Speed discrimination in the far monocular periphery: A relative advantage for interocular comparisons consistent with self-motion

Devon A. Greer

Center for Perceptual Systems,
Department of Psychology,
The University of Texas at Austin, Austin, TX, USA ✉

Kathryn Bonnen

Center for Perceptual Systems,
Department of Psychology, Institute for Neuroscience,
The University of Texas at Austin, Austin, TX, USA ✉

Alexander C. Huk

Center for Perceptual Systems,
Department of Psychology, Institute for Neuroscience,
The University of Texas at Austin, Austin, TX, USA ✉

Lawrence K. Cormack

Center for Perceptual Systems,
Department of Psychology, Institute for Neuroscience,
The University of Texas at Austin, Austin, TX, USA ✉

Some animals with lateral eyes (such as bees) control their navigation through the 3D world using velocity differences between the two eyes. Other animals with frontal eyes (such as primates, including humans) can perceive 3D motion based on the different velocities that a moving object projects upon the two retinae. Although one type of 3D motion perception involves a comparison between velocities from vastly different (monocular) portions of the visual field, and the other involves a comparison within overlapping (binocular) portions of the visual field, both compare velocities across the two eyes. Here we asked whether human interocular velocity comparisons, typically studied in the context of binocularly overlapping vision, operate in the far lateral (and hence, monocular) periphery and, if so, whether these comparisons were accordant with conventional interocular motion processing. We found that speed discrimination was indeed better between the two eyes' monocular visual fields, as compared to within a single eye's (monocular) visual field, but only when the velocities were consistent with commonly encountered motion. This intriguing finding suggests that mechanisms sensitive to relative motion information on opposite sides of an animal may have been retained, or at some point independently achieved, as the eyes became frontal in some animals.

Introduction

When a bee flies through the world, its (lateral) eyes each extract different velocities to gauge its 3D heading (Srinivasan, Zhang, Altwein, & Tautz, 2000). When a human views an object flying towards them, their (frontal) eyes are stimulated by different velocities, which are used to estimate a 3D direction (Harris, Nefs, & Grafton, 2008; Regan & Gray, 2009). There are many differences between these two domains: insect versus primate, monocular visual fields versus binocular vision, and visually guided navigation versus object perception. However, both fundamentally involve extracting eye-specific velocities and comparing them to estimate a 3D direction.

Humans and other primates are able to perceive the 3D direction of an object based on velocities within their central visual field. In the primate object motion literature, this differential velocity cue is called the interocular velocity difference (IOVD). Conventionally, this term refers to the dichoptic comparison of velocities from overlapping portions of the left and right eyes' visual fields (Cumming & Parker, 1994; Czuba, Rokers, Huk, & Cormack, 2010; Fernandez &

Farell, 2005; Regan & Beverley, 1973; Rokers, Cormack, & Huk, 2008; Shioiri, Kakehi, Tashiro, & Yaguchi, 2009). Alternatively, many animals have relatively little binocular overlap because of the lateral placement of their eyes. These animals, despite their lack of stereoscopic vision, are quite adept at navigating at high speeds through complex environments. A growing body of work shows that they accomplish this by comparing the velocities viewed separately in each eye to arrive at a 3D heading (Bhagavatula, Claudianos, Ibbotson, & Srinivasan, 2011; Clark et al., 2014; Eckmeier et al., 2008; Götz, 1968; Martin, 2009; Martin & Shaw, 2010; Schiffner & Srinivasan, 2015; Srinivasan, Lehrer, Kirchner, & Zhang, 1991).

Considering both scenarios, interocular velocity differences per se may not be limited to encoding motion-through-depth of objects relative to the observer. The concept could be extended to describe the intermonocular velocity comparisons used for navigation by animals with lateral eyes. Both processes involve differential velocity information between the eyes, which is used to encode a 3D motion direction. In fact, the only structural difference between these interocular velocity differences is the portion of the visual field which is being used. Put another way, there may be not only a system sensitive to central binocular IOVDs in primates, but also a system sensitive to peripheral monocular IOVDs (mIOVDs).

For these reasons, we sought to better understand whether the primate visual system processes IOVDs in the monocular and binocular fields similarly, or whether it can be said to process mIOVDs at all. To do so, we developed a paradigm that links conventional binocular motion perception studies with approaches from visually guided bee navigation literature. This was accomplished by simultaneously presenting a pair of drifting gratings exclusively in the monocular visual fields of humans. Using a range of speeds that a walking observer would view in their peripheral vision (through a hallway or forest, for example), we compared speed discrimination performance between and within the monocular fields.

One might expect that, like for most visual functions, speed discrimination performance drops considerably as the speeds are viewed at greater eccentricity (McKee & Nakayama, 1984; Wright & Johnston, 1983). However, we have found a scenario in which this decline in performance is remarkably spared. Human observers were substantially better at speed comparisons when speeds were compared across our vastly separate monocular fields, and the velocities encountered by the right eye and left eye monocular views were consistent with either forward or backward self-motion than when the same moving stimuli were presented within the same monocular field. In general, sensitivities were markedly worse for patterns of motion that could not be easily produced by a combination of self-motion and smooth pursuit eye movements. We suggest that this robustness of intermonocular velocity comparisons demonstrates that humans are indeed also sensitive to mIOVDs.

General methods

Observers

Data were collected from three observers (aged 25–26, one naive, plus two of the authors), all with normal or corrected-to-normal visual acuity. Observers needing correction wore contact lenses rather than glasses to insure unobstructed peripheral vision. Two subjects (authors) were experienced psychophysical observers, while the naive subject had no previous psychophysical experience. All observers completed every experiment. Each observer gave written consent, and procedures were approved by The University of Texas at Austin Institutional Review Board. All data were collected at UT Austin, and all observers were recruited from the UT Austin community.

Apparatus and setup

Stimuli were generated using MATLAB (MathWorks, Inc., Natick, MA) and the Psychophysics Toolbox (Brainard, 1997; Kleiner et al., 2007; Pelli, 1997) on a Quad-Core Intel (Intel Corporation, Santa Clara, CA) Mac Pro computer (Apple, Inc., Cupertino, CA) with an ATI Radeon HD 4870 graphics card (Advanced Micro Devices, Inc., Sunnyvale, CA), and displayed on three 23 in. monitors (NEC MultiSync PA231W LCD displays; NEC Display Solutions, Ltd., Minato-ku, Tokyo, Japan). The luminance functions of the three displays were linearized using standard gamma-correction procedures. The displays were connected via a multidisplay adaptor (Matrox TripleHead2Go; Matrox Graphics, Inc., Dorval, QC, Canada), creating a merged display of 1920×480 at 60 Hz resolution.

As shown in Figure 1, we used a triptych stimulus display comprising three monitors in portrait orientation (i.e., longer dimension vertical). The center monitor occupied the majority of the observer's binocular field, and the lateral monitors, each perpendicular to the center one, almost entirely filled the observer's monocular fields. Note that the nose obstructed the left display from the right eye, and vice versa. A chin cup and forehead rest minimized observer's head movements. The forehead rest was constructed so not to occlude any peripheral vision.
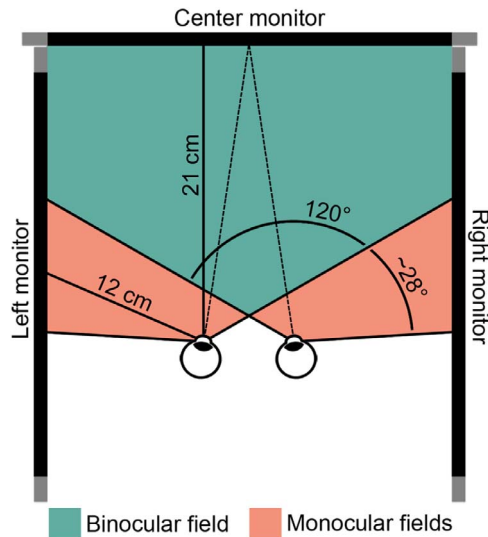
Figure 1. Top view schematic of the three-monitor setup, observer viewing location, and visual field locations. The observer simultaneously viewed three monitors: one at 21 cm directly in front, and one each to the left and the right, positioned such that stimuli could be presented in the center of the monocular fields (orange) at roughly 12 cm from the nearest eye. The typical observer's binocular field (teal) in this setup was measured to span approximately 120 visual degrees and monocular fields spanned approximately 28 visual degrees on each side.

Because of the heat generated by the monitors, a small USB fan was used to circulate air through the interior of the monitor setup during the experiments.

Task

On each trial, observers viewed two simultaneously presented drifting gratings and indicated which of the two appeared to have moved faster. Locations of the stimulus elements (grating patches) varied, depending upon the condition (described below). Observers were instructed to maintain gaze on a fixation cross that remained in the middle of the center monitor. The stimuli were presented for 750 ms and, following a 200 ms blank period, the observer had a 2 s interval in which to respond with a button press. Auditory feedback indicated if the observer was correct, incorrect, or did not respond, and this was followed by a 300 ms delay before presentation of the next trial.

Stimuli

The stimuli were drifting compound gratings consisting of three superposed sinusoids with spatial frequencies of ¼, ⅓, and ½ cycles·deg^{-1}. The starting phase of each component grating was randomized from trial to trial so that a trivial spatial changing-phase cue could not be used to do the task. The contrast of the components was scaled to yield a maximum Michelson contrast of 50% for the compound grating on each trial. The gratings were windowed with a spatial Gaussian function with a space constant (σ) of 3° and truncated at $\pm 3.5\ \sigma$. Because the stimuli were large and close, the viewing distance within a stimulus varied slightly across the extent of the stimulus. The spatial numbers (and the speeds to follow) are thus slight approximations computed with respect to the stimulus center, but this does not affect the experimental comparisons of interest.

Baseline velocities (5, 10, 20, 30, 40 deg·s^{-1}) were determined roughly by the range of speeds seen in the peripheral vision by a person, walking (1.4 m·s^{-1}) down a hallway (Browning, Baker, Herron, & Kram, 2006; Mohler, Thompson, Creem-Regehr, Pick, & Warren, 2007) or, by extension, a moderately dense wooded area. An individual walking at a normal pace through a 6-ft (approx. 182.88-cm) wide hallway, no closer than 1.5 ft from a wall, would experience speeds ranging from 25–55 deg·s^{-1}. Considering that walking through many environments (such as wooded areas with an average tree spacing greater than 6 ft) would generate slower velocities, we included 5 and 10 deg·s^{-1} baseline velocities. These additional velocities also allowed for comparison with other studies in the literature.

The velocities shown involved temporal frequencies that were within hardware refresh rate limits. If, due to the staircase, the maximal velocity (60 deg·s^{-1}) was reached more than five times in a run, that run was discarded (however this only occurred in initial practice sessions).

Procedure

Before performing the main experiments, we mapped the visual fields of our observers using the same apparatus and monitor configuration described above. This was necessary to insure that our monocular stimuli were placed exclusively in the monocular visual fields, including conditions requiring two stimuli to fit in the same monocular field. Each eye was tested in a separate perimetry session. Observers were instructed to respond if they saw the stimulus (a white circle 20 pixels in diameter) by pushing a button; no response correspondingly indicated that the stimulus was not visible. Because the stimuli were large and bright, they were also very conservative; the blind spots, for example, were below the resolution of this perimetry. Figure 2 shows the resulting visual field of one observer, with the stimulus locations shown by the black circles. For two of the observers, the monocular
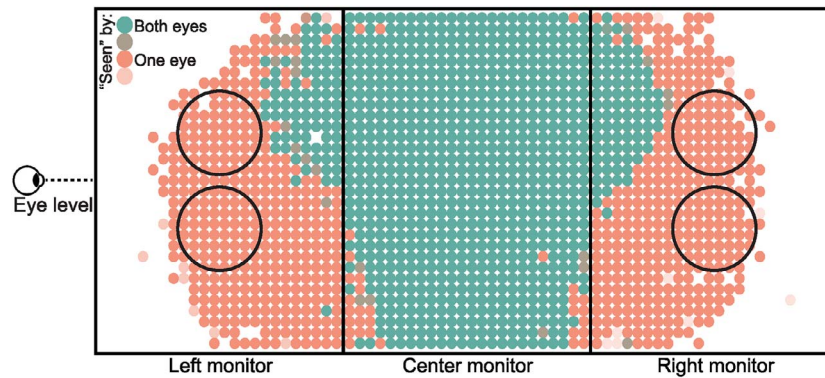
Figure 2. Perimetry visualization from the naive observer confirmed stimuli placement exclusively in the monocular fields. Observer visual field was estimated by superimposing the left and right eye perimetry results. Teal areas show locations in which the subject reported seeing the stimulus in both left and right eye (both eyes response). Areas of blended teal and orange specify locations in which the observer provided mixed responses as to if the stimulus was seen with one eye or both. Orange areas show locations in which the observer reported seeing the stimulus in only one eye (one eye response). Lighter orange areas mark locations that the observer reported seeing the stimulus at that location for 50% of the trials in one eye. Blank areas were not reported as seen. The black circles show the locations of one of the peripheral stimulus configurations (left and right conditions), demonstrating that our monocular stimuli did indeed fall only in the truly monocular fields. The eccentricities along the vertical and horizontal meridian are specified at a few critical locations on the three-monitor setup. The stimuli were too large and bright to detect the blindspots, so the monocular field boundaries are very conservative estimates.

stimuli were in the monocular fields when centered on the lateral monitors (as shown). For the third observer, the stimuli were displayed 5° lower.

All observers completed between two and 12 full-length practice sessions to become familiarized with the task prior to participating in the main experiment. Practice sessions continued until performance stabilized. The observer with little psychophysics experience was monitored during practice sessions in order to confirm correct eye/head position. These practice sessions were identical to the experiment sessions and averaged to 720 trials per session.

There were three basic experimental conditions, in which the two gratings were either: (a) both within the central binocular visual field (separated either vertically or horizontally; Figure 3C and D); (b) both within the same monocular visual field (either to the far right or far left, separated vertically; Figure 3A); or (c) distributed across the monocular visual fields (separated horizontally; Figure 3B). We used both vertically and horizontally separated stimuli in the central field so that each peripheral monocular condition could be paired with a central condition for which the grating patches differed only in eccentricity. Figure 3 shows the directions tested specifically in Experiment 1; however, the locations shown describe the experimental conditions tested for all experiments.

Given that the gratings within the same monocular field could be either on the left or the right, and the central binocular stimuli could be separated either horizontally or vertically, the three basic conditions

actually yielded five total stimulus location combinations. These location combinations were tested in separate sessions. Observers ran at least two sessions for each stimulus location combination. Thus, each observer completed a total of 10 or more sessions for each of the experiments described below.

Performance for baseline velocities was determined from four to eight staircases for each observer. No more than two staircases for a baseline velocity were tested in a single session. A staircase terminated when either six reversals or 100 trials were collected. With each reversal, the step size of the staircase decreased slightly. Observers took breaks during sessions as needed.

The velocity difference yielding 79% correct performance was estimated with a three down, one up staircase. Threshold was defined as the average of the velocity differences for the last five trials of each staircase. We describe performance using Weber fractions (speed discrimination threshold divided by baseline speed). The results shown were determined by averaging the Weber fractions calculated for every staircase for all observers. Uncertainty was estimated using bootstrapping methods (resampling 10,000 times with replacement); as the performance across conditions was very similar for all observers, thresholds were resampled for each condition without regard to observer identity. Unless otherwise indicated, error bands indicate ± 1 standard error of the mean (i.e., the central 68% of the sampling distribution).
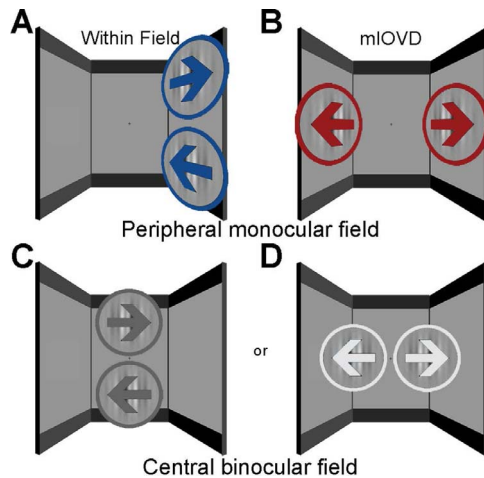
Figure 3. Speed discrimination conditions in Experiment 1 consisted of spatially separate, oppositely drifting gratings presented simultaneously. Arrows show the drift direction of the gratings. In the monocular within-field condition (A), stimuli were presented exclusively within a single monocular field of the observer. The mIOVD condition stimuli (B) were presented separately in each monocular field. Note that the radial eccentricities of the stimuli in A and B were slightly different, but not importantly so, given their large size and huge overall eccentricity. The central binocular field condition stimuli (C, D) were presented in the central area of the observer's binocular field. The stimuli in this condition are vertically (C) or horizontally (D) offset across the fixation point. Note that Figure 3 and the other similar Figures are not to scale; in the horizontally offset central binocular field condition (D), for example, the stimuli were entirely on the center monitor.

Results

Experiment 1

In this experiment, we compared speed discrimination performance *within* a single eye's monocular field versus *across* both eye's monocular fields (as shown in Figure 3). We reasoned that if mIOVDs are processed in a privileged fashion, observers should be better at speed discrimination when the two moving patches were separated across the left and right eyes, as compared to within a single eye.

Methods

In the monocular within-field condition, the two gratings were both presented within the same monocular field (left or right). Gratings were placed vertically relative to each other to allow constant stimulus size while maximizing use of the monocular field (see Figure 3A; also Figure 2). The gratings were vertical (i.e., horizontal contrast energy) and were presented simul-

taneously, drifting horizontally in opposite directions. The left and right monocular fields were tested in separate sessions.

In the mIOVD condition, the two gratings were located in separate monocular fields (Figure 3B). The centers of the gratings were located at an eccentricity of 70°. The gratings had an approximate radius of 10.5° (refer to Figures 1 and 2). The two gratings were presented simultaneously, and drifted horizontally in opposite directions within their Gaussian spatial envelopes.

Finally, two additional central binocular field conditions (Figure 3C and D) tested gratings in the central area of the binocular field, offset either vertically or horizontally across the fixation point. In one condition, the two stimuli were placed side by side about the fixation point in the center display. In the other, the stimuli were placed vertically about the fixation point. These central binocular conditions provided straightforward baselines for comparison to the peripheral monocular field conditions in that each monocular stimulus condition differed from its binocular counterpart only in eccentricity. There was no reason to suspect, however, that performance in the two binocular conditions would differ greatly, and this proved to be the case in Experiment 1 (a slight difference was seen in Experiment 2, discussed later).

Results

If interocular velocity differences extracted between the two monocular portions of the visual field are processed in some privileged way, observers should have a lower threshold to speed differences (i.e., lower Weber fractions) in the mIOVD condition compared to the monocular within-field condition. In Figure 4A, the gray curve shows the thresholds measured centrally. The blue curve shows the thresholds that result when we increased the stimulus eccentricity, either to the left or to the right, moving the stimuli into an exclusively monocular portion of the visual field (monocular within-field condition). Not surprisingly, thresholds are worse at every baseline speed. The bands on the plots show bootstrapped 68% confidence intervals. The red curve shows the thresholds we obtained when we again increased the stimulus eccentricity, but this time in opposite directions such that the two gratings occupied opposite monocular fields on either side of the head (mIOVD condition). This increase in eccentricity also yielded an increase in thresholds but, crucially, the increase was much less than for the within-field data.

The dark gray curve in Figure 4B shows the discrimination thresholds for two grating patches separated vertically in the central binocular visual field as a function of pedestal speed. The light gray curve in Figure 4B shows the central binocular data when the
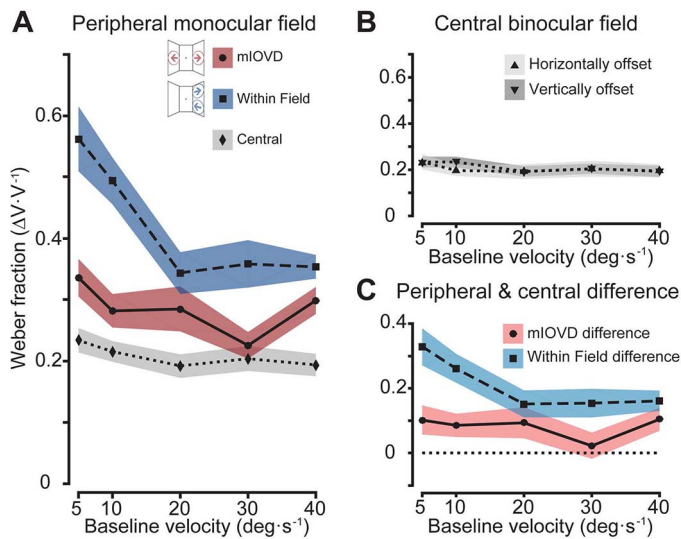
Figure 4. Speed discrimination thresholds for Experiment 1. (A) Sensitivity for speed differences within a single monocular field (within-field condition, blue) and for the mIOVD condition (red). Average sensitivity for the central binocular field is shown in gray. Icons illustrate stimulus configurations. (B) Sensitivity to speed differences in the central binocular field condition with vertically offset gratings (dark gray) and with horizontally offset gratings (light gray). (C) Difference in average thresholds for the peripheral monocular field and the central binocular field conditions. Monocular within-field threshold difference is shown in light blue and mIOVD threshold difference is shown in pink. The colored regions indicate the bootstrapped 68% confidence intervals.

two gratings were separated horizontally instead of vertically; this change in configuration had no discernible effect on threshold (the two gray curves are the same within measurement error). Put another way, when the stimuli moved from the central visual field to the far monocular periphery, relative discrimination performance was actually better when the two gratings to be discriminated were on opposite sides of the head than when they were in the same visual field.

To quantify the drop in performance when the stimulus eccentricity increased, we calculated the difference between the peripheral monocular field sensitivity and the central binocular field sensitivity. Specifically, we took the difference in sensitivity for the monocular within-field condition and compared it to the central binocular (vertically offset) condition sensitivity (Figure 4C, light blue). For the mIOVD condition, a similar difference in sensitivity was estimated by comparing to the horizontally offset central binocular condition (Figure 4C, pink). As there were negligible differences between the two central binocular field conditions, these differences simply recapitulate the differences between mIOVD and monocular within-field conditions seen in Figure 4A. But these central binocular conditions are important

for testing whether the relative directions of the gratings affect sensitivity, independent of their locations in various monocular field locations (an issue that becomes more important in Experiment 2).

Discussion

Observers were better at monocular field speed discrimination when the speeds were presented in separate eyes rather than the same eye. We note that this effect was observed using stimuli that were consistent with local velocity vectors seen by an observer walking forward or backward either at different average distances from two surfaces, or while turning slightly while walking between the two surfaces. Moreover, these same basic stimuli are known to cause bees to change their flight to null the velocity difference between the lateral visual fields (Srinivasan et al., 1991).

Experiments 2 and 3 are designed to further test the theory that speed discrimination is enhanced for self-motion, and also serves to rule out other effects like simple crowding.

Experiment 2

Experiment 2 examined speed discrimination for drifting gratings that move in the same direction, as schematized in Figure 5. Given the unique viewing geometry of these experiments, a brief aside on terminology is warranted here. By "move in the same direction," we mean that both gratings drifted to the left or both to the right when viewed in the central binocular field (Figure 5C and D). Note that when the eccentricity of the components was increased, one to the left and one to the right, as in the mIOVD condition (Figure 5B), one component ended up drifting forward and the other drifting backward due to the configuration of the three-monitor setup. However, from the observer's perspective, both gratings drifted in the same relative direction—both either to the left or to the right—in each eye's visual field. A comparison of Figure 3 (opposite direction) and Figure 5 (same direction) should make this point clear.

The same direction motion used in this experiment is not consistent with self-motion for primates with mobile eyes, but it does occur during smooth pursuit of a moving target (it could also occur in insects, or any animal with fixed eyes or without a VOR, that were turning in place but were slightly closer to one of two parallel walls). This experiment will thus help test whether mIOVD in humans is confined to velocity differences commonly encountered by animals with mobile frontal eyes, or whether it generalizes to other kinds of velocity differences.
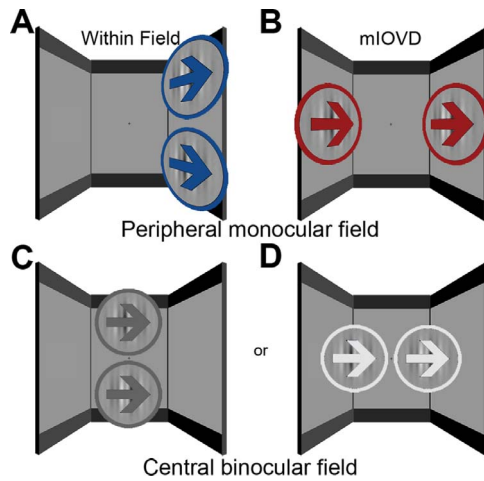
Figure 5. Experiment 2 speed discrimination conditions in which simultaneously presented gratings drifted in the same relative direction (same general format as described for Figure 3). Arrows indicate the relative drift directions of the gratings (same horizontal drift direction for vertically oriented gratings in Experiment 2).

Methods

The stimuli and procedures were identical to those in Experiment 1, with one exception: rather than the stimuli moving in opposite horizontal directions (relative to each eyes' field of view), stimuli moved in the same direction (Figure 5). Like Experiment 1, the observer was instructed to indicate which stimulus was moving the fastest.

Results

Just as in Experiment 1, when the gratings were moved from the central binocular visual field into the same peripheral monocular field, thresholds were elevated (Figure 6A). For the slowest speeds, the peripheral thresholds were slightly lower for these same-direction stimuli than they were for the opposite-direction stimuli of Experiment 1.

Unlike Experiment 1, however, the mIOVD thresholds (Figure 6A, red) were elevated by an amount that surpassed the monocular within-field thresholds (Figure 6A, blue) at lower speeds. The peripheral monocular field conditions were compared to the equivalent central binocular field condition (to quantify the drop in sensitivity as stimulus eccentricity increased). As shown in Figure 6C, both peripheral monocular field conditions actually showed a similar drop in performance. Thus, in Experiment 2, when the gratings were moved into the far periphery, velocity discrimination suffered by a similar amount regardless of whether the grating patches were moved to opposite monocular fields (mIOVD) or to the same peripheral field.
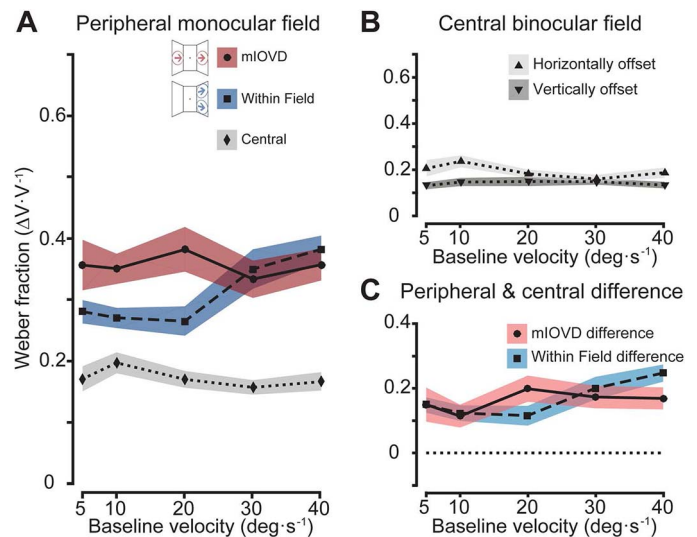

Figure 6. Speed discrimination thresholds for Experiment 2. (A) Weber fractions for speed differences within either the left or right monocular field (blue) and for the mIOVD stimulus (red). Averaged central binocular thresholds (gray) are shown for reference. (B) Speed discrimination thresholds for the central binocular field with vertically offset gratings (dark gray) and for the central binocular field with horizontally offset gratings (light gray). (C) The difference in average thresholds of the peripheral monocular field conditions (monocular within-field, light blue; mIOVD, pink) and the equivalent central binocular field condition. Plotting conventions are as in Figure 4.

In summary, the threshold elevation for stimuli in the periphery (relative to central vision) was about the same whether the stimuli were moved into the same or into opposite monocular fields. This is in contrast to Experiment 1, in which thresholds were noticeably poorer when the stimuli were in the same field.

Discussion

In Experiment 1, observers were better at speed discrimination in the far periphery when the stimuli to be discriminated were actually presented in separate eyes on opposite sides of the head rather than to the same eye in relatively close proximity to one another. In Experiment 2, when the relative directions of gratings were changed, there was no longer any advantage to comparing speeds across the monocular fields as opposed to comparing speeds within a monocular field.

We also observed higher sensitivity to speed differences in the vertical central binocular condition (compared to the horizontal central binocular condition). This is possibly due to the stimulus configuration in this condition in which observers could use changing relative phase information when comparing speeds. As humans are thought to be largely phase

blind in the periphery (Bennett & Banks, 1987; Rentschler & Treutwein, 1985; Stephenson & Braddick, 1983), this information is unlikely to have been used in the monocular within-field condition. If this is the case, the threshold difference between these conditions may actually be smaller than our results show.

It is perhaps worth briefly pausing to consider the difference between Experiment 1 and Experiment 2, both in terms of the stimuli per se as well as their ecological validity. With respect to the stimuli themselves, the difference between the two experiments seems trivial; the only difference is a reversal of the velocity sign of one of the two gratings. Ecologically, however, this reversal makes a profound difference when the stimuli are placed in opposite monocular fields in the far periphery. For a primate (having mobile frontally located eyes), the stimuli from Experiment 1 are rough approximations of what is experienced when walking along a path in a forest or along a hallway. By flipping the direction of one grating, however, one renders the stimuli consistent with the stimulation resulting from smooth pursuit (or, alternatively, what would be experienced by rotating the head in place with the eyes fixed in the head).

To further this line of argument—that speed discriminations in the periphery are best for stimuli that are ecologically valid—we tested observers in speed discrimination for directions that were completely inconsistent with any type of self-motion or eye movement.

Experiment 3

To remove any possible ecologically valid motion pattern from stimuli, we used gratings that drifted in orthogonal directions. In no (survivable) situation would an observer view these velocity vectors during self-motion or smooth pursuit in a roughly rigid environment. We anticipated that mIOVD performance would be no better than speed discrimination within a monocular field in this scenario.

Methods

The stimuli in this experiment were identical to those used in the previous two experiments, except that one of the two gratings drifted vertically as shown in Figure 7. The only way a human observer could experience this type of motion naturally would be during a fleeting moment of consciousness while the structural integrity of the head was being severely compromised. We speculate that psychophysical reports from such an observer would be difficult if not
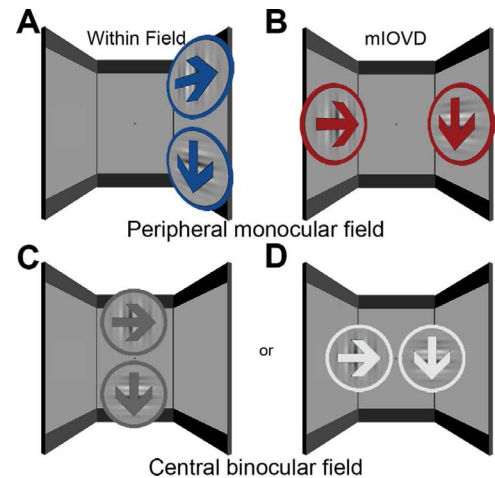

Figure 7. Speed discrimination conditions in Experiment 3, in which gratings drifted orthogonally. Conventions are as in Figures 3 and 5. For each condition, one grating was oriented vertically and drifted horizontally, the second grating was oriented horizontally and drifted vertically. See text for details.

impossible to obtain. In this experiment, we tested only 5, 10, and 20 deg·s^{-1} baseline velocities as these were the most diagnostic speeds in the first two experiments and because the faster speeds resulted in thresholds too high to measure.

Results

In Experiment 3, we found little difference between the central binocular field conditions (Figure 8B, gray) so, as in Experiment 1, it did not matter if the patches flanked the fixation point vertically (dark gray) or horizontally (light gray). Thresholds were elevated when we moved the stimuli into the periphery, either into the same monocular field (Figure 8A, blue) or into monocular fields on the opposite sides of the head (mIOVD; Figure 8A, red). Threshold elevation was the same for the two conditions because the central thresholds were also higher than in Experiments 1 and 2. Thus, like in Experiment 2 but unlike in Experiment 1, there was no less of a drop in performance for mIOVD compared to within a monocular field speed comparisons.

Discussion

For a rigid environment, the stimuli used in this experiment are not ecologically valid, in that they could not be produced by self-motion or common eye movements. Overall, thresholds were higher in central vision than for the other two experiments, and sensitivities in the periphery were quite bad, closely matching the ones measured in Experiment 1 for stimuli in the same monocular visual field.
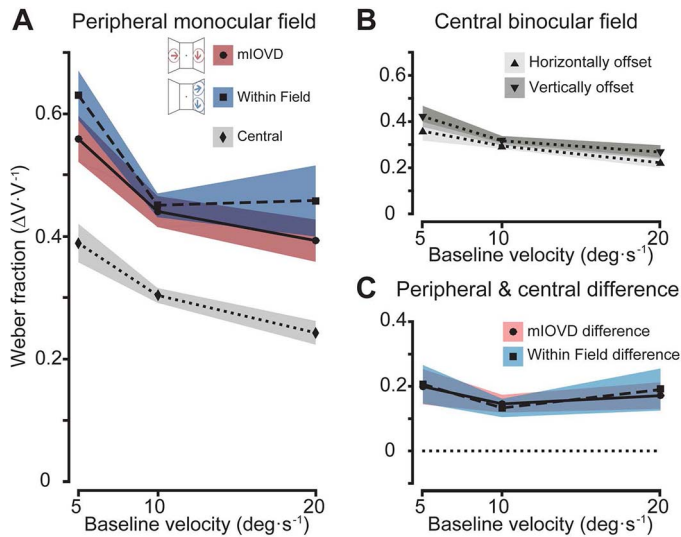
Figure 8. Speed discrimination thresholds for orthogonal motion. (A) Weber fractions for speed differences within a single monocular field ("within-field" blue) and for between both monocular fields (mIOVD, red). Averaged central binocular thresholds (gray) are shown for comparison. (B) Speed difference thresholds in the central binocular field with vertically offset gratings (dark gray) and for the central binocular field with horizontally offset gratings (light gray). (C) The difference in average thresholds measured the drop in performance of the peripheral monocular field conditions (monocular within-field,light blue; mIOVD, pink) after the equivalent central binocular field condition was deducted. Plotting conventions are as in Figures 4 and 6.

General discussion

Our results support the hypothesis that inter-monocular speed comparisons can actually be quite good. The sensitivity of velocity discrimination of our observers was highly dependent upon the relative directions of motions to be compared, and discrimination was best when the velocities seen in the two monocular visual fields were consistent with either forward or backward self-motion, or a smooth pursuit eye movement. When one looks at the data across all three experiments, a couple of striking patterns emerge.

First, in the central visual field, thresholds in Experiments 1 and 2 are relatively good. In Experiment 3, in which the stimuli simulated impossible or at least unlikely patterns of motion, the Weber fractions were elevated. Empirically, it is thus easier to judge the magnitude of two velocity vectors when they are parallel, even if they are pointing in opposite directions, than it is when they are orthogonal.

Second, all the peripheral thresholds from Experiment 2 (both within-field and mIOVD conditions) and the mIOVD thresholds from Experiment 1 are all very similar. Moreover, they stand in contrast to the thresholds from Experiment 3 (the ecologically invalid stimuli) and, interestingly, the thresholds from the within-field condition of Experiment 1. Categorically then, there seem to be two distinct classes of peripheral Weber fractions: those resulting from implausible stimuli (Experiment 3) and oppositely moving stimuli in the same visual field on the one hand, and all of the rest on the other hand.

If we explain the data of Experiment 3 by appealing to the stimuli being ecologically invalid, we are left with the question: among all the conditions of Experiments 1 and 2, why are Weber fractions so bad when oppositely moving stimuli are placed in the same monocular field? As has already been noted, motion in accord with all the stimuli from Experiment 2 can be produced by smooth pursuit of a moving target. As also noted, the mIOVD stimuli from Experiment 1 (Figure 3B and D) can be produced by a moving observer looking forward. The situation depicted in Figure 3C, vertically separated motion on the midline moving in opposite directions, is also a familiar one, as it is the stimulus for motion parallax (as produced by an observer translating forward while fixating a fixed point on the ground place off to the side). The situation shown in Figure 3A, however, is different. It would only occur (in a rigid environment) for an observer translating forward and making a smooth pursuit eye movement that resulted in the image of a peripheral point on the ground plane being fixed on the peripheral retina. Another way to think about this is that, for a forward moving observer, it would require that a fixed point on the peripheral retina remain aligned with a fixed point on the ground plane.

We propose that interocular velocity differences are used for processing both object and ego motion. When used for estimating the 3D direction of objects, the requisite eye-specific velocity signals come from corresponding locations within the overlapping binocular field from both eyes (the conventional IOVD). When used for estimating the direction an observer is moving, these IOVD signals come from the far peripheral (temporal) portions of each eye's view, including large portions of completely monocular visual fields, which we have termed here the mIOVD. The relevance of IOVDs to navigation is perhaps best understood in the ecological context of optic flow. If one considers an observer that fixates straight ahead while moving forward, the resulting radial flow field would contain velocities that emanate from a common central point, the focus of expansion (FOE). Although classical conceptions of optic flow (Gibson, 1950; Koenderink, 1986) are effectively cyclopean (i.e., a single optic flow field is considered), our results suggest that it is important to appreciate that both eyes receive optic flow, and that the spatial patterns of velocities differ in lawful ways between the two eyes due to the relative

positions of the eyes in the head (as well as the occlusions that features of the head and face pose to each eye's view).

In animals with lateral eyes, scene structure to the sides of these animals projects primarily to one eye or the other, and in the simple case of an animal moving forward, these velocities both "point" backward, which means that the left eye receives leftward oculocentric velocities and the right eye receives rightward oculocentric velocities. The differential directions and speeds are directly indicative of the animal's motion relative to the scene. Although it is straightforward to think about this pattern as involving a comparison between the far lateral portions of the visual field, it may be more appropriate to consider these comparisons as going on between the two eyes.

One possible explanation for these results is that some of the increase in thresholds seen when both gratings are placed in the same monocular visual field is due to crowding or some other form of spatial interference. To confirm crowding effects did not produce these results, a control experiment we piloted included additional flanker gratings directly above the mIOVD stimuli that were irrelevant to the speed discrimination task. These flankers had the same spatial properties as the test stimuli, but their speeds ranged between the test and reference speeds in a given trial, and did not give the observer any extra information to perform the task (i.e., they were completely task-irrelevent). Performance was unaffected, mitigating our initial concern of crowding being an issue as we began the experiments. More direct evidence against crowding comes from considering the different stimulus directions examined throughout Experiments 1 through 3 (see e.g., Bex, Dakin & Simmers, 2003; Levi, Hariharan, & Klein, 2002). Specifically, if crowding was a key factor in Experiment 1 (in which sensitivity was higher for motions in different eyes compared to motions in the same monocular field), a similar difference would have been present in the results of the other experiments, but it was not (although the exact amounts of interaction between target and flankers might be tuned for direction and speed; Bex & Dakin, 2005).

In summary, it seems that some directions of relative motion discrimination in the periphery are better than others. Discrimination was poor when the motion direction was orthogonal, regardless of position in the visual field (Figure 3). For conditions in which the motion was parallel (Experiments 1 and 2) discrimination was generally good, except for the condition in which opposite directions of motion were presented in the same monocular peripheral field. Interestingly, this also corresponds to a pattern of motion that, unlike the others in Experiments 1 and 2,

would not usually be produced by some combination of smooth pursuit and self motion. Further, it is possible that the comparisons of velocities between the monocular fields might be supported by a mechanism related to the IOVD computations currently studied in the context of 3D motion perception (Brooks, 2002; Czuba et al., 2010; Fernandez & Farell, 2005; Rokers et al., 2008; Shioiri et al., 2009). It is tempting to speculate that this mechanism, which computes IOVDs for a single object and thus operates in the same portion of the visual field in the two eyes, is perhaps derived from an older mechanism that compares velocities between opposite sides of the head, and that this mechanism indeed remained or was modified as the eyes migrated forward in the head. These findings reinforce the utility of eye-specific motion signals and suggest it may be possible to integrate interocular computations across multiple visual domains and species. More generally, we have established that, in some cases, the brain is as good at comparing stimuli presented to different eyes on opposite sides of the head as it is to comparing adjacent stimuli in the same eye. We find this intriguing and propose that it be addressed with further investigation.

Acknowledgments

Commercial relationships: none.
Corresponding author: Devon A. Greer.
Email: devong@utexas.edu.
Address: Center for Perceptual Systems, Department of Psychology, The University of Texas at Austin, Austin, TX, USA.

References

Bennett, P. J., & Banks, M. S. (1987). Sensitivity loss in odd-symmetric mechanisms and phase anomalies in peripheral vision. *Nature*, *326*, 873–876.

Bex, P. J., & Dakin, S. C. (2005). Spatial interference

among moving targets. *Vision Research*, *45*, 1385–1398.

Bex, P. J., Dakin, S. C., & Simmers, A. J. (2003). The shape and size of crowding for moving targets. *Vision Research*, *43*, 2895–2904.

Bhagavatula, P. S., Claudianos, C., Ibbotson, M. R., & Srinivasan, M. V. (2011). Optic flow cues guide flight in birds. *Current Biology*, *21*, 1794–1799.

Brainard, D. H. (1997). The Psychophysics Toolbox. *Spatial Vision*, *10*, 433–436.

Brooks, K. R. (2002). Interocular velocity difference contributes to stereomotion speed perception. *Journal of Vision*, *2*(3):2, 218–231, doi:10.1167/2.3.2. [PubMed] [Article]

Browning, R. C., Baker, E. A., Herron, J. A., & Kram, R. (2006). Effects of obesity and sex on the energetic cost and preferred speed of walking. *Journal of Applied Physiology*, *100*, 390–398.

Clark, D. A., Fitzgerald, J. E., Ales, J. M., Gohl, D. M., Silies, M. A., Norcia, A. M., & Clandinin, T. R. (2014). Flies and humans share a motion estimation strategy that exploits natural scene statistics. *Nature Neuroscience*, *17*, 296–303.

Cumming, B. G., & Parker, A. J. (1994). Binocular mechanisms for detecting motion-in-depth. *Vision Research*, *34*, 483–495.

Czuba, T. B., Rokers, B., Huk, A. C., & Cormack, L. K. (2010). Speed and eccentricity tuning reveal a central role for the velocity-based cue to 3D visual motion. *Journal of Neurophysiology*, *104*, 2886–2899.

Eckmeier, D., Geurten, B. R., Kress, D., Mertes, M., Kern, R., Egelhaaf, M., & Bischof, H. J. (2008). Gaze strategy in the free flying zebra finch (*Taeniopygia guttata*). *PLoS One*, *3*, e3956–e3956.

Fernandez, J. M., & Farell, B. (2005). Seeing motion in depth using interocular velocity differences. *Vision Research*, *45*, 2786–2798.

Gibson, J. J. (1950). *The perception of the visual world*. Boston, MA: Houghton Mifflin.

Götz, K. G. (1968). Flight control in *Drosophila* by visual perception of motion. *Kybernetik*, *4*, 199–208.

Harris, J. M., Nefs, H. T., & Grafton, C. E. (2008). Binocular vision and motion-in-depth. *Spatial Vision*, *21*, 531–547.

Kleiner, M., Brainard, D., Pelli, D., Ingling, A., Murray, R., & Broussard, C. (2007). What's new in Psychtoolbox-3. *Perception*, *36*(14), 1–16.

Koenderink, J. J. (1986). Optic flow. *Vision Research*, *26*, 161–179.

Levi, D. M., Hariharan, S., & Klein, S. A. (2002). Suppressive and facilitatory spatial interactions in peripheral vision: Peripheral crowding is neither size invariant nor simple contrast masking. *Journal of Vision*, *2*(2):3, 167–177, doi:10.1167/2.2.3. [PubMed] [Article]

Martin, G. R. (2009). What is binocular vision for? A birds' eye view. *Journal of Vision*, *9*(11):14, 1–19, doi:10.1167/9.11.14. [PubMed] [Article]

Martin, G. R., & Shaw, J. M. (2010). Bird collisions with power lines: Failing to see the way ahead? *Biological Conservation*, *143*, 2695–2702.

McKee, S. P., & Nakayama, K. (1984). The detection of motion in the peripheral visual field. *Vision Research*, *24*, 25–32.

Mohler, B. J., Thompson, W. B., Creem-Regehr, S. H., Pick, H. L., Jr, & Warren, W. H., Jr. (2007). Visual flow influences gait transition speed and preferred walking speed. *Experimental Brain Research*, *181*, 221–228.

Pelli, D. G. (1997). The VideoToolbox software for visual psychophysics: transforming numbers into movies. *Spatial Vision*, *10*, 437–442.

Regan, D., & Beverley, K. I. (1973). Some dynamic features of depth perception. *Vision Research*, *13*, 2369–2379.

Regan, D., & Gray, R. (2009). Binocular processing of motion: Some unresolved questions. *Spatial Vision*, *22*, 1–43.

Rentschler, I., & Treutwein, B. (1985). Loss of spatial phase relationships in extrafoveal vision. *Nature*, *313*, 308–310.

Rokers, B., Cormack, L. K., & Huk, A. C. (2008). Strong percepts of motion through depth without strong percepts of position in depth. *Journal of Vision*, *8*(4):6, 1–10, doi:10.1167/8.4.6. [PubMed] [Article]

Schiffner, I., & Srinivasan, M. V. (2015). Direct evidence for vision-based control of flight speed in budgerigars. *Scientific Reports*, *5*, 10992.

Shioiri, S., Kakehi, D., Tashiro, T., & Yaguchi, H. (2009). Integration of monocular motion signals and the analysis of interocular velocity differences for the perception of motion-in-depth. *Journal of Vision*, *9*(13):10, 1–17, doi:10.1167/9.13.10. [PubMed] [Article]

Srinivasan, M. V., Lehrer, M., Kirchner, W. H., & Zhang, S. W. (1991). Range perception through apparent image speed in freely flying honeybees. *Visual Neuroscience*, *6*, 519–535.

Srinivasan, M. V., Zhang, S., Altwein, M., & Tautz,

J. (2000). Honeybee navigation: Nature and calibration of the "odometer." *Science*, *287*, 851–853.

Stephenson, C., & Braddick, O. (1983). Discrimination of relative spatial phase in fovea and periphery *Investigative Ophthalmology and Visual Science (Suppl.)*, *24*, 146.

Wright, M. J., & Johnston, A. (1983). Spatiotemporal contrast sensitivity and visual field locus. *Vision Research*, *23*, 983–989.