Sensitivity and bias in the discrimination of two-dimensional and three-dimensional motion direction

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Sensory systems are faced with an essentially infinite number of possible environmental events but have limited processing resources. Posed with this challenge, it makes sense to allocate these resources to prioritize the discrimination of events with the most behavioral relevance. Here, we asked if such relevance is reflected in the processing and perception of motion. We compared human performance on a rapid motion direction discrimination task, including monocular and binocular viewing. In particular, we determined sensitivity and bias for a binocular motion-in-depth (three-dimensional; 3D) stimulus and for its constituent monocular (two-dimensional; 2D) signals over a broad range of speeds. Consistent with prior work, we found that binocular 3D sensitivity was lower than monocular sensitivity for all speeds. Although overall sensitivity was worse for 3D discrimination, we found that the transformation from 2D to 3D motion processing also incorporated a pattern of potentially advantageous biases. One such bias is reflected by a criterion shift that occurs at the level of 3D motion processing and results in an increased hit rate for motion toward the head. We also observed an increase in sensitivity for 3D motion trajectories presented on crossed rather than uncrossed disparity pedestals, privileging motion trajectories closer to the observer. We used these measurements to determine the range of real-world trajectories for which rapid 3D motion discrimination is most useful. These results suggest that the neural mechanisms that underlie motion perception privilege behaviorally relevant motion and provide insights into the nature of human motion sensitivity in the real world.

Introduction

A key function of vision is to encode the direction and speed of moving objects. Research on the encoding and perception of motion largely has focused on motion trajectories that lie within the frontoparallel plane (i.e., two-dimensional [2D] motion; for review see Born & Bradley, 2005; Burr & Thompson, 2011). Comparatively less is known about how motion trajectories through three-dimensional (3D) space are encoded. To address this question, work in recent years has focused on understanding the mechanisms that underlie 3D motion perception from binocular cues. These binocular cues are derived from differences in the two monocular retinal images produced by a moving object (Harris, Nefs, & Grafton, 2008). In particular, neurophysiological and brain-imaging studies have identified a central role for area MT/MT+, which previously has been described as a key area for 2D motion processing (Czuba, Huk, Cormack, & Kohn, 2014; Rokers, Cormack, & Huk, 2009; Sanada & DeAngelis, 2014; Zeki, 1974). This work suggests that receptive fields that are useful for encoding binocular 3D motion could form via neurons that are tuned for different 2D directions of motion in the two eyes.

However, the principles that underlie the encoding of binocular 3D motion via the integration of two monocular motion cues are not yet well characterized. For example, recent perceptual work showed that temporal integration of motion-in-depth signals differs fundamentally from integration of lateral motion signals and suggested that this difference might reflect the particular ecological importance of making judg-ments of toward versus away motion (Katz, Hennig, Cormack, & Huk, 2015). That is, the ability to rapidly detect motion toward the head may confer a benefit in terms of self-preservation over the detection of receding motion. Here, we examined this idea further by characterizing changes in both sensitivity and bias that

are associated with the transformation from monocular to binocular motion encoding.

Prior evidence for a "motion toward the head" advantage has been mixed. Work with looming stimuli has shown that objects on a collision course with the head or body have a privileged perceptual role (Lin et al., 2008, 2009; Schiff et al., 1962). On the other hand, work that investigated centripetal and centrifugal motion (which represent cues to receding and approaching trajectories, in 3D) suggests a perceptual privilege for motion receding from the observer (Edwards & Badcock, 1993; Raymond, 1994; but see Ball & Sekuler, 1980). These previous studies examined only monocular cues to motion in depth, and thus it is unknown which, if any, of these perceptual differences are reflected in binocular motion perception.

In the present study, we aimed to identify potential specializations associated with the transformation from 2D (monocular) to 3D (binocular) motion processing. We therefore directly compared the sensitivity and biases in 2D and 3D motion direction discrimination in human observers across a broad range of speeds. Importantly, by selectively manipulating binocular motion cues, we differentiated 3D motion–specific biases from those that might exist in the constituent monocular signals. The effects uncovered in our study suggest that the transformation from 2D to 3D motion processing incorporates behaviorally relevant biases.

Materials and method

Participants

Seven observers (ages 19–41 years; two females and five males) participated. All had normal or corrected-to-normal vision and were experienced psychophysical observers. Three observers were the study authors, and the remaining four were naive to the study's purpose. The procedure was approved by the University of Wisconsin–Madison Institutional Review Board and carried out in accordance with the Declaration of Helsinki. One participant was excluded from the group analysis because they were unable to perform the task and almost exclusively responded that slow speeds moved toward them and fast speeds moved away.

Experimental setup

The setup consisted of a stereoscopic 3D–enabled Planar LCD 23-in. display (120-Hz refresh rate, 1920 × 1080 pixels) and a chin rest located 75 cm from the monitor (Figure 1a). Observers viewed the display through NVIDIA 3D Vision 2 glasses. The mean
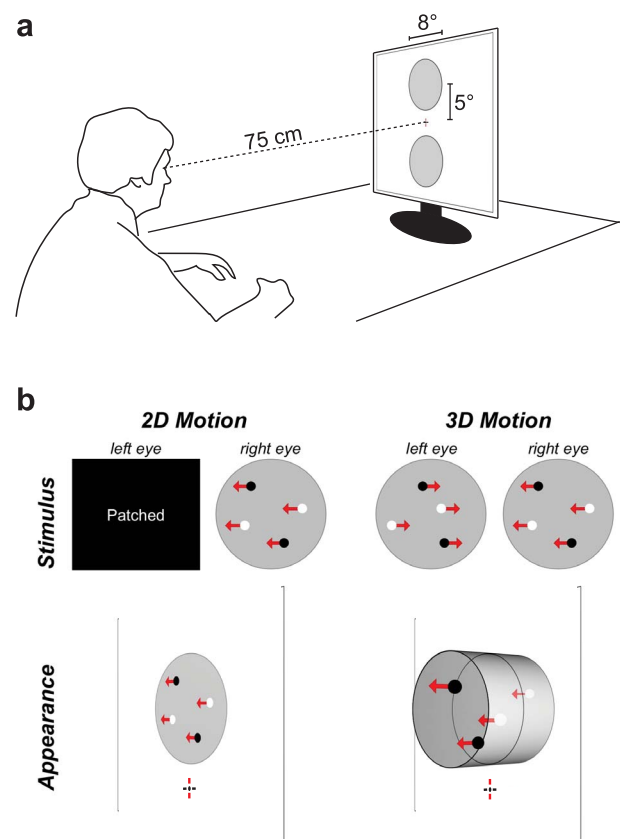

Figure 1. Schematic of the setup, stimulus, and appearance. (a) Observers viewed the screen from 75 cm and fixated a nonius crosshair. On each trial, moving dots appeared randomly either 5° above or 5° below fixation within an 8° aperture. (b) The stimulus was viewed either monocularly (2D motion) or binocularly (3D motion). In the 3D condition, dots moved in opposite directions in the two eyes and specified a range of binocular disparities. Thus, the dots appeared to move toward or away from the observer within a fixed volume in depth (right column). In the 2D condition, the left eye was patched so the dots appeared to move laterally on the display plane (left column).

luminance through the glasses was 5.37 cd/m^2. The maximum luminance ("white") was 13.8 cd/m^2, and the minimum luminance ("black") was 0.03 cd/m^2. Vergence stability was facilitated by a 1/f noise background that covered the entire display with the exception of two stimulus apertures. A fixation dot and nonius lines were presented in the center of the display to help monitor vergence, and observers were instructed to maintain fixation at all times.

Stimuli

Stimuli were generated using an Apple Mac Pro (Apple, Cupertino, CA) running MATLAB (Mathworks Inc., Natick, MA) and Psychophysics Toolbox 3

(Brainard, 1997; Kleiner, Brainard, Pelli, Ingling et al., 2007; Pelli, 1997). All stimulus elements were anti-aliased to achieve subpixel resolution. The motion stimuli were presented within one of two circular apertures with a solid background at mean luminance (8° diameter) directly above and below the fixation point (Figure 1a). Each motion stimulus consisted of 16 black and white dots (8-pixel diameter) presented in a 4° diameter region centered on the aperture. The dots were randomly distributed and moved laterally in opposite directions for each eye at the following speeds: 0.14°, 0.27°, 0.55°, 1.10°, 2.19°, 3.29°, 4.39°, 6.58°, 8.78°, and 13.16°/s. Faster speeds initially were included but were removed from analysis because of potential motion artifacts at the monocular frame rate (60 Hz/ eye). 3D motion direction sensitivity was measured in three conditions, each at a different pedestal: middle, near, and far. In each condition the binocular disparity range was limited, creating a perception of dots continuously wrapping through a cylindrical volume (Figure 1b). Individual dots that reached the limit of the stimulus volume were extinguished and redrawn in a random position at the opposite end of the volume. In the middle condition, this volume contained disparities ±0.55° from the fixation plane. In the near and far conditions, this volume was placed on a disparity pedestal and contained disparities between 0° and 1.10° either crossed or uncrossed, respectively. Thus, in the middle condition the volume appeared to straddle the display plane, and in the near and far conditions the entire volume was in front of or behind the display, respectively. Lateral motion sensitivity was measured by covering the left eye and presenting the middle stimulus.

Procedure

On each trial, stimuli were presented pseudorandomly in either aperture, so the observer was unable to make anticipatory eye movements. In each aperture, 15 repetitions of each speed and motion direction were presented in pseudorandom order. For four of the participants, presentation duration was 133 ms. Two participants had difficulty performing the task at this duration, so the time was extended to 200 ms. After each presentation, observers performed a two-alternative forced-choice task on the direction of motion (either toward/away or left/right, depending on the session). Participants underwent training on the task prior to starting their first session but did not receive feedback. The middle condition was always the first condition tested. The far and near trials were randomly ordered in a block design, with two blocks each. The monocular lateral task was completed last. In a follow-up control experiment conducted after the initial study,

three participants repeated the lateral motion task binocularly.

Data analysis

For each condition, we calculated the percentage of correct responses for each participant and each speed. The hit and false alarm rates were used to compute the sensitivity index (d'):

$$d' = n(\text{hit}) - n(\text{false}). \quad (1)$$

Here, $n(.)$ denotes the inverse of the cumulative of the normal distribution. By way of convention, correct responses on trials in which motion was leftward (monocularly) or toward (binocularly) were considered hits. The response criterion (c) was computed as

$$c = \frac{-\left(n(\text{hit}) + n(\text{false})\right)}{2}. \quad (2)$$

Results for sensitivity and percent correct as a function of speed were fit in MATLAB via nonlinear least squares regression using the trust region algorithm. The fitting function ($g(x)$) was parameterized as a scaled skew-Gaussian distribution:

$$g(x) = 2\alpha \left(\frac{1}{\sigma\sqrt{2\pi}} e^{\frac{-(x-\mu)^2}{2\sigma^2}} \right)$$
$$\times \left(0.5 \left[1 + \text{erf}\left(\frac{\beta(x-\mu)}{\sigma\sqrt{2}} \right) \right] \right), \quad (3)$$

where μ and σ are the mean and standard deviation, respectively; α is a scale term that determines the amplitude of the function; β is the skewness; and x is the logarithm (base 10) of the monocular retinal speed. For 2D accuracy data, the skew term was fixed at zero in order to achieve a stable fit. Criterion data were fit with least squares linear regression.

Conversion to world speeds

It is useful to consider these retinal motion sensitivities in terms of the corresponding object speeds in the world. Here, we describe a simple conversion between object distance/speed in the world and the angular speed cast on the retinas. The conversion assumes that fixation distance is held constant in the midsagittal plane such that retinal motion is caused by object motion only. In applying this conversion to our angular motion sensitivity data, we furthermore assume that motion sensitivity in angular units is independent of fixation distance—similar to static binocular disparity (Hillis & Banks, 2001).

We define a left-handed 3D coordinate system with the origin at the midpoint of the interocular axis. The x-axis is parallel to the interocular axis and positive to the right. The y-axis is orthogonal to the x-axis in the plane of the forehead and positive toward the top of the head. The z-axis is positive in front of the observer. If the observer has an interocular separation of $2a$, then the right and left eyes are located on the x-axis with coordinates $(a, 0, 0)$ and $(-a, 0, 0)$, respectively.

The function $P(t) = [X(t), Y(t), Z(t)]$ is the position of an object in this coordinate system as a function of time (t). For simplicity, we consider only objects in the midsagittal plane: $X(t) = 0$ for all t. The object's azimuth ($\Theta(t)$, the angle relative to the z-axis in the xz-plane) on the right eye's retina is

$$\Theta(t) = \tan^{-1}\left(\frac{a}{Z(t)}\right). \quad (4)$$

If for all points in time $Z(t)$ is much larger than a, then the small angle approximation—$\phi = \tan(\phi)$—can be applied to yield

$$\Theta(t) \approx \frac{a}{Z(t)}. \quad (5)$$

To examine the angular horizontal retinal velocity signals generated by the object's motion, we differentiate $\Theta(t)$ with respect to time, yielding

$$\frac{d\Theta(t)}{dt} \approx \frac{a\left(dZ(t)/dt\right)}{Z^2(t)}. \quad (6)$$

We denote this angular velocity at a given moment in time t_0 as

$$\delta \approx \frac{av}{b^2}, \quad (7)$$

where δ, v, and b correspond to $d\Theta(t)/dt$, $dZ(t)/dt$, and $Z(t)$, respectively, each evaluated at $t = t_0$. These are the horizontal retinal velocity in the right eye, the object velocity in depth, and the object distance, respectively. Recall that this calculation yields the retinal velocity in the right eye. If we consider only motion directly toward and away from the observer in the midsagittal plane, then the angular velocity in the left eye will be equal in magnitude (speed) but opposite in sign. Thus, we can generically describe the monocular horizontal retinal speed ω cast by an object with world speed in depth $s = |v|$ as

$$\omega \approx \frac{as}{b^2}. \quad (8)$$

Using this equation, we can now examine how the performance on 3D direction discrimination expressed in retinal speeds translates to performance for moving objects with different combinations of world speeds (s) and distances (b). We assume an interocular distance of 6.4 cm ($a = 3.2$) and convert ω from radians per unit time to degrees per second.

Note that this analysis considers only horizontal displacements on the retina, not vertical ones. Horizontal disparities result when a point in the world projects to unequal azimuths in the two eyes; vertical disparities result when a point projects to unequal elevations in the two eyes. Disparities and interocular velocity differences created by natural stimuli will have both a horizontal and a vertical component. However, we are assuming here that fixation is near the midsagittal plane and that the retinal eccentricities involved are always small, and therefore vertical disparities will also tend to be small (Read, Phillipson, & Glennerster, 2009).

Results

As expected, both the ability to discriminate 2D lateral motion direction (left, right) and 3D motion direction (toward, away) varied as a function of speed (Figure 2a; Czuba, Rokers, Huk, & Cormack, 2010; De Bruyn & Orban, 1988; Tyler, 1971). 2D sensitivity (d') exceeded 3D sensitivity for all tested speeds, but the peak sensitivity for both tasks occurred at similar speeds (5.5°/s for 2D and 3.3°/s for 3D). The 3D condition data plotted here are for the middle disparity pedestal only (near and far pedestal data are shown in Figure 3). Note that the positions of the moving dots updated and "wrapped" within the aperture in both the 2D and 3D conditions, potentially making both tasks more difficult at fast speeds. The reduction in 3D sensitivity relative to 2D is generally consistent with the idea that the computation of 3D motion direction is accomplished by comparing the 2D signals between the two eyes and that the additional computation results in lower signal-to-noise (Katz et al., 2015; Tyler, 1971). Using a strict test for statistical differences (nonoverlap of the 95% confidence intervals), we found that the amplitude, mean, and standard deviation were greater for the 2D motion curve than for the 3D curve (Table 1). The ratio of the sensitivity values (yellow line) followed a shallow U shape, showing that the discriminability of 3D motion relative to 2D motion is best and nearly constant for midrange speeds; however, it worsens for relatively fast and slow speeds. Plotting the same results in terms of percent correct responses revealed that performance was well above chance for all conditions (Figure 2b). This is impressive given the brief presentation intervals and wide range of speeds. Discrimination for 2D motion was also above threshold (75%) for all but the slowest speed, and discrimination for 3D motion was above threshold for seven out of the 10 speeds tested.
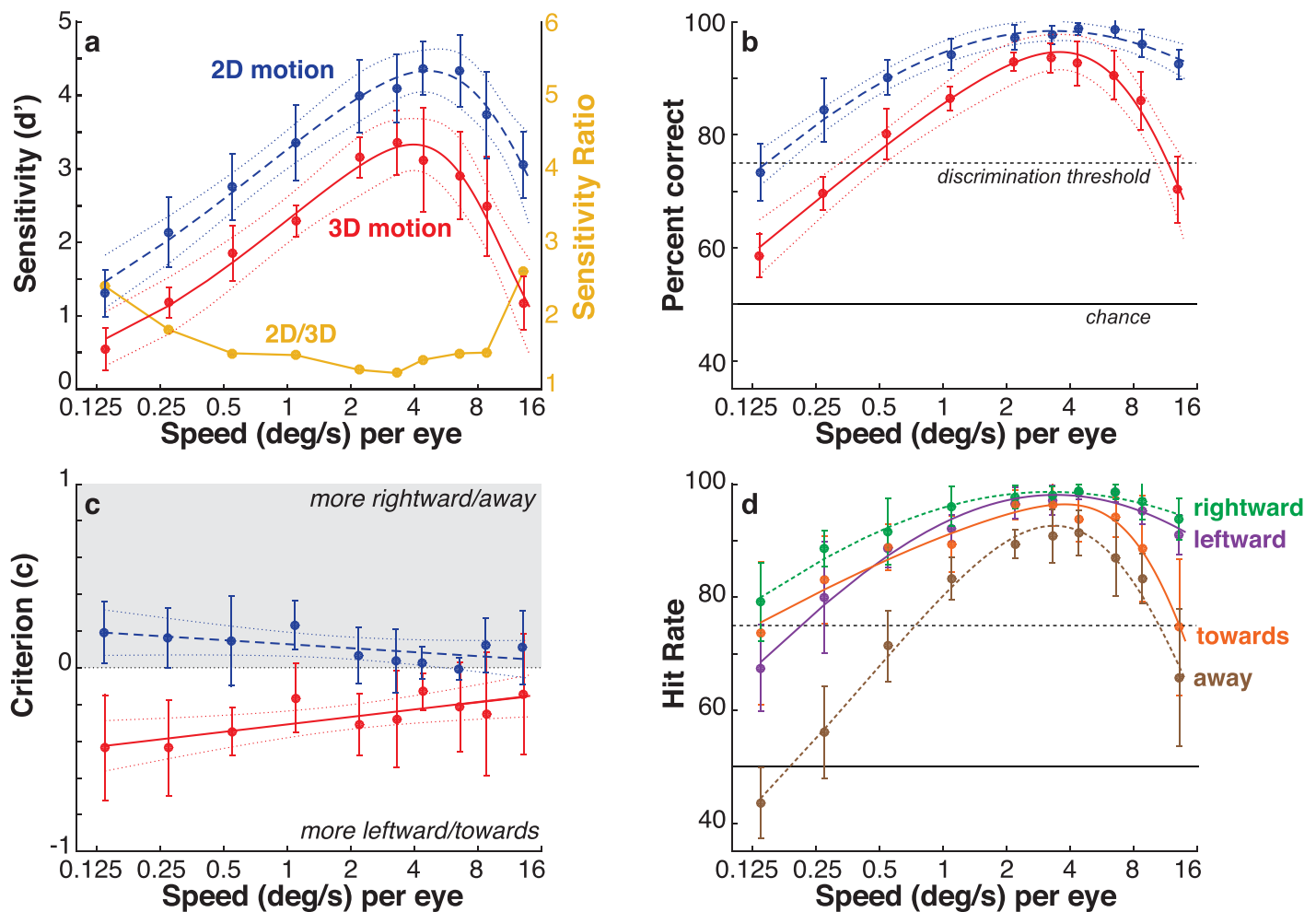
Figure 2. Performance comparison for 2D and 3D motion. (a) Between-subjects mean and 95% confidence intervals for motion direction sensitivity as a function of retinal speed are plotted for 2D (blue circles) and 3D (red circles) motion. Best-fitting skew-Gaussians and 95% confidence bands (simultaneous) for the fitted curves are shown. The yellow line indicates the ratio between the 2D and 3D data points. (b, c) Data for percentage of correct trials and for response criterion are plotted in the same manner as in panel a. (d) Hit rates are plotted in the same manner as in panel a, separately for each of the four motion directions. Confidence bands are excluded for clarity.

Next, we asked whether there were any systematic biases in the determination of motion direction. We did this by comparing the response criterions for each task. If the performance on the 3D motion task was completely determined by performance on the 2D motion task (plus a lower signal-to-noise ratio), we would expect both tasks to have a similar response criterion. However, our results clearly contradict this idea (Figure 2c). For the 2D task, we found a slight bias toward rightward motion: Observers tended to have a higher hit rate for rightward moving trials. Because all observers performed the 2D task with their right eye, this is generally consistent with a slight increase in sensitivity for nasalward motion on the retina (Raymond, 1994). Interestingly, the 3D motion task was associated with a criterion shift such that the response bias reversed and strengthened. The 3D bias strongly

favored motion toward the head, which produces the opposite direction of 2D motion in the right eye (leftward). In both cases, the response bias systematically decreased as a function of stimulus speed. However, it is unclear whether this trend is also related to the change in sensitivity with speed. Individual observer data for Figure 2a and c are included in Supplementary Figure S1.

Three of the observers participated in a control experiment: They performed the 2D motion discrimination binocularly rather than monocularly. This condition was designed to test whether the criterion shift observed in the binocular 3D task was specific to 3D motion and not to binocularity per se. Both the sensitivity and criterion data for the observers in this control condition were highly similar to the monocular 2D task (Supplementary Figure S2). Thus, the negative

| | Sensitivity | | | | Percent correct | | | |
| | 2D versus 3D | | 3D near versus far | | Leftward versus rightward | | Toward versus away | |
Variable	2D	3D (middle)	Near	Far	Leftward	Rightward	Toward	Away
Amplitude	**8.3 (7.7, 8.8)**	**4.8 (4.5, 5.2)**	**5.9 (5.6, 6.2)**	**4.7 (4.3, 5.1)**	**4.1 (3.7, 4.4)**	**5.2 (4.7, 5.8)**	**3.7 (3.3, 4.1)**	**2.1 (2.1, 2.3)**
Mean	**1.2 (1.1, 1.3)**	**1.0 (1.0, 1.1)**	1.0 (1.0, 1.1)	1.0 (1.0, 1.1)	0.5 (0.5, 0.6)	0.5 (0.4, 0.6)	1.3 (1.2, 1.5)	1.3 (1.2, 1.3)
Standard dev.	**1.3 (1.2, 1.4)**	**1.0 (0.9, 1.1)**	1.0 (0.9, 1.1)	1.0 (0.9, 1.2)	**1.6 (1.5, 1.8)**	**2.1 (1.9, 2.3)**	**2.9 (2.5, 3.3)**	**1.6 (1.4, 1.7)**
Skew	−4.1 (−6.2, −2.0)	−4.1 (−6.0, −2.2)	−3.9 (−5.2, −2.5)	−4.9 (−7.4, −2.4)	—	—	−8.6 (−13.3, −3.8)	−3.1 (−4.5, −1.6)

Table 1. Parameters of fitted curves (Equation 3) to sensitivity and percent correct as a function of log (base 10) retinal speed. Four comparisons are shown: 2D versus 3D sensitivity, 3D near versus 3D far sensitivity, leftward versus rightward percent correct, and toward versus away percent correct. Values in parentheses are 95% confidence intervals. Parameters are bold if the 95% confidence intervals do not overlap.

criterion shift appears to be specific to the 3D motion direction judgment.

To determine how much this criterion shift affects performance, we also plotted the hit rate separately for each direction of motion. That is, the percentage of correct responses was split up by trials for each motion direction: leftward, rightward, toward, and away (Figure 2d). The hit rates for leftward (solid purple line) and rightward (dashed green line) motion were similar to each other, and both were high across all speeds. For speeds up to approximately 6°/s, the hit rate for motion toward the head (solid orange line) was quite similar to the leftward and rightward hit rates. Although the toward-motion hit rate at faster speeds declined steeply, all speeds except the fastest and the slowest were above the 75% threshold. In contrast, the hit rate for motion away from the head (dashed brown line) was substantially worse than that for all other motion directions. This makes sense because the 3D motion criterion shift necessitates that a substantial number of "toward" false alarms must occur to reach the same hit rate for a given motion sensitivity. Both the amplitude and standard deviations of the fitted curves were greater for rightward (versus leftward) and toward (versus away) motion (Table 1).

Next, we asked whether 3D motion sensitivity also differed as a function of binocular disparity. We presented the 3D motion stimulus on either a crossed or an uncrossed disparity pedestal, consistent with motion occurring nearer to or farther than the fixation distance, respectively. Note that the addition of a binocular disparity pedestal only creates a relative position shift in the monocular locations of dots presented to the two eyes and thus would not affect the monocular speed sensitivity. In terms of monocular retinal speeds, the near and far conditions are identical. For each speed tested, the sensitivity in the near condition was greater than that in the far condition, and the ratio between near and far sensitivity was essentially constant across all tested speeds (Figure 3a; Table 1). In addition, we observed that the response criteria for both near and far motion were quite similar to each other: The near criteria were slightly but not significantly more negative (Figure 3b). Individual observer data for these two plots are included in Supplementary Figure S3.

Interestingly, greater motion sensitivity at the near pedestal was observed in both the upper and lower visual field regions of our stimulus (not shown in the figure). This is surprising because there is a well-known asymmetry between the upper and lower visual fields related to static depth perception from binocular disparity. Specifically, the visual system is more sensitive to crossed (near) binocular disparities in the lower visual field and to uncrossed (far) disparities in
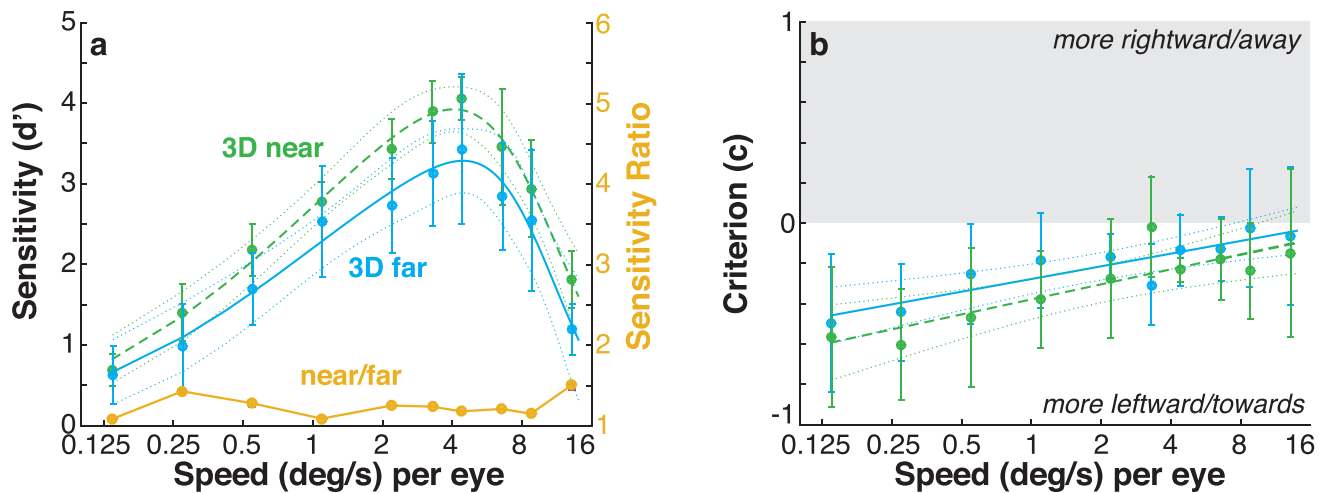
Figure 3. Performance comparison for 3D motion presented nearer or farther relative to fixation. (a, b) Data for sensitivity and criterion for 3D motion direction discrimination when the stimulus was either on a crossed pedestal (nearer than fixation; green circles) or on an uncrossed pedestal (farther than fixation; cyan circles) are plotted in the same manner as in Figure 2a and c.

the upper visual field (Harrold & Grove, 2015; Julesz, Breitmeyer, & Kropfl, 1976). This is likely due to systematic biases in the disparities between empirical corresponding points—the locations on the two retinas that correspond to the same perceived direction in space and relative to which depth discriminations are most precise (Blakemore, 1970; Cooper, Burge, & Banks, 2011; von Helmholtz, 1962). These biases in corresponding points are thought to be related to statistical regularities in the typical distance of objects in the upper and lower visual fields (Hibbard & Bouzit, 2004; Sprague, Cooper, Tošić, & Banks, 2015). Based on this binocular disparity literature, one might predict that 3D motion sensitivity would have a similar visual field–dependent asymmetry, with an advantage for 3D motion at relatively near depths observed only in the lower visual field. But we did not find evidence for this asymmetry in the current study; instead, we found that sensitivity was better at the crossed pedestal in both visual field locations.

Discussion

The accurate perception of object motion is critical for survival. Although the phenomenology and neural mechanisms underlying 2D motion perception have been studied extensively, it has not been clear how these mechanisms contribute to the perception of motion in depth. Here, we show that although the transformation from monocular to binocular motion-in-depth signals involves a loss in sensitivity, the range of speeds over which observers can discriminate 3D motion direction is nonetheless quite broad. Our results examining sensitivity and bias suggest that the

computations involved in binocular 3D motion encoding may favor behaviorally important features of the environment. That is, the combination of monocular motion and depth signals required to detect 3D motion may be thought of not as a simple comparison between two monocular patterns but rather as a specific reweighting of stimulus information that reflects fundamental asymmetries in our 3D world.

Relationship to prior work

One possible explanation for the broad range of speed sensitivity found in our experiment is that there are two distinct and complementary binocular motion mechanisms: one tuned for binocular disparity and slow speeds and one tuned for fast speeds independent of disparity (Allen, Haun, Green, Hanley, & Rokers, 2015; Cumming & Parker, 1994; Czuba et al., 2010; Regan, 1993). However, the fact that we observed an effect of binocular disparity pedestal (crossed vs. uncrossed disparities) across a large range of retinal speeds suggests that both of these mechanisms contribute over a wider range of speeds than has previously been recognized.

Several prior studies have manipulated disparity pedestal in binocular 3D motion tasks as a way of examining these two purported mechanisms (Brooks, 2002; Brooks & Stone, 2004; Cumming, 1995; Portfors-Yeomans & Regan, 1996). One of these studies directly compared performance with a crossed versus an uncrossed pedestal (Brooks & Stone, 2004) but did not find a similar advantage at the crossed (near) pedestal. However, participants were performing a speed-discrimination task rather than a
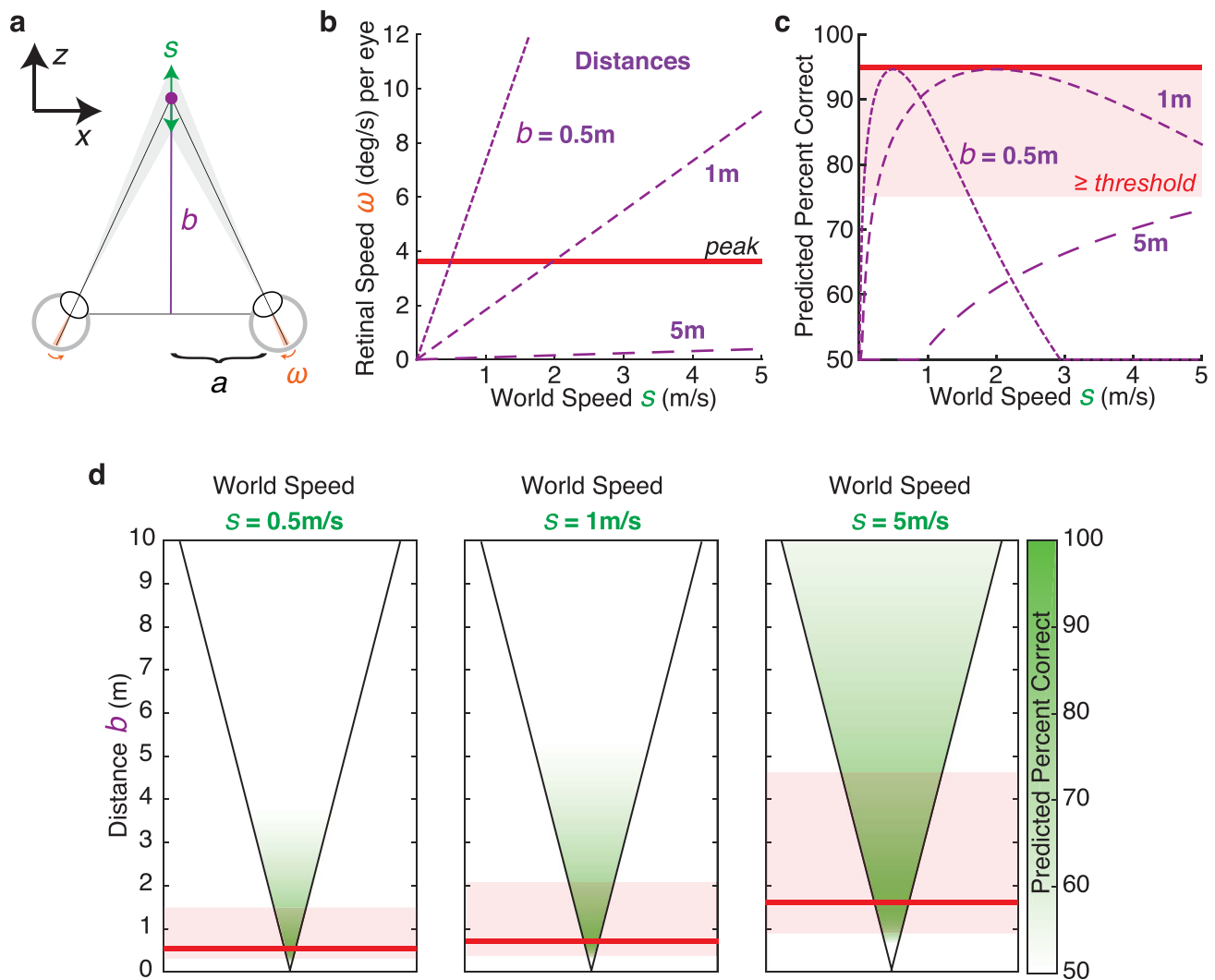
Figure 4. Predicted 3D direction discrimination performance as a function of object distance and speed. (a) Top-down view of the assumed viewing geometry. (b) Each purple line shows the relationship between world (abscissa) and retinal (ordinate) speed for a different object distance. The retinal speed associated with peak percent correct (red line) is shown for the 3D motion direction discrimination data in Figure 2b. (c) Retinal speed sensitivity is best for the discrimination of 3D motion direction of relatively nearby objects. The predicted percent correct for direction discrimination for each world distance and speed from panel b is shown. The red shaded region represents values that are above threshold. (d) Similar to panel c, except that predicted performance for three object speeds is plotted as a function of distance using a heat map. The peak percent correct and threshold region are plotted as in the previous panels.

direction-discrimination task. In a related study, observers reported the perceived direction of motion of small targets moving in a horizontal plane containing the eyes (Fulvio, Rosen, & Rokers, 2015). For high-contrast stimuli at both near and zero disparity pedestals, observers had a tendency to misreport motion away from the head as being motion toward the head, consistent with the results of the current study. However, with low-contrast stimuli, this trend reversed and more misreports were made in the opposite direction. Future work can further examine how other monocular cues may interact to affect the decision criterion used in these types of judgments.

Sensitivity to motion trajectories in the world

Although manipulating stimuli in terms of retinal velocities is advantageous for directly comparing sensitivity for 2D and 3D motion, it is more behaviorally relevant to think about 3D motion sensitivity in terms of the speeds with which objects move in the world. In the following section, we examine how the sensitivities measured in our experiment can inform our understanding of 3D motion perception in the natural world.

We determined the combinations of object distance (b) and speed in depth (s) in the world that could generate the retinal speeds (ω) used in our experiments, assuming the scenario illustrated in Figure 4a

(see Materials and methods). Note that our experiment required observers to make direction judgments from very brief stimulus presentations (200 ms or less), so these predictions are relevant for making rapid discriminations.

Figure 4b shows how the retinal speed cast by a moving object increases as a function of world speed (abscissa) and decreases with greater distances (purple lines). The red horizontal line indicates the retinal speed associated with the peak percent correct responses (from the fitted curve to the middle condition in our experiment: 3.6°/s per eye). For an object at 0.5 m this retinal speed translates to a world speed of 0.5 m/s, for an object at 1 m the world speed is 2.0 m/s, and for an object at 5 m the world speed is a very fast 49 m/s (beyond the speeds shown in the plot).

We can replot these lines in terms of the percent correct responses for each retinal speed to show in detail how performance should vary as a function of the world parameters (Figure 4c). The red line again indicates the peak percent correct (95%), and the shaded red region indicates the retinal speeds for which performance was above threshold (75%). For example, when an object is relatively close to the observer (0.5 m), discrimination is predicted to be above threshold for a range of reasonable world speeds (0.06–1.6 m/s). For objects at 1 m, discrimination would be above threshold over a very broad range of world speeds, even up to very fast ones (0.2–6.5 m/s). However, for objects that are relatively far away (5 m), motion would have to be faster than 5.8 m/s for the retinal speed to exceed threshold.

In addition, we can select a specific world speed and examine the sensitivity of the visual system as a function of object distance (Figure 4d). Here, we show the expected percent correct, as well as the peak and thresholds, for three world speeds: 0.5, 1, and 5 m/s. Data are plotted as a heat map for a fixed visual angle in front of the observer. In each case, performance is best for relatively nearby viewing distances (<5 m) and peaks at 0.5, 0.7, and 1.6 m, respectively. This analysis shows that for the particular task of making fast judgments of 3D motion direction, the visual system may be most sensitive for relatively nearby objects. Objects at distances greater than 5 m would have to move exceedingly fast to reach threshold.

It should be noted that the current set of experiments examined sensitivity to very brief presentations of motion in a relatively small region of the visual field. The speed sensitivities we observed generally are consistent with previous 3D measurements (Czuba et al., 2010). However, similar paradigms for 2D motion sensitivity have produced a range of peak speeds, with some showing substantially faster speeds at peak sensitivity (De Bruyn & Orban, 1988). It is also important to note that the conversion from retinal to world speed here relies on the assumption that motion sensitivity in angular units is independent of fixation distance (i.e., that the same retinal speed results would be obtained for arbitrary fixation distances). To fully understand the space of stimulus parameters that contribute to both 2D and 3D motion sensitivity, future work will need to explore the effects of factors such as longer exposure durations, changes in fixation location, and more fully realized naturalistic stimuli. For example, when objects move at locations away from the midsagittal plane, frontoparallel motion can also produce different speeds in the two eyes, and 3D motion produces speeds that are no longer equal and opposite.

Relatedly, the current analysis does not consider the potential contribution of vertical disparities to perception of motion in depth. In natural viewing situations, the disparities between the two eyes images' have both a horizontal and a vertical component (except for points falling on the horizontal and vertical meridians of the eyes). Vertical disparities can contribute to perceived depth (Howard & Rogers, 2002). However, to our knowledge the contribution of vertical interocular velocity differences has not been explored.

Finally, the stimuli in our experiment consisted of constant retinal speeds for the full presentation duration. It is clear from Equation 8 that an object in the world moving at a constant speed in depth (s) will have a different retinal speed as its distance (b) changes. Indeed, an object moving toward an observer at a constant velocity will project to an accelerating retinal speed (as b decreases, ω increases). An object moving away from an observer at a constant velocity will project to a decelerating retinal speed. It then follows that stimuli with constant retinal velocities are consistent with objects that are decelerating as they approach an observer or accelerating as they recede. In future work, it would be interesting to examine whether 2D and 3D motion sensitivities are differentially affected by changes in velocity.

To conclude, by directly comparing sensitivity and biases in 2D and 3D motion direction discrimination in human observers, we present evidence that the encoding of motion trajectories through 3D space brings with it specific sensitivities and biases well suited to detecting stimuli that are nearby and moving toward the observer. Identifying the emergence of such biases and sensitivities in neural populations in the dorsal stream will ultimately help reveal the mechanisms that close the sensation–perception–action loop.

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References

Allen, B., Haun, A. M., Green, C. S., Hanley, T., & Rokers, B. (2015). Optimal combination of the binocular cues to 3D motion. *Investigative Ophthalmology & Visual Science, 56*(12), 7589–7596. [PubMed] [Article]

Ball, K., & Sekuler, R. (1980). Human vision favors centrifugal motion. *Perception, 9*(3), 317–325.

Blakemore, C. (1970). The range and scope of binocular depth discrimination in man. *Journal of Physiology, 211*(3), 599–622.

Born, R. T., & Bradley, D. C. (2005). Structure and function of visual area MT. *Annual Review of Neuroscience, 28,* 157–189.

Brainard, D. H. (1997). The Psychophysics Toolbox. *Spatial Vision, 10*(4), 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]

Brooks, K. R., & Stone, L. S. (2004). Stereomotion speed perception: Contributions from both changing disparity and interocular velocity difference over a range of relative disparities. *Journal of Vision, 4*(12):6, 1061–1079, doi:10.1167/4.12.6. [PubMed] [Article]

Burr, D., & Thompson, P. (2011). Motion psychophysics: 1985–2010. *Vision Research, 51*(13), 1431–1456.

Cooper, E. A., Burge, J., & Banks, M. S. (2011). The vertical horopter is not adaptable, but it may be adaptive. *Journal of Vision, 11*(3):20, 1–19, doi:10.1167/11.3.20. [PubMed] [Article]

Cumming, B. G. (1995). The relationship between stereoacuity and stereomotion thresholds. *Perception, 24*(1), 105–114.

Cumming, B. G., & Parker, A. J. (1994). Binocular mechanisms for detecting motion-in-depth. *Vision Research, 34*(4), 483–495.

Czuba, T. B., Huk, A. C., Cormack, L. K., & Kohn, A. (2014). Area MT encodes three-dimensional motion. *Journal of Neuroscience, 34*(47), 15522–15533.

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*(5), 2886–2899.

De Bruyn, B., & Orban, G. A. (1988). Human velocity and direction discrimination measured with random dot patterns. *Vision Research, 28*(12), 1323–1335.

Edwards, M., & Badcock, D. R. (1993). Asymmetries in the sensitivity to motion in depth: A centripetal bias. *Perception, 22*(9), 1013–1023.

Fulvio, J. M., Rosen, M. L., & Rokers, B. (2015). Sensory uncertainty leads to systematic misperception of the direction of motion in depth. *Attention, Perception, & Psychophysics, 77*(5), 1685–1696.

Harris, J. M., Nefs, H. T., & Grafton, C. E. (2008). Binocular vision and motion-in-depth. *Spatial Vision, 21*(6), 531–547.

Harrold, A. L., & Grove, P. M. (2015). Binocular correspondence and the range of fusible horizontal disparities in the central visual field. *Journal of Vision, 15*(8):12, 1–17, doi:10.1167/15.8.12. [PubMed] [Article]

Hibbard, P. B., & Bouzit, S. (2004). Stereoscopic correspondence for ambiguous targets is affected by elevation and fixation distance. *Spatial Vision, 18*(4), 399–411.

Hillis, J. M., & Banks, M. S. (2001). Are corresponding points fixed? *Vision Research, 41*(19), 2457–2473.

Howard, I. P., & Rogers, B. J. (2002). *Seeing in depth, Volume 2: Depth perception*. Ontario, Canada: I Porteous.

Julesz, B., Breitmeyer, B., & Kropfl, W. (1976). Binocular-disparity-dependent upper-lower hemifield anisotropy and left-right hemifield isotropy as revealed by dynamic random-dot stereograms. *Perception, 5*(2), 129–141.

Katz, L. N., Hennig, J. A., Cormack, L. K., & Huk, A. C. (2015). A distinct mechanism of temporal integration for motion through depth. *Journal of Neuroscience, 35*(28), 10212–10216.

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

Lin, J. Y., Murray, S. O., & Boynton, G. M. (2009). Capture of attention to threatening stimuli without perceptual awareness. *Current Biology, 19*(13), 1118–1122.

Lin, J. Y., Franconeri, S., & Enns, J. T. (2008). Objects on a collision path with the observer demand attention. *Psychological Science, 19*(7), 686–692.

Pelli, D. G. (1997). The VideoToolbox software for visual psychophysics: Transforming numbers into movies. *Spatial Vision, 10*(4), 437–442.

Portfors-Yeomans, C. V., & Regan, D. (1996). Cyclopean discrimination thresholds for the direction and speed of motion in depth. *Vision Research, 36*(20), 3265–3279.

Raymond, J. E. (1994). Directional anisotropy of motion sensitivity across the visual field. *Vision Research, 34*(8), 1029–1037.

Read, J. C. A., Phillipson, G. P., & Glennerster, A. (2009). Latitude and longitude vertical disparity. *Journal of Vision, 9*(13):11, 1–37, doi:10.1167/9.13.11. [PubMed] [Article]

Regan, D. (1993). Binocular correlates of the direction of motion in depth. *Vision Research, 33*(16), 2359–2360.

Rokers, B., Cormack, L. K., & Huk, A. C. (2009). Disparity- and velocity-based signals for three-dimensional motion perception in human MT. *Nature Neuroscience, 12*(8), 1050–1055.

Sanada, T. M., & DeAngelis, G. C. (2014). Neural representation of motion-in-depth in area MT. *Journal of Neuroscience, 34*(47), 15508–15521.

Schiff, W., Caviness, J. A., & Gibson, J. J. (1962). Persistent fear responses in rhesus monkeys to the optical stimulus of "looming." *Science, 136*(3520), 982–983.

Sprague, W. W., Cooper, E. A., Tošić, I., & Banks, M. S. (2015). Stereopsis is adaptive for the natural environment. Science Advances, 1(4), e1400254.

Tyler, C. W. (1971). Stereoscopic depth movement: Two eyes less sensitive than one. *Science, 174*(4012), 958–961.

von Helmholtz, H. (1962). *Treatise on physiological optics*. New York, NY: Dover. (Original work published 1867)

Zeki, S. M. (1974). Cells responding to changing image size and disparity in the cortex of the rhesus monkey. *Journal of Physiology, 242*(3), 827–841.