Spatial variability in localization biases predicts crowding performance

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Visual processing varies substantially across individuals, and prior work has shown significant individual differences in fundamental processes such as spatial localization. For example, when asked to report the location of a briefly flashed target in the periphery, different observers systematically misperceive its location in an idiosyncratic manner, showing different patterns of reproduction error across visual field locations. In this study, we tested whether these individual differences may propagate to other stages of visual processing, affecting the strength of visual crowding, which depends on the spacing between objects in the periphery. We, therefore, investigated the relationship between observers' idiosyncratic biases in localization and the strength of crowding to determine whether these spatial biases limit peripheral object recognition. To examine this relationship, we measured the strength of crowding at 12 locations at 8° eccentricity, in addition to the perceived spacing between pairs of Gaussian patches at these same locations. These measurements show an association between variability in crowding strength and perceived spacing at the same visual field locations: at locations where a participant experienced stronger crowding, their perceived spacing was smaller, and vice versa. We demonstrate that spatial heterogeneity in perceived spacing affects observers' ability to recognize objects in the periphery. Our results support the idea that variability in both spatial sensitivity and bias contribute to variability in the strength of crowding and bolster the account that variability in spatial coding may propagate across multiple stages of visual processing.

Introduction

Much of the literature in experimental psychology relies on measuring average performance across

observers to understand the fundamental mechanisms underlying perceptual processes. However, much of visual perception is also idiosyncratic, and two observers who see the same scene may perceive it differently. Critically, these differences can shape how we interact with the world across many situations, from the process of finding our wallet in our bag to accurately localizing where a pedestrian is on the road. A growing body of work has shown that there is, in fact, considerable variability between individuals in terms of how we perceive our individual visual environment, even for quite simple, seemingly unambiguous, stimuli. Previous work has shown significant variability in visual perception, ranging from fundamental visual processes, such as location perception (Kosovicheva & Whitney, 2017), size perception (Moutsiana et al., 2016), surface and figure-ground interpretations (Finlayson, Neacsu, & Schwarzkopf, 2020; Wexler, Duyck, & Mamassian, 2015), to higher level processes such as face perception (Afraz, Pashkam, & Cavanagh, 2010).

Recent work has shown significant individual variability in the perceived locations of brief peripheral targets (Kosovicheva & Whitney, 2017; Wang, Murai, & Whitney, 2020). One might think that a briefly presented target, in isolation, would be localized accurately by all observers. In fact, when participants report the locations of these targets, their responses reveal systematic errors that are participant-specific and vary across the visual field. These idiosyncratic patterns of error are stable temporally and robust to different measurement methods, ranging from free cursor movement to speeded saccades, demonstrating individual variability for a seemingly simple task. A possibility raised by this work is that this spatial variability in perceived location may propagate to other stages of visual processing, and, in particular, may be reflected in measures of visual crowding.

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Crowding is the impairment in peripheral object identification owing to the presence of surrounding objects (Whitney & Levi, 2011). Notably, crowding varies across the visual field and depends strongly on target-flanker spacing, such that when the spacing is smaller, the target is harder to identify (Bouma, 1970). The strength of crowding is typically measured by determining the critical spacing—the minimum target-flanker separation necessary to identify the target. Previous work has also shown that there are consistent individual differences in critical spacing, across participants and throughout the visual field (e.g., Petrov & Meleshkevich, 2011; Veríssimo, Hölsken, & Olivers, 2021). The variability in the strength of crowding across the visual field limits peripheral object identification to varying degrees at different locations, and has some similarities with the localization work described earlier.

Given these findings, one possibility is that individual variability in perceived location (e.g., Kosovicheva & Whitney, 2017) may alter perceived spacing throughout the visual field and produce idiosyncrasies in the strength of crowding between objects, essentially helping to explain these individual differences in crowding. In other words, in locations where the target-flanker spacing is perceived as smaller (i.e., spatial compression in one area of the visual field), crowding may be stronger. In contrast, in other locations, the target–flanker spacing may be perceived as larger, resulting in weaker crowding and making it easier for the observer to identify a crowded object. This prediction aligns with previous work showing that crowding critically depends on the perceived, rather than physical, separation between the target and flankers (Dakin, Greenwood, Carlson, & Bex, 2011; Maus, Fischer, & Whitney, 2011; although see Chambers, Johnston, & Roach, 2018 for a counter-example). However, these studies manipulated perceived separation by introducing changes to the stimulus directly (i.e., by adding motion). There may be additional individual variability in the perceived location between individuals, in the absence of an illusion or other stimulus manipulation, that contributes to variability in crowding. Here, we asked whether variability in perceived spacing, in the absence of physical changes in the image, can account for idiosyncrasies in crowding strength.

Previous research suggests that individual differences in localization may propagate across multiple levels of visual processing. Wang et al. (2020) measured individual variability in perceived location across the visual field, converting participants' directional localization errors to measures of spatial compression and expansion at different visual field locations. They then correlated this measure (i.e., their spatial distortion index) with a measure of spatial precision (observers' Vernier acuity). This process demonstrated that areas

of spatial compression were associated with higher position sensitivity, whereas areas of expansion were associated with lower position sensitivity. Additionally, Greenwood, Szinte, Sayim, and Cavanagh (2017) found a relationship between spatial precision and crowding, demonstrating that areas of greater precision in object localization (higher position sensitivity) were associated with reduced crowding. Conversely, in areas of decreased spatial precision, where participants were less accurate in reporting where an object was, crowding was stronger.

Together, these studies suggest that idiosyncrasies in spatial representations are likely to be related across several domains of visual processing, and they span localization and crowding tasks. However, these results point to a potential counterintuitive prediction: if visual field locations that exhibit spatial compression are associated with higher spatial precision (Wang et al., 2020), and visual field locations where there is higher spatial precision are associated with weaker crowding (Greenwood et al., 2017), it remains possible that locations with relative spatial compression should be associated with weaker crowding. That is, the relationship between perceived spacing and critical spacing would move in the opposite direction (i.e., in areas where targets appear closer together, crowding would be weaker, not stronger). To clarify this point, we sought to test these different predictions to determine the relationship between individual variability in perceived location and crowding—specifically, whether areas of perceived spatial compression are associated with stronger crowding or decreased crowding.

In sum, crowding is an inherent limitation on peripheral object identification associated with variability in spatial precision at different visual field locations. Yet, we do not know how crowding and individual spatial localization biases interact. Understanding the relationships between individual differences in crowding, localization biases, and spatial precision will provide a more complete account of constraints that apply to peripheral object recognition and the mechanisms underlying individual variability in crowding. Because prior research has identified consistent idiosyncrasies in crowding and in localization, we predict that individual differences in how participants perceive space at different locations in the visual field will subsequently influence how much crowding is experienced at these locations. To test this hypothesis, we measured perceived separation between pairs of brief, peripheral targets, and compared this measure of perceived spacing with participants' critical spacing values from a separate crowding task. This approach allowed us to address our key question directly and to determine if there is a link between spatial heterogeneity in perceived spacing and peripheral object recognition.

Methods

Participants

Twelve observers with normal or corrected-to-normal vision participated in the experiment, including one author. Following exclusions (see Analysis), the final sample consisted of 10 participants (ages 19–30 years; 2 male, 8 female; mean age, 21 years). Procedures were approved by the Research Ethics Board at the University of Toronto, and the study was carried out in accordance with all relevant regulations regarding human participants research. All procedures were preregistered. Preregistration information, as well as data and materials, can be found on the Open Science Framework (https://osf.io/3j57e/). Participants gave informed consent before participating in the study.

Apparatus and stimuli

Participants completed the task in a dark, soundattenuated room. Stimuli were presented on an ASUS ROG Swift PG278Q 27" monitor with a 2,560- \times 1,440-pixel resolution and a refresh rate of 120 Hz. All visual stimuli were generated using MATLAB and the Psychophysics Toolbox (Brainard, 1997; Kleiner et al., 2007; Pelli, 1997), and the experiment program was run on a Lenovo Legion C730 computer with an NVIDIA GeForce GTX 1060 graphics card. Participants viewed the stimuli binocularly, using a chin rest to maintain a stable viewing distance of 57 cm. All stimuli were shown on a uniform gray background (50.2 cd/m²). The same experimental setup was used in both tasks. During the experiment, participants were instructed to maintain fixation throughout each trial on the black fixation dot at the center of the screen, and fixation compliance was monitored in each task using an Eyelink 1000 eye tracker (see Eye Tracking).

Crowding task stimuli

The crowding task was adapted from previous work (Greenwood et al., 2017), in which participants identified the orientation of a central clock hand surrounded by two flankers to induce crowding (Figure 1A). All stimuli were presented in black (0.18 cd/m²),

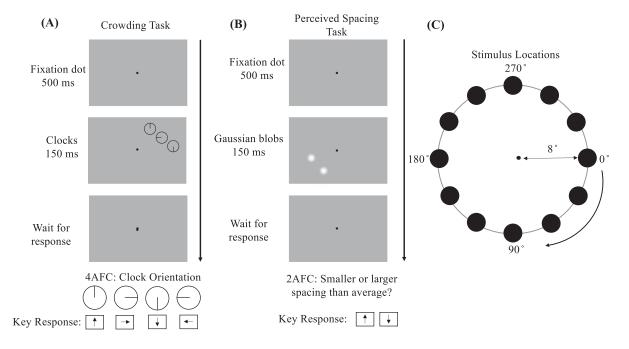


Figure 1. Experimental paradigm for the crowding and perceived spacing tasks, including stimulus presentation locations.

(A) Crowding task. Participants fixated the center of the screen, and three clock stimuli were flashed briefly (150 ms) in the periphery. The central clock was shown at 1 of 12 possible locations at 8° from fixation (shown in [C], with flankers positioned tangentially as shown, relative to each location). Participants' task was to identify the clock-hand orientation of the central stimulus and report whether it was pointing up, down, left, or right with the arrow keys. (B) Perceived spacing task. Participants fixated the center of the screen, and two Gaussian blobs were shown briefly (150 ms) in the periphery centered at one of the same 12 possible locations at 8° from fixation (as seen in [C]). The participants' task was to determine whether the spacing between the two stimuli was smaller or larger than the average of all the spacings seen before, using the arrow keys to indicate larger (up arrow) or smaller (down arrow). (C) Depicts 12 stimulus locations used in both conditions.

including the fixation dot (0.45° diameter) at the center of the screen. On each trial, the central clock was shown at a distance of 8° from the fixation point at 1 of 12 evenly spaced angular locations (Figure 1C). Angular locations were separated by 30° of rotation angle between each location, and included locations directly above, below, and to the left and right of fixation. Each clock stimulus had a total diameter of 1.4°. The line width for the circle and the inner hand stroke was 0.07°. At each visual field location, flanker stimuli were presented tangentially on either side of the central target, with the target–flanker spacing varying between trials. We note that, although crowding is stronger with radial flankers (Toet & Levi, 1992), stimuli were arranged tangentially in both the crowding and perceived spacing tasks to match the methods of previous studies that have shown systematic and highly consistent angular biases (i.e., clockwise and counter-clockwise errors) in observers' localization errors at a given eccentricity (Kosovicheva & Whitney, 2017; Wang et al., 2020). The orientations of the lines inside the target clock and each of the surrounding clocks were randomly and independently selected on each trial from one of four orientations (0°, 90°, 180°, or 270°).

Each trial began with a blank interval with only the fixation dot shown, and stimulus presentation was withheld until the participant maintained continuous fixation for 500 ms (see Eye tracking). Participants maintained fixation at the center of the screen throughout the entire trial. The stimuli were presented for 150 ms and then immediately removed from the display. After that, participants reported the orientation of the central clock hand (up, down, left, or right) with the arrow keys on the keyboard and had an unlimited duration in which to do so The next trial began immediately after the participant made their response.

Target–flanker spacing for each trial was controlled by a set of 12 randomly interleaved staircases (80 trials each), with one staircase running independently per location using a modified three-down, one-up rule. This strategy allowed measurement of critical spacing, defined as the distance between the target and flankers needed for each participant to identify the central target at 80% accuracy, for each location. The staircase procedure was modified as follows: the spacing on the first trial of each staircase was 5° with an initial step size of 1°, which decreased to 0.25° after six reversals. To maximize efficiency, the staircase followed a one-up, one-down rule until the second reversal, and then switched to a three-down, one-up rule. A reversal is a change in the direction of the staircase (from ascending to descending, or vice versa). If there were 10 consecutive trials with no reversals, the staircase was reset to the initial starting parameters. Psychometric functions were fit to participants'

responses to estimate critical spacing at each location (see Analysis).

Perceived spacing task

This task measured perceived spacing between pairs of brief targets using the method of single stimuli, and was adapted from previous work (McGraw, Roach, Badcock, & Whitaker, 2012; Morgan, Watamaniuk, & McKee, 2000; Wang et al., 2020). This procedure allows estimation of the perceived spacing between pairs of targets at each location without requiring the use of a simultaneous reference stimulus. As shown in Figure 1B, participants were shown pairs of Gaussian blobs ($\sigma = 0.15^{\circ}$; peak luminance = 120.7 cd/m²) at 8° eccentricity. Similar to the crowding task, pairs of Gaussian blobs were arranged tangentially relative to the fixation point and centered on each of the same 12 possible locations as the crowding task, with the location on each trial randomly interleaved. This task used pairs of Gaussian blobs, rather than the clock stimuli from the crowding task, to increase task difficulty by maximizing uncertainty about target location. On each trial, the blobs were separated by one of six randomly selected spacings (2.25°, 2.50°, 2.75°, 3.00°, 3.25°, or 3.50°), and participants identified whether the spacing between the stimuli was larger or smaller (up arrow key, larger; down arrow key, smaller) relative to the average of all the previously seen spacings across all locations. Participants were first given an opportunity to practice the task with feedback (see Procedure) to familiarize themselves with the range of possible spacings. Stimulus timings were identical to the crowding task; participants were required to fixate continuously on a dot for 500 ms on a grey background, followed by the two blobs for 150 ms.

Procedure

Participants completed the experiment across two separate sessions that were no more than 3 weeks apart. Each session consisted of one block of the crowding task and one block of the spacing task, with the order counterbalanced across participants to mitigate potential order effects. Each crowding block consisted of twelve 80-trial staircases, one per location, with location randomly interleaved (960 trials in total). Each spacing block consisted of 864 trials in the perceived spacing task, with 72 trials per location (with 12 trials for each of the 6 spacings at each location), with location and spacing randomly interleaved. Before each block, participants completed a 72-trial practice of the task with auditory feedback, where they heard high- and low-pitched beeps for correct and incorrect responses, respectively (600 Hz high and 280 Hz low for 250 ms). Participants did not receive feedback regarding response accuracy during the actual experiment. During the experiment, they received breaks every 80 trials and were encouraged to take a break between tasks. After completing each session, participants were compensated \$15 for their time; after the first session, they were scheduled for their second session. Once both sessions were complete, participants received an additional \$15 as a completion bonus.

Eye tracking

For all participants, gaze position was monitored binocularly using an Eyelink 1000 eye tracker (1,000 Hz sampling rate). Stimulus presentation was withheld until the participant had maintained continuous fixation on the fixation dot for 500 ms, and participants were required to maintain fixation within 1.5° of the fixation dot while the stimulus was on the screen. If the participant's point of gaze drifted from this region, a buzzer sound (sum of 600, 1000, and 1500 Hz tones) was played for 250 ms to cue the participant to return their gaze to the fixation point.

Analysis

Exclusions

For each task, thresholds were calculated based on fitting psychometric functions to participants' responses, aggregated over the two sessions. For the crowding task, we estimated critical spacing, and for the perceived spacing task, we estimated the point of subjective equality (PSE) (see Threshold calculations). Before fitting psychometric functions to the data, we excluded any unreliable threshold estimates based on the following pre-registered criteria. Locations with unreliable threshold estimates from either task were removed from the analysis based on the slope of linear fits to participants' responses. Presentation locations where the linear slope in the crowding task was less than 0.05 (i.e., a less than 5% increase in accuracy for every 1° increment in target–flanker spacing) or where the linear slope in the perceived spacing task was less than 0.25 (i.e., less than 25% increase in "larger" responses for every 1° increment in physical separation) were removed from the analysis. Also, if more than one-half of the estimates in either the crowding or the perceived spacing tasks were removed for a given participant, all responses from that participant were removed from the analysis.

Based on these criteria, one participant was excluded because they did not have six thresholds that met these preregistered criteria. Another participant was removed from the analysis, because they were unable to return for a second session. In addition, we excluded two outlier data points (critical spacing estimates of more than 10°) that were not captured by our preregistered exclusion criteria. Both points were more than 2.5 standard deviations away from the mean (3.71 and 3.10). Their removal does not change our results appreciably (for completeness, we have included the correlation analysis with these data points in Figure S1). Out of the remaining participants, 9.6%, or 23 of 240 thresholds (12 locations × 2 tasks × 10 participants) were removed from the analysis.

Threshold and just noticeable difference (JND) calculations

In the crowding task, psychometric functions were fitted to the data to determine the critical spacing, defined as the target–flanker separation at which performance reached 80% accuracy for a given location. In the perceived spacing task, for each location, we identified the PSE—the separation at which participants perceived the space between the two patches to be equal to the average of all spacings across all locations. Therefore, psychometric functions were based on fits to the proportion of "larger" responses at each separation, rather than accuracy like in our crowding task. From this, we determined the PSE from the 50% point on the function, where participants reported "larger than average" on one-half of the trials.

Previous work has also shown that spatial precision, as measured by Vernier acuity, is associated with both the strength of visual crowding (Greenwood et al., 2017) and with localization errors (Wang et al., 2020). Therefore, we also tested whether spatial sensitivity, as measured by the JND for the judgments of perceived spacing, was associated with the strength of crowding. The JND was derived from each participant's psychometric functions in the perceived spacing task by taking one-half of the distance between the 75% and 25% points on the function. Higher JND values correspond with shallower slopes and lower JND values correspond with steeper slopes.

For both tasks, two-parameter logistic functions (slope and horizontal shift) were fit to the data using a maximum likelihood criterion. For the crowding task, the floor and ceiling were constrained at 25% (chance performance) and 100%, respectively. For the spacing task, they were set to 0% and 100%. We also repeated the analyses using the lapse rate as an additional parameter to the psychometric fits and observed similar results.

Next, we determined the relationship between participants' critical spacing estimates in the crowding task and the PSE and JND estimates from the perceived spacing task using a linear mixed model (see Results). This process quantified the relationship between the target—flanker spacing each participant required to identify the orientation of the central clock (crowding) and participants' perceived spacing between pairs of

Gaussian blobs, as well as their position sensitivity at those same locations. This analysis was performed on matched pairs of points per location for each participant (i.e., all 12 data points were plotted per participant, minus any exclusions). This analysis was based on 97 matched pairs of thresholds (194 thresholds in total) between the crowding task and critical spacing task (i.e., locations for which there were measurable thresholds in both the crowding task and the perceived spacing task).

Results

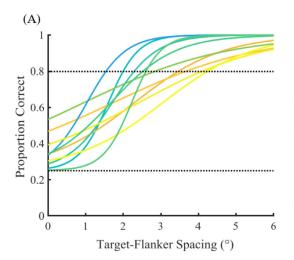
Critical spacing estimates

To compute critical spacing thresholds for all participants, we plotted the proportion of correct responses in the crowding task as a function of the spacing between target and flanker stimuli; critical spacing was defined as the 80% point on the function. Figure 2A shows a set of psychometric functions for critical spacing, with one for each location for a representative participant. Figure 3A shows the average critical spacing at each of the 12 locations tested across all participants. The average critical spacing thresholds for all participants and locations was 3.08°

 \pm 1.12°, consistent with the expected critical spacing at 8° eccentricity (Bouma, 1970; Toet & Levi, 1992).

Perceived spacing estimates

To estimate the perceived spacing between the Gaussian blobs at each location, we calculated the proportion of trials in which the participants responded "larger than average" for each spacing. The PSE was used as a measure of the perceived spacing. This point on the function indicates the physical separation required for the spacing to look like the average across all trials. In other words, we defined the PSE as the spacing at which the proportion of "larger" responses was 50% on the best-fit function. Larger PSE values correspond with a smaller perceived separation between the Gaussian blobs at a given location, and smaller PSE values correspond with a larger perceived separation. Figure 2B shows a set of psychometric functions for perceived spacing, with one for each location for a representative participant, where the line plot colors correspond with the critical spacing values shown in Figure 2A. Figure 3B shows the average PSE values across all participants. Across all participants and locations, the average PSE was $2.97^{\circ} \pm 0.21^{\circ}$ for the spacing task. Figure 3C shows the average JND values across all participants estimated from the same task, with an average JND of $0.27^{\circ} \pm 0.07^{\circ}$.



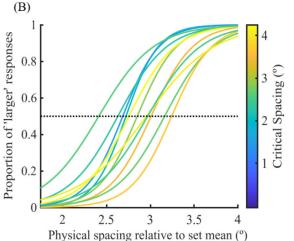


Figure 2. (A). Psychometric functions for the crowding task from a representative participant. The plot visualizes the proportion of correct responses (y axis) at different target-flanker spacings (x axis). Each psychometric function corresponds with one tested location. Critical spacing was defined as the target-flanker separation needed to reach 80% accuracy (upper dotted line). The lower dotted line indicates chance performance (25%). These results demonstrate at what target-flanker distance a participant is able to just identify the orientation of the clock. (B) Twelve psychometric functions based on a representative participant's responses in the perceived spacing task, where each function is plotted based on the proportion of larger responses (y axis) at different physical spacings (x axis); the physical set mean in Experiment 2 was 2.875°. This finding demonstrates the variability in perceived separation at each visual field location as measured with the point of subjective equality (PSE). The colors of each graph correspond with the measured critical spacing value from the crowding task.

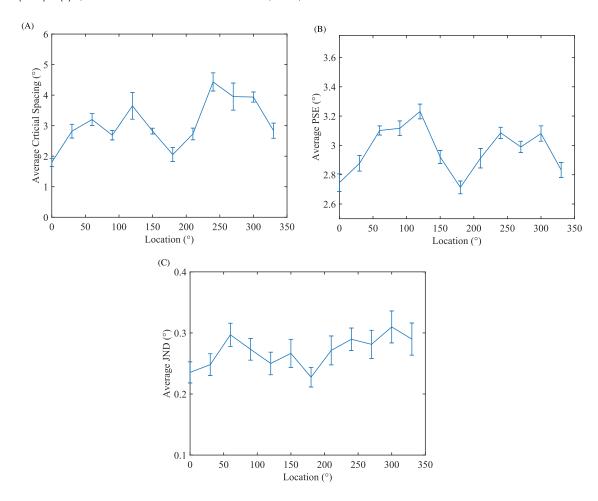


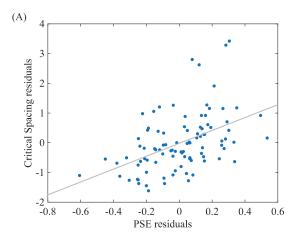
Figure 3. Group means for all 12 locations tested, showing (A) critical spacing as measured in the crowding task, as well as (B) average perceived spacing (point of subjective equality [PSE]), and (C) average just noticeable difference (JND), as measured in the perceived spacing task. Locations on the x axis correspond with the locations indicated in Figure 1C, where 0° indicates the location directly to the right of fixation and 90° indicates the location directly below fixation. Error bars represent \pm 1 standard error of the mean.

Linear mixed model analysis

We next fit a linear mixed model to the data to examine the relationship between critical spacing estimates, perceived spacing (PSE), and position sensitivity (JND). Specifically, we fit a linear model with critical spacing as the dependent variable, with fixed effects of PSE and JND value, calculated from the perceived spacing task. To account for repeated measures between observers, each participant was entered as a random effect, with a separate intercept estimated for each participant.

The results of the linear model showed a significant, positive relationship between critical spacing and PSE values, with a fixed effect coefficient of 2.17 (standard error: 0.42), F(1,94) = 26.94, p < 0.001. Figure 4A shows the unique relationship between PSE and critical spacing after taking into account the other variables in the model. These results support our hypothesis that, in

areas where crowding is stronger (as indicated by larger critical spacing values), the point of subjective point of equality (PSE) was also larger. Larger PSE values correspond with smaller perceived spacing. Therefore, in locations where crowding is stronger, perceived spacing is smaller. The direction of this relationship was also consistent across participants (as shown in Figure S2 in the Supplemental materials; all participants had a positive slope when fitted individually). Furthermore, the results of the model showed a significant, positive relationship between the JND and critical spacing (Figure 4B) with a fixed effect coefficient of 6.46 (standard error: 1.27), F(1,94) = 25.688, p < 0.001. These results demonstrate that position sensitivity is also positively associated with the strength of crowding. Areas with a higher JND (i.e., less sensitivity to changes in perceived spacing) were associated with larger critical spacing values, which means that participants experienced stronger crowding at those locations.



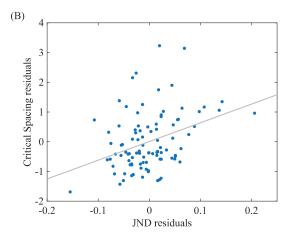


Figure 4. (A) Partial regression (i.e., added variable) plot showing the unique relationship between perceived spacing (point of subjective equality [PSE]) and critical spacing, after taking into account the effects of the other variables. Each point represents one pair of estimates for a single location. The *y* axis (critical spacing residuals) shows the residuals for critical spacing when predicted by all variables except PSE, and the *x* axis (PSE residuals) shows the residuals from regressing PSE against the other independent variables. (B) Partial regression plot showing the unique relationship between the just noticeable difference (JND) and critical spacing, following the same conventions as in (A).

In addition, we verified that these effects were not dependent on our choice of parameters for fitting the psychometric functions. Rerunning the model with the addition of a lapse rate parameter to the psychometric fits revealed similar results, with a significant positive relationship between PSE and critical spacing, F(1,94) = 25.15, p < .001, and a significant, positive relationship between JND and critical spacing, F(1,94)= 22.07, p < .001 (see the Supplemental Materials). We also verified that these results were consistent between sessions by analyzing the data separately for session 1 and session 2 (in contrast with the main analysis, which pooled responses from both sessions before fitting). In this analysis, we observed significant relationships between both the PSE and critical spacing and between the JND and critical spacing separately for each session, consistent with the finding that pairs of sessions within a given participant were well-correlated with one another (see the Supplemental Materials).

One possibility is that there may be similarities in crowding and perceived spacing across participants that are seen at the group level. For example, on average, crowding is typically stronger in the upper visual field compared with the lower visual field (He, Cavanagh, & Intriligator, 1996) and weaker along the horizontal meridian (Liu, Jiang, Sun, & He, 2009). Given that critical spacing values and PSE values were similar across participants, we determined how much the effects from the main analysis are driven by participant idiosyncrasies compared with group-level effects. If PSE values show similar asymmetries, this process could produce a significant correlation that is driven by group-level effects. In other words, we

separately analyzed the degree to which between-subject differences in perceived spacing are related to between-subject variability in crowding. To do this, we subtracted out the mean threshold estimates (the 80%) and 50% estimates for critical spacing and PSE values, respectively) for each location (across participants) from every participant's threshold estimate at that location. These resulting values provide an estimate, for a given location, of the strength of crowding (or the size of the PSE values) for a participant relative to the group mean. We then proceeded to fit the same model to these values. The results indicate a significant positive relationship between the mean subtracted JND estimates and the critical spacing values, F(1.94) = 9.28, p = 0.003, with a coefficient of 3.82 (standard error, 1.25), indicating that the relationship between critical spacing and the JND was not driven exclusively by commonalities across participants and that individual differences in position sensitivity are associated with individual differences in crowding at different visual field locations. However, we did not observe the same positive relationship between the mean subtracted PSE values and the critical spacing estimates, F(1.94) = 0.65, p = 0.42. This finding suggests that, although stronger crowding is associated with smaller perceived separation, this factor is driven by group-level effects rather than individual idiosyncrasies.

Discussion

We investigated spatial variability in perceived spacing as one explanation for variability in the strength

of crowding. We based our work on prior findings demonstrating participant-specific idiosyncrasies in crowding by location (e.g., Greenwood et al., 2017; Petrov & Meleshkevich, 2011; Veríssimo et al., 2021). Building on this work, we compared participants' differences in the strength of visual crowding around the visual field with their variability in perceived spacing between pairs of stimuli at those same locations. We predicted that, in locations where participants perceived the space between objects to be smaller, crowding would be stronger; conversely, in locations where participants perceived space between objects to be larger, crowding would be weaker. We show a significant positive relationship between critical spacing and perceived spacing (PSE) values), supporting our hypothesis. Additionally, we showed that participant-level idiosyncrasies in position sensitivity were also associated with the strength of visual crowding, such that areas with greater position sensitivity were associated with lower critical spacing estimates. However, the relationship between perceived spacing and critical spacing reflects commonalities between participants.

Our findings are consistent with previous research demonstrating similar effects, which have been shown with briefly presented Gabor patches and either flickering or drifting flankers (Dakin et al., 2011; Maus et al., 2011). Critically, in these experiments, a motion-induced shift in the perceived locations of the flankers toward the target increased crowding, and an illusory shift in perceived flanker location away from the target decreased crowding. We show similar effects in the absence of such an illusory shift, showing that crowding can be influenced by heterogeneity in perceived spacing around the visual field. However, other work has shown that the strength of crowding does not always follow illusory displacements in perceived position (e.g., Chambers et al., 2018) and can also depend on perceptual grouping and flanker arrangement (Herzog, Sayim, Chicherov, & Manassi, 2015; Manassi, Sayim, & Herzog, 2013). Critically, these results likely reflect that crowding occurs at multiple stages of visual processing and future studies could extend our paradigm to examine how these factors intersect with spatial variability in visual space

We also demonstrate that participants' sensitivity in spatial judgments to be correlated with the strength of crowding. Our results are consistent with those of Greenwood et al. (2017), who reported that areas of greater precision in spatial localization were associated with decreased crowding. Notably, in our data, participants' bias and sensitivity were associated independently with the strength of visual crowding when we controlled for the effects of the other. This finding suggests that multiple mechanisms may contribute to individual spatial variability in

the strength of crowding. In other words, greater precision would decrease crowding by helping to segregate the target from the flankers visually; spatial expansion would decrease it by increasing the apparent target–flanker separation.

More generally, our results suggest that early variability in spatial coding propagates across multiple stages of visual processing and influences processes like crowding. Although there is considerable variability in the anatomy and physiology of the visual system, less is known about how these individual anatomical differences propagate to different stages of visual processing and whether they are associated with variability in visual function. One possibility is that differences in spatial sampling at the retinal level may contribute to variability in spatial precision and bias, propagating to later cortical stages of visual processing and influencing object identification and the strength of crowding. These ideas are broadly consistent with previous studies showing large individual variability in photoreceptor density (Curcio, Sloan, Kalina, & Hendrickson, 1990), variability in the sizes of early visual areas (Andrews, Halpern, Purves, 1997), and correlations within individuals as to the size of their visual areas (Andrews et al., 1997).

Although our results show clear relationships between spatial heterogeneity in perceived spacing and crowding, further work is needed to understand fully the relationships between spatial precision, bias, and the strength of crowding. Previous work has shown that visual field locations that exhibit spatial compression are associated with higher spatial precision (Wang et al., 2020), and visual field locations where there is higher spatial precision are associated with weaker crowding (Greenwood et al., 2017). Together, this result would predict that locations with relative spatial compression should be associated with weaker crowding. That is, the relationship between perceived spacing and critical spacing would be opposite to what we observed. One possibility is that this relationship between perceived spacing and crowding might require changing the stimulus used to measure these effects. For example, there may be differences in spatial precision when measured across larger and smaller areas of the visual field. For example, Wang et al. (2020) used a Vernier task used to measure acuity, a fine scale task that measures spatial resolution limits. In contrast, we measured perceived location with relatively large peripheral patches, similar to our measures of spatial precision and bias. In addition, estimates of spatial compression in their study were based on a single stimulus shown at a time, which might produce different location estimates compared with pairs of images shown at the same time. Future studies may need to bear these differences in mind to examine position sensitivity and bias at different spatial scales.

Our research expands on the subject-specific nature of crowding and demonstrates a relationship between idiosyncratic variability in spatial precision and the strength of crowding. Because visual crowding plays a large role in our daily interactions, like identifying the pedestrian in the road, understanding individual variability underlying this process might allow a better understanding of how it impacts real-world behavior. Driving is a prime example where the effects of crowding have the ability to result in catastrophic events (Xia, Manassi, Nakayama, Zipser, & Whitney, 2020), and understanding what might influence crowding could help us to mitigate its effects outside the laboratory, because it may help to explain the individual variability in crowding at specific locations.

Future studies could also examine the relationship between space perception and other tasks where crowding may limit performance, like visual search. Veríssimo et al., (2021) demonstrated that crowding constrains participants' ability to find items in a display and related it to differences in individual visual search performance. We speculate that it may be possible to trace differences in search performance back to individual variability in spatial precision and heterogeneity in perceived spacing, because it affects crowding, which may, in turn, impact visual search performance. It may be informative to think about crowding within a search array as varying for each individual as a function of their spatial idiosyncrasies across the visual field. This point might mean that the effects of crowding at specific visual field locations (e.g., more crowding in one area versus another) may impact where an observer looks next and how well (or easily) they can find their target. Future work might also benefit from investigating a larger sample size to capture the full range of individual differences in spatial coding.

We demonstrate that spatial heterogeneity in perceived spacing affects observers' ability to recognize objects in the periphery. Our results support the account that multiple mechanisms may contribute to individual spatial variability in the strength of crowding and provide further evidence, supporting the idea that variability in spatial coding propagates across multiple stages of visual processing. We suggest that future work examining how crowding contributes to behavior should incorporate an understanding of each participant's idiosyncrasies to fully explain why each participant perceives the world the way they do, rather than ignoring these stable idiosyncrasies and simply looking at the group as a whole.

Keywords: crowding, perceived spacing, individual differences, perception

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