Radial bias alters high-level motion perception

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Abstract

The visual system involves various orientation and visual field anisotropies, one of which is a preference for radial orientations and motion directions. By radial, we mean those directions coursing symmetrically outward from the fovea into the periphery. This bias stems from anatomical and physiological substrates in the early visual system. We recently reported that this low-level visual anisotropy can alter perceived object orientation. Here, we report that radial bias can also alter another higher-level system, the perceived direction of apparent motion. We presented a bistable apparent motion quartet in the center of the screen while participants fixated on various locations around the quartet. Participants (N=22) were strongly biased to see the motion direction that was radial with respect to their fixation, controlling for any biases with center fixation. This was observed using a vertical-horizontal quartet as well as an oblique quartet (45° rotated quartet). The latter allowed us to rule out the contribution of the hemisphere effect where motion across the midline is perceived less often. These results extend our earlier findings on perceived object orientation, showing that low-level structural aspects of the visual system alter yet another higher-level visual process, that of apparent motion perception.

Keywords: radial bias, apparent motion, bistable motion

Introduction

We recently reported a striking visual illusion where an object was often seen in a nonveridical orientation biased toward radial with respect to fixation (Menceloglu, Nakayama, & Song, 2022). We presented a peripheral Landolt C placed in one of eight orientations and eight locations along four meridians (vertical, horizontal, 45°, 135°). Participants indicated the gap position of the Landolt C using a continuous response measure. Their error patterns indicated that the perceived gap was attracted toward the radial axis. We reasoned that our findings reflected an altered population coding of objects involving a stronger weighting of radial over tangential orientations. This was a novel example of a low-level visual anisotropy influencing high-level perception.

Past research has already shown that the visual system prefers radial over tangential orientations. In particular, extrafoveal visual stimuli that are aligned with a line intersecting the center of gaze are more easily seen or discriminated in psychophysical studies (Bennett & Banks, 1991; Westheimer, 2003; Westheimer, 2005; Rovamo et al., 1982; Sasaki et al., 2006; Temme et al., 1985). Neural evidence for a radial orientation bias has been found in the retina, LGN, and cortex in cat and monkey (Levick and Thibos, 1982; Leventhal and Schall, 1983; Schall et al., 1986), as well as in the LGN and cortex in humans (Mannion et al., 2010; Sasaki et al., 2006; Ling et al., 2015), which may stem from radially added cells during eye development (Leventhal and Schall 1983).

Similar to radial bias for orientation, radial bias for motion direction has been reported. Single-cell studies have shown robust radial bias for motion direction in the middle temporal visual area (MT) (Albright, 1989), posterior parietal cortex (Steinmetz et al., 1987), and the frontal eye fields (Xiao, Barborica, & Ferrera, 2006) of the macaque monkey and the lateral suprasylvian cortex of the cat where cortical motion detectors are situated (Rauschecker et al., 1987). In humans, neuroimaging studies have reported enhanced responses to radial motion (both centrifugal and centripetal) relative to tangential (circular) motion in V1, V2, and V3 (Clifford et al., 2009; Raemaekers et al., 2009). Further, Hong (2015) showed that radial motion as well as radially oriented static stimuli have privileged access to visual awareness. Notably, such evidence concerns real motion involving increments of small steps in the position of a visual stimulus. Here, we explored whether radial bias could also alter motion direction using apparent motion displays.

Apparent motion refers to the spontaneous perception of motion between alternating still frames (e.g., Burt & Sperling, 1981; Anstis, 1980). Perception of apparent motion from stimuli such as the ones used here likely relies on the hypothesized high-level motion system. In particular, in motion perception literature, two different motion systems have been proposed with slight variations (e.g. Anstis, 1980; Braddick, 1980; Sperling, 1989; Seiffert & Cavanagh, 1998): a low-level motion system that extracts energy-based motion signals from the local motion detectors and a high-level motion system that uses feature-based motion signals and attentively tracks an object’s changing location. Such distinction has been shown in the context of apparent motion. For example, patients with right parietal lobe damage show bilateral losses in the perception of apparent motion despite intact low-level motion perception (Battelli et al. 2001). Relatedly, Claeys et al. (2003) reported distinct neural substrates for the two systems with a bilateral higher-level system in the inferior parietal lobule. Therefore, we reasoned that if radial bias affected the perceived direction of apparent motion, it would mean that a low-level visual anisotropy can influence high-level motion processing.

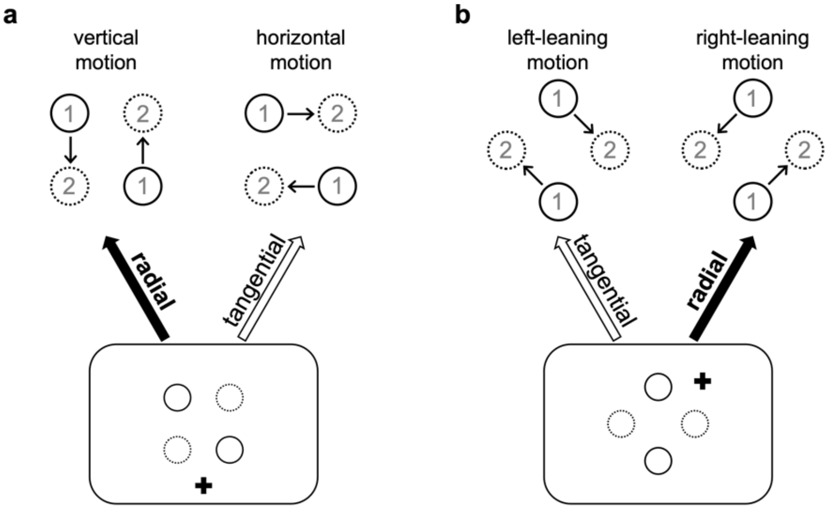

Figure 1. Illustration of how apparent motion is perceived for square (a) and diamond (b) bistable quartets. Each dot pair in a given quartet (marked 1s and 2s) is presented in succession creating bistable apparent motion. **a)** Top: Square quartet and two major perceived motion directions (vertical and horizontal) are depicted. Bottom: As an example, when fixating below the quartet (on the fixation cross), the radial bias account predicts that vertical motion would be perceived more often than horizontal motion, over and above any baseline motion direction bias measured with center fixation. **b)** Top: Diamond quartet and the two major perceived motion directions (left- and right-leaning) are depicted. Bottom: When fixating on the upper right side of the quartet (on the fixation cross), the radial bias account predicts that right-leaning motion would be perceived more often than left-leaning motion, over and above any baseline motion direction bias measured with center fixation.

The perceived direction of apparent motion can become ambiguous if the display has multiple motion paths. In a typical motion quartet (Gengerelli, 1946) complementary pairs of dots are presented in each frame where each dot in a pair appears on the diagonal corners of an imaginary square (see **Fig. 1a**). The perception of moving dots is bistable as the dots on a given presentation can appear to be moving up and down or left or right (**Fig. 1a**). The dot quartet can be rotated such that the dot pairs correspond to the corners of an imaginary diamond (e.g., Anstis & Ramachandran, 1987) (see **Fig. 1b**). In that case, the dots can appear to be moving diagonally in either a left-leaning or right-leaning manner (**Fig. 1b**). Consequently, given its bistable nature, using motion quartets allowed us to probe whether there is a preponderance of apparent motion in radial or tangential directions with respect to fixation (see **Fig. 1** for examples and **Fig. 2a** for all possible fixation locations).

Methods

Participants. Twenty-two Brown University undergraduate students were recruited to participate in the study. All had normal or corrected-to-normal vision. Participants received partial course credit or monetary compensation ($10/hr) for their participation, which lasted approximately one hour. Our sample included 22 participants (17 women, 5 men) between the ages of 18 and 35 years (M = 20.18 years, SD = 3.99). The protocol was approved by the Institutional Review Board at Brown University. Participants gave informed consent and were treated according to the guidelines of the Institutional Review Board.

Stimuli and procedure. Stimuli were presented using a Dell OptiPlex 5090 computer running MATLAB (Version 2015b; MathWorks) and Psychtoolbox (Version 3.0.14; Brainard, 1997; Kleiner, Brainard, & Pelli, 2007; Pelli, 1997). Stimuli were displayed on a Dell P2213 LCD monitor with a refresh rate of 60 Hz and using 1024 x 768 resolution. Visual stimuli were white (42.3 cd/m^2), black (0.27 cd/m^2), or green (31 cd/m^2), presented on a gray (9 cd/m^2) background under slightly dimmed lighting. The viewing distance was about 40 cm.

Each trial began with the fixation dot consisting of a black cross on a white circle with a black outline (fixation diameter: 0.43°) (see **Fig. 2** for details). The fixation could appear in the center of the screen or one of equally spaced eight locations along an imaginary circle with a 9.7° visual angle diameter. In the square block, the polar angle of the peripheral fixation location was 0° (right), 90° (top), 180° (left), or 270° (bottom) (**Fig. 2a,** left). In the diamond block, it was 45° (top-right), 135° (top-left), 225° (bottom-left), or 315° (bottom-right) (**Fig 2a,** right). Because the position of the fixation varied across trials, we briefly presented two green circles around the fixation as a location cue, a large one (cue diameter: 1.88°) for 600 ms followed by a small one (cue diameter: 1.07°) for 600 ms. This allowed participants to easily locate the fixation dot and fixate before the onset of the quartet (see **Fig. 2b**, green circles). The fixation dot alone then remained on the screen for 1000 ms.

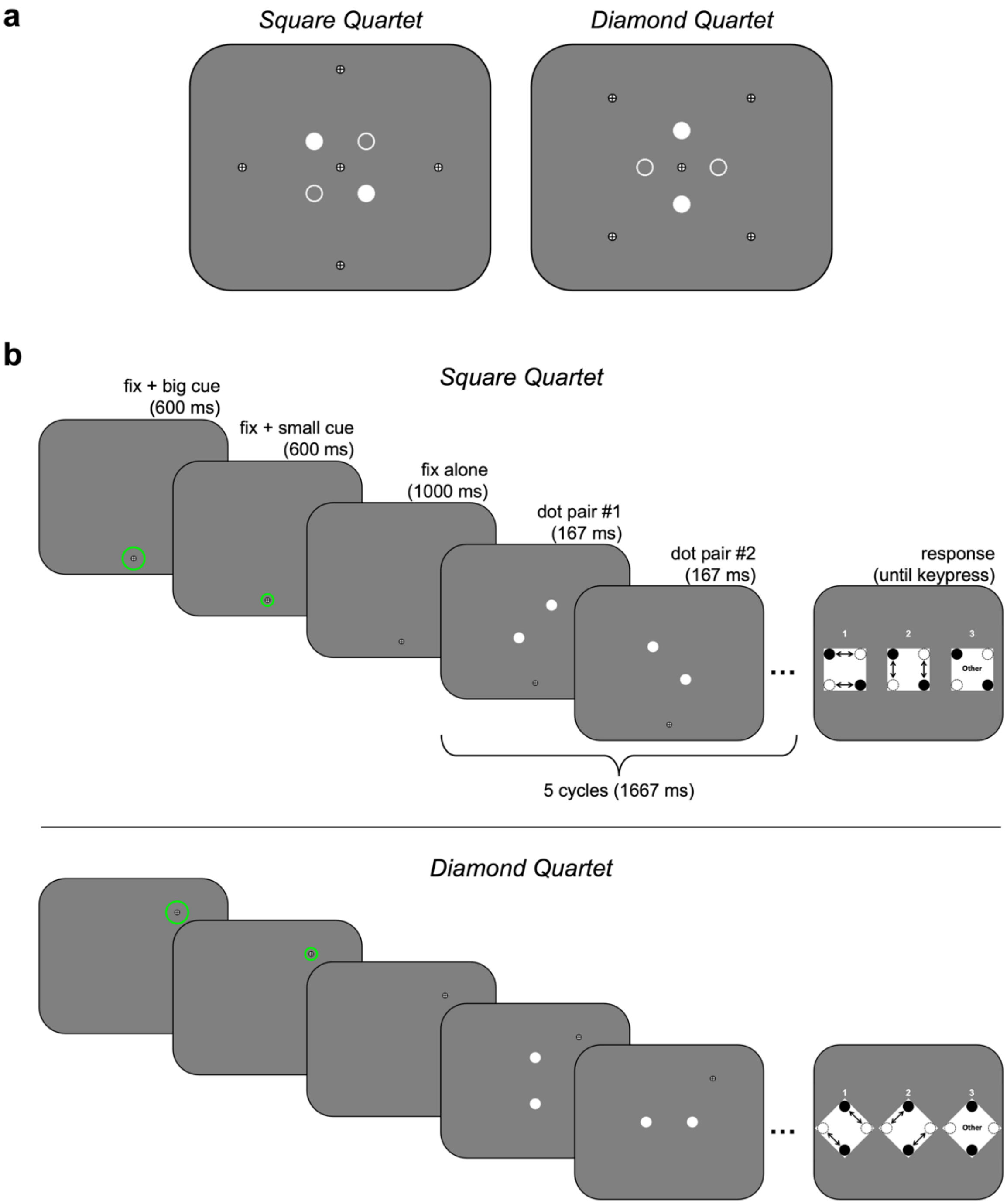

Figure 2. a) All possible fixations, including the center fixation, in square quartet trials (left) and diamond quartet trials (right) with respect to the quartet dots are shown. Filled and empty dots represent the separate pairs of dots presented consecutively that make up the bistable quartet. **b)** Example sequence of trial events in a square quartet trial (top) and a diamond quartet trial (bottom). Each trial began with a fixation dot and cues to aid the quick localization of the fixation, followed by the quartet presentation and the response display. Square and diamond quartets were presented in separate blocks.

Then, we presented the quartet display that consisted of two complementary dot pairs (dot diameter: 0.86°). In the square block, the dot pairs corresponded to the corners of an imaginary square (2.58° by 2.58° square). In the diamond block, the imaginary square was rotated such that the dot pairs corresponded to the corners of an imaginary diamond. In both quartet configurations, each dot pair was presented for ~167 ms (10 frames on a 60Hz monitor). We presented the bistable quartet (consecutive presentation of two dot pairs) for five cycles totaling ~1667 ms.

We then presented the response display which illustrated the two major possible perceived motion directions, and also the “other” option if participants could not perceive either of the major directions. In the square block, the major perceived direction options were horizontal and vertical. In the diamond block, the major perceived direction options were left leaning and right leaning (see **Fig 2b**, response screens). Participants pressed 1 for horizontal or left-leaning direction, 2 for vertical or right-leaning direction, and 3 for “other” on the number pad. Once participants recorded their responses, we presented a dynamic gray-scale noise pattern for 1000 ms and the next trial began.

Participants were instructed to fixate on the fixation dot throughout the quartet presentation. We monitored and recorded participants’ eye positions using an eye tracker (Eyelink-1000 Plus with the Tower Mount) to ensure proper fixation. We also gave online feedback about the accuracy of their fixations.

Participants completed two blocks of trials: one square block and one diamond block. Each block of trials included 14 practice trials followed by 126 experimental trials where each minimum condition cell contained 18 repetitions. Before each block, we presented a demo of the quartet where participants could freely view the quartet and experience bistable motion. We ensured that participants could see the two main motion directions in each quartet by providing aids such as covering opposing dots to disambiguate the motion direction and asking them to hold that direction in mind when viewing the full quartet as well as presenting a line along either motion direction in the center of the quartet to bias the perceived motion direction in either direction.

We intermixed three trial types: center fixation trials, peripheral fixation trials, and center fixation trials with a line across the quartet. In the center fixation trials, participants viewed the quartet display while fixating on the center of it. This served as a control condition as it provided a baseline measure of any existing bias in perceived motion direction per participant per quartet type. In the peripheral fixation trials, we presented the fixation outside of the quartet (location depended on the quartet type, see above). This trial type provided a measure of whether or not there was a preponderance of radial vs. tangential perceived motion direction. Lastly, in the center fixation with line trials, we presented the fixation in the center and also a line across the quartet that was either horizontal or vertical in the square quartet block and 45° or 135° oriented in the diamond quartet block. The details and results of these trials are not discussed here as they do not directly relate to the main question of the paper.

Data analysis. We only analyzed the trials in which participants correctly fixated on the fixation point. We first defined nine interest areas corresponding to all nine possible fixation locations including the center fixation using EyeLink Data Viewer. We then determined for each fixation, the interest area it fell within or it was nearest to during the target presentation. We included trials where participants had fixations that were assigned to the correct interest area (fixation point for a given trial) with a total duration of at least 75% of the length of the target presentation. With this approach, on average we included 94% (Range = 85-100%; SD = 0.04%) of the trials across both blocks. We then separately analyzed data from the square block and diamond block.

In the square block, we computed the proportion of horizontal, vertical, and “other” responses per participant per fixation location (center, 0°, 90°, 180°, and 270°). We then averaged the same meridian fixations to calculate horizontal meridian (0° and 180°) and vertical meridian (90° and 270°) responses. We also calculated a difference score (vertical minus horizontal), ignoring “other” responses. We then tested this difference score measured for the center, horizontal meridian, and vertical meridian fixations against zero using three separate one-sample t-tests.

Similarly, in the diamond block, we computed the proportion of left-leaning, right-leaning, and “other” responses per participant per fixation location (center, 45°, 135°, 225°, and 315°). We then averaged the same meridian fixations to calculate left-leaning meridian (135° and 315°) and right-leaning meridian (45° and 225°) responses. We calculated a difference score (right-leaning minus left-leaning) and tested this difference score measured for the center, left-leaning meridian, and right-leaning meridian fixations against zero using three separate one-sample t-tests.

In both blocks, we planned to follow up any significant differences from zero in peripheral fixation conditions with a comparison against center fixation using a paired sample t-test to ensure that these differences were not simply due to an overall preference for a given motion direction which would be reflected in center fixation.

Results

Square quartet. We had participants fixate along the vertical or the horizontal meridian while viewing a square quartet. As a control condition, we also had participants fixate in the center of the quartet to measure their inherent motion direction bias and account for it in the peripheral fixation trials. This is important for the square quartet because it is well documented that with a square configuration and center fixation, there is already a bias to see vertical motion. This has been attributed to the greater efficiency of intra-hemispheric motion processing compared with inter-hemispheric motion processing (Gengerelli, 1946; Chaudhuri & Glaser, 1991; Genç et al., 2011).

Figure 3a illustrates the proportion of vertical (connected by red dashed line), horizontal (connected by blue dashed line), and "other" (connected by gray dashed line) responses for each fixation location category, which are center fixation, horizontal meridian fixations (combining left and right fixations), and vertical meridian fixations (combining upper and lower fixations). At each fixation category, the sum of the proportion of responses equals 100%. For instance, at center fixation, on average, participants reported seeing vertical in 82% of the trials (red), horizontal in 17% of the trials (blue), and "other" in 1% of the trials (gray). Notably, the relative proportions of vertical and horizontal responses change as a function of fixation, which we elaborate on in **Figure 3b**.

Figure 3b illustrates the extent of direction dominance calculated as a difference score (vertical minus horizontal responses), as a function of center fixation, horizontal meridian fixations, and vertical meridian fixations. This approach ignores the "other" responses and directly measures the relative dominance of horizontal and vertical responses. Here, positive values mean the dominance of vertical over horizontal responses, and negative values mean the dominance of horizontal over vertical responses. Note that for vertical meridian fixations, a positive difference indicates radial bias (see **Fig. 3b**, filled red arrow) while a negative difference indicates tangential bias (see **Fig. 3b**, empty red arrow). For the horizontal meridian fixations, a negative difference indicates radial bias (see **Fig. 3b**, filled blue arrow) while a positive difference indicates tangential bias (see **Fig. 3b**, empty blue arrow). We also plot individual participant data (see the transparent dots in **Fig. 3b**) along with the group means to highlight the distribution of responses.

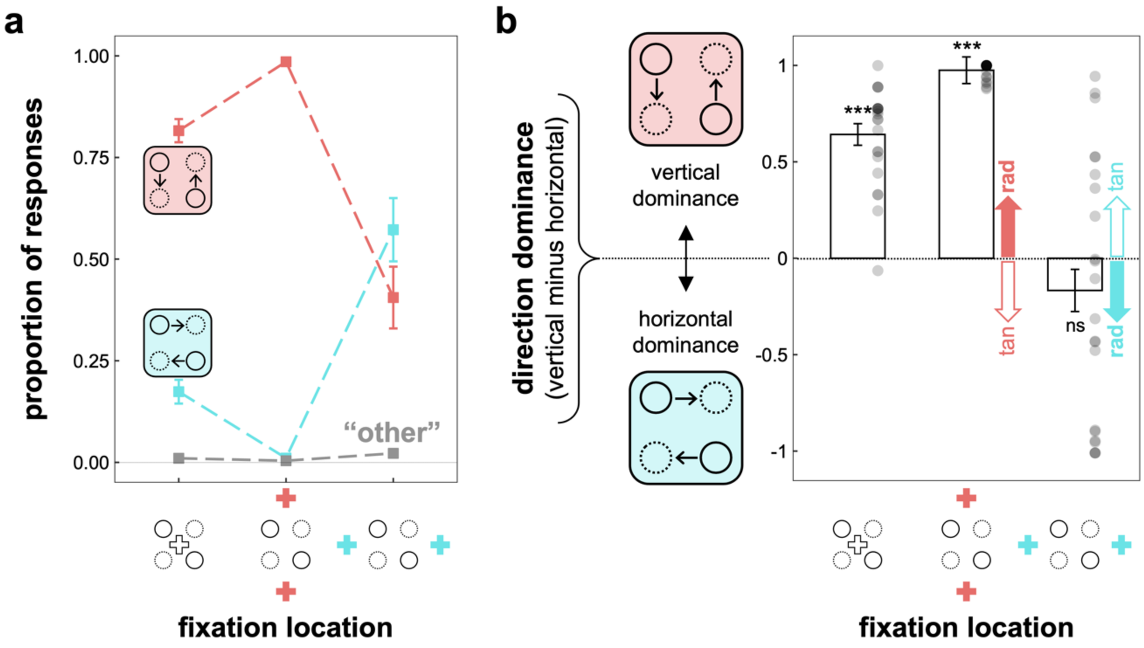

Figure 3. Results from square quartet trials. **a)** Proportions of vertical (red), horizontal (blue), and “other” (gray) responses are plotted as a function of fixation location which are center (white cross) or along the vertical meridian (red crosses) and horizontal meridian (blue crosses). **b)** Direction dominance which is measured as the difference between vertical and horizontal responses is plotted as a function of fixation location (ignoring “other” responses). Bars reflect group mean data; dots reflect individual participant data. Individual data points are drawn with 30% opacity, with darker regions reflecting greater numbers of overlapping data points. The red and blue arrows indicate the relative direction of perceived motion for vertical and horizontal meridian fixations, respectively (rad = radial; tan = tangential). Error bars represent ±1 SEM, adjusted for within-participant comparison (Morey, 2008). *** $p < .0005$.

As can be seen from the figure, in the center fixation trials which are the control condition (see **Fig. 3b**, first bar), participants reported seeing the vertical more often than the horizontal motion direction, $t(21) = 12.73$, $p < .0001$, $d = 2.71$. The vertical motion dominance was robust, with all but one participant showing the effect. As mentioned before, this effect has been previously shown and attributed to the hemisphere effect (Gengerelli, 1946; Chaudhuri & Glaser, 1991; Genç et al., 2011).

In the vertical meridian fixation trials (see **Fig. 3b**, second bar), participants also reported seeing the vertical more often than the horizontal motion direction, $t(21) = 90.48$, $p < .0001$, d

= 19.29. In other words, participants more often reported seeing the radial than tangential motion direction. Notably, the vertical motion dominance with vertical meridian fixations was significantly greater than the vertical motion dominance with center fixation (control), $t(21) = 6.49$, $p < .0001$, $d = 1.38$. This indicates that radial bias measured along the vertical meridian cannot be solely explained by the vertical motion dominance due to the abovementioned hemisphere effect. Nevertheless, the combined effects led to a very strong vertical dominance near ceiling, as indicated by all participants clustering at or near 100%. Gengerelli (1946) also reported a numerically greater vertical dominance when participants fixated below the quartet compared with when they fixated on the center of the quartet, although he did not statistically compare or interpret this difference.

In the horizontal meridian fixation trials (see **Fig. 3b**, third bar), we did not find evidence for dominance of either perceived motion direction, $t(21) = 1.21$, $p = .24$, $d = 0.26$. This null effect was due to greatly distributed data points with some participants showing horizontal dominance, vertical dominance, or neither. Similarly, Gengerelli (1946) reported a lack of evidence for dominance of either direction when participants fixated to the right of the quartet. Individual participant data suggested that this was also due to heterogeneity in the dominance direction instead of a consistent lack of dominance in either direction.

We then examined the potential relationship between difference scores measured at center fixation, vertical meridian fixations, and horizontal meridian fixations using Pearson's correlation. We found a significant positive correlation between difference scores measured at center fixation and vertical meridian fixations, $r(20) = .44$, $p = .042$, as well as between those measured at center fixation and horizontal meridian fixation scores, $r(20) = .44$, $p = .040$. In other words, participants who showed greater vertical motion dominance at center fixation also showed greater vertical motion dominance with vertical meridian fixations and greater vertical motion dominance (or lesser horizontal motion dominance) with horizontal meridian fixations. Although correlational, this finding may suggest that a general dominance of vertical motion may have overshadowed radial bias along the horizontal meridian. The exact reason for such individual differences and thus a lack of evidence of a consistent bias along horizontal meridian requires further investigation.

Diamond quartet. We had participants fixate along the oblique meridians while viewing a diamond quartet. As a control condition, we also had participants fixate in the center of the quartet. Note that using a diamond quartet instead of the typical square quartet eliminates the contribution of the hemisphere effect in motion processing and thus provides a clearer measure of radial bias in our study.

Figure 4a illustrates the proportion of right-leaning (connected by the dashed purple line), left-leaning (connected by the dashed green line), and "other" (connected by the dashed gray line) responses for each fixation location category, which are center fixation, right-leaning meridian fixations (combining upper-right and lower-left fixations), and left-leaning meridian fixations (combining upper-left and lower-right fixations). As before, at each fixation category, the sum of the proportion of responses equals 100%. For instance, at center fixation, on average, participants reported seeing right-leaning motion in 46% of the trials, left-leaning motion in 39% of the trials, and "other" motion in 15% of the trials. Notably, the relative proportions of right-leaning and left-leaning motion responses change as a function of fixation, which we focus on in **Figure 4b**.

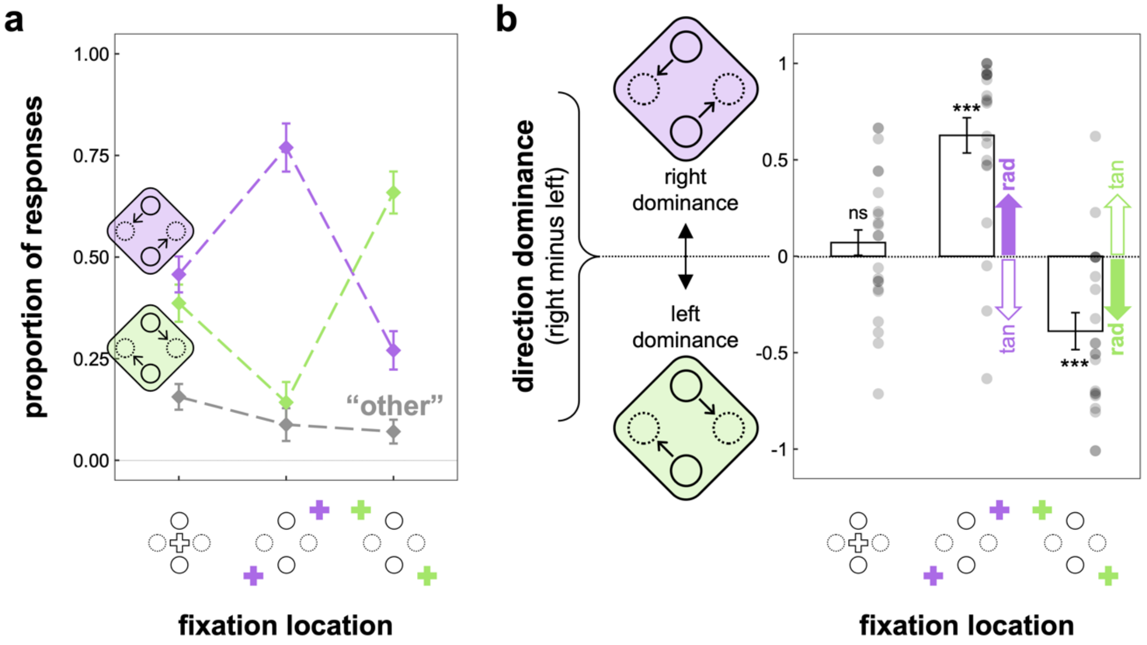

Figure 4. Results from diamond quartet trials. **a)** Proportion of right-leaning (purple), left-leaning (green), and "other" (gray) responses are plotted as a function of fixation location which can be center (white cross) or along the right-leaning meridian (purple crosses) and left-leaning meridian (green crosses). **b)** Difference between right- and left-leaning responses are plotted as a function of fixation location (ignoring "other" responses). Bars reflect group mean data; dots reflect individual participant data. Individual data points are drawn with 30% opacity, with darker regions reflecting greater numbers of overlapping data points. The purple and green arrows indicate the relative direction of perceived motion for right-leaning and left - leaning meridian fixations, respectively (rad = radial; tan = tangential). Error bars represent ±1 SEM, adjusted for within-participant comparison (Morey, 2008). *** *p* < .0005.

Figure 4b illustrates the extent of direction dominance calculated as a difference score (right-leaning minus left-leaning responses) as a function of center fixation, right-leaning meridian fixations, and left-leaning meridian fixations. Positive values mean dominance of right-leaning over left-leaning motion direction and negative values mean dominance of left-leaning over right-leaning motion direction. Note that for right-leaning meridian fixations, a positive difference indicates radial bias (see **Fig. 4b**, filled purple arrow) while a negative difference indicates tangential bias (see **Fig. 4b**, empty purple arrow). For the left-leaning meridian fixations, a negative difference indicates radial bias (see **Fig. 4b**, filled green arrow) while a positive difference indicates tangential bias (see **Fig. 4b**, empty green arrow). We also plot individual participant data (see the transparent dots in **Fig. 4b**) along with the group means to highlight the distribution of responses.

In the center fixation trials, which serve as the control condition (see **Fig. 4b**, first bar), as expected, and unlike the square quartet, we did not find dominance of either direction, $t(21) = 0.89$, $p = .38$, $d = 0.19$. In the right-leaning meridian fixation trials (see **Fig. 4b**, second bar), participants reported seeing the right-leaning more often than the left-leaning motion direction, $t(21) = 6.57$, $p < .0001$, $d = 1.40$. In the left-leaning meridian fixation trials (see **Fig. 4b**, third bar), participants reported seeing the left-leaning more often than the right-leaning motion direction, $t(21) = 4.52$, $p = .0002$, $d = 0.96$. These results indicate that participants more often reported seeing the radial than tangential motion directions along both meridians.

We also examined the potential relationship between difference scores measured at center fixation, right-leaning meridian fixations, and left-leaning meridian fixations using Pearson's correlation. Unlike the square quartet and as expected, difference scores at center fixation did not significantly correlate with difference scores at right-leaning meridian fixations, $r(20) = .31$, $p = .16$, or left-leaning meridian fixations, $r(20) = .13$, $p = .57$. In other words, any dominance measured at center fixation was not related to the dominance measured at peripheral fixations.

Overall, we found evidence for robust radial bias for motion direction along all meridians except for the horizontal meridian, controlling for existing motion direction bias measured with center fixation when necessary. These results demonstrate that the visual systems' preference for radial motion directions can be manifested as the dominance of radial apparent motion in bistable motion displays.

Discussion

In the current study, we found that when viewing an extrafoveally presented bistable apparent motion quartet, participants were biased to see radial motion with respect to their fixation.

The visual system has various visual field and orientation anisotropies. For instance, visual performance is better along the horizontal than the vertical meridian, and in the lower than the upper visual field (e.g., Mackeben, 1999; Altpeter, Mackeben, & Trauzettel-Klosinski, 2000; Carrasco, Talgar, & Cameron, 2001; Barbot, Xue, & Carrasco, 2021). Visual performance is also better for stimuli with cardinal than with oblique orientations (e.g. Appelle,1972; Girshick, Landy, & Simoncelli, 2011). More directly related to our study, the visual system also prefers radial over tangential orientations (e.g. Leventhal & Schall, 1983; Westheimer 2003; Sasaki et al., 2006; Ling et al., 2015; Mannion et al., 2010) as well as motion directions (e.g. Albright, 1989; Rauschecker et al., 1987; Steinmetz et al., 1987; Xiao et al., 2006; Clifford et al., 2009; Hong 2015).

Prior studies have used simple visual stimuli such as static and moving sine gratings to establish radial bias for orientation and motion direction, respectively. We recently observed an illusion where radial bias altered the population coding of simple shapes thereby wrongly shifting the perceived orientation of an object toward radial (Menceloglu et al., 2022). Here, we have also extended the preference for radial real motion direction by showing that radial bias can alter the perceived direction of apparent motion stimulus that does not contain low-level motion signals. Taken together, these findings demonstrate the robust influence of low-level anisotropies on high-level perception.

How is radial bias for motion direction related to radial bias for orientation? It has been argued that the two forms of radial bias may reflect a common underlying anisotropy in the visual field (e.g. Clifford et al., 2009; Hong, 2015). Specifically, radial bias for motion direction may stem from radial bias for orientation of static stimuli when considering the role of “motion streaks” in fast motion and relatedly, the populations of neurons that show common selectivity of orientation and motion direction in fast motion processing (Geisler, 1999). When a visual stimulus moves fast enough it is proposed that it becomes smeared in space due to temporal integration and creates a “motion streak”. This spatial signal that is oriented in the direction of the motion is then used by the visual system to improve the precision of the encoding of motion direction (Geisler, 1999). Thus, streaky fast motion should produce a maximal response in the population of neurons with preferred orientation that is parallel to the direction of motion. As predicted, Geisler et al. (2001) found that many orientation-selective neurons in the V1 of macaque monkeys were also direction selective for parallel motion. Using moving spots as motion stimuli, they found that the cells' response shifted as motion speed increased such that for fast speeds, cells responded more strongly to motion parallel to their preferred orientation. Further support for separate slow and fast motion processing systems, comes from studies reporting orientation-selective suppression in binocular rivalry (Apthorp et al., 2009) and successful decoding in the early visual cortex of the direction of fast but not slow motion after training with oriented static stimuli (Apthorp et al., 2013).

How can radial bias for direction of real motion that contains actual changes in energy along the path of motion alter the perceived direction of apparent motion? In our experiment, we used apparent motion with an inferred speed that was well above the minimum speed (of real motion) that is thought to be processed by fast motion detectors (Geisler, 1999; Burr, 2000). Thus one may assume that apparent motion stimuli used in the current study stimulate fast motion detectors which would show radial bias. Indeed, apparent motion can activate overlapping visual areas as real motion. Monkey neurophysiology studies have revealed that direction-selective cells in V1 and MT contribute to apparent motion perception (Mikami et al., 1986a, 1986b; Newsome et al., 1986), with MT cells being the more prominent contributors as they support apparent motion perception for a wider range of speeds and distances. Human fMRI studies have shown neural activation in early visual areas as well as MT+ (the human motion complex) along the path of real motion and apparent motion against control stimuli such as flicker (e.g., Goebel et al., 1998; Liu et al., 2004; Muckli et al., 2005). Further, evidence for the neural representation of perceptual “filling-in” (Yantis & Nakama, 1998) of intermediate steps in apparent motion was observed in V1 (Chong et al., 2015; Larsen et al., 2006), MT+ (Muckli et al., 2002; Liu et al., 2004) and the lateral occipital complex involved in object processing (Liu et al., 2004). Sterzer et al. (2006) later showed that the activations of V1 representing the motion path reflected feedback from MT+ and emphasized the potential role of V1 in generating dynamic object representations based on motion through feedback signals. Overall, given the overlap between the neural activation by real and apparent motion, the neural mechanisms responsible for radial bias observed for real motion are likely driving the same bias for apparent motion.

Here, we tested radial bias for motion direction along the cardinal meridians and 45° oblique meridians. We found consistent radial motion dominance along all meridians except for the horizontal meridian. This result is in line with our recent findings where radial bias altered perceived object orientation along the vertical and oblique meridians but not along the horizontal meridian (Menceloglu et al., 2022). This was related to the greater perceptual sensitivity along the horizontal meridian and also for the vertically oriented object (Landolt C) as reflected by overall smaller errors for both conditions independently. In the current study, we observed that a general vertical motion dominance might be the reason behind the lack of radial bias for motion along the horizontal meridian.

As previously mentioned, it has already been demonstrated that vertical motion is seen more often than horizontal motion when viewing a square quartet with center fixation. This is explained by the perception of vertical motion requiring only intra-hemispheric processing while the perception of horizontal motion requiring integration across hemispheres (inter-hemispheric), which is less efficient (Gengerelli, 1946; Chaudhuri & Glaser, 1991; Genç et al., 2011). Chaudhuri & Glaser (1991) reported that for a square quartet to yield equivalent vertical and horizontal motion judgments, the vertical displacement of the dots needed to be greater than the horizontal displacement and that the ratio (parity ratio) varied among observers. Using diffusion tensor imaging, Genç et al. (2011) further demonstrated that an observer’s parity ratio correlated with the properties of fibers of their corpus callosum segments connecting MT+ of the two hemispheres. This was interpreted as larger-diameter axons in the corpus callosum connecting the hemispheres allowing for faster conduction velocities, and thus leading to less vertical dominance.

While the hemisphere effect explains the vertical dominance with center fixation in our data, it does not explain the lack of consistent radial bias along the horizontal meridian, or in other words, the persistence of vertical dominance with horizontal fixation in which perception of both horizontal and vertical motion requires only intra-hemispheric processing. Thus, understanding why some people see vertical more often than horizontal motion direction independently of the hemisphere effect needs further investigation.

In conclusion, we have demonstrated that when apparent motion signals are bistable such that both radial and tangential perceived motion directions are possible, observers are biased to see radial motion. The visual system’s increased sensitivity to radial orientations and, likely relatedly, to radial motion directions appears to be the substrate for this phenomenon. These results are another demonstration of the pervasive structural influences throughout the visual system and its highly interconnected nature.

Open practices statement. Materials and raw data for the experiments reported here are available online at https://osf.io/wpqhz. The experiments were not preregistered.

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