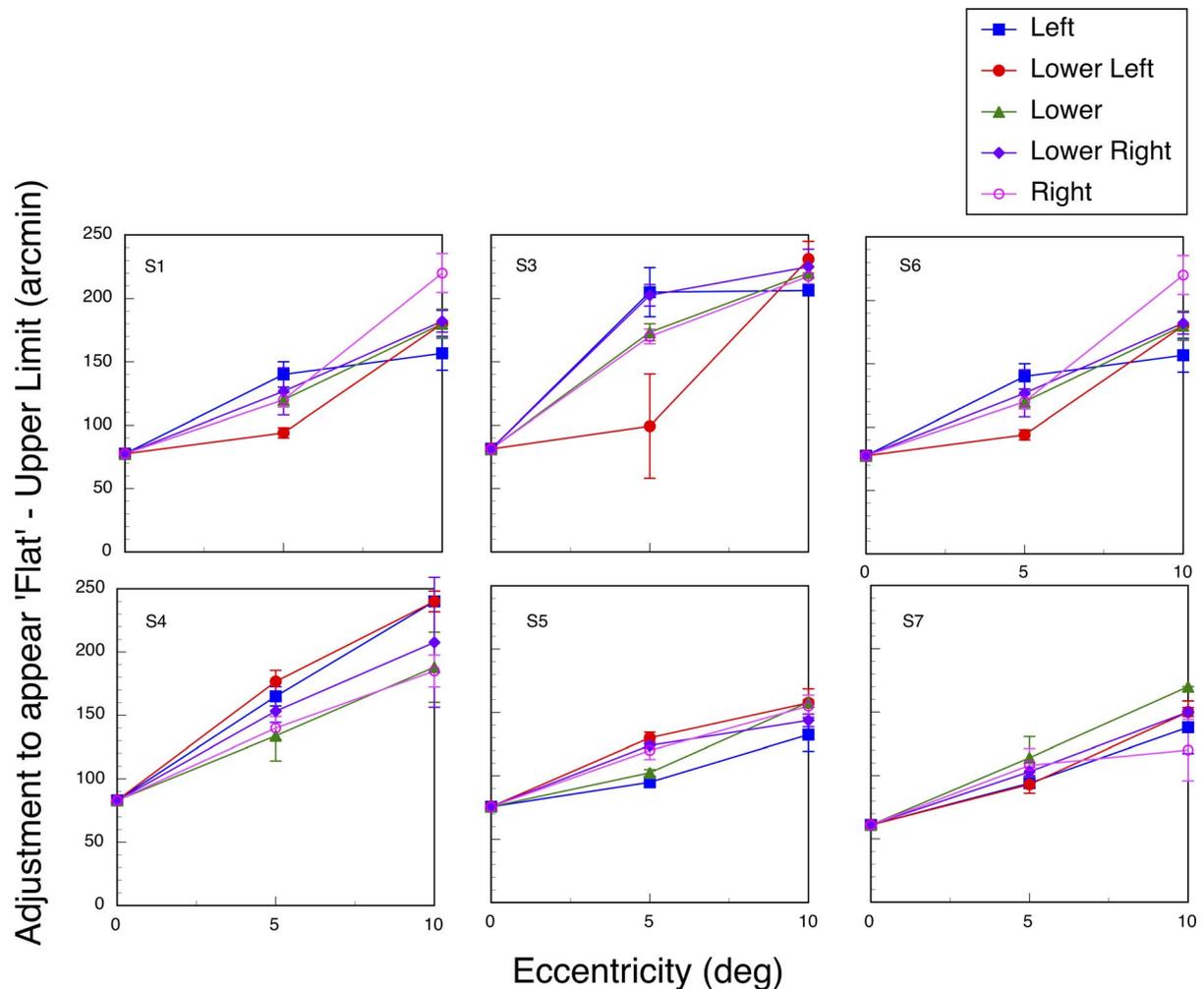
Figure 4. Upper limit of depth range as a function of eccentricity in Experiment 2. Data are plotted for each observer and for different meridians, when a flat percept was reported.

reference over a narrow disparity range. Like incremental width judgments, incremental disparity judgments follow Weber's law (McKee et al., 1990).

At the value where the disparity thresholds merge with the width thresholds, observers are using the space between the two diplopic half-images of the test patch to judge disparity—or more exactly, using the incremental changes in their lateral separation to judge whether the test disparity is large or small. Thus, if the test patches were wider—for example, 4°—there would be no space between the half-images even at moderately large disparities (>3°). Moreover, the monocular increment thresholds for comparable widths—for example, 4° ± Δwidth—would generally be higher than the disparity thresholds, so that the improvement in disparity thresholds seen in Figure 2 (arrows) would not be evident. In general, this threshold approach is only useful for targets of 1° or less in width. We believe that narrower targets would produce the same results as those shown in Figure 2, because McKee et al. (1990)

found the same upper limit in the fovea, using very thin bright lines.

It is also interesting to note that the magnitude of increment thresholds as a function of PD in the range below the upper disparity limit (10–50 arcmin) do not increase substantially with eccentricity. As can be seen in Figure 3, which compares the data in Experiment 1 across eccentricity, increment thresholds for observer S1 are roughly invariant across eccentricity, whereas increment thresholds for observer S2 at 10° eccentricity are about twice the thresholds at the fovea. These disparity increment thresholds determine how precisely one can judge the *z*-axis distance between features (e.g., the distance from peg to hole in Verghese et al., 2016) and possibly control the size of the grasp aperture. Thus, they may be more important than stereoacuity for controlling hand movements. Note how little the disparity increment thresholds change with eccentricity—a surprising result in light of the steep increase of stereoacuity thresholds with eccentricity. The shallow increase of disparity increment thresholds with eccen-
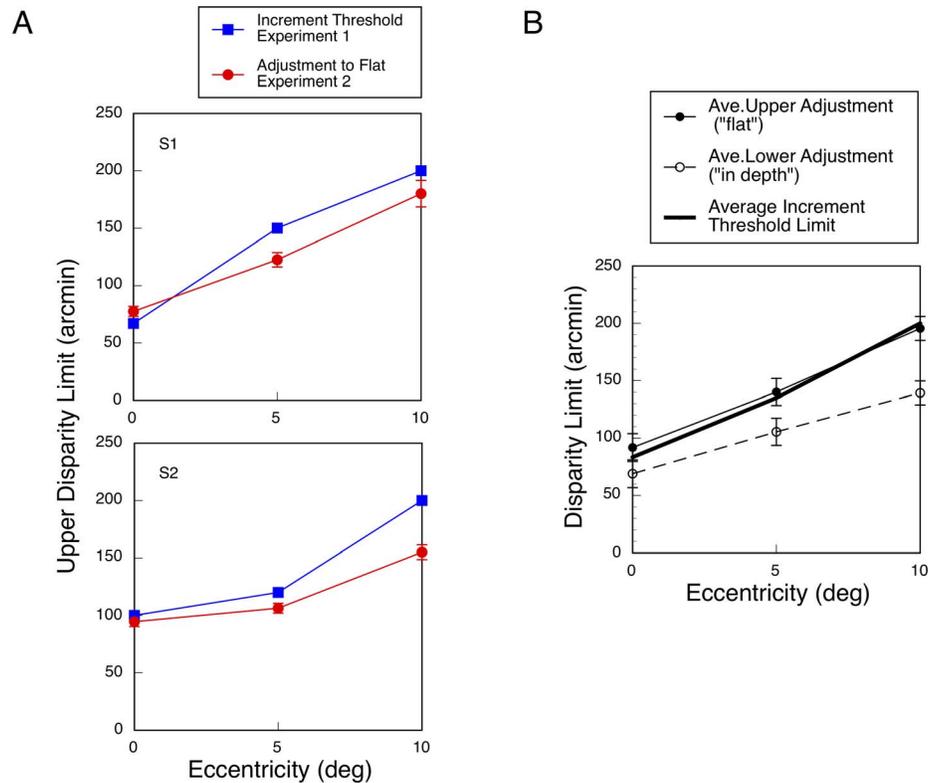
Figure 5. (A) Upper limit of depth versus eccentricity for both the increment threshold method (Experiment 1; blue squares) and the method of adjustment (Experiment 2; red circles) for observers S1 and S2, along the lower vertical meridian. (B) The average increment threshold for S1 and S2 (Experiment 1; thick solid line) and the upper adjustment limit, averaged over all observers and all meridians in Figure 4 (Experiment 2; thin solid line). The average lower adjustment in Experiment 2 corresponding to the disparity where the test target appeared in depth, although unfused, is also plotted (dashed line).

tricity indicates that for disparities ranging from 10 to 50 arcmin (1–4 cm at arm's length), observers are nearly as precise at judging disparity intervals at 10° eccentricity as they are in the fovea.

Experiment 2: The shallow function holds across other meridians

The increase in the upper limit of depth perception with eccentricity, although shallow, emphasizes the potential of peripheral vision for stereopsis. Individuals with binocular macular degeneration often have a preferred retinal locus that places the binocular scotoma in the upper visual field (Fletcher & Schuchard, 1997; Fletcher, Schuchard, Livingstone, Crane, & Hu, 1994), so that they can use the lower visual to explore the world around them. The question arises whether there is a specific meridian along which there is a wider range for potential depth perception. To address this, we measured the upper limit of depth perception along all meridians in the lower visual field.

The method in Experiment 1 is very time consuming: Each data point in Figure 2 comprises at least 360–600 trials, in addition to pilot studies to determine the disparity step for a given PD, resulting in at least 10,000 trials per observer; and the observers could do only a few blocks of trials in a day. Therefore, in Experiment 2 we used the method of adjustment.

Design

Eccentricity (0°, 5°, and 10°) and meridian (left, right, lower vertical, lower left, and lower right) were measured in separate experimental blocks. The reference patch was always presented above the test patch, and the eccentricity of the stimulus was the distance between the fixation point and the vertical midpoint of the reference/test configuration. We randomized the order in which meridians were tested across participants, and within a meridian we randomized the order in which eccentricity was tested for a given participant. We ensured that the stimuli did not fall in the blind spot for any observer. Stimuli were presented dichoptically; the half-images of the test patch had crossed

disparity. Six observers completed the task in all meridians tested. Only the lower vertical meridian was tested for S2.

Procedure

The task was to report the disparity at which the test patch transitioned from the appearance of a different-depth ("in depth") percept to a same-depth ("flat") one. We started the trial by presenting the test patch at a disparity for which it appeared single and in depth. Then the participant increased the disparity (using the right arrow key) until the test patch appeared diplopic but still in depth. The participant kept increasing the disparity until the test patch appeared diplopic but no longer in depth. At this point, the participant recorded a flat percept. The test-patch disparity was then increased by a random disparity (chosen from a set of 10 disparity values), after which the participant decreased the disparity (by pressing the left arrow key) until the test patch appeared diplopic *and* in depth. At this point, the participant recorded an in-depth percept. There were at least three trials for each experimental condition.

Results

Figure 4 shows the mean and standard deviation (*SD*) along each meridian separately for each of the six observers. Data are for the large disparity at which a flat percept was reported. Idiosyncratic patterns of adjustment were found for different meridians within and between observers. Overall, the increase in depth range with eccentricity was shallow along all meridians. We did not find a systematic effect of meridian on the upper depth range.

Figure 5B shows the average of the means pooled over meridian as a function of eccentricity for when the reported percept was flat or in depth. The disparities corresponding to the flat percept are higher than those corresponding to the in-depth percept, and have a similar slope with eccentricity. Note that the appearance of being in depth corresponds not to the point where the half-images are fused but rather to the point at which the diplopic half-images appear in a different plane from the reference target. The average upper limit estimated from the increment thresholds in Experiment 1 are plotted for comparison in Figure 5A and 5B.

Note that the pooled average adjustment for the flat percept is essentially identical to the average estimate from the threshold approach (Figure 5B). The increase in depth range with eccentricity is similar and shallow for both measures, showing that the results from the method of adjustment confirm the trend obtained with the more time-consuming measurement of increment thresholds.

Discussion

Upper limit of disparity for stereopsis

In patients with central vision loss due to macular degeneration, residual stereopsis can help with tasks that require eye-hand coordination in depth (Verghese et al., 2016). For these patients to perceive depth from disparity, they need to have intact retina in both eyes at roughly corresponding points with overlapping receptive fields, despite asymmetries in the shape of monocular scotoma and possible small eye misalignments. Neurons close to the fovea, because of their small receptive fields, are more susceptible to a lack of correspondence, whereas neurons in the periphery with larger receptive fields and coarse disparity detectors are likely less sensitive to the effects of macular degeneration. In this work, we set out to determine the largest disparity as a function of eccentricity that supports stereopsis in people with healthy vision, to find the potential for stereopsis in individuals with central vision loss.

Our results, using two different methods, showed that the upper depth limit for crossed disparity at an eccentricity of 10° is about 180–200 arcmin (~3° or more). Other studies that have looked at the upper limit have found similar values for stimuli that extend to eccentricities between 5° and 10°. Tyler (1975) measured the maximum depth limit for a 15° vertical line that varied sinusoidally in depth and found the peak-to-peak amplitude at 0.03 c/° to be 300–600 arcmin, equivalent to a crossed disparity limit (half-amplitude) of 150–300 arcmin. Schor et al. (1984) found that 200 arcmin was the upper limit for a coarse difference-of-Gaussians target (peak spatial frequency = 0.075 c/°) that extended across the central 13° of the visual field. Kane, Guan, and Banks (2014) measured the upper limit as a function of the spatial frequency of a triangular-wave corrugated stimulus, composed of small random dots; their 9°-wide target was placed 0.5° laterally from the fixation point, so the edges of the target extended to an eccentricity of 9.5°. At a corrugation frequency of 0.06, the upper depth limit reached an amplitude of ~500 arcmin, for a crossed disparity limit (half-amplitude) of about 250 arcmin.

Few studies have looked systematically at either fusion or the upper depth limit as a function of eccentricity. An exception is Ogle's (1952b) study, which measured Panum's limit for line targets from the fovea to 12° eccentricity. In Figure 6A, we have plotted Ogle's data with our own upper-limit data, based on
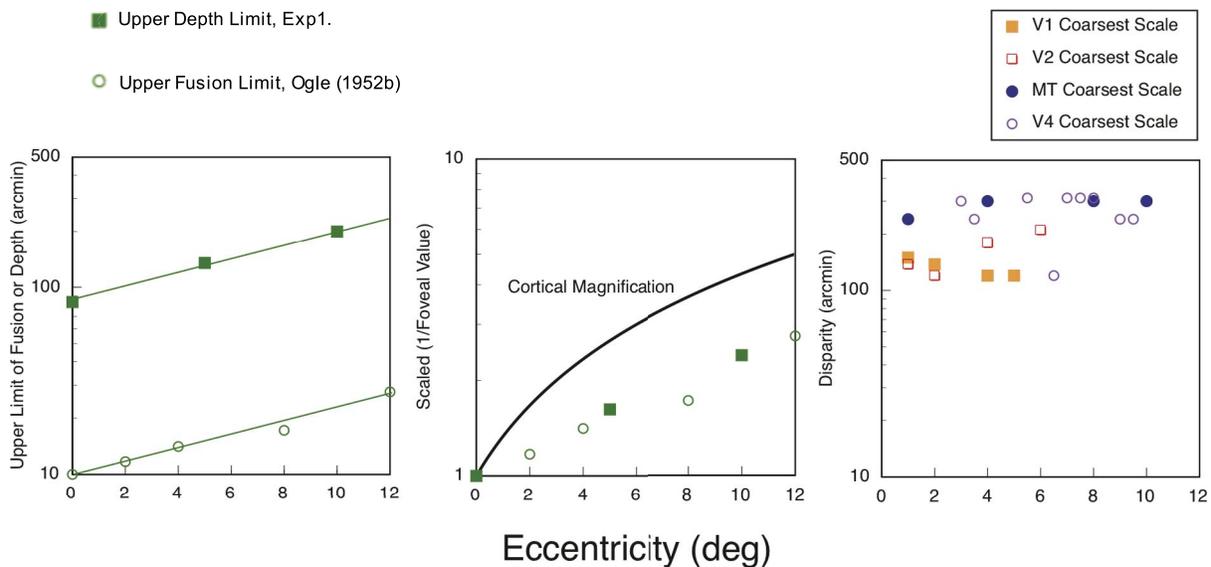
Figure 6. Shallow increase in the upper depth limit and fusion limit with eccentricity. (A) Data replotted from Experiment 1 (filled squares) compared with Ogle (1952b). (B) Same data normalized by foveal value. The cortical magnification factor (Virsu & Rovamo, 1979) is plotted for comparison. (C) Disparity tuning of the coarsest scales in primate cortex, based on data from Parker (2007, figure 1).

our increment threshold measurements. The lines, based on best-fitting exponential functions, have nearly identical slopes, which suggests that the upper depth limit is a scaled-up version of the upper limit set by the finest scale mechanism for measuring disparity. As Schor et al. (1984) have argued, when target disparity exceeds the range of the finest disparity detectors, perfect fusion—represented by Panum's limit—breaks down. We suppose that when target disparity exceeds the range of the coarsest disparity detectors, both the appearance of depth and thresholds based on *disparity,* rather than the lateral separation between the half-images, breaks down. The values for the upper depth limit are about 10 times Panum's limit, which suggests that at each eccentricity, the largest disparity detectors are about 10 times the size of the smallest, assuming a self-similar organization across scales.

Note that the slope of the lines in Figure 6A is very shallow, increasing only by about a factor of 3 over 12° eccentricity. To emphasize this point we have replotted both data sets in Figure 6B, scaled by their foveal value, and accompanied by the cortical magnification function (Virsu & Rovamo, 1979). Clearly, the increase in the disparity values for both measures is substantially less than cortical magnification, a function that predicts the change in visual acuity and contrast sensitivity with eccentricity (Levi, Klein, & Aitsebaomo, 1985; Saarinen, Rovamo, & Virsu, 1989; Virsu & Rovamo, 1979). Apparently, the spatial scales that determine the fusion limit (Ogle, 1952b) and upper disparity limit (our data) are different from the scales that mediate those other visual functions.

What does account for the upper disparity limits? In Figure 6C, we have replotted the disparity tuning of the coarsest scales from a number of visual areas in primate cortex, based on data plotted in Figure 1 of Parker's (2007) review. The tuning of these coarse-scale disparity neurons is not very different from our psychophysical estimates of the upper disparity limits. Moreover, the change in coarse-scale disparity tuning with eccentricity exhibits the same shallow slope as the human data, which suggests that disparity neurons in this range determine human limits.

Relation between upper disparity limit and statistics of images in the real world

The upper range for stereopsis sets a limit on coarse disparities supported by the visual system. It is possible that this range has adapted to efficiently encode the statistics of disparities in the real world (Atick & Redlich, 1992; Barlow & Földiák, 1989). If so, the visual system only needs to support the range of coarse disparities that it actually encounters. A study by Sprague, Cooper, Tošić, and Banks (2015) supports this conjecture. It shows that statistically, crossed disparities are more common in the lower visual field, whereas uncrossed disparities are more common in the upper visual field, given that objects in the lower visual field are usually closer than the point of fixation. Sprague et al. hypothesized that if disparity detectors are tuned efficiently, neurons with receptive fields in the lower visual field should be more selective for crossed

disparities, whereas neurons with receptive fields in the upper visual field should be more selective to uncrossed disparities. They analyzed data from other studies that measured both the preferred disparities and visual-field locations of V1 neurons in macaque monkeys (e.g., Durand, Celebrini, & Trotter, 2006; Prince et al., 2002; Samonds, Potetz, & Lee, 2012) and found that neurons in the lower visual field were indeed biased to be selective for crossed disparity, whereas neurons representing the upper visual were biased toward uncrossed disparity. Thus, the statistics of disparity in real-world situations are correlated with the preferred disparity distribution of neurons.

Liu, Bovik, and Cormack (2008) used data on the distribution of fixation distances in depth (Yang & Purves, 2003) and compared it to the distribution of binocular disparities in the real world, obtained from range maps. They showed that the distribution of disparity is a Laplacian function centered near zero at fixation, with a mean disparity that increases as a function of eccentricity. At an eccentricity of 10°, 95% of the disparity range was within 2°, and at an eccentricity of 30°, the 95% range increased to about 3°. Thus the upper disparity limit of around 200 arcmin (3.3°) that we measured at an eccentricity of 10° is consistent with the range of disparities that we encounter in the real world.

Chauhan, Masquelier, Montlibert, and Cottereau (2018) looked at how the statistics of disparity in natural scenes can affect the development of V1 receptive fields. Using a simple Hebbian coincidence-detector unsupervised neural network, they showed that the disparities found in natural scenes accounts for the emergence of binocular, disparity-selective receptive fields. They used the Hunter–Hibbard database of stereo images (Hunter & Hibbard, 2015) as input to their network. In their simulated network, they had neurons in the central visual field (0°–3°) receiving inputs from the central part of the images, and neurons in the periphery (6°–10°) receiving input from the peripheral parts of the images. They looked at the development of receptive fields in central and peripheral vision. After training, the receptive-field size ranges for horizontal disparity detectors were 0.5° and 1.5°, respectively, for central and peripheral neurons; note again a shallow increase in the receptive-field size!

Disparity judgments of brief targets

It has been known for more than half a century that observers can correctly judge the sign (crossed or uncrossed) of briefly presented targets (≤100 ms) for disparities ranging up to 20° (Blakemore, 1970; Dengler & Kommerell, 1993; Foley, Applebaum, & Richards, 1975; Richards & Foley, 1974; Richards & Kaye, 1974;

Westheimer & Tanzman, 1956). Yet if targets with these large disparities are presented for longer durations, they appear completely diplopic and located in the fixation plane (no depth), as our results demonstrate. Wilcox and Allison (2009) have argued that there may be special neural mechanisms that respond to these transient disparity signals—mechanisms that are not driven by the stimuli typically used to measure disparity tuning in cortical neurons, for example, those in Figure 6C. Given the sparsity of naturally occurring disparities in the range from 4° to 20°, what is the functional value of being able to identify the disparity sign of these large disparities? Voluntary convergence is slow, with a latency of about 160 ms (Rashbass & Westheimer, 1961), so these large disparities may initiate a convergence response in the correct direction, thereby avoiding the delay associated with a start in the wrong direction (Wilcox & Allison, 2009). However, given their transience, these large disparities would not be useful in guiding hand or other prolonged body movements that require continuous information.

Conclusion

Our results place stringent constraints on the degree of retinal correspondence required to support stereopsis. Even at 10° eccentricity, the upper disparity limit is about 3°, and the useful range, where disparity can supply precise information about z-axis distances, is roughly half that value. In addition, for a given standing pedestal, sensitivity does not change much as a function of eccentricity. Thus, individuals with macular degeneration and healthy vision in corresponding locations in the periphery can use disparity information to guide hand movements, although those lacking stereopsis can still utilize the other depth cues to grasp and to position objects within arm's length—albeit at a slower pace (Verghese et al., 2016). The good news is that disparity increment thresholds for disparities ranging from 10 to 50 arcmin (1–4 cm at arm's length) are nearly as precise at 10° eccentricity as in the fovea. Thus, for those who have healthy retina at eccentric locations that fall at or near correspondence, stereo precision at grasping and positioning objects can be nearly as good as in those with healthy foveas.

Keywords: periphery, disparity limit, central-field loss, eye-hand coordination

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Corresponding author: Saeideh Ghahghaei.
Email: saeideh@ski.org.
Address: The Smith–Kettlewell Eye Research Institute, San Francisco, CA, USA.

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