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Anisotropic representations of visual space modulate visual numerosity estimation

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Abstract

Humans can estimate the number of visually displayed items without counting. This capacity of numerosity perception has often been attributed to a dedicated system to estimate numerosity, or alternatively to the exploitation of various stimulus features, such as density, convex hull, the size of items, and occupancy area. The distribution of the presented items is usually not varied with eccentricity in the visual field. However, our visual fields are highly asymmetric. To date, it is unclear how inhomogeneities of the visual field impact numerosity perception. Besides eccentricity, a pronounced asymmetry is the radial-tangential anisotropy. For example, in crowding, radially placed flankers interfere more strongly with target perception than tangentially placed flankers. Similarly, in redundancy masking, the number of perceived items in repeating patterns is reduced when the items are arranged radially but not when they are arranged tangentially. Here, we investigated whether numerosity perception is subject to the radial-tangential anisotropy of spatial vision to shed light on the underlying topology of numerosity perception. In Experiment 1, observers were presented with varying numbers of discs, predominantly arranged radially or tangentially, and asked to report their perceived number. In Experiment 2, observers were presented with the same displays as in Experiment 1, and were asked to encircle items that were perceived as a group. We found that numerosity estimation depended on the arrangement of discs, suggesting a radial-tangential anisotropy of numerosity perception. Grouping among discs did not seem to explain our results. We suggest that the topology of spatial vision modulates numerosity estimation and that asymmetries of visual space should be taken into account when investigating numerosity estimation.

Keywords: numerosity estimation, spatial vision, crowding, redundancy masking, radial-tangential anisotropy

Introduction

Humans can perform numerosity estimations without counting. When the number of items is small - usually up to 4 items - people apprehend the number of items rapidly and without errors (i.e., subitizing (Atkinson et al., 1976; Kaufman et al., 1949)). However, estimating higher numbers of objects is usually imprecise compared with subitizing. Different mechanisms have been proposed to underlie numerosity estimation. A prominent account of numerosity perception suggests that it is accomplished by a dedicated system - the approximate number system (ANS, also known as the "number sense"). The ANS has been suggested to extract the numerosity independently from other physical properties of the stimulus (Barth et al., 2003; Burr et al., 2018; Dehaene, 1992, 2011; Dehaene et al., 1998; Feigenson et al., 2004; Gilmore et al., 2011; Halberda & Feigenson, 2008; Lipton & Spelke, 2003; Xu et al., 2005).

Other accounts suggest that numerosity perception is not performed by independent mechanisms dedicated to numerosity but by exploiting stimulus properties such as item density (Dakin et al., 2011; Durgin, 2008), occupancy area (Allïk & Tuulmets, 1991), or by combining and weighting multiple visual cues (Gebuis & Reynvoet, 2012b, 2012c). Studies investigating the role of density in numerosity perception have shown diverging results. Burr and Ross (2008) demonstrated that numerosity, just like other primary visual properties, is subject to adaptation, and the effect was dependent on the number of items but not on other properties such as size or density. Hence, the authors suggested that numerosity is an independent visual property (see also Ross & Burr, 2010). Anobile et al. (2014) also suggested separate mechanisms for numerosity and density, supported by evidence that discrimination thresholds of high and low-density displays followed two distinct psychophysical functions (Weber's law and a square root function for low- and high-density displays, respectively). However, density and numerosity are physically indivisible, as density is calculated by dividing numerosity by the total area (Tibber et al., 2012). Dakin et al. (2011) showed that both numerosity and density judgments were biased by the size of the stimulus, which was interpreted to imply that numerosity perception and density perception share a common metric (see also Tibber et al., 2012).

In addition to density, several other physical properties of displays have been shown to affect numerosity perception. For example, in the occupancy model, Allïk and Tuulmets (1991) proposed that each presented item occupies a given circular region, and the total area collectively occupied by items (instead of the number of items per se) determined the perceived numerosity: When items are positioned too close to each other, the occupied regions overlap, resulting in lower perceived numerosity (see also, Allik & Raidvee, 2021). While proximity according to the occupancy model yields underestimation, varying proximity between subgroups of displayed items can yield more accurate performance. Specifically, when the presented items could be perceptually separated into subgroups, the number of items was enumerated more accurately and quickly ("groupitizing", Giovanni Anobile et al., 2020; Ciccione & Dehaene, 2020; Maldonado Moscoso et al., 2020; Pan et al., 2021). Hence, the spatial organization and perceptual grouping of items can modulate perceived numerosity. A similar effect of grouping has been shown with uniform versus regular patterns: Uniform patterns are often perceived to be more numerous than patterns that can be grouped into clusters (Frith & Frut, 1972; Ginsburg, 1976; Taves, 1941). Chakravarthi and Bertamini (2020) investigated numerosity estimation and crowded target discrimination using identical stimulus configurations, varying spacing and similarity among items that are both known to affect numerosity perception and crowding (see below). Based on their results that spacing and similarity impacted crowded discrimination and numerosity estimation differently, they suggested that underestimation in numerosity perception was not due to crowding but due to clustering among items, and that grouping may moderate both. Similarly, Im et al. (2016) found that the number of perceived groups predicted perceived numerosity, with smaller numerosity estimates when items were arranged in subgroups (yielding fewer perceived groups), suggesting that grouping between items plays a role in numerosity perception

Another suggestion for factors modulating or determining numerosity estimates is that observers combine (and weight) information from various visual cues (including item size, aggregate surface, convex hull, and density) to estimate numerosity (Gebuis & Reynvoet, 2012a, 2012b, 2013, 2014). What most experiments on numerosity perception have in common is that they usually apply stimulus features homogenously to the entire display, independent of stimulus locations in the visual field. However, our visual field has strong inhomogeneities (Abrams et al., 2012; Carrasco et al., 2001; Greenwood et al., 2017) which are likely to affect numerosity perception. One of the key factors that modulates perception is the eccentricity in the visual field. For example, a decrease in performance with increasing eccentricity has been shown for various tasks, including letter recognition (Gurnsey et al., 2011; Wolford & Hollingsworth, 1974; Zahabi & Arguin, 2014), conjunction search (Carrasco et al., 1995; Scialfa & Joffe, 1998), target detection (Meinecke & Donk, 2002), and vernier offset discrimination (Harris & Fahle, 1996; Levi & Waugh, 1994). How eccentricity modulates numerosity perception has also been investigated (Mengal & Matathia, 1980; Valsecchi et al., 2013). For example, it was found that the perceived number of items was lower when stimuli were presented in the periphery compared to central vision (Valsecchi et al., 2013). The authors suggested that the underestimation in the periphery could have been due to crowding where targets that are easily identified in isolation become difficult to discern when flanked by other items (Figure 1a, 1b; Bouma, 1970; Levi, 2008; Pelli & Tillman, 2008; Strasburger et al., 1991; Strasburger et al., 2011; Whitney & Levi, 2011). As crowding occurs when multiple objects interact, it is a plausible mechanism that could underlie underestimation in numerosity perception where multiple - often close-by - items are presented. Importantly, while crowding is usually assumed to affect target identification but not detection (Livne & Sagi, 2007; Pelli et al., 2004), recent studies showed that target parts were often unnoticed under crowding (Coates et al., 2017; Sayim & Taylor, 2019; Sayim & Wagemans, 2017). A particularly strong case of such 'omission errors' occurred when flankers and the target were the same. For example, when presenting three identical letters Ts in the periphery, observers frequently reported only 2 letters (see also, Sayim & Taylor, 2019). This effect was termed "redundancy masking": The reduction of the number of perceived items in repeating patterns (Sayim & Taylor, 2019; Yildirim et al., 2020, 2021, 2022). Redundancy masking has been shown to occur when as few as 3 items were presented (Sayim & Taylor, 2019; Yildirim et al., 2020, 2021, 2022). Notably, redundancy masking – as crowding - has a pronounced radial-tangential anisotropy: In crowding, radially placed flankers interfere more strongly with target perception than tangentially placed flankers (see Figure 1c, Greenwood et al., 2017; Kwon et al., 2014; Toet & Levi, 1992); redundancy masking is strong with radially arranged lines and absent with tangentially arranged lines (Figure 1d, e, f; Yildirim et al., 2020). As performance in most tasks deteriorates with increasing eccentricity (even if no contextual elements are presented), anisotropies such as the radial-tangential anisotropy are better suited to investigate to what extent numerosity perception is determined by similar contextual interactions as crowding and redundancy masking.

Here, we investigated whether numerosity perception is subject to a radial-tangential anisotropy to shed light on the underlying topology of numerosity perception. Specifically, we created displays that favored or did not favor these effects to occur (in 2 different alignment conditions: *tangential* and *radial*). We presented two types of arrangements of discs to produce weak or strong interference among the presented discs. To obtain a weak interference condition, close-by discs were predominantly arranged tangentially (*tangential* condition; Figure 2a); to obtain strong interference, they were predominantly arranged radially (*radial* condition; Figure 2b). In the *tangential* condition, elliptical zones around each disc that were expected to yield strong interference from neighboring discs within the zones ("crowding" zones) were "protected" by preventing discs from being positioned in these regions (hence, allowing tangential arrangements of discs, radial "protection zones" were used). In the *radial* condition, "protection zones" were perpendicular to these interference regions (i.e., tangential oriented), allowing discs to fall into other discs' interference regions (Figure 2e). We varied the size of the interference and protection zones as a function of eccentricity. Other physical properties (convex hull, occupancy area, density etc.) did not differ in the two conditions. In two experiments, participants viewed *tangential* and *radial* displays and were asked to perform the numerosity estimation task (Experiment 1) and the grouping task (Experiment 2). In Experiment 1, we tested whether the alignment condition (*radial* vs. *tangential*) influenced the perceived numerosity. Observers were asked to indicate the number of discs on each display. We found that the estimates of the number of discs were lower in the *radial* (strong interference) compared to the *tangential* (weak interference) condition. In Experiment 2, we tested whether there were any differences in the perceived number of groups in the two conditions, and thereby whether grouping could underlie the observed results in Experiment 1. For that aim, we asked participants to encircle the discs that they perceived to form groups. Interestingly, the results of Experiment 2 showed the opposite effect of the alignment condition on the perceived number of groups than the main experiment: The average number of groups reported by observers was larger in the *radial* compared to the *tangential* condition. This result suggests that the relatively lower estimates in the *radial* condition compared to the *tangential* condition (Experiment 1) was not likely caused by factors related to perceptual grouping as tested in Experiment 2. Overall, our results showed a pronounced radial-tangential anisotropy of numerosity perception, suggesting a similar underlying topology of spatial vision as in other types of contextual interactions.

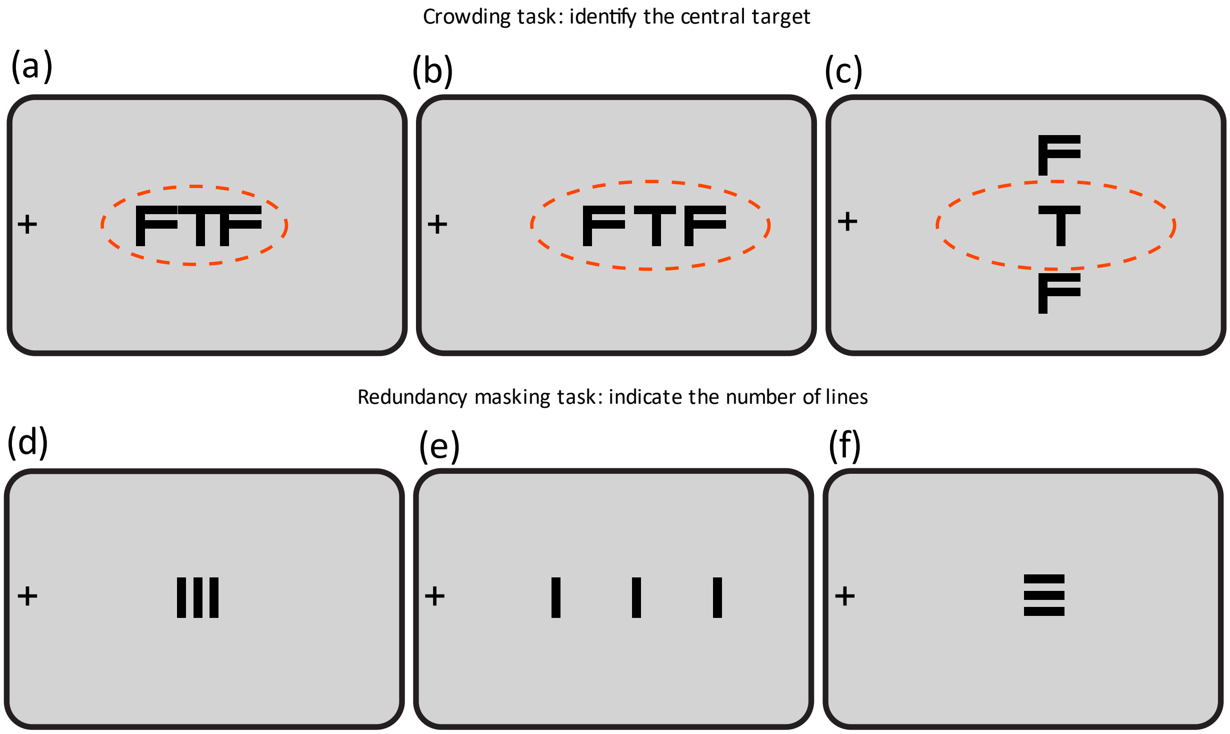


Figure 1 Illustration of crowding and redundancy masking. (a) When fixating the cross, identifying the target "T" that is surrounded by 2 flankers "F", is usually difficult when flankers are positioned inside the interference ("crowding") region (indicated by the dashed ellipse). (b) The interference region is eccentricity-dependent: increasing target eccentricity increases the size of the interference region. (c) The interference region is anisotropic: Flankers cease to interfere at smaller distances in tangential (c) compared to radial (b) directions. (d) Redundancy masking is the reduction of the number of perceived items in repeating patterns. When presenting 3 close-by aligned vertical lines in the periphery, most observers reported only 2 lines. (e) Redundancy masking was weaker with large compared to small (d) spacings (Yildirim et al., 2020). (f) There was no redundancy masking when lines were arranged tangentially.

Method

Experiment 1: Numerosity Estimation

In Experiment 1, we tested whether the radial-tangential anisotropy of visual space impacted perceived numerosity.

Participants

Twenty-one healthy participants (7 males, 14 females; mean age: 24.1 years, ranging from 19 to 31) participated in the experiment. All participants were naïve as to the purpose of the study. Participants either received monetary compensation or participated without compensation. All participants reported normal or corrected-to-normal visual acuity and signed informed consent prior to the experiment. The experiment was approved by the ethics committee of the Ulille SHS, University of Lille.

Apparatus

The experiment was programmed in PsychoPy coder v3.1.2 (Peirce, 2009) and ran on a desktop PC. All stimuli were presented on a Vision Master Flat Square CRT monitor (Iiyama MS103DT), with a resolution of 1280 × 1024 pixels (refresh rate was set at 100 Hz). During the experiment, participants sat in front of the monitor with a chin rest at a distance of 57 cm from the monitor. All experiments were conducted in a dim experimental room.

Stimuli

Stimuli consisted of black discs (0.9 cd/m^2; radius: 0.25°) presented on a gray background (25 cd/m^2). In five numerosity range conditions, discs were presented within rectangular regions of different sizes (width × height: 19.5 × 11.5; 21.5 × 13.5; 25 × 16.5; 27 × 18.5; 30 × 21 degrees of visual angle that occupy 30%, 40%, 50%, 60%, and 70% of the screen, respectively), each corresponding to one of the 5 different numerosity ranges (21 –25; 31 – 35; 41 – 45; 49 – 53; 54 - 58). No discs were presented within a circular region (radius: 3.8°) around fixation. There were two types of disc arrangements: tangential and radial, illustrated in Figure 2. We surrounded each disc with a virtual "protection zone" free of any other disc. The size of the "protection zone" was based on common estimates of the size of the interference region in crowding (e.g., Bouma (1970), Toet & Levi (1992)). Both the major axis and the minor axis of the "protection zone" were determined by target eccentricity: the major axis was set to 0.25 × eccentricity and the minor axis to 0.1 × eccentricity (corresponding to a minimum distance of 0.2 and 0.5 × eccentricity when two discs were tangentially or radially aligned). To generate a *tangential* display (Figure 2a, c and f), a random position was chosen to place the first disc with its corresponding (radially extended) "protection zone." All the other discs were added with their "protection zones" iteratively on the displays with the constraint not to overlap with any of the "protection zones" of other discs, until no disc could be positioned onto the display without overlapping "protection zones." In the *radial* condition (Figure 2b, d, and g), displays were generated the same way as the *tangential* displays, except that the "protection zones" were rotated by 90° compared to the *tangential* condition. Therefore, in the *radial* condition, "protection zones" were orthogonal to the major axis of the interference region (Figure 2d, e). For each numerosity range, we generated 5000 displays for each condition (*tangential* and *radial*). We calculated convex hull, occupancy area, average spacing, average eccentricity, and density for each generated display and selected displays from the *tangential* and *radial* conditions that matched their physical properties (see Supplementary Table S1). The density was measured by dividing numerosity by occupancy area, excluding the central region where no discs were presented. As an insufficient number of displays in the smallest numerosity range could be matched, we generated an additional 5700 *radial* displays to obtain the required matches.

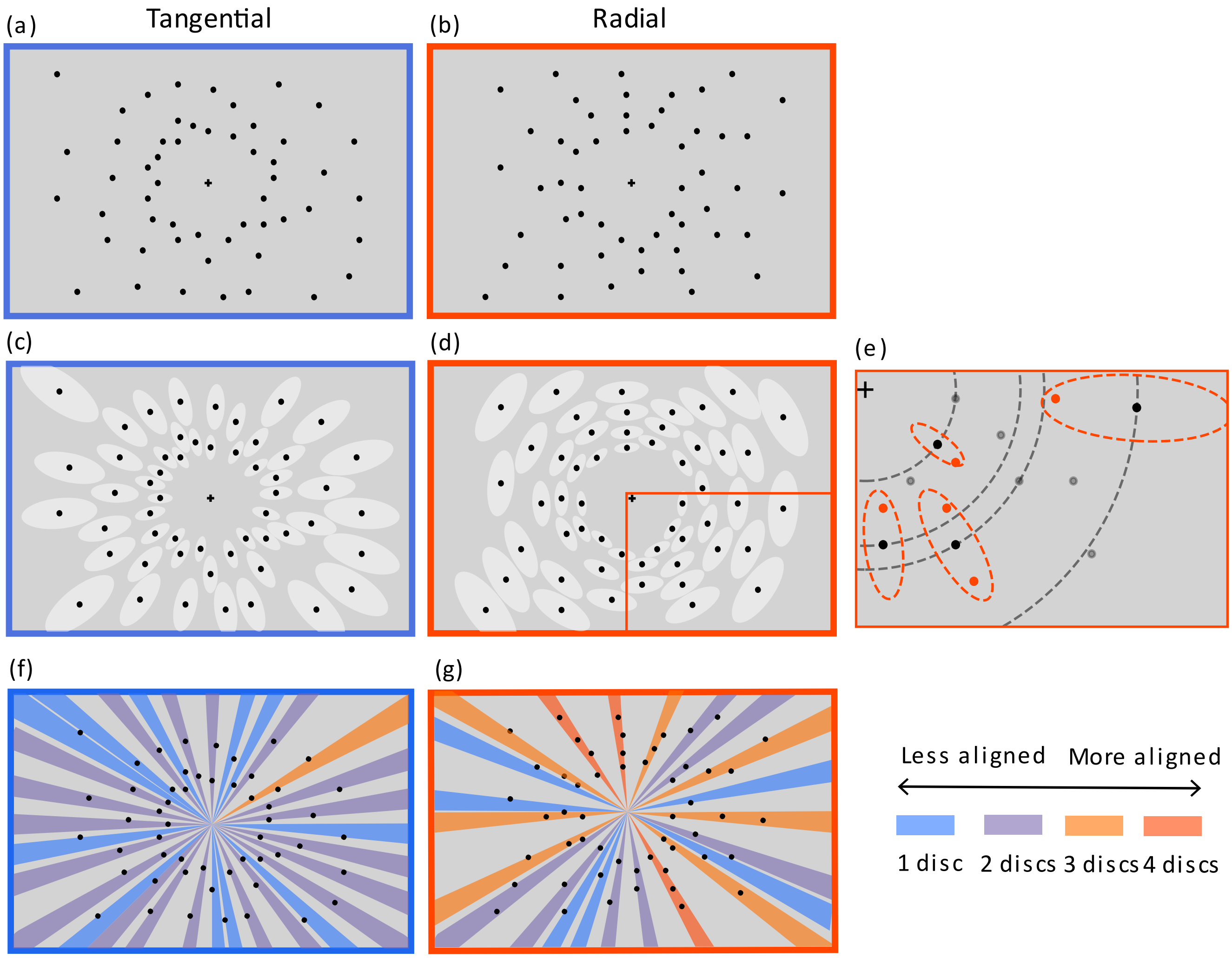


Figure 2

Illustration of displays in the (a) *tangential* and (b) *radial* conditions. (c) and (d): Illustration of the geometric principles of the *tangential* and *radial* conditions. (c) In the *tangential* condition, each disc is surrounded by a "protection zone" (indicated by the ellipses), allowing predominantly tangential alignments of discs. No discs were positioned into any other disc's interference region zones. (d) Rotated protection zones in the radial condition, favoring stronger interference. Here, a certain number of discs was positioned inside other discs' interference regions. (e): Detail of the *radial* display, illustrating discs (shown in red for illustration) in the interference region of other discs. (f) and (g) illustrate radial-tangential alignment scores for the *tangential* and *radial* conditions, respectively.

Design and Procedure

At the start of each trial, a black fixation cross (0.75° × 0.75°) was presented at the center of the screen. Observers initiated each trial by pressing the spacebar. The stimulus display was presented for

150 ms. Participants were instructed to respond by entering their best estimation of the number of presented discs with the numeric keypad. No feedback was provided. There was no time limit for participants to respond. Participants were not informed about the numerosity ranges prior to the experiment. Prior to each experimental block, participants viewed 5 reference displays in random order. The numerosities of the 5 reference displays were equally distributed around the averaged numerosity of the block (± 0.125 and ± 0.25 times of the mean numerosity of the block). Each reference display was presented for 150 ms, and participants were informed about the actual numerosity of the display after the reference display offset.

There were two factors: Alignment condition (*tangential* vs. *radial*) and numerosity range (5 levels: 21-25, 31-35, 41- 45, 49-53, and 54-58; for convenience, we use the first numerosity of each numerosity range to denote the actual numerosity range, i.e., N21, N31, N41, N49 and N54 denote numerosity range 21-25, 31-35, 41- 45, 49-53, and 54-58, respectively). Each participant performed 10 blocks of 50 trials each. Within each block, each numerosity was presented 10 times (5 different displays, each repeated twice). Participants first completed each of the 5 numerosity ranges (in random order), followed by 5 blocks in the opposite order. The dependent variable was the deviation score (DV) of participants, calculated by subtracting the actual numerosity from participants' estimation for each trial. Hence, positive DVs represent overestimation; negative DVs represent underestimation. We also calculated the relative estimation error by dividing the DV by the numerosity of the display.

Data Analysis

We conducted a within-subject ANOVA on DV scores with alignment condition and numerosity range as within-subject factors. We expected lower DVs in the radial compared to the tangential condition. The ANOVA and pairwise analysis were performed with an open-source Python package, Pingouin version 0.5.1 (Vallat, 2018). Estimates outside of 3 standard deviations around the mean were discarded independently for each numerosity range (0.4% of all trials). The same analyses were conducted on relative estimation error.

Radial alignment scores (RAs). We calculated RAs as measures of how well discs were radially aligned in a display. RAs were calculated individually for each display by rotating a circle sector with an angle of 6° (half the angle of the minor axis of the protection zones) around fixation for a complete rotation and counting the number of discs falling in the sector at each location a new disc fell into the trailing edge of the sector (i.e., when the edge of the circle sector aligned with a disc center; Figures 2f and 2g). Neighboring circle sectors ("alignment regions") did not overlap. The procedure was repeated with each disc in the display as starting disc, always performing a complete rotation. For each rotation, the proportion of the circle sectors that contained 3 (the minimum number of items to obtain redundancy masking) or more discs was calculated. For example, if there were 20 circle sectors in one rotation and 10 of them contained 3 (or more) discs, the proportion would be 0.5. The RA of that display was the averaged proportion across all rotations for that display.

Crowding strength. The number of discs that was positioned in other discs' interference regions varied in the *radial* condition but not in the *tangential* condition since no discs could be positioned into the interference region of other discs (Figure 2c; by definition, what we denote as the "crowding strength" was 0 in all tangential displays). To quantify "crowding strength" in the *radial* condition, we calculated the number of discs per display that were positioned in other discs' interference regions. The average crowding strength was 1.3 ± 1.1, 2.6 ± 1.3, 4.8 ± 2.4, 6.6 ± 2.9, and 7.1 ± 3.1 for N21, N31, N41, N49, and N54, respectively.

Partial correlations. We calculated partial correlations between (1) RAs and DVs and (2) crowding strength and DVs, controlling for numerosity. To ensure that RAs, crowding strength, and DVs were comparable across numerosity ranges, they were normalized in the linear regression to predict numerosity.

Experiment 2: Grouping into clusters

In Experiment 2, we tested whether the number of perceived groups in the *radial* and *tangential* conditions differed. If the number of perceived groups was lower in the *radial* than in the *tangential* condition, grouping among discs could be a factor contributing to the effect found in Experiment 1. If the number of perceived groups was similar in the *radial* and the *tangential* displays, the results would suggest that grouping is an unlikely factor underlying the effect observed in Experiment 1.

Participants

Thirty healthy participants (4 males, 26 females; mean age: 19.7 years, ranging from 18 to 24) participated in Experiment 2. All participants were students at the University of Lille or the KU Leuven, and naïve as to the purpose of the study. All participants received course credits for their participation. All participants reported normal or corrected-to-normal visual acuity and signed informed consent prior to the experiment.

Apparatus

The experiment was programmed in PsychoPy coder v2.1.0 (Peirce, 2009) and ran on a desktop PC. All stimuli were presented on an LCD display with a resolution of 1960 × 1080 pixels. During the experiment, participants sat in front of the monitor with a chin rest at a distance of 57 cm from the monitor.

Stimuli

The stimuli were identical to the stimuli in Experiment 1.

Design and Procedure

The design and procedure were identical to Experiment 1 except for the following changes: Participants were asked to encircle the discs that they perceived as a group, using the mouse (as a 'pen'). Each display was presented until participants had finished the trial (unlimited viewing time). Participants were presented with the same displays that were used in Experiment 1. Each participant was presented with one-third of the total number of displays (250 displays) of Experiment 1 to limit the duration of the experiment (about 100 minutes per participant). There were 30 participants (hence, 10 responses per display).

Data Analysis

The analyses were identical to the ANOVA analysis in Experiment 1, except that the dependent variable was the number of perceived groups. The number of groups that participants encircled for each display corresponded to the number of perceived groups in the analysis.

Results

Experiment 1: Numerosity Estimation

Figure 3a shows the average deviation scores (DVs) for the *tangential* and the *radial* condition separately for each numerosity range. A repeated measures ANOVA with alignment condition (*tangential* and *radial*) and numerosity range (N21, N31, N41, N49, and N54) as factors showed a main effect of alignment condition ($F(1, 20) = 13.45$, $p < .005$, $\eta_p^2 = .40$) on DVs. Participants reported fewer discs in the *radial* (DV = 1.64 ± 8.65) compared to the *tangential* condition (DV = 2.66 ± 8.78). Pairwise comparisons with Hochberg FDR correction showed significant differences between the *tangential* and the *radial* conditions in all numerosity ranges (N31: $t(20) = 2.66$, $p < .05$, Cohen's $d = 0.12$; N41: $t(20) = 2.32$, $p < .05$, Cohen's $d = 0.10$; N49: $t(20) = 3.43$, $p < .005$, Cohen's $d = 0.15$; N54: $t(20) = 3.55$, $p = .005$, Cohen's $d = 0.16$), except for the smallest one (N21: ($t(20) = 0.85$, $p = .40$, Cohen's $d = 0.04$). We also found a main effect of numerosity range with lower DVs for small numerosities. ($F(4, 80) = 3.96$, $p < .05$, $\eta_p^2 = .17$). A significant interaction between alignment condition and numerosity range ($F(4, 80) = 2.68$, $p < .05$, $\eta_p^2 = .12$) indicated that the difference between the *tangential* and the *radial* conditions increased with larger numerosities. Figure 3b shows the average relative estimation error for each condition. We also conducted a repeated measures ANOVA on average relative estimation error with alignment condition and numerosity range as within-subject factors. We observed a main effect of alignment condition (*F*(1, 20) = 8.79, $p < .01$, $\eta_p^2 = .31$) on relative estimation errors. No other significant effect was observed (*p*s > .05).

To test whether radial alignment predicted DVs, we correlated radial-alignment scores (RAs) and DVs while controlling for numerosity (partial correlation, Figure 3b). For all numerosity ranges combined, the partial correlation was r = -0.40 ($p < .0001$, CI 95% [-0.50 -0.29]), showing higher deviations scores with increasing RAs. Except for N21, the partial correlation between DVs and RAs showed a clear negative correlation when controlling for the effect of numerosity. These results showed that estimates were smaller when discs were more strongly radially aligned, at least for larger numerosities (N31 and above). The averaged RAs for separate numerosity ranges for both *tangential* and *radial* displays are shown in Supplementary Table S2. The partial correlations for the separate numerosity ranges are shown in Supplementary Table S3.

To test whether "crowding strength" predicted DVs, we correlated crowding strength and DVs while controlling for numerosity (partial correlations, Figure 3c). Results showed that the overall partial correlation coefficient was r = -0.40 ($p < .0001$, CI 95% [-0.50 -0.29]). Hence, there was a clear negative correlation between the number of discs falling into the interference zone of other discs and numerosity judgments: The more discs were presented in other discs' interference zones, the lower the numerosity judgments. Supplementary Table S3 shows the partial correlations analysis of each numerosity range separately.

Experiment 2: Grouping into clusters

Figure 4 illustrates the task and response format in the grouping task for tangential and radial displays, respectively. A repeated measures ANOVA with alignment condition and numerosity range as factors showed a main effect of alignment condition (*F*(1, 9) = 6.91, $p < .005$, $\eta_p^2 = .43$) on the perceived number of groups. Participants reported more groups in the *radial* (13.0 ± 4.25) compared to the *tangential* condition (11.4 ± 3.78). Pairwise comparisons with Hochberg FDR correction showed significant differences between the *tangential* and the *radial* conditions in N21 (t(9) = 4.11, $p < .01$, Cohen's d = 1.10), but not in the other numerosity ranges (N31: t(9) = 2.08, $p = .09$, Cohen's d = 0.70; N41: t(9) = 2.08, p =.09, Cohen's d = 0.67; N49: t(9) = 1.58, $p = .15$, Cohen's d = 0.40, N54: t(9) = 2.07, $p = .09$, Cohen's d = 0.58). Unsurprisingly, there was also a main effect of numerosity range on the perceived number of groups ($F(4, 36) = 101.94$, $p < .001$, $\eta_p^2 = .92$), showing that more groups were perceived with larger numerosities. No interaction between alignment condition and numerosity range was observed ($F(4, 36) = 0.58$, $p = .68$, $\eta_p^2 = .06$). Supplementary Table S4 summarizes the average perceived number of groups for each numerosity range in the *tangential* and the *radial* condition. Importantly, the two alignment conditions affected numerosity estimations (Experiment 1) and the perceived number of groups (Experiment 2) differently: numerosity estimation was lower and the perceived number of groups higher in the *radial* compared to the *tangential* condition.

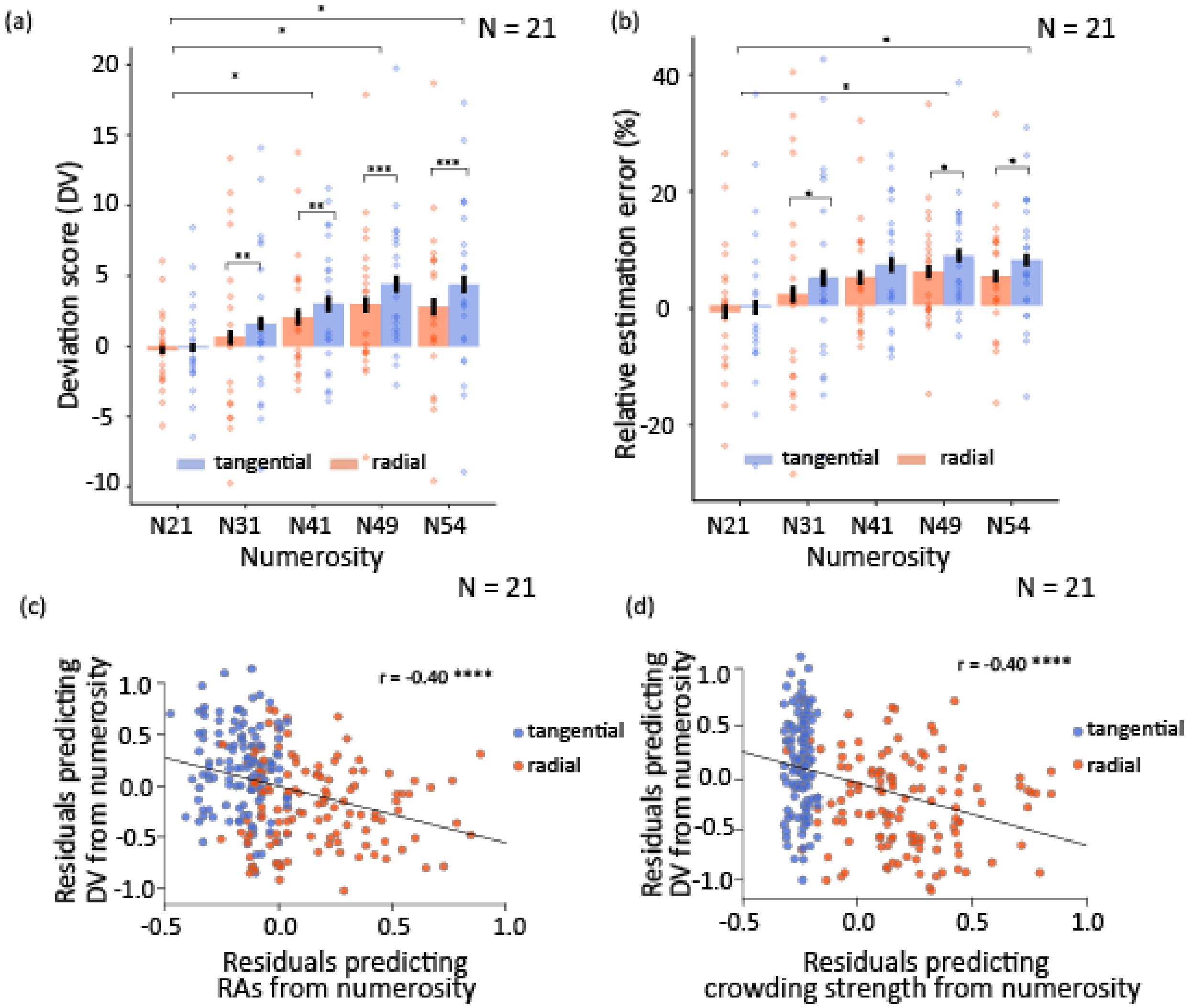


Figure 3. Results of Experiment 1. (a): Deviation score (DV) as a function of numerosity. DVs of 0 represent no deviation from correct responses, negative DVs represent underestimations, and positive DVs represent overestimations. Error bars indicate (+/-1) standard errors of the mean. Significant pairwise comparisons are indicated with asterisks. Each data point shows the average scores for one observer. (b): Relative estimation error as a function of numerosity. Error bars indicate (+/-1) standard errors of the mean. Each data point represents the average percent changes of one observer. (c): Partial correlation between DVs and radial alignment scores (RAs). when controlling for the effect of numerosity. (d): Partial correlation between DVs and crowding strength when controlling for the effect of numerosity. (*p < .05. **p < .005. ***p < .001. ****p < .0001.)

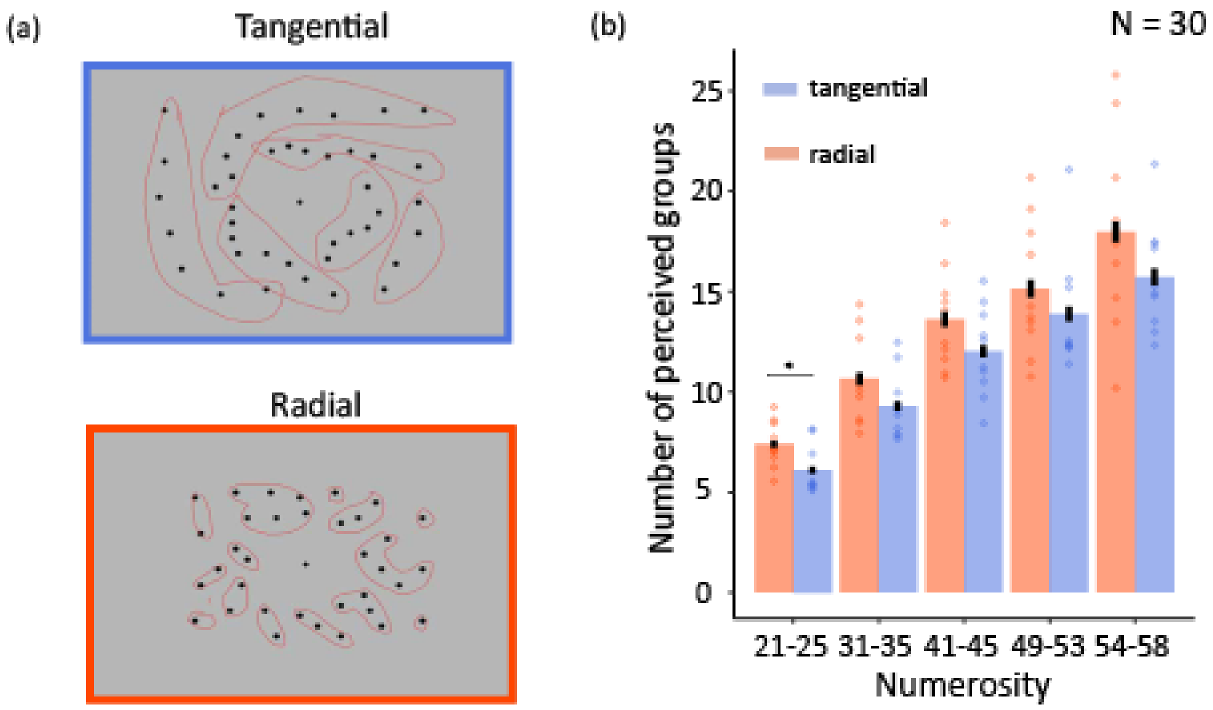


Figure 4. Results of Experiment 2. (a) Illustration of Experiment 2 with possible responses for tangential and radial displays. Each closed red shape was counted as one group of items. (b) The number of perceived groups as a function of numerosity separated for the radial and tangential conditions. Error bars indicate (+/-1) standard errors of the mean. Each data point shows the average scores for one observer. (*p < .05).

Discussion

We investigated to what extent the topology of spatial vision determined numerosity estimation. In particular, based on the radial-tangential anisotropy of spatial interactions in the peripheral visual field, we sought to investigate if numerosity estimation was subject to a similar radial-tangential anisotropy as crowding and redundancy masking. For that aim, we created displays in which neighboring items were predominantly arranged in either tangential or radial directions while keeping other features of the two types of displays, such as inter-item spacing, average eccentricity, convex hull, and density as similar as possible. In Experiment 1, we asked participants to report the number of discs they perceived. We found that numerosity estimates were lower in the *radial* compared to the *tangential* condition. The analysis of radial alignment scores (RAs) showed that higher RAs yielded lower numerosity estimates. In the *radial* condition, the number of items falling into the interference regions of other items was taken as a measure of "crowding strength." We found that crowding strength predicted deviation scores (DVs): high crowding strength was associated with smaller numerosity estimates and vice versa. Grouping among items is a good predictor of crowding strength (Livne & Sagi, 2007; Manassi et al., 2012; Sayim et al., 2010; Sayim et al., 2011; but see Melnik et al., 2018; Rummens & Sayim, 2019a). Grouping has also been shown to modulate numerosity perception (Chakravarthi & Bertamini, 2020; Ciccione & Dehaene, 2020; Im et al., 2016; Pan et al., 2021). To test whether the number of perceived groups was related to the relative underestimation in the *radial* compared to the *tangential* condition, we asked observers in Experiment 2 to encircle the discs they perceived as a group. We used the same displays in the grouping task as in Experiment 1. The results showed that the number of perceived groups in the *radial* condition was higher than in the *tangential* condition, i.e., the opposite pattern of results compared to Experiment 1: lower estimations (Experiment 1) and higher number of groups (Experiment 2) in the *radial* compared to the *tangential* condition. Hence, the perceived number of groups and the perceived numerosity were affected by alignment conditions differently. These results indicate that grouping is unlikely the cause for the different numerosity estimates in the *radial* and the *tangential* condition.

Crowding strongly limits peripheral vision (Bouma, 1970; He et al., 1996; Levi et al., 2002; Pelli et al., 2004), and was proposed to play a role in numerosity estimates (Anobile et al., 2015; Valsecchi et al., 2013). In particular, the relative underestimation of numerosities in dot displays presented in the fovea compared to the periphery suggested that mechanisms related to crowding might be an important factor in numerosity perception (Valsecchi et al., 2013). A potential role of crowding was also shown when varying eccentricity: Numerosity estimates varied with eccentricity similar to crowding, with stronger interference (lower estimates) farther in the periphery (Valsecchi et al., 2013). However, performance in most tasks deteriorates with increasing eccentricity. For example, besides crowding (Levi, 2008; Pelli et al., 2004; Strasburger, 2020; Toet & Levi, 1992), performance in other tasks, including letter recognition (Gurnsey et al., 2011; Wolford & Hollingsworth, 1974; Zahabi & Arguin, 2014), conjunction search (Carrasco et al., 1995; Scialfa & Joffe, 1998), target detection (Gruber et al., 2014; Meinecke & Donk, 2002), visual search (Carrasco & Frieder, 1997; Carrasco et al., 1998) and vernier offset discrimination (Harris & Fahle, 1996; Levi & Waugh, 1994) deteriorates with increasing eccentricity. Hence, eccentricity dependence is not sufficient to conclude that crowding-like mechanisms underlie numerosity estimation. In a recent study, crowding and numerosity perception were directly compared using identical stimulus configurations (Chakravarthi & Bertamini, 2020). Inter-item spacing and item similarity (same or opposite contrast polarity), both known to modulate crowding as well as numerosity estimates were varied. The results showed that spacing and similarity affected numerosity perception (in a 2AFC numerosity comparison task) and crowding (in an identification task) differently, suggesting a dissociation between numerosity perception and crowding. However, the different tasks and different task-relevancy of the presented items – a single relevant target or many relevant targets – render definite conclusions about the dissociation of crowding and numerosity perception difficult. For example, whether items are task-relevant or not has recently been shown to strongly modulate crowding, inverting the similarity rule of crowding (Rummens & Sayim, 2019b): When all items were task-relevant, performance was superior with target and flankers of the same compared to opposite contrast polarity. Similarly, small spacing between target and flankers does not always yield stronger crowding: Emergent features between the target and a flanker improved performance at small compared to larger distances in a crowding task (Melnik et al., 2020).

Importantly, crowding is usually assumed to impair target identification but not target detection (Andriessen & Bouma, 1976; Levi, 2008; Pelli et al., 2004; but see Allard & Cavanagh, 2011; Sayim & Wagemans, 2017). As underestimation in numerosity perception implies failures of detection, not discrimination, it might be suggested that crowding is an unlikely candidate to play a role in numerosity perception in general. However, recently it was shown that parts of the targets are often lost in crowding (Sayim & Wagemans, 2017). Such "omission errors" may well be due to the recently discovered phenomenon of redundancy masking, the reduction of the number of perceived items in repeating patterns (Sayim & Taylor, 2019; Yildirim et al., 2020, 2021). Although related to crowding, a key difference is that redundancy masking, unlike crowding, impairs the perception of the number of items (not their identity). As in numerosity estimation, a typical task to investigate redundancy masking is to ask participants to report the number of perceived items (however, see Sayim & Taylor, 2019, for a free verbal report and drawing task). Hence, there are obvious parallels between redundancy masking and numerosity perception, and redundancy masking could underlie underestimation in numerosity perception. Importantly, redundancy masking occurs for as few as three presented items, i.e., in the subitizing range (Yildirim et al., 2020) where reports are usually accurate (Atkinson et al., 1976; Jensen et al., 1950; Kaufman et al., 1949). Although clearly present for larger numbers of items, redundancy masking does not scale linearly with the number of items. For example, with three presented items of which only two are reported, one-third of all items are lost due to redundancy masking. While the absolute number of items lost due to redundancy masking increases with the number of presented items, the ratio decreases (Yildirim et al., 2020). Hence, the exact relation between redundancy masking and numerosity estimation still needs to be investigated, with future studies closing the gap between the paradigms typically used in numerosity perception and in redundancy masking, and shedding light on the extent of their similarities. Importantly, redundancy masking – as crowding – has a pronounced radial-tangential anisotropy: When peripherally presented lines were arranged radially, redundancy masking was strong; when they were arranged tangentially, there was no redundancy masking (Yildirim et al., 2020). Here, we used this radial-tangential anisotropy to manipulate displays where discs were predominantly arranged tangentially or radially to test if radial arrangements would yield lower estimates than tangential arrangements. As expected, radial arrangements yielded lower estimates than tangential arrangements. Taken together, contextual interactions subject to radial-tangential anisotropy, and in particular redundancy masking, are promising phenomena that share characteristics with numerosity perception beyond eccentricity dependence.

Many physical characteristics of displays used in experiments on numerosity perception are potentially confounded with numerosity per se (Gebuis & Reynvoet, 2012c). Importantly, in our *tangential* and *radial* arrangements, we kept physical properties of the displays that have been shown to play a role in numerosity estimation as similar as possible, matching them in regard to items size (Allik et al., 1991; Ginsburg & Nicholls, 1988), occupancy area (Allïk & Tuulmets, 1991), convex hull (Gilmore et al., 2016; Katzin, 2018), regularity (Franconeri et al., 2009; Ginsburg, 1976; Liu et al., 2018; Zhao & Yu, 2016), spatial clustering (Bertamini et al., 2018; Bertamini et al., 2016; Chakravarthi & Bertamini, 2020; Koesling et al., 2004), and texture density (Dakin et al., 2011). Controlling for these possibly confounding physical properties in the two conditions minimized the probability of factors related to these properties to account for the effect of our manipulation. Given the predominantly *tangential* or *radial* arrangements in the two conditions, some systematic structural differences are unavoidable. In particular, the discs in the *tangential* displays tend to be arranged into concentric patterns around fixation and in the *radial* displays into ray patterns. Importantly, while these structural differences between the displays may be a variable that modulates numerosity estimates, the findings in redundancy masking show strong differences between *tangential* and *radial* arrangements without any global, structural differences between *tangential* and *radial* arrangements. Moreover, redundancy masking has been shown to increase – not decrease – with diffused compared to focused attention

(Yildirim et al., in preparation). As focused spatial attention is considered not required in numerosity estimation (at least with relatively sparse displays; Anobile et al., 2020; Burr et al., 2010), redundancy masking would not be expected to cease in displays with larger numerosities.

While the number of discs, average eccentricity, average spacing, convex hull, and density were matched in the *tangential and radial* conditions, all displays contained density gradients with higher density in more central regions and decreasing density with increasing eccentricity. Hence, differences of the spatial distributions of the discs as a function of eccentricity in the two conditions were possible. For example, relatively more discs could be close to the center in one display, forming a higher local density region, compared to fewer discs close to the center in another display (with the same number of discs). The local density as a function of eccentricity (Supplementary Figure S1) captures such variations of display density. Differences in local densities could be a factor influencing numerosity estimates, for example, by yielding higher numerosity estimates for displays with high local densities compared to displays with low local densities. Such an effect would be expected if central regions were weighted more strongly than peripheral regions (Cheyette & Piantadosi, 2019; see also, Dandan et al., in preparation). A small subset of displays in the *tangential* condition had relatively high local densities compared to the average (Figure S1). However, the majority of these displays were not judged as more numerous than displays with lower local density, suggesting that local density differences between the *tangential* ('concentric') and the *radial* ('ray') conditions did not underlie differences of numerosity estimates. Note that relatively low density (due to relatively larger item size or smaller convex hull) has also been reported to yield higher numerosity estimates compared to displays with relatively high densities (Gebuis & Reynvoet, 2012c), however, in relatively uniform displays, without any systematic density variation with eccentricity as in our displays. If the structural differences per se irrespective of other variables (e.g., local density, overall density, convex hull, etc.) modulated numerosity perception, with generally lower estimates in ray compared to concentric patterns, radial-tangential anisotropies may well underlie such a difference. Systematic investigations to explore if – and how – such structural differences and local density differences modulate numerosity estimations will shed light on their role in numerosity perception.

Our results showed that the relative underestimation in the *radial* compared to the *tangential* condition was primarily driven by larger numerosities, with significant differences observed in N31 to N54 but not for N21. Consistently, in the partial correlation analysis, we found that both RAs and crowding strength negatively correlated with estimations with large numerosities but not small numerosities (see Supplementary Table S3). The pronounced effect on large but not small numerosity ranges is not surprising as the radial-tangential manipulation of displays did not yield strong differences in the smallest numerosity (N21, see RAs, Supplementary Table S2). While density did not differ between the *radial* and *tangential* conditions within each numerosity range, densities did vary between numerosity ranges: Relative higher density in N21 compared to the other numerosity (see Supplementary Table S1). Anobile et al. (2014) suggested that numerosity discrimination and judgments based on density depend on the density of the displayed items, with numerosity discrimination occurring when display densities are less than 0.25 items/deg^2 and judgments based on density with larger densities of the displays. In our displays, the densities in the large numerosity ranges (N41, N49 and N54) where we found differences between the *radial* and *tangential* displays fell into the 'numerosity judgment' range suggested by Anobile et al. (2014). Hence, it is unlikely that judgments in these conditions were based on density (but see Dakin et al., 2011; Durgin, 2008).

In contrast to smaller numerosities (N21) where the number of discs was rather accurately estimated, it was overestimated with larger numerosities (N31 and more). The overestimation with larger numerosities diverged from the general underestimation found in most numerosity studies (Anobile et al., 2020; Au & Watanabe, 2013; Chakravarthi & Bertamini, 2020; Krueger, 1982, 1984; Liu et al., 2017; Liu et al., 2018). The direct estimation task, in contrast to the typical discrimination task, could be one reason for the overestimation in our study. Similar overestimations were found when presenting regular and irregular dots array (28 – 46 dots), asking observers to estimate the number of dots (Alam et al., 1986). Also, when asking participants to report the number of items, Gebuis and Reynvoet (2012c) found that half of the participants overestimated and the other half underestimated the numerosities. We can exclude that the overestimation was due to the overall distribution of numerosities in different blocks as the same pattern of results also occurred in the first block that observers completed. Importantly, irrespective of the overall overestimation, which suggests a general bias, it is the relative underestimation in the *radial* compared to the *tangential* condition that shows the key estimation difference between the two conditions.

Perceptual grouping has been shown to modulate perceived numerosity (Chakravarthi & Bertamini, 2020; Im et al., 2016; Mazza & Caramazza, 2012). When items were arranged into clusters (Chakravarthi & Bertamini, 2020; Frith & Frut, 1972), perceived to contain a larger number of groups (Im et al., 2016), were grouped by connectedness (Franconeri et al., 2009) or by similarity grouping (connectedness, shape, proximity, and common region (Yu et al., 2019), observers tended to underestimate the numerosity compared to similar displays with weaker grouping. Hence, grouping among items may have modulated the perceived numerosity in the present study as well. For example, the relative underestimation in the *radial* compared to the *tangential* condition could have been driven by more grouping (and therefore fewer groups) in the *radial* compared to the *tangential* displays. In Experiment 2, we investigated how the discs in our displays were perceived to groups and whether grouping differences between the conditions could underlie the pattern of results in Experiment 1. Interestingly, the average number of perceived groups was higher in the *radial* than in the *tangential* condition, in contrast to number estimates which were lower in the *radial* compared to the *tangential* condition. Hence, this result shows that displays with low (high) numbers of perceived groups did not yield low (high) numerosity estimates. These results suggest that the relative underestimation in the *radial* compared to the *tangential* displays was not due to a smaller number of groups in the *radial* compared to the *tangential* condition: Grouping into clusters seems unlikely to play an important role in our results. However, while the same stimuli were used in the estimation (Experiment 1) and the grouping task (Experiment 2), viewing conditions were different: peripheral viewing with limited presentation time (150 ms) in the estimation task and free viewing with unlimited presentation time in the grouping task. Hence, retinal stimulus locations and presentation time could have influenced the results in the two experiments. For example, different sets of discs could have appeared to group when viewed peripherally compared to when viewed freely. However, as proximity was the principal grouping factor, differences that would systematically reverse grouping strength of the same displays in the two experiments are implausible. Rather, proximity as a grouping factor should be stable and maintain the ordinal relationships among displays across eccentricities. Importantly, in the realm of contextual interactions, i.e., crowding, the very same effects of grouping (and ungrouping) have been observed in the fovea (Sayim et al., 2008; Sayim et al., 2010) and in the periphery (Manassi et al., 2012; Rosen & Pelli, 2015). Similarly, variations of presentation time should maintain the order of grouping strengths across displays (Haladjian & Mathy, 2015). Interestingly, investigations of grouping and ungrouping in a backward masking paradigm showed that complex Gestalts needed more time to yield ungrouping compared to basic features; however, presentation times were very short (20ms), and no modulation occurred beyond the presentation time in our Experiment 1 (150 ms, Sayim et al., 2014; see also Feldman, 2007; Kimchi, 1998). One possible explanation for the divergent numerosity estimation results of Experiment 1 and grouping results of Experiment 2 is that only single - or subsets of – grouped discs were sampled in a given trial in Experiment 1. As the number of (perceived) groups was larger in the *radial* compared to the *tangential* condition (Experiment 2), and therefore the average number of discs per group was smaller, numerosity estimates based on single (or a few) groups would be lower. However, given the frequent overestimation in the current study, it is unlikely that such sub-sampling (without overcompensation) has occurred. Another factor that could underlie the diverging results in Experiments 1 and 2 is that different groups of observers participated in the two experiments. In recent experiments with similar stimuli (including the radial-tangential manipulation), we found similar results with a different group of observers (66 participants), providing further evidence that numerosity estimates depend on the (*radial* or *tangential*) arrangement of items. In Experiment 2 of the current study, 87% of the observers indicated more groups in the radial than in the *tangential* condition (on average for all numerosities), while only 13% showed the opposite pattern, indicating a robust pattern of results across participants. Hence, it is unlikely that a different group of observers would show the opposite pattern of results, i.e., higher numerosity estimates and a larger number of perceived groups in the radial condition compared to the tangential condition.

Overall, we demonstrated that numerosity perception was anisotropic in regard to *radial* versus *tangential* arrangements. We suggest that redundancy masking is one of the potential determining factors in numerosity estimation. Going beyond purely physical stimulus descriptions by taking into account asymmetries of the visual field in spatial vision will help to shed light on the underlying mechanisms of numerosity perception.

Appendix

Supplementary Table S1

A summary of physical properties for the radial and the tangential displays across all numerosity ranges.

	Numerosity range 21-25		Numerosity range 31-35		Numerosity range 41-45		Numerosity range 49-53		Numerosity range 54-58	
	Tan*(SD)*	Rad*(SD)*	Tan*(SD)*	Rad*(SD)*	Tan*(SD)*	Rad*(SD)*	Tan*(SD)*	Rad*(SD)*	Tan*(SD)*	Rad*(SD)*
Average spacing (°)	6.80*(0.07)*	6.74*(0.06)*	7.93*(0.07)*	7.91*(0.05)*	9.16*(0.09)*	9.16*(0.08)*	10.41*(0.09)*	10.37*(0.09)*	11.44*(0.09)*	11.38*(0.09)*
Convex hull (°)	35.47*(1.04)*	36.57*(0.98)*	48.28*(0.78)*	48.49*(0.67)*	60.93*(0.98)*	61.49*(0.96)*	73.78*(1.12)*	74.29*(0.96)*	84.43*(1.39)*	85.38*(0.98)*
Average eccentricity (°)	5.07*(0.05)*	5.03(0.05)	5.88*(0.05)*	5.86*(0.04)*	6.71*(0.07)*	6.72*(0.06)*	7.54*(0.07)*	7.54*(0.06)*	8.21*(0.06)*	8.20*(0.07)*
Occupancy area (Convex hull 2D volume)	88.83*(3.60)*	90.81*(3.22)*	157.45*(4.04)*	156.30*(4.05)*	249.79*(4.69)*	251.38*(5.06)*	367.54*(6.48)*	368.95*(6.79)*	482.35*(10.79)*	485.45*(8.17)*
Density (item/deg^2)	0.54*(0.02)*	0.52*(0.01)*	0.31*(0.01)*	0.30*(0.01)*	0.21*(0.01)*	0.21*(0.01)*	0.16*(<0.01)*	0.16*(<0.01)*	0.13*(<0.01)*	0.13*(<0.01)*

Note. Tan: Tangential displays; Rad: Radial displays. SD: Standard deviation. Convex hull and occupancy area were computed using the Qhull library (Barber et al., 1996) with Python. Density was calculated using the numerosity divided by occupancy area, excluding the empty central region (46.28 deg^2).

Supplementary Table S2

Averaged radial alignment scores (RAs) for each numerosity range

Numerosity range	Radial (*SD*)	Tangential (*SD*)
21-25	0.075(*0.255*)	0 (*0*)
31-35	0.466 (*0.532*)	0 (*0*)
41-45	1.378 (*0.808*)	0.049 (*0.165*)
49-53	2.939 (*1.080*)	0.525 (*0.461*)
54-58	3.378 (*1.207*)	1.447 (*0.914*)

Supplementary Table S3

Partial correlations (partial r_1 and $CI_1$95%) between deviation scores (DVs)and radial alignment scores (RAs) controlling for numerosity and partial correlations (partial r_2 and $CI_1$95%) between DVs and crowding strength controlling for numerosity

Numerosity range	partial r_1	$CI_1$95%	partial r_2	$CI_2$95%
21-25	0.10	[-0.19 - 0.36]	-0.17	[-0.43 - 0.12]
31-35	-0.23	[-0.48 - 0.05]	-0.49***	[-0.68 - 0.25]
41-45	-0.31*	[-0.54 - 0.03]	-0.31*	[-0.54 - 0.03]
49-53	-0.52***	[-0.7 - 0.28]	-0.44**	[-0.64 - 0.18]
54-58	-0.50***	[-0.68 - 0.25]	-0.52***	[-0.7 - 0.28]
all	-0.40****	[-0.5 - 0.29]	-0.40****	[-0.5 - 0.29]

Note. *p < .05. **p < .005. ***p < .001. ****p < .0001

In addition to circle sectors of 6°, we varied the size of the sectors from 1° to 12°, following the same method as described above in Method. Too small and too large angles were expected to yield weaker (or no) correlations with RAs as alignments would be rare (when angles were very small) or counted when far beyond plausible interference zones (when angles were large). The results showed that this was the case, with overall higher correlations for medium angle sizes (from about 5° to 9°).

Supplementary Table S4

Descriptive Statistics: means and standard deviations of perceived groups in the tangential and the radial condition for each numerosity range

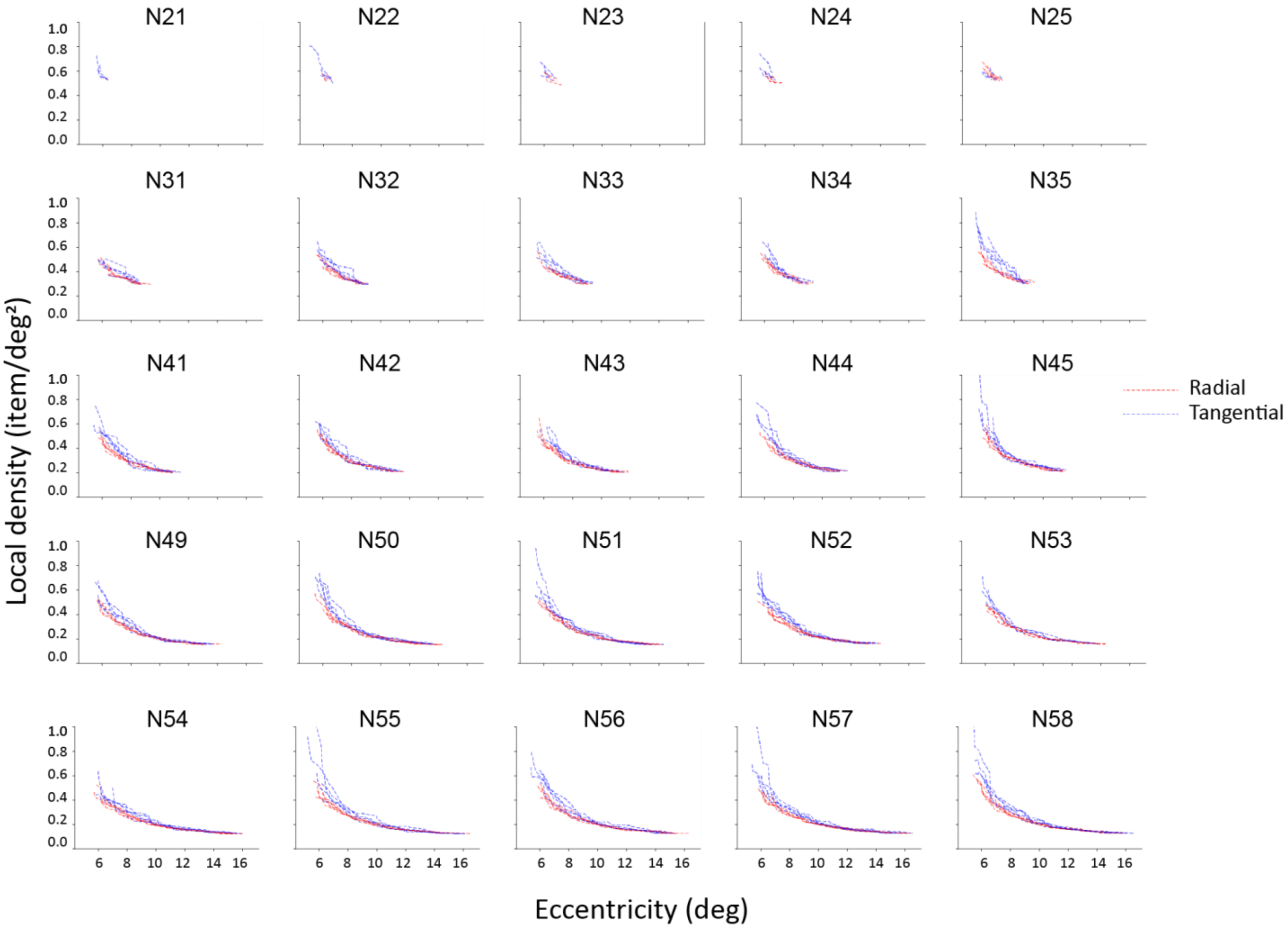
Numerosity range	Alignment condition	Mean (*SD*)
21-25	Tangential	6.13(*2.50*)
	Radial	7.37(*2.66*)
31-35	Tangential	9.3(*3.66*)
	Radial	10.7(*4.72*)
41-45	Tangential	12.0(*4.74*)
	Radial	13.6(*5.72*)
49-53	Tangential	13.9(*5.95*)
	Radial	15.1(*6.91*)
54-58	Tangential	15.7(*7.80*)
	Radial	18.0(*6.48*)

Supplementary Table S5

Partial correlations between the number of perceived groups and deviation scores (DVs) controlling for numerosity

Numerosity range	Alignment condition	Partial r	CI95%
21-25	Tangential	0.18	[-0.25 – 0.54]
	Radial	-0.21	[-0.56 – 0.21]
31-35	Tangential	0.30	[-0.11 – 0.63]
	Radial	0.36	[-0.05 – 0.67]
41-45	Tangential	0.07	[-0.35 – 0.46]
	Radial	-0.22	[-0.57 – 0.2]
49-53	Tangential	0.34	[-0.07 – 0.65]
	Radial	0.02	[-0.38 – 0.42]
54-58	Tangential	-0.11	[-0.49 – 0.3]
	Radial	0.10	[-0.31 – 0.49]

Note. All *p*s > .05



Supplementary Figure S1. Local density as a function of eccentricity. Local density was measured using the number of discs of displays (that fall into the local convex hull region) divided by occupancy area, excluding the empty central region. Each curve represents the local density for a single display.

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