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Keywords

Redundancy masking, visual field asymmetries, peripheral vision, crowding, regularity perception, spatial compression

Author Contributions

B.S., D.R.C., and F.Z.Y. designed the study and prepared the manuscript. F.Z.Y. collected and analyzed the data and prepared the figures. All authors interpreted the data and reviewed the manuscript.

Competing interests

The authors declare no competing interests.

Abstract

Redundancy masking is the reduction of the perceived number of items in repeating patterns. It shares a number of characteristics with crowding, the impairment of target identification in visual clutter. Crowding strongly depends on the location of the target in the visual field. For example, it is stronger in the upper compared to the lower visual field, and usually weakest on the horizontal meridian. This pattern of visual field asymmetries is common in spatial vision, as revealed by tasks measuring, e.g., spatial resolution and contrast sensitivity. Here, to characterize redundancy masking and reveal its similarities and differences to other spatial tasks, we investigated whether redundancy masking shows the same typical visual field asymmetries. Observers were presented with three to six radially arranged lines at 10° eccentricity at one of eight locations around fixation and were asked to report the number of lines. We found asymmetries that differed pronouncedly from those found in crowding. Redundancy masking did not differ between upper and lower visual fields. Importantly, redundancy masking was stronger on the horizontal meridian than on the vertical meridian, the opposite of what is usually found in crowding. These results show that redundancy masking diverges from crowding in regard to visual field asymmetries, suggesting different underlying mechanisms of redundancy masking and crowding. We suggest that the observed atypical visual field asymmetries in redundancy masking are due to the superior extraction of regularity and a more pronounced compression of visual space on the horizontal compared to the vertical meridian.

Keywords

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Introduction

In redundancy masking (RM), the perceived number of identical items is reduced (Sayim & Taylor, 2019; Taylor & Sayim, 2018; 2020; Yildirim, Coates, & Sayim, 2020, 2021). For example, when presented with three identical, nearby letters in the visual periphery, observers frequently reported only two letters (in a free naming and drawing task; Sayim & Taylor, 2019; Figure 1a). Recently, several characteristics of RM have been revealed (Yildirim et al., 2020, 2021). RM shows a pronounced radial-tangential anisotropy: when items were arranged radially relative to fixation, there was strong RM; when they were arranged tangentially, there was no RM (Yildirim et al., 2020). RM has also been shown to depend on the spacing between items: Larger spacing between items decreased RM compared to smaller spacings (Yildirim et al., 2020). Also, size affected the strength of RM: Increasing the width of items decreased RM (Yildirim et al., 2020). Importantly, the strength of RM strongly depended on the spatial regularity of the stimulus. Varying the regularity of peripherally presented line arrays by vertically or horizontally jittering the positions of the lines, it was found that there was strong RM with items that were arranged regularly and no RM with items that were arranged irregularly (Yildirim et al., 2020). A similar dependence on regularity was observed when observers indicated the number of tilted lines, with strong RM when all (three) lines were tilted in the same direction and no RM when one of the lines was tilted in the opposite direction (Rummens & Sayim, in revision).

RM seems to be one way the visual system copes with large amounts of information: redundant information in regular, repeating patterns is discarded and does not enter conscious awareness (see also Brady, Konkle, & Alvarez, 2009). However, the underlying mechanisms of RM are still unknown. A recent finding suggests that RM is linked to compressions of visual space (Yildirim, Coates, & Sayim, 2019).

Observers were asked to indicate the number of lines, and judge the spacing between the outermost lines (i.e., the overall horizontal extent of the entire line array) or - in a different experiment - the spacing between adjacent lines (alternative choices from varying spacings) (Yildirim, Coates, & Sayim, 2019). We found that in trials in which RM occurred (in particular when 3 lines were presented and 2 reported), but not in trials in which no RM occurred (3 lines presented, 3 reported), observers reported a smaller overall extent and a larger spacing between adjacent lines compared to the correct extent. Investigating the perceived centroid of the line arrays, we found further evidence for a compression of space, and the loss of the central (of three) lines in RM: Observers accurately reported the location of a probe relative to the centroid of the line array in both RM and no RM trials (if the perceived location of the probe deviated from the correct centroid of the line array in RM trials, it would suggest that an outer line, rather than a central line (especially when three lines were presented), was lost due to RM). These results suggest that RM goes hand in hand with compressions of peripheral visual space (Yildirim et al., 2019). Irrespective of the compression of visual space, RM could be due to insufficient attentional resolution in peripheral vision similar to what was proposed for crowding, the impairment of object recognition in clutter (Figure 1a) (Chakravarthi & Cavanagh, 2007; He, Cavanagh, & Intriligator, 1996, 1997; Intriligator & Cavanagh, 2001). In attentionally demanding tasks, such as crowded target discrimination, superior performance was found in the lower compared to the upper visual field. This asymmetry was attributed to higher attentional resolution in the lower than the upper visual field (He et al., 1996). Limits of attentional resolution might well underlie RM. If that was the case one would expect a similar upper/lower visual field asymmetry as in crowding.

RM is related to crowding (Bouma, 1970, 1973; Herzog, Sayim, Chicherov, & Manassi, 2015; Levi, 2008; Melnik, Coates, & Sayim, 2018, 2020; Pelli, Palomares, & Majaj, 2004; Rummens & Sayim, 2019; 2021; Sayim & Cavanagh, 2013; Sayim, Greenwood, & Cavanagh, 2014; Strasburger, Harvey, & Rentschler, 1991; Strasburger, 2020; Whitney & Levi, 2011). A loss of information possibly related to RM, such as the omissions or truncations of elements (Sayim & Wagemans, 2017) was shown in a number of recent crowding studies (Coates, Wagemans, & Sayim, 2017; Coates, Bernard, & Chung, 2019; Sayim & Wagemans, 2017; see also Korte, 1923). For example, using a gaze-contingent peripheral presentation and appearance capture (drawing) paradigm, frequent omissions and truncations of elements in letter and letter-like targets indicated target diminishment in crowding (Sayim & Wagemans, 2017). Similar results – possibly due to 'self-crowding' (Martelli, Majaj, & Pelli, 2005; Zhang, Zhang, Liu, & Yu, 2009) - were found with complex, peripherally presented letters and letter-like shapes in isolation (Melnik, Coates, & Sayim, 2021). The investigation of errors in peripherally presented lower-case letter trigrams revealed a similar pattern of diminishment in crowding: Letter features appearing in both a flanking letter and the target letter (such as an ascender or descender) were often omitted in the reported target (Coates et al., 2019). Common characteristics of RM and crowding include radial-tangential anisotropies (Greenwood, Szinte, Sayim, & Cavanagh, 2017; Petrov & Meleshkevich, 2011a; Toet & Levi, 1992; Yildirim et al., 2020), a reduction of interference with increasing spacing between items (Bouma, 1970; Levi, Hariharan, & Klein, 2002; Pelli et al., 2004; Strasburger et al., 1991; Yildirim et al., 2020), and a dependence on spatial regularity (Manassi, Sayim, & Herzog, 2012; Saarela, Westheimer, & Herzog, 2010; Sayim, Westheimer, & Herzog, 2011; Yildirim et al., 2020). In addition to the radial-tangential anisotropy, crowding has been shown to be subject to a number of other asymmetries. For example, flankers on the outer (peripheral) side of the target yield more crowding than flankers on the inner (central) side, the 'inner-outer asymmetry' of crowding (Banks, Bachrach, & Larson, 1977; Petrov & Meleshkevich, 2011a, 2011b; Shechter & Yashar, 2021). Importantly, the strength of crowding is asymmetric across isoeccentric locations in the visual field. Specifically, at a fixed eccentricity, crowding is stronger in the upper compared to the lower visual field (i.e., vertical meridian asymmetry: VMA) (Fortenbaugh, Silver, & Robertson, 2015; Greenwood et al., 2017; He et al., 1996; Intriligator & Cavanagh, 2001), and usually weaker on the horizontal meridian compared to the vertical meridian (i.e., horizontal-vertical asymmetry: HVA) (Greenwood et al., 2017; Nazir, 1992). This pattern of visual field asymmetries (Figure 1b) is common in vision, and has been found for spatial resolution (Altpeter, Mackeben, & Trauzettel-Klosinski, 2000; Barbot, Xue, & Carrasco, 2021; Greenwood et al., 2017; Nazir, 1992), contrast sensitivity (Abrams, Nizam, & Carrasco, 2012; Cameron, Tai, & Carrasco, 2002; Carrasco, Talgar, & Cameron, 2001), motion (Fuller & Carrasco, 2009; Lakha & Humphreys, 2005), hue (Levine & McAnany, 2005), saccadic precision and spatial localization (Greenwood et al., 2017), saccadic latency (Greene, Brown, & Dauphin, 2014; Greenwood et al., 2017; Petrova & Wentura, 2012) and texture segmentation (Talgar & Carrasco, 2002). Not all tasks, however, show all of the typical anisotropies. For example, performance in a three-dot bisection task was better in the lower than upper visual field, but not different between horizontal and vertical meridians (Greenwood et al., 2017). Performance in vernier acuity for horizontally and vertically aligned target lines seemed not to differ between horizontal and vertical meridians (Westheimer, 2005). Here, we investigated whether RM shows the same typical visual field asymmetries as several related phenomena.

We presented three to six radially arranged lines at one of the eight locations at 10° eccentricity around fixation (in cardinal and inter-cardinal directions), and asked observers to report the number of lines. We found asymmetries that differ pronouncedly from those found in most spatial tasks. RM did not differ between the upper and lower visual fields (i.e., no VMA). We did find a strong horizontal-vertical asymmetry (HVA), however, in the opposite direction of what is usually found: RM was stronger on the horizontal meridian than on the vertical meridian. Our results show atypical visual field asymmetries in RM. Although related to crowding, these results suggest that RM and crowding have different underlying mechanisms. We suggest that different sensitivities for the extraction of regularity on the vertical and horizontal meridian, and stronger compression of visual space on the horizontal than vertical meridian underlie the observed pattern of results.

Methods

Participants

19 students (age range: 19-47 years, seven male) from the University of Bern participated in the experiment in exchange for course credit or on a voluntary basis. All observers reported normal or corrected-to-normal visual acuity. Observers were naïve regarding the aim of the study. Before the experiment, participants signed a consent form and were informed about the general procedure. The experimental protocols were approved by the local ethics committee at the University of Bern. All procedures were in accordance with the Declaration of Helsinki.

Stimuli and Procedure

Stimuli were generated with Psychopy v2.7.11 (Peirce, 2007) and displayed on a 22" CRT monitor with a resolution of 1152 × 864 and a refresh rate of 110 Hz. The experiment was conducted in a dimly illuminated room. Observers viewed the monitor from a distance of 57 cm, and were supported by a chin and head rest. A black disc (diameter=0.2°; 2 cd/m^2) at the center of the screen served as a fixation point throughout the experiment. Stimuli consisted of black (1 cd/m^2) lines that were 1° in length and 0.04° in width, presented on a uniform grey background (42 cd/m^2). The number of presented lines ranged from three to six (Figure 2a). The center-to-center spacing between adjacent lines within a line array was identical, but varied randomly across trials to preclude the use of spacing and overall extent as cues (see example stimuli in Figure 2a). The center-to-center spacing was 0.42°, 0.57°, or 0.85° yielding a maximum extent of the line array of 2.1º, 2.85º, or 4.25º, respectively (when six lines were presented). The lines were arranged radially with respect to fovea, and presented at one of eight cardinal (i.e., left, right, upper, lower) and inter-cardinal (i.e., upper-left, upper-right, lower-left, lower-right) directions (Figure 2b). In total there were 96 (four numbers of lines x three spacings x eight locations) stimulus conditions. The line array was centered at 10° eccentricity. The position of the line array was slightly varied at random across trials (centered at 10º or jittered 0.07° either up, down, left or right).

Figure 2c illustrates a schematic depiction of the procedure. At the beginning of the experiment, the fixation disc was presented for 1 s. Observers were instructed to keep fixating on the center. Next, a stimulus was presented for 145 ms at one of eight target locations. Observers were required to indicate the number of lines they perceived with a key press on the number pad (0-9). Observers were not informed about the range of the number of presented lines. Response time was unconstrained. The next trial began 454 ms after the response. The stimulus location (eight locations), the number of lines (three to six), and the spacing (0.42°, 0.57°, and 0.85°) were randomized within each block. Observers completed 48 blocks with 80 trials (40 trials for each stimulus condition) with self-paced breaks taken between blocks.

Before the experiment, for each participant we verified that the spacing between adjacent lines was above their resolution limit. A two-line discrimination task was performed at the farthest eccentricities of lines in the main experiment (11.7°, when six lines were presented): one or two lines with varying spacings (0.42°, 0.57°, and 0.85°) were presented at the eight locations of the main experiment. Observers were presented with one line in half of the trials, and two lines in the other half. There were 480 trials in total (eight locations x three spacings x ten trials = 240 trials for each number of lines). Participants were asked to indicate whether they perceived one or two lines. Performance was equal to - or above - 95% correct in the majority of trials (87% of the trials; and above 80% correct in the remaining 13% of the trials).

Analysis

To assess the strength of RM, deviation scores were calculated by subtracting the correct number of lines from the reported number of lines (Yildirim et al., 2020). Hence, if the number of lines reported was the same as the number of lines presented, the deviation score was zero; reporting more lines than presented yielded scores above zero; and reporting fewer lines than presented yielded scores below zero. When discussing the magnitudes of deviation scores, we refer to absolute values throughout the manuscript (most deviation scores were negative).

All statistical analyses were performed in R Studio (version 1.2.5033) running the R software package (version 3.6). The deviation scores were analyzed by a generalized linear mixed-effects model using the glmmTMB package (Brooks, Kristensen, Benthem, Magnusson, Berg, Nielsen, Skaug, Machler, & Bolker, 2017). The number of lines presented, the location of the lines, and the spacing conditions were specified as fixed effects, and subject as a random effect. Predicted values were calculated with the ggpredict function of the ggeffects package (Lüdecke, 2018). The marginal (R^2_m) and conditional (R^2_c) pseudo *R* squared statistics were computed to quantify goodness-of-fit using the r.squaredGLMM() function from the MuMIn package (Barton & Barton, 2015; Johnson, 2014). R^2_m represents the variance explained by fixed effects and R^2_c the variance explained by both fixed and random effects. Assumptions underlying the models were checked with diagnostic plots of residuals using the DHARMa package (Hartig, 2017). Analysis of Deviance Tables (using Type II Wald Chi-Square tests) for the model were calculated using the car package. For significant effects with $p < 0.05$, planned post hoc comparisons were performed with Tukey P adjustment using the emmeans package. Contrasts with $p < 0.05$ were considered as significant (corrected p values are reported).

A second-degree polynomial regression was used to fit the deviation scores on the number of lines presented ($R^2_m = 0.17$; $R^2_c = 0.82$). The random effect structure contained random slopes and random intercepts for each subject. The strength of RM varied considerably between observers (but the overall pattern of results was similar across observers, Supplementary Figure 4).

To assess the variability of observers' responses, we calculated the standard deviations (SD) of observers' responses for each stimulus location, spacing condition, and number of lines. A three-way repeated measures ANOVA with the factors location, spacing, and number of lines was performed on the SDs of observers' responses. A model without interaction effects was used as the interaction effects were not significant (number of lines and location, $f(21) = 0.81$, $p = .71$; number of lines and spacing, $f(6) = 0.28$, $p = .95$; location and spacing, $f(14) = 0.25$, $p = .99$; number of lines, location, and spacing, $f(42) = 0.17$, $p = 1.0$). ANOVA Tables (using Type II tests) for the model were calculated using the car package. For significant effects with $p < 0.05$, planned post hoc comparisons were performed with Tukey P adjustment using the emmeans package. Contrasts with $p < 0.05$ were considered as significant (corrected p values are reported).

Results

Mean deviation scores are shown as a function of visual field location in Figure 3. The eight points at cardinal and inter-cardinal directions on the polar plots correspond to the eight target locations. Mean deviation scores ranged between -0.74 (±*SE* 0.12) (strong RM; right horizontal meridian, 6 lines) and 0.1 (±*SE* 0.12) (no RM, reporting on average more lines than presented; lower-left location, 4 lines), with clear differences between the different locations. Overall, deviation score magnitudes were larger (i.e., RM was stronger) on the horizontal meridian (left and right visual field) than any other locations (note that 'magnitude' refers to absolute deviation scores; nearly all average deviation scores were negative). We refer to this effect as ‘reverse horizontal-vertical meridian asymmetry’ (rHVA; apparent in the vertically-elongated and horizontally-compressed patterns in Figure 3). We found a significant main effect of location ($\chi 2(7) = 749.11$, $p < .0001$). Figure 3a shows mean deviation scores averaged over all numbers of lines and spacings as a function of location. Comparisons between each two locations showed that deviation score magnitudes were significantly larger (RM stronger) on the horizontal meridian (left: -0.53±0.10; right: -0.59±0.10; with no differences between the left and right horizontal meridians (HMA)) than at any other location (Supplementary Table 1a). Deviation scores magnitudes were smaller (but still slightly negative) at the lower-left location (-0.097±0.10) compared to all other locations (except for the lower-right location (-0.17±0.10); Supplementary Table 1a).

We found significant two-way interactions between location and number of lines ($\chi 2(14) = 41.86$, $p < 0.001$) and location and spacing ($\chi 2(14) = 110.1$, $p < .0001$). There was no two-way interaction between number of lines and spacing ($\chi 2(4) = 2.98$, $p = 0.56$), and no three-way interaction between number of lines, location, and spacing ($\chi 2(28) = 20.44$, $p = 0.85$). Importantly, significant interactions did not undermine the main effect of location (i.e., rHVA), which holds at nearly all levels of number of lines and spacing (see below). Figure 3b shows the interaction between location and number of lines with mean deviation scores averaged over all spacings. Comparisons between each two locations performed separately for each number of lines showed that the deviation score magnitudes were larger on the horizontal meridian compared to any other location (for all numbers of lines). Figure 3c shows the interaction between location and spacing with mean deviation scores averaged over all numbers of lines. Comparisons between each two locations performed separately for each spacing condition showed that the deviation score magnitudes were larger on the horizontal meridian than at any other location for each spacing (with the exception that there was no difference between the left and the upper location at the largest spacing). These results showed that although visual field location interacted with number of lines and spacing, its main effect, i.e., rHVA, holds at nearly all levels of number of lines and spacing.

We also found significant main effects of the number of lines ($\chi2(2) = 48.07$, $p < .0001$) and spacing ($\chi2(2) = 35.99$, $p < .0001$). Comparisons between each two numbers of lines showed that the deviation score magnitudes were larger for 3 lines (-0.37±0.096) compared to 4 lines (-0.13±0.11), and 6 lines (-0.47±0.12) compared to 4 (-0.13±0.11) and 5 lines (-0.16±0.12) (Supplementary Figure 1a and Supplementary Table 1b). This pattern of deviation scores (larger at the endpoints of the number range, and smaller at the midrange) is consistent with our previous findings (Yildirim et al., 2020). Comparisons between each two spacings showed that the deviation score magnitudes were smaller with the smallest spacing 0.42° (-0.16±0.11) than the other two spacings 0.57° (-0.31±0.10) and 0.85° (-0.38±0.09) (Supplementary Figure 1b and Supplementary Table 1c). These results replicated a trend we found in a previous study where small spacing tended to be associated with slightly weaker RM (Yildirim et al., 2020), possibly because observers used density cues (e.g., Dakin, Greenwood, Kingdom, & Morgan, 2011), and therefore reported larger numbers than with intermediate spacings (at spacings larger than 2.5° at 10° eccentricity, RM ceased, Yildirim et al., 2020).

Figure 4 shows the mean deviation scores separately for each number, location, and spacing condition. The deviation scores ranged between -0.83 (±0.09; right horizontal meridian, 6 lines) and 0.28 (±0.16; upper vertical meridian, 5 lines). The pattern of results reported above (i.e., different RM with different numbers of lines and different spacings), including the main effect of location, is apparent for the different numbers of lines and spacings: Deviation score magnitudes were larger on the horizontal meridian than at all other locations for each number of lines presented and all spacings.

Figure 5 shows summary plots for the (a)symmetries we found (i.e., VMA, HMA, HVA, vertical vs. diagonal meridians, and horizontal vs. diagonal meridians). Deviation scores were averaged over visual field locations and plotted for two different dimensions in each subplot. For example, for the “Horizontal vs. Vertical (HVA)” subplot, the deviation scores of left and right locations vs. lower and upper locations were plotted (illustrating the horizontal vs. vertical asymmetry (HVA)). Deviation of at least one standard error away from the diagonal were considered asymmetries. Asymmetries occurred only for “Horizontal vs. Vertical (HVA)” and “Horizontal vs. Diagonal” comparisons. RM was stronger on the horizontal compared to the vertical and on the horizontal compared to the diagonal meridians. There were no asymmetries between lower vs. upper locations, right vs. left locations, and vertical vs. diagonal meridians.

To assess the ambiguity of observers’ percepts at each location, we analyzed the variability of responses by calculating the mean standard deviations (SD; Supplementary Figure 2). There was a main effect of location ($f(7) = 7.52$, $p < .0001$). Comparisons between each pair of locations showed that SDs for the horizontal meridian were lower than SDs for all other locations (Supplementary Table 2a). There was also a main effect of the number of lines ($f(3) = 21.09$, $p < .0001$). Comparisons between each two numbers of lines showed that the SD for 3 lines was lower than the SDs for 4, 5, and 6 lines (Supplementary Table 2b). Lastly, there was a main effect of spacing ($f(2) = 14.36$, $p < .0001$). Comparisons between each two spacings showed that SD for 0.42° spacing was higher than SDs for 0.57° and 0.85° spacings, and SD for 0.57° spacing was higher than SD for 0.85° spacing (Supplementary Table 2c).

Taken together, these results show that RM was stronger (i.e., deviation score magnitudes were larger) and responses were less varied (i.e., SDs were lower) on the horizontal meridian than the other locations.

Discussion

We investigated whether RM was subject to typical visual field asymmetries. Our results showed that visual field dependencies in RM clearly differed from those in most other visual tasks. RM was stronger on the horizontal meridian than at any other of the tested locations, including the vertical meridian. Hence, we found the opposite of what is typically observed - a “reverse horizontal-vertical asymmetry”. There was also no upper/lower visual field asymmetry: on the vertical meridian, RM was equally strong in the lower and the upper visual field. This pattern of visual field asymmetries suggests that the underlying mechanisms of RM diverge from those of related spatial tasks, including crowding.

The typical visual field asymmetries - superior performance on the horizontal than on the vertical meridian (HVA), on the lower vertical than on the upper vertical meridian (VMA), on the right horizontal than on the left horizontal meridian (HMA), and intermediate performance on the intercardinal locations - are well documented for a variety of visual tasks. For example, spatial resolution (e.g., Altpeter et al., 2000; Wertheim, 1894), contrast sensitivity (e.g., Cameron et al., 2002), and spatial localization (e.g., Carrasco et al., 2001) were all shown to be better on the horizontal than on the vertical meridian (HVA), and on the lower vertical than on the upper vertical meridian (VMA). Word and letter recognition were shown to be better on the right horizontal than on the left horizontal meridian (e.g., Hagenbeek, & Van Strien, 2002; Worrall & Coles, 1976; Simola, Holmqvist, & Lindgren, 2009). Performance in orientation discrimination, detection, spatial localization, and contrast sensitivity tasks on the intercardinal locations (upper-right, upper-left, lower-right, and lower-left) was shown to be in between the horizontal and the vertical meridians (Carrasco et al., 2001; Cameron et al., 2002; Carrasco, Giordano, & McElree, 2004). Also for crowding, which shares a number of characteristics with RM, the same typical asymmetries have been reported (Greenwood et al., 2017; He et al., 1996; Kurzawski, Burchell, Thapa, Majaj, Winawer, & Pelli, 2021; Nazir, 1992; Petrov & Meleshkevich, 2011a). For example, crowding zones have been shown to be smaller, that is, flankers interfered over smaller distances with target perception, on the horizontal than on the vertical meridian (Greenwood et al., 2017; Kurzawski et al., 2021), on the lower vertical than on the upper vertical meridians (Greenwood et al., 2017; Kurzawski et al., 2021; Petrov & Meleshkevich, 2011a), and on the right horizontal than on the left horizontal meridians (Greenwood et al., 2017; Kurzawski et al., 2021). Thus, our results diverge from typical visual field asymmetries (Altpeter et al., 2000; Barbot et al., 2021; Carrasco et al., 2001; Mackeben, 1999).

The effects of RM are most evident when observers do not have to estimate or count the number of items but can subitize them (or see them at a glance; Mandler & Shebo, 1982), i.e., when only very few items (3-4) are presented (Yildirim et al., 2020, 2021). Here, when three lines were presented, deviation scores were -0.56 (±0.08) on the horizontal meridian (with no difference between the left and right visual field), and -0.32 (±0.10) on the vertical meridian (with no difference between the upper and lower visual field), showing a clear reversal of the horizontal-vertical meridian asymmetry. Importantly, subitizing versus estimating the number of presented items usually differs not only in regard to accuracy but also in regard to observers' confidence. For example, we recently showed that confidence was higher when RM occurred compared to when RM did not occur (Yildirim & Sayim, in revision). With the exact same stimulus (three lines as in the present experiment), observers were more confident when they reported two lines (i.e., RM occurred) than three lines (correct response; no RM). This pattern of confidence judgments was also reflected in the proportion of trials with and without RM: observers reported 2 lines in most of the trials (80%), and 3 and more than 3 lines in the remaining trials (18% and 2%, respectively) (Yildirim & Sayim, in revision). In the present experiment, we did not measure confidence but used the variability of responses to assess the ambiguity of observers' percepts. The variability of responses (SDs, Supplementary Figure 2) was smaller on the horizontal meridian compared to all other locations, including the vertical meridian. Particularly, when 3 lines were presented on the horizontal meridian, SDs were smaller than for the other numbers of lines as observers almost exclusively reported 2 (66% of the trials) and 3 lines (26% of the trials; more than three lines in 8%; see Supplementary Figure 3). Hence, it seems that there was not only stronger RM on the horizontal meridian, but also lower ambiguity: Observers perceived less items than were presented and did so comparably consistently.

There are several possible reasons for the atypical horizontal-vertical asymmetry we found in RM. First, it could arise from the same underlying mechanisms of tasks that show similar atypical visual field asymmetries. However, it seems that the results found here are uncommon and that the pattern of results found in studies which revealed atypical asymmetries, differed from the pattern we found here. For example, a three-dot bisection task, measuring the ability of spatial localization did not show the typical HVA: performance was similar on the horizontal and vertical meridians (Greenwood et al., 2017). Although the bisection results differed from the typical HVA, they did not resemble the pattern found here, showing how atypical visual field dependencies in spatial vision may vary across tasks. Perceiving the number of items, especially when only a few items are presented, should be closely related to other spatial capacities such as localization (Carrasco et al., 2001) and resolution (Carrasco et al., 2002; Greenwood et al., 2017; Nazir, 1992), but there are clear differences regarding their visual field asymmetries, and the relations between the underlying processes remain obscure.

One possible explanation is that the pattern of results could be a by-product of a process, such as regularity extraction, that negatively affects enumeration but not related phenomena such as localization and crowding. As noted in the introduction, one of the key factors that determine RM is stimulus regularity. Previously, we found that disrupting the regularity of line patterns by jittering the lines either horizontally or vertically abolished RM (Yildirim et al., 2020). For example, as little as 0.28° of horizontal jitter of a subset of lines, corresponding to 33% of the regular spacing between lines (at 10 degrees eccentricity), was sufficient to abolish RM. Stimulus regularity also determined whether observers reported two or three lines when presented with three equally spaced lines that were slightly tilted to the left or right from vertical

(Rummens & Sayim, in revision). When the stimulus was highly regular with all lines of the same tilt direction, observers frequently reported two lines, yielding strong RM; when one line had the opposite tilt direction of the two other lines, no RM occurred (Rummens & Sayim, in revision). Hence, it seems that a certain level of regularity is mandatory for RM. Here, we suggest that any factors that interfere with the extraction of regularity from the presented patterns might also interfere with the occurrence of RM. As perceiving the regularity of the presented line patterns requires accurate (relative) localization of the lines, any interference with accurate localization may as well interfere with the extraction of regularity and therefore reduce or prevent RM, yielding the pattern of results found here. Earlier studies showing superior performance in spatial localization (Carrasco et al., 2001) and regularity extraction (Corballis & Roldan, 1975; Jenkins, 1985; Pashler, 1990; Wagemans, Van Gool, & D'ydewalle, 1991) along the horizontal meridian compared to the vertical meridian support this hypothesis. Observers were better at localization tasks when the targets were placed along the horizontal meridian compared to the vertical meridian (Carrasco et al., 2001; Greenwood et al., 2017; Li, Yildirim, Alp, & Sayim, 2021; Smith, 2022). Studies on symmetry perception showed that vertical axis symmetries were more salient compared to horizontal and oblique symmetries (Corballis & Roldan, 1975; Jenkins, 1985; Pashler, 1990; Wagemans, Van Gool, & D'ydewalle, 1991; for reviews see: Wagemans, 1995; Wenderoth, 1994), suggesting that regularity extraction might be better along the horizontal than the vertical meridian. Following this reasoning, strong RM on the horizontal meridian may be partly driven by accurate extraction of the regularity of the line pattern. By contrast, on the vertical meridian, inaccuracies to extract the positions of the individual lines may interfere with the perceived overall regularity of the line arrays. The higher SDs of responses on the vertical compared to horizontal meridian are in line with this interpretation: The inaccuracies of encoding the positions of individual lines may interfere with the perceived regularity of the line array, yielding higher variability of responses. We speculate that such a reduction of the perceived regularity of the line pattern, just as actual irregularities of the stimulus, may underlie the weaker RM on the vertical compared to the horizontal meridian. In addition to stronger RM along the horizontal than the vertical meridian, we also found stronger RM on the horizontal than the diagonal meridians (± 45°) and no difference between the vertical and diagonal meridians. Stronger RM on the horizontal than the diagonal meridians may similarly be due to superior capacities to extract regularities along the horizontal than the diagonal meridians; however, further studies are needed to better understand the relationship between regularity extraction, visual field dependencies and redundancy masking.

A compression of peripheral visual space as found in previous studies could underlie the atypical horizontal-vertical asymmetry in RM. Previous studies have shown that perceptual space is distorted along both the horizontal and vertical meridians in peripheral vision (Osaka, 1977; Sheth & Shimojo, 2001; Wang, Murai, & Whitney, 2020; Yildirim et al., 2019). For example, a target that was briefly presented on the horizontal or vertical meridian was systematically mislocalized as closer to the center of gaze, indicating a compression of visual space between the target and fixation (Sheth & Shimojo, 2001). In another peripheral localization study, observers were asked to fixate a point and to manually point at a target stimulus which appeared briefly at large eccentricities (10° to 50°) along the vertical and horizontal meridians (Osaka, 1977). The observers made systematic errors, reporting the target location closer to fixation than its actual location, indicating again that visual space between fixation and the target was compressed. The magnitude of mislocalizations depended on visual field location, with larger mislocalizations seemingly occurring on the horizontal than vertical meridian (Osaka 1977; a significant effect of location, but no comparisons between the locations were reported). In a position matching task, participants indicated the position of a target (shown at 48 different angular positions) with a mouse cursor after the target disappeared (Wang, Murai, & Whitney, 2020). Calculating the angular distance between two adjacent reported locations revealed whether visual space was compressed (when smaller distances were reported) or expanded (when larger distances were reported). It was found that on average visual space was compressed along the horizontal meridian and expanded along the vertical meridian. We found the same pattern of compression along the horizontal meridian in a previous study on RM (Yildirim et al., 2019). In two RM experiments, observers were asked to report the spacing between the two outermost lines (that is, the overall extent of the array) or the spacing between adjacent lines. We found that observers reported the spacing between the outermost of three lines (presented on the horizontal meridian) as smaller than the actual spacing and the spacing between adjacent lines as larger than the actual spacing when RM occurred, but not when no RM occurred (Yildirim et al., 2019). Importantly, the spacing estimations in RM trials were approximately the same in both experiments, indicating that the perceived spacing between the two remaining (of the three presented) lines was similar for two adjacent and the two outermost lines (Yildirim et al., 2019) (In contrast, in 'correct' trials, the spacing between two adjacent lines was accurately estimated while the spacing between the two outermost lines was overestimated). There are two alternative explanations for the observed results: either, one of the outer lines was redundancy-masked, corresponding to an expansion of space, or the central line was masked, corresponding to a compression of space. An experiment assessing the perceived centroid of the line arrays ruled out that an outer line was masked: whether RM occurred or did not occur, observers reported the centroid of the line arrays similarly accurately, indicating the loss of the central line and compression of space in RM (Yildirim et al., 2019). Taken together, we suggest that greater spatial compression on the horizontal meridian compared to the vertical meridian might underlie the reverse horizontal-vertical asymmetry we found in RM. Note that spatial compression and reduced capacities to extract regularities are not mutually exclusive. While it is unclear how the two mechanisms are related, they may well be correlated (strong spatial compression going hand in hand with superior regularity extraction), for example, because of irregular spatial compression. Investigating to what extent regularity perception and spatial compression correlate will shed light on the relation of the two mechanisms.

In addition to the horizontal-vertical meridian asymmetry, another important deviation from other visual tasks was the absence of an upper/lower visual field asymmetry (VMA). The typical VMA is characterized by a lower visual field advantage: Performance is usually superior in the lower visual field compared to the upper visual field (Altpeter et al., 2000; Barbot et al., 2021; Carrasco et al., 2001;

Greenwood, et al., 2017; Talgar & Carrasco, 2002; but see Previc, 1990; Zito, Cazzoli, Müri, Mosimann, & Nef, 2016 for upper visual field advantages). The VMA has been attributed to higher attentional resolution in the lower compared to the upper visual field (He et al., 1996, 1997; Intriligator & Cavanagh, 2001). According to this explanation, performance for attentionally demanding tasks is better in the lower visual field because of higher attentional resolution in the lower compared to the upper visual field. Consistent with this explanation, a lower visual field advantage in the subitizing range (1-5) was found when observers performed an enumeration task for moving targets among distractors (Lakha & Humphreys, 2005). In contrast, when no distractors were presented, i.e., when targets required no segmentation from distractors, performance was the same in the lower and upper visual fields, suggesting that high attentional demands are required for VMA to occur (Lakha & Humphreys, 2005). The absence of the VMA was also reported in studies investigating orientation discrimination for a single target across the visual field (Kristjánsson & Sigurdardottir, 2008; Zito et al., 2016). For example, a lower visual field advantage was found only when the target was presented among distractors, but not when it was presented in isolation (Kristjánsson & Sigurdardottir, 2008). It was argued that added distractors increased attentional demands of the task, thereby giving rise to the VMA (Kristjánsson & Sigurdardottir, 2008). However, a number of studies also showed the VMA when attentional demands of the task were low (Baldwin, Meese, & Baker, 2012; Cameron et al., 2002; Carrasco et al., 2001), suggesting that the VMA - while it is usually stronger with higher attentional demands - can also occur when attentional demands are relatively low. Taken together, the absence of the VMA in our results may be related to the low attentional demands in enumerating a small number of static lines. The absence of the VMA is also relevant for distinguishing RM from crowding. As mentioned in the introduction, the VMA is a hallmark of crowding (He et al., 1996; He, Cavanagh, & Intriligator, 1997; Intriligator & Cavanagh, 2001). Attentional resolution accounts suggest that crowding occurs due to insufficient resolution of attention, yielding weaker crowding in the lower than in the upper visual field (He et al., 1996; He, Cavanagh, & Intriligator, 1997; Intriligator & Cavanagh, 2001; but see, Fortenbaugh et al., 2015). As we did not find the lower field advantage in RM we suggest that attentional mechanisms play different roles in crowding and RM.

Conclusions

To conclude, we found atypical visual field asymmetries in RM: RM was stronger on the horizontal meridian than on the vertical meridian, which is the opposite of the typical horizontal-vertical asymmetry. We also found no evidence for an upper/lower visual field asymmetry: RM was similar in the upper and lower visual field. Our results show that visual field asymmetries in RM diverge from most related perceptual phenomena, including crowding. We suggest that relatively noisy extraction of location information on the vertical compared to the horizontal meridian could contribute to the observed asymmetries: A reduction of perceived regularity may decrease RM and increase ambiguity, yielding the observed pattern of results. Similarly, the atypical visual field asymmetries in RM may be related to a stronger compression of visual space along the horizontal than along the vertical meridian.

Data availability

The datasets generated during the study are available on OSF (https://osf.io/6t4qh/).

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Figure Legends

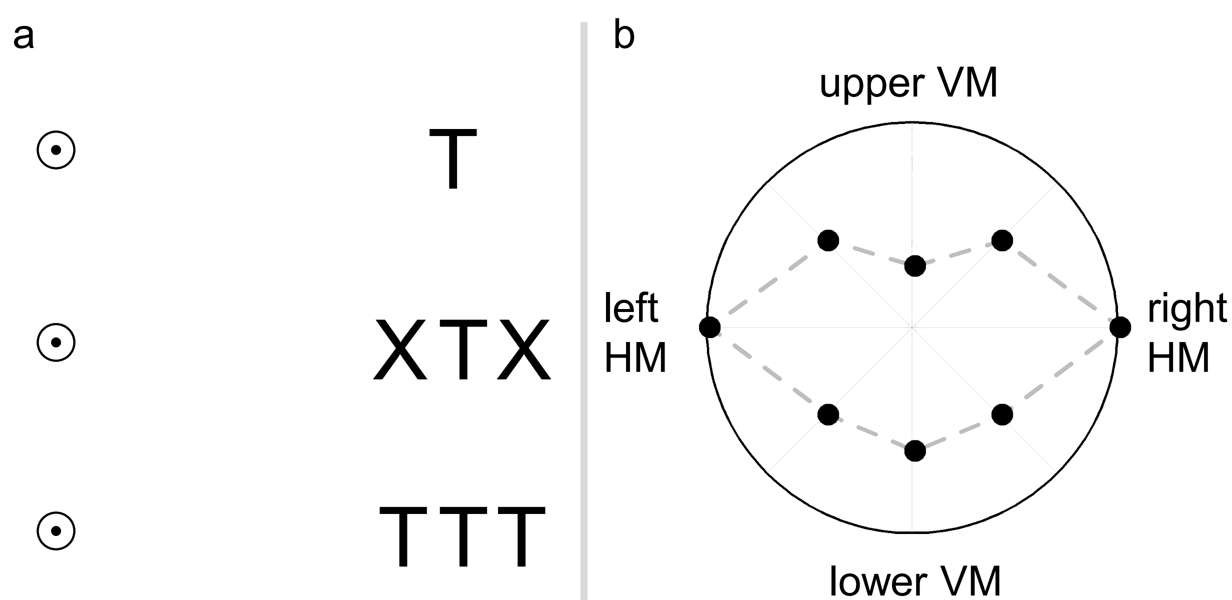

Figure 1. (a) Illustration of crowding and RM. When fixating the dot on the left, an isolated letter T that is relatively easy to identify (top row) becomes difficult to discern when flanked by nearby letters (middle row; crowding). Observers can identify the repeating letter T (bottom row; RM), but mostly report only two Ts instead of three. (b) Illustration of visual field asymmetries. Each dot denotes performance as a function of polar angle at a fixed eccentricity. The center of the polar plot represents chance level performance. Highest performance is typically observed along the horizontal meridian (HM). Performance on the HM is usually better than on the vertical meridian (VM; horizontal-vertical asymmetry), and better in the lower VM than in the upper VM (vertical meridian asymmetry). Performance along the diagonals (± 45°) is usually comparable and in between the horizontal and the vertical meridians (Figure adapted from Barbot et al., 2021).

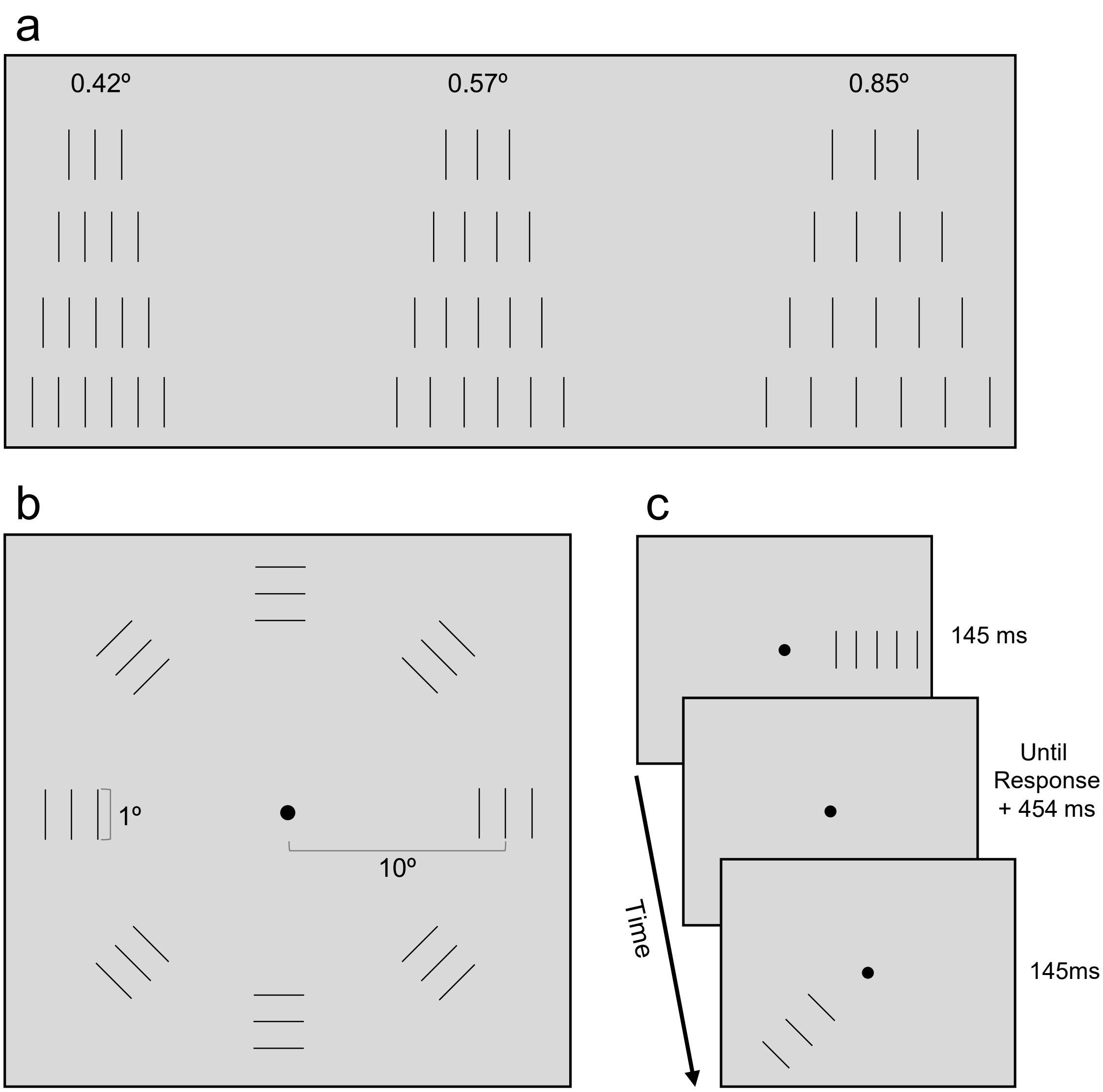

Figure 2. (a, b) Illustration of the stimuli. (a) Three to six lines with the different spacings (0.42°, 0.57°, and 0.85°). (b) The eight stimulus locations with exemplary stimuli shown at each location (only one stimulus at a time was presented in the experiment). (c) Schematic depiction of the experimental procedure. (Stimuli are not drawn to scale).

Figure 3. Mean deviation scores averaged over (a) all spacings and number of lines (main effect of location), (b) all spacings (interaction of location and number of lines), and (c) all number of lines (interaction of location and spacing) as a function of visual field location. The center of each polar plot (-1) indicates strong RM (negative deviations scores), 0 indicates correct responses, and the most eccentric polar coordinate (0.5) indicates overestimation (positive deviations scores). Error bars show ±SEM. RM was stronger on the horizontal meridian than all other locations (i.e., rHVA). The rHVA holds at nearly all levels of number of lines and spacing.

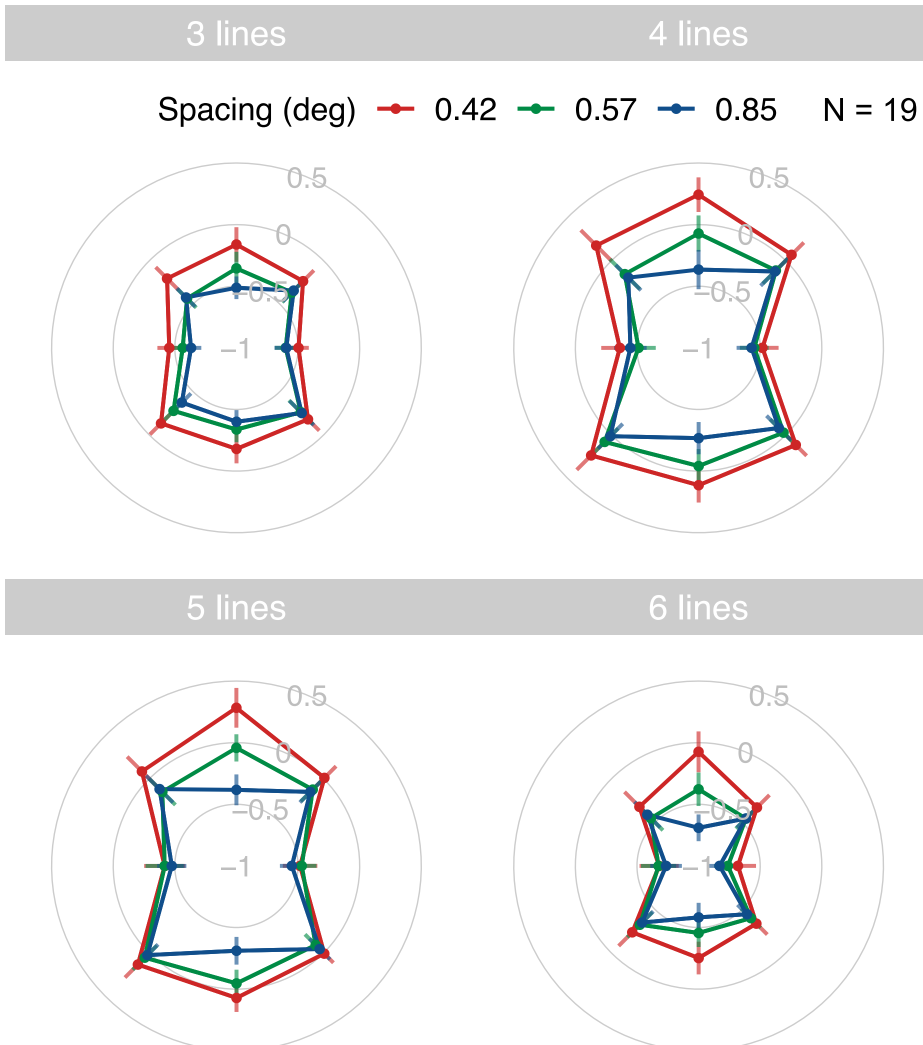

Figure 4. RM as a function of visual field location. Mean deviation scores for each number, location, and spacing condition are shown in polar coordinates. The center of each polar plot (-1) indicates strong RM (negative deviations scores) whilst the most eccentric polar coordinate (0.5) indicates an absence of RM (positive deviations scores). Error bars show ±SEM. RM was stronger on the horizontal meridian than all other locations.

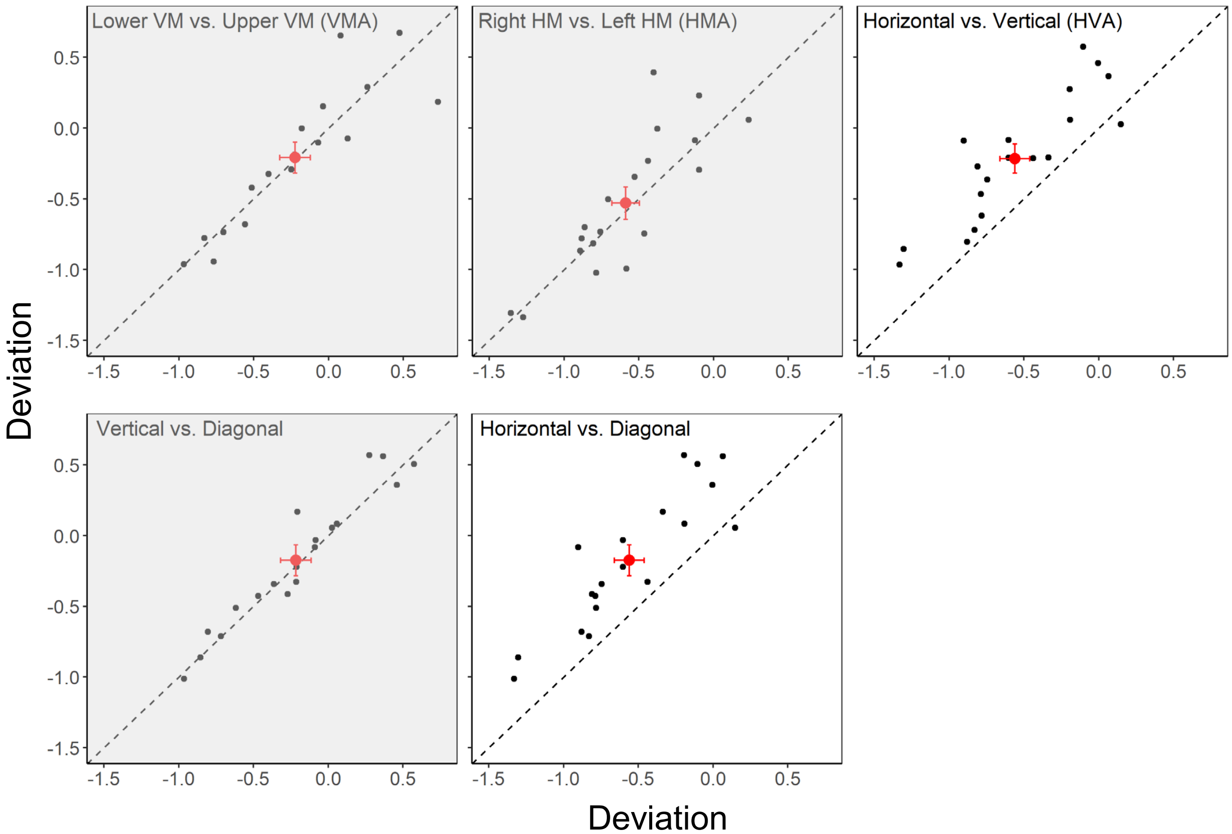

Figure 5. Illustration of various (a)symmetries of RM. Deviation scores for different visual fields and axes are shown in each subplot. The first and second visual field locations in the titles of each subplot denote the *x*- and *y*-axis, respectively. For example, in the "Lower VM vs. Upper VM (VMA)" subplot, lower VM (*x*-axis) is plotted with upper VM (*y*-axis). Each black disk represents the average deviation score of an individual observer. Points above the diagonal indicate that RM was stronger along the *x*-axis than the *y*-axis; points below the diagonal indicate that RM was stronger along the *y*-axis than the *x*-axis. For the (1) 'horizontal', (2) 'vertical' and (3) 'diagonal' meridians, (1) the 'left HM and right HM', (2) the 'lower VM and upper VM', and (3) the 'lower-right, lower-left, upper-right, and upper-left locations' were averaged, respectively. The red disks with error bars (±SEM) display the average of all observers. The shaded subplots show the results for which no asymmetries were observed.

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