Simultaneously and sequentially presented arrays evoke similar visual working memory crowding

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Abstract

Visual crowding is a widely observed perceptual phenomenon in which the representation of a target item is degraded in the presence of adjacent flanker items. Recently, crowding has also been observed between location-specific items maintained in visual working memory (VWM), and such VWM crowding has achieved importance as a way to evaluate shared mechanisms between memory and perception. However, some previous studies that investigated VWM crowding claimed that VWM crowding errors stemmed from inter-item competition or failures of item-location binding during encoding, rather than crowding during maintenance. In the current study, we tested VWM crowding using simultaneously presented arrays. We evaluated two indices of crowding: anisotropy of crowding for radially vs. tangentially configured arrays, and proximity of targets to the remainder of the array (array middle vs. array edge targets). Simultaneously presented arrays evoked both VWM crowding and crowding anisotropy. We then compared the data from the current study to that from our previous study that used sequential array presentation, which are generally taken to rule out encoding-based explanations for crowding effects. We predicted that we would observe greater crowding for simultaneous than sequential crowding because simultaneous array presentations allow for two opportunities for crowding—encoding and maintenance—while sequential array presentations only allow for maintenance-based crowding. Surprisingly, we observed that both crowding indices were similar across simultaneous and sequential array presentations. These results indicate that VWM crowding does not have an additive error mechanism across encoding and maintenance stages, and is influenced by retinotopy in the early visual cortex whether the VWM arrays are presented sequentially or simultaneously.

Keywords: Visual working memory, crowding, sensory recruitment, simultaneous versus sequential

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Visual crowding is a perceptual phenomenon in which report of a target item is impaired by proximity to other items, termed flankers. There are at least two theoretical explanations for crowding. First, visual crowding is sometimes attributed to a failure of target individuation, such that target and flanker item features are pooled into a common representation (Freeman, Chakravarthi & Pelli, 2011; Whitney & Levi, 2011). Second, visual crowding is sometimes attributed to a failure of the visual system to reliably select the target from among the other item representations, leading to substitution of a flanker for a target at report on some trials (Ester, Klee & Awh, 2014; Ester, Zilber & Serences, 2015). These explanations are not mutually exclusive (Tamber-Rosenau, Fintzi & Marois, 2015). Regardless of mechanism, the effect of visual crowding is that the accuracy of target reports is reduced when the targets are surrounded by adjacent flanker items (Bouma, 1970; Whitney & Levi, 2011). The crowding effect decreases as target-flanker separation increases. Moreover, the critical distance—the maximum distance between the target and flanker items at which crowding is observed—is determined by the ratio between the target-flanker distance and the target item's eccentricity (Bouma's law: Bouma, 1970). Visual crowding is most easily observed in peripheral vision because the critical target-flanker separation is vanishingly small in central vision (Coates, Levi, Touch & Sabesan, 2018); the scaling of critical separation with eccentricity is thought to be due to cortical magnification, mostly in the retinotopic early visual cortical regions (Holmes, 1918; Horton & Hoyt, 1991). Thus, crowding can be at least partially localized to the early visual cortex.

Visual crowding is not determined only by target-flanker separation and target eccentricity; a variety of other features of the stimulus array can modulate it. In particular, a hallmark of visual crowding is radial-tangential anisotropy (Toet & Levi, 1992), in which the crowding effect is stronger when the stimulus array is configured radially (perpendicular to an imaginary circle that is surrounding the central visual field), rather than tangentially (parallel to an imaginary circle that is surrounding the central visual field). This radial-tangential anisotropy is thought to be explained by the retinotopic organization of the early visual cortex because, for a given real-world target-flanker separation, flankers in a radial array are represented closer to the target in cortical retinotopic maps than are flankers in a same-real-world-distance tangential array. This relation between visual eccentricity and cortical distance is claimed to be possibly explained by the number of neurons in early visual cortex, with the number of neurons that are representing the visual stimulus logarithmically decreasing as the target eccentricity increases (Pelli, 2008). The decrease in the number of neurons leads to a higher rate of crowding effect for radially configured perceptual arrays than the tangentially configured ones due to the retinotopic mapping in early visual cortex (Harrison & Bays, 2018; Pelli & Tillman, 2008; Toet & Levi, 1992). Further evidence for this explanation comes from fMRI studies that utilized retinotopic mapping of early visual areas (Engel, Glover & Wandell, 1997; Qiu et al., 2005). Decreases in BOLD signal in V1 were found to be correlated with the strength of crowding effect (Millin, et al. 2014), and the reduction in BOLD signal was greater when the stimuli was configured radially compared to tangentially (Kwon et al., 2014; Malania et al., 2020). Because crowding, in general, is at least partially explained by the organization of the early visual cortex and the radial-tangential crowding anisotropy, in particular, is thought to be mainly or entirely explained by the organization of the early visual cortex, the observation of crowding—and, especially, radial-tangential anisotropy—in behavioral reports suggest that those reports depend on representations in early visual cortex (Harrison & Bays, 2018). The ability to infer the locus of representation in the brain from behavioral reports has made visual crowding an important measure in visual cognition research.

Recently, visual crowding has been used to investigate the locus of visual working memory (VWM) representations by asking whether crowding can be observed among items represented in VWM in accordance with the predictions of the sensory recruitment model (Harrison & Bays, 2018; Tamber-Rosenau et al., 2015; Yörük et al., 2020). The sensory recruitment model predicts that VWM representations rely on the same cortical machinery as perceptual vision, and thus, VWM representations should show hallmarks of perceptual representations in the early visual cortex. The sensory recruitment model of VWM has been supported by the observation of sustained neural representations in early visual areas when the perceptual stimuli are no longer available (Ester, Serences & Awh, 2009; Harrison & Tong, 2009) as well as a range of other evidence (Adam, Rademaker & Serences, 2021).

According to a strong version of the sensory recruitment model, both perceptual and VWM representations are maintained in the same retinotopic neural population. On the other hand, according to a more flexible form of the sensory recruitment model, VWM information is still represented in the early visual cortex (Ester, Serences & Awh, 2009; Rademaker, Chunharas & Serences, 2019; Yörük, et al., 2020), but those representations can be more global or rely on distinct neural populations from ongoing visual processing. Indeed, previous studies show that when a VWM task did not require spatially specific encoding, activity for memory content can be decoded from the cortex that is either contralateral or ipsilateral to the visual stimuli (Ester et al., 2009). On the other hand, when the VWM task required location-bound representations, classification of the memory activity from contralateral visual areas was higher than the ipsilateral areas to the stimuli, suggesting that VWM representations were encoded in a spatially specific manner (Pratte & Tong, 2014).

In an early study, Emrich and Ferber (2012) investigated whether competition among the representation of target and not-target VWM items occur during the encoding stage, before VWM maintenance. To achieve that, they varied set size and proximity of color patches and reported more swap errors (in which a non-target item was reported) with greater inter-item proximity in a VWM delayed estimation task. However, Emrich and Ferber (2012) concluded that this phenomenon was a product of encoding error, not VWM representation per se, because presenting the color patches sequentially instead of simultaneously abolished the effect. Thus, this study could not adjudicate the locus of sustained VWM representations.

Subsequently, Tamber-Rosenau et al. (2015) examined the crowding of oriented bars in VWM. While Tamber-Rosenau et al. (2015) used only simultaneous arrays, they compared a memory condition to a perceptual condition in which the visual arrays remained on screen during the response period. By comparing errors on VWM trials to those on perceptual trials, they were able to conclude that crowding could arise between items held in VWM. Specifically, while they observed similar amounts of crowding for perception and VWM, VWM crowding was primarily explained by swap errors while perceptual crowding was explained by a mixture of swap errors and reduced representational precision. Critically, Tamber-Rosenau et al. (2015) required participants to report target location (rather than orientation) on half of the trials, with the to-be-reported feature cued only at the end of the delay period, and thus, only after there was an opportunity for crowding to occur in VWM. The timing of the report cue coupled with the need to report precise spatial locations on half of the trials enforced representation of precise spatial locations, which may explain why Tamber-Rosenau et al. (2015) observed crowding within

VWM representations and Emrich & Ferber (2012) did not. Tamber-Rosenau et al. (2015) concluded that their observations supported the sensory recruitment model in that similar error magnitude was observed for perception and VWM, but they also concluded that the ongoing item representations in VWM were transformed from visual representations. In essence, they argued for a flexible form of sensory recruitment rather than a strong form of sensory recruitment in which the exact perceptual representations are sustained over time in order to create VWM representations.

Another subsequent study (Ahmad et al., 2017) varied presentation timing and proximity for color patches and found, like Emrich & Ferber (2012), that crowding was abolished via sequential array presentations. However, crowding was restored, even for sequential presentations, when participants were required to sometimes report item location instead of color (c.f., Tamber-Rosenau et al., 2015). Thus, these important results explain the differential findings of Emrich & Ferber (2012) and Tamber-Rosenau et al. (2015) while supporting the idea that crowding may arise both at encoding and during maintenance.

Harrison & Bays (2018) questioned the interpretation of prior studies as reflecting sensory recruitment. Specifically, they examined orientation crowding for radial and tangential arrays of oriented bars, but used sequential presentation of the target/flanker arrays to prevent crowding during encoding. They observed no radial-tangential crowding anisotropy, which, they suggested, rejects the sensory recruitment model because crowding anisotropy is thought to arise in the early visual cortex, as detailed above. However, their study also did not require participants to maintain location information.

Recently, we conducted a study to further test the sensory recruitment model of visual working memory (Yörük, et al., 2020) by replicating and extending Experiment 1 from Harrison and Bays (2018). Like Harrison and Bays (2018), we displayed VWM arrays consisting of three sequentially-presented oriented bars with the central array item positioned at 10 degrees of eccentricity. Unlike Harrison and Bays, we presented the arrays at random locations on an imaginary circle around central fixation instead of using a single fixed location. This allowed us to post-cue report of either target location (50% of trials) or orientation, rather than requiring report of target orientation only. With the requirement to maintain location information, we observed both significant crowding (greater error in orientation delayed estimation for the middle array element vs. the edge elements) and significant crowding anisotropy (greater error in orientation delayed estimation for radial vs. tangential arrays). Critically, in a further control experiment in which we did not require location report on any trials (while keeping the rest of the experiment design the same), we no longer observed the radial-tangential crowding anisotropy nor did we observe statistically significant crowding (Yörük, et al., 2020). Overall, these results indicated that, when spatially detailed information is needed, VWM items are represented in the early visual cortex—consistent with the sensory recruitment model. However, when encoding of the spatial information is no longer necessary, VWM items might be represented more globally in a flexible manner (also see Ester et al., 2009; Pratte & Tong, 2014).

In general, past VWM crowding research has assumed that crowding may take place at encoding (Ahmad et al., 2017; Emrich & Ferber, 2012; Tamber-Rosenau et al., 2015) and during maintenance (Ahmad et al., 2017; Tamber-Rosenau et al., 2015; Yörük, et al., 2020). However, this assumption has had limited tests (Ahmad et al., 2017; Emrich & Ferber, 2012). Moreover, no past research has examined radial-tangential crowding anisotropy in VWM as a function of sequential vs. simultaneous arrays; put differently, no past research has examined the difference between simultaneous and sequential array presentations for the index of VWM crowding that is most clearly attributable to retinotopic representations in early visual cortex. As reviewed above, previous studies demonstrated VWM crowding for both simultaneous (Tamber-Rosenau et al., 2015) and sequential (Yörük, et al., 2020) arrays of oriented bars. However, these two studies used very different array and cue parameters, making it difficult to compare results across them. Moreover, Tamber-Rosenau et al. (2015) used only (roughly) tangential arrays, meaning that that study did not estimate radial-tangential anisotropy at all. Thus, in the present study, we evaluated VWM for simultaneously presented arrays but with other parameters identical to Yörük et al. (2020). This allowed novel estimates of VWM crowding and radial-tangential crowding anisotropy. In addition, we compared these new data to the previously-reported crowding and crowding anisotropy estimates from Yörük et al. (2020). We reasoned that, with simultaneous array presentations, we would expect errors stemming from both perceptual competition during encoding and additional errors stemming from competition during ongoing VWM maintenance—in other words, we would expect greater VWM crowding for simultaneous than sequential arrays. To anticipate the results, we instead observed similar amounts of crowding regardless of the array presentation sequence.

Method

Participants

Twenty-four adult participants (15 females, 8 males, 1 preferred not to answer, mean age 20.13 years, range 18-26) were recruited from the University of Houston, under a protocol approved by the University of Houston Institutional Review Board. An initial model-based analysis[1] (Harrison & Bays, 2018; Yörük, et al., 2020) was fit to each participant, which ensured that the present data were comparable to that of Yörük et al. (2020). One participant's data could not be fit by the model. Based on this quality-control measure, this participant was excluded from all analyses. Thus, a total of 23 participants were included in all analyses reported in the present work. We provided participants either extra credit in their coursework or Amazon.com gift cards as compensation.

Task

We followed the procedure of the main experiment from Yörük et al. (2020), with some modifications. Briefly, participants viewed an array of oriented bars in either a radial or tangential arrangement (Figure 1). The middle item of the array was always presented at 10 degrees of eccentricity. In contrast to Yörük et al. (2020), which used sequential presentation of array items with a 500 ms ISI, the present experiment presented all array items simultaneously. The presentation phase lasted for 500 ms (the same amount of time for which each item was presented in Yörük et al., 2020). We chose to present the arrays for 500 ms (rather than 1500 ms, i.e., the summed presentation time from Yörük et al., 2020) for efficiency and because past evidence suggests that simultaneously-presented arrays are encoded in parallel, not serially (Bays et al., 2011). As in Yörük et al. (2020), participants viewed a blank screen following array presentation (i.e., during the delay period). At the end of this period, they heard a verbal post-cue to report either the “tilt” (orientation) or “place” (location). Then, they saw a visual cue

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[1] In this analysis, the data were fit using maximum likelihood estimation to a model which estimates frequencies of correct reports of the cued item, swaps in which a non-target item from the sample is reported, or guess trials in which an orientation is reported at random (Bays, Catalao & Husain, 2009). Two versions of this model were compared. Specifically, one model assumed separate sets of parameters for radial and tangential trials, while the other model fit a single set of parameters to radial and tangential trials.These model fit analyses are not included in the current paper because fit indices showed that neither model provided a good fit for the data in either Yörük et al. (2020) or the present novel data. The analysis code was adapted from code kindly provided by William J. Harrison (William J. Harrison, personal communication, 18 July 2018).

indicating which array item should be reported before engaging in a delayed estimation procedure. To equilibrate the (mean) delay period between item presentation and the delayed estimation cue with that from Yörük et al. (2020), we set the delay period to 1500 ms. In the main experiment of Yörük et al. (2020), the temporal order of the target item was considered as a factor and counterbalanced across the trials. With the simultaneous presentation of the current experiment, the temporal order factor was eliminated, therefore the total number of trials was reduced to one-third of the sequential experiment. As a result, data from each participant was collected in a single session, instead of the 3-session experiment of Yörük et al. (2020). All other task parameters were identical to Yörük et al. (2020). Thus, the experiment consisted of 216 trials in total, with 12 trial types (two response types – location or orientation; two stimulus array configurations – radial or tangential; and three spatial array positions).

In perceptual crowding research, reports generally refer to the array elements as a singular target (typically the center element of the array) and one or more flankers (all other array elements). This language is not applicable to VWM crowding because, in order to incentivize encoding of the entire array, it is critical that each array element is sometimes probed. In other words, each array position is sometimes a target and sometimes a flanker. Thus, for the remainder of this paper, we adopt distinct language from the visual crowding literature: instead of targets and flankers, we refer to *middle* and *edge* elements of the array. In contrast to most visual crowding research, edge elements may be targets.

Apparatus and Procedure

The experiment was run on a computer operating on KUbuntu Linux 16.04 LTS and displayed on a 21-in CRT (40 cm x 30 cm) monitor with a resolution of 1600 x 1200 pixels. The participants sat at a 60 cm (approximate) viewing distance from the monitor. With a 60 cm viewing distance, one pixel corresponds to approximately 0.023 deg visual angle (43.4 pixels per degree of visual angle). Central fixation was monitored by an Eyelink 1000 Plus eye tracker at a 500-Hz sampling rate. The eye tracker was configured in remote mode, meaning that participant head location was monitored and compensated for by the eye tracker, but the head location was not fixed. This ensures participant comfort and thus limits distraction during relatively long task sessions. The experiment was programmed in MATLAB using Psychophysics Toolbox (Kleiner, Brainard, & Pelli, 2007) and the Eyelink Toolbox (Cornelissen, Peters, & Palmer, 2002), and was based on the task of Harrison and Bays (2018), with code generously shared by W. Harrison (personal communication, 18 July 2018).

Each trial (Figure 2) began with the presentation of a fixation dot at the center of the screen for 500 ms. After the initial fixation, the three-element stimulus array appeared and stayed on the screen for 500 ms. The stimulus array consisted of three randomly oriented bars (sized 2 x 0.2 degrees of visual angle). Each bar was colored either red, blue, or green, in order to facilitate later cueing of one bar for report. On each trial, the center of the middle target item in the array was positioned at a random location on an imaginary circle (radius: 10 degrees of visual angle) around a fixation point. In half of the trials, the stimulus array was configured radially (perpendicular to the imaginary circle). In the other half, the array was configured tangentially (parallel to the imaginary circle). Radial and tangential configuration conditions were randomly mixed across trials throughout the whole experiment. In both configurations, the distance between center points of the middle and edge targets was 2 degrees of visual angle. After the stimulus array was displayed for 500 ms, it was replaced by a fixation-only VWM delay screen lasting 1500 ms. Following the delay, participants were randomly cued to report either the location or orientation of a randomly selected bar from the array.

On orientation-report trials, participants heard a voice saying “tilt,” and the target item was indicated by the color of a centrally presented response probe circle. After the response type and target color cues, a response probe bar appeared at central fixation upon mouse movement, and the participants rotated the response probe bar using the mouse until it matched their recollection of the orientation of the cued bar. Participants completed their responses with a left-click of the mouse.

On location-report trials, participants heard a voice saying “place,” and a colored response probe circle indicated the color of the target item. Upon the mouse movement, a colored response dot appeared, and the participants were asked to move the response dot to the remembered location of the target stimulus. Participants completed their responses by clicking the left mouse button.

Central fixation was monitored throughout each trial by the eye tracker. When the distance between the locus of the gaze of the participant and the central fixation dot exceeded 2 degrees of visual angle, that trial was terminated and a warning message reminded the participant of the central fixation requirement. Terminated trials were replaced by trials of the same condition and added to the end of the experiment with the same parameters.

Before the main experiment procedure, participants completed practice trials in order to become familiar with the task. Practice trials consisted of two six-trial mini-blocks (with three radially and three tangentially configured arrays per block) for orientation and location report tasks, separately.

Sequential Experiment

The sequential experiment data that are used in this paper were initially reported in a previous publication (Yörük et al., 2020). That experiment's procedure was identical to the (novel) simultaneous experiment reported here, except for the stimulus presentation phase and delay duration. In the sequential experiment, each bar was presented one after another for 500 ms, with 500 ms of fixation-only inter-stimulus intervals in between. After the presentation of the last stimulus, another fixation-only VWM delay screen was presented for 500 ms.

Results

Simultaneous Experiment

In this experiment, we estimated VWM crowding and radial-tangential crowding anisotropy for simultaneously-presented arrays. We used circular standard deviation (expressed in radians) to characterize the error between the orientation reports and the actual orientations of the target items (Harrison & Bays, 2018); this descriptive statistic was calculated using the cstd.m MATLAB code retrieved from the Paul Bays' lab website (https://www.paulbays.com/toolbox), which implements the circular standard deviation as described by Fisher (1995). This circular standard deviation approach takes into account the fact that errors "wrap around" a circle. We compared orientation report errors using both standard and Bayesian paired sample t-tests.

Initially we performed a 2-way within-subjects ANOVA with the stimulus array configuration (radial vs. tangential) and position (middle vs. edge) conditions. We observed a significant main effect of position ($F(1,22) = 16.528$, $p < .001$, $\eta_p^2 = 0.429$, BF (in favor of inclusion) = 447.171), with higher orientation report errors for the middle targets compared to edge targets. This effect is evidence of crowding because the middle targets are flanked on two sides by non-targets and the edge targets are flanked on only one side by a non-target. We also observed a main effect of stimulus configuration ($F(1,22) = 6.525$, $p = .018$, $\eta_p^2 = 0.229$, BF (in favor of inclusion) = 5.017), with higher errors for radial configurations than tangential. This effect is evidence of the radial-tangential crowding anisotropy. There was also a significant position X configuration interaction effect ($F(1,22) = 5.571$, $p = .028$, $\eta_p^2 = 0.202$, BF (in favor of inclusion) = 5.265). Interpretation of these effects is complicated by the different eccentricities for middle targets and tangential edge targets (10 degrees) compared to radial edge targets (8 or 12 degrees), motivating further analyses of crowding anisotropy for middle targets only, and separate consideration of crowding (edge vs. middle targets) for radial and tangential configurations, as reported below.

To estimate crowding anisotropy, we compared the orientation-report errors of middle targets across radial and tangential arrays. This analysis revealed significantly higher errors for radial configurations ($M = 1.35$, $SD = 0.35$) compared to tangential configurations ($M = 1.14$, $SD = 0.43$), $t(22) = 2.79$, $p = 0.005$, Cohen's d = 0.58, BF (in favor of a difference) = 9.26, one-tailed (Figure 3).

We also estimated overall crowding by comparing orientation report errors for middle vs. edge targets, and we performed this comparison separately for the radial and tangential arrays because of the known anisotropy that was also observed in the present data (see preceding paragraphs), and to better understand the nature of the interaction between crowding and anisotropy. For the radial configurations, orientation report errors were significantly higher for middle targets ($M = 1.35$, $SD = 0.35$) than edge targets ($M = 1.06$, $SD = 0.34$), $t(22) = 5.11$, $p < 0.001$, Cohen's d = 1.06, BF (in favor of a difference) = 1221.45, one-tailed (Figure 4).

Consistent with the anisotropy measured by comparing middle items across array configurations, there was less crowding for tangential arrays. Specifically, the difference between middle (M = 1.14, SD = 0.43) and edge (M = 1.04, SD = 0.30) target orientation reports revealed a smaller crowding effect that did not achieve statistical significance ($t(22) = 1.44$, $p = 0.082$, Cohen's d = 0.30, BF (in favor of a difference) = 0.98, one-tailed) (Figure 5).

In addition, we evaluated another hallmark of visual crowding, the inner-outer anisotropy for radially configured arrays. Typically, more visual crowding is obtained from flankers positioned further from fixation than the target compared to flankers positioned closer to fixation than the target (Petrov et al., 2007; Whitney & Levi, 2011). To evaluate this effect in the present data, we compared the inner-edge (more eccentric flankers) and outer-edge (less eccentric flankers) targets, and, consistent with the typical visual crowding results, the orientation report errors were significantly higher for the inner-edge targets (M = 1.31, SE = 0.079), compared to outer-edge targets (M = 0.968, SE = 0.078), t(22) = 2.436, p = .012, one-tailed, Cohen's d = 0.508, BF (in favor of a difference) = 4.78. It should be noted that inner vs. outer is confounded with eccentricity such that inner targets would be expected to have less error than outer targets, were it not for this inner-outer crowding anisotropy effect.

Sequential Experiment

As previously reported (Yörük et al., 2020), the sequential experiment supported the existence of crowding anisotropy. Here, we first present a 2-way repeated-measures ANOVA with configuration (radial vs tangential) and position (middle vs edge) on the sequential data from Yörük et al. (2020). This analysis showed that there was a significant effect of configuration with higher orientation report errors for the radial configurations than the tangential configurations ($F(1,23) = 43.625$, $p < .001$, $\eta_p^2 = 0.655$, BF (in favor of inclusion) =

2.513). There was a main effect of position with higher orientation report errors for middle targets than the edge targets ($F(1,23) = 5.322$, $p = .030$, $\eta_p^2 = 0.188$, BF (in favor of inclusion) = 4.037×10^6). The configuration X position effect was just above the threshold for statistical significance ($F(1,23) = 4.194$, $p = .052$, $\eta_p^2 = 0.154$, BF (in favor of inclusion) = 3.556).

Orientation report errors for the middle items were significantly higher when the arrays were radially configured (M = 1.45, SE = 0.07), compared to tangentially configured arrays (M = 1.32, SE = 0.06):, $t(23) = 2.49$, $p = .01$, one-tailed, Cohen's d = 0.509, Bayes factor (in favor of a difference) = 5.31. Also, the overall VWM crowding effect was supported by the comparisons of middle and edge target errors. When the arrays were configured radially, orientation report errors for middle targets (M = 1.45, SE = 0.07) were significantly higher than edge targets (M = 1.18 rad, SE = 0.05), $t(23) = 6.17$, $p < .001$, one-tailed, Cohen's d = 1.259, Bayes factor (in favor of a difference) = 14316.04. For the tangential arrays, middle target errors were significantly higher (M = 1.32, SE = 0.06) compared to edge targets (M = 1.17, SE = 0.05), $t(23) = 3.53$, $p < .001$, one-tailed, Cohen's d = 0.720, Bayes factor (in favor of a difference) = 41.86 (Yörük et al., 2020).

A further analysis that was not reported by Yörük et al. (2020) revealed significant effects of temporal order. A two-way ANOVA on middle target errors with configuration (radial vs. tangential) and temporal order (1^{st}, 2^{nd}, and 3^{rd} item in the sequence) showed that there was a significant main effect of temporal order ($F(2,46) = 111.23$, $p < .001$, $\eta_p^2 = 0.829$, BF (in favor of inclusion) approaches infinity), while the radial and tangential difference were not observed in this analysis ($F(1,23) = 0.009$, $p = .925$, $\eta_p^2 < 0.001$, BF (in favor of inclusion) = 0.239). According to a post-hoc comparison of the temporal order conditions, orientation report errors were significantly lower for the 3^{rd} item in the sequence compared to the 1^{st} ($t = 13.35$, $p_{bonff} <$

0.001) and 2nd (t = 12.433, $p_{bonff} < 0.001$) items, while the errors for the 1st and 2nd items were similar to one another (t = 0.917, $p_{bonff} = 1.000$). These results revealed a strong recency effect for the sequentially presented visual working memory displays that appears to swamp the radial-tangential crowding anisotropy effect.

Comparison of Simultaneous vs. Sequential Experiments

Critically, though the present data were acquired in a new set of participants, the task was identical to that of Yörük et al. (2020) except that VWM arrays were presented simultaneously, not sequentially. This enables comparison of the present results to the previously-published VWM crowding and crowding anisotropy results, which can address the prediction that simultaneous arrays should lead to greater crowding because they are crowded during both encoding and maintenance. Therefore, we compared orientation report errors from the simultaneously presented VWM memory array in the present study to the sequentially presented VWM arrays in the Yörük et al. (2020) study.

For the experiment-wise comparison analysis, we conducted a 3-way ANOVA including the position (middle vs. edge) and configuration (radial vs. tangential) as within-subjects variables, and experiment (sequential vs. simultaneous) as a between-subjects variable. The 3-way ANOVA revealed that there was a main effect of position ($F(1,45) = 50.945$, $p < 0.001$, $\eta_p^2 = 0.531$, BF (in favor of inclusion) = 3.992×10^9) and configuration ($F(1,45) = 11.766$, $p = 0.001$, $\eta_p^2 = 0.207$, BF (in favor of inclusion) = 87.496). However, the main effect of experiment was not significant ($F(1,45) = 2.831$, $p = 0.099$, $\eta_p^2 = 0.059$, BF (in favor of inclusion) = 0.615), and the difference between experiments was numerically opposite the predicted direction: the simultaneous experiment had numerically less error compared to the sequential experiment. The position X configuration ($F(1,45) = 9.821$, $p = 0.003$, $\eta_p^2 = 0.179$, BF (in favor of inclusion) = 18.388) interaction was significant; however, the position X experiment ($F(1,45) = 0.141$, $p = 0.709$, $\eta_p^2 = 0.003$, BF (in favor of inclusion) = 0.361), configuration X experiment ($F(1,45) = 0.759$, $p = 0.388$, $\eta_p^2 = 0.017$, BF (in favor of inclusion) = 0.371), and position X configuration X experiment ($F(1,45) = 0.474$, $p = 0.495$, $\eta_p^2 = 0.010$, BF (in favor of inclusion) = 0.135) interactions were not statistically significant.

As an additional comparison of radial-tangential crowding anisotropy across experiments, we conducted a mixed ANOVA with a between-subjects factor of experiment (simultaneous vs. sequential) and a within-subjects factor of array configuration (radial vs. tangential) on middle targets only. There was a main effect of configuration ($F(1,45) = 13.999$, $p < .001$, $\eta_p^2 = 0.237$, BF (in favor of inclusion) = 39.774); however we observed neither a significant main effect of experiment ($F(1,45) = 2.47$, $p = 0.12$, $\eta_p^2 = 0.052$, BF (in favor of inclusion) = 0.83), nor an experiment x configuration interaction ($F(1,45) = 0.79$, $p = 0.38$, $\eta_p^2 = 0.017$, BF (in favor of inclusion) = 0.75) (Figure 6). These results suggest that, contrary to expectations, VWM radial-tangential crowding anisotropy is similar for simultaneous and sequential stimulus presentations. Though the BFs are close to 1.0 and thus not dispositive, the effect sizes—particularly for the interaction of radial-tangential anisotropy and experiment—are miniscule.

As an additional investigation of the overall crowding effects identified in the omnibus ANOVA, we examined the effects of position (middle vs. edge) and experiment by looking at the orientation report error differences between middle vs. edge targets, separately for radial and tangential arrays. For radial arrays, there was no main effect of experiment ($F(1,45) = 1.746$, $p = 0.193$, $\eta_p^2 = 0.037$, BF (in favor of inclusion) = 0.648) and no experiment x position interaction

($F(1,45) = 0.033$, $p = 0.858$, $\eta_p^2 < 0.001$, BF (in favor of inclusion) = 0.527). Again, while the BFs were not dispositive, the standardized effect size of the interaction was miniscule (Figure 7).

For tangential configurations, there was a marginal main effect of experiment ($F(1,45) = 3.513$, $p = 0.067$, $\eta_p^2 = 0.072$, BF (in favor of inclusion) = 1.148) with higher errors in the sequential experiment than the simultaneous errors. However, there was again no experiment x position interaction ($F(1,45) = 0.490$, $p = 0.488$, $\eta_p^2 = 0.011$, BF (in favor of inclusion) = 0.776). Once again, the interaction effect size was miniscule, and the marginal main effect was opposite to the prediction of greater crowding for simultaneous (compared to sequential) arrays (Figure 8). Together, these results are contrary to our predictions: we expected relatively high crowding errors in the simultaneous experiment due to accumulation of crowding errors over perceptual crowding (at encoding) and VWM crowding (during maintenance). We thus expected relatively low crowding errors in the sequential experiment, because no crowding could take place at encoding. Instead, we observed similar amounts of crowding for both array presentation procedures.

Location-report trials were included only to enforce spatially-localized VWM representations, and they are not informative for the central questions of the present study. In particular, in contrast to orientations, locations of array items were not independent of one another, complicating the interpretation of any location analysis. Moreover, there are not clear predictions for how they should vary across conditions because of cortical magnification—for further discussion, see Tamber-Rosenau et al. (2015) and Yörük et al. (2020). Nevertheless, for the sake of completeness, we report an analysis of location report errors. Specifically, we compared targets presented in the middle (pooled across radial and tangential conditions) across the sequential and simultaneous experiments. A t-test showed that the participants who were run on the sequential experiment had significantly higher location-report errors (M = 85.64 pixels, SD = 16.07), compared to the simultaneous experiment (M = 72.47, SD = 18.94), $t(45) = 2.58$, $p = 0.007$, Cohen's d = 0.75, BF (in favor of a difference) = 7.709, one-tailed[2]. This result is not surprising because all arrays took on one of two possible configurations, radial or tangential. Thus, reporting a location could be accomplished with support from both individual stimulus location information and from long-term knowledge of the array configurations coupled with knowledge of the global position of the sample on any given trial. The sample's position might be more easily encoded for the simultaneous array because the simultaneous array allows for ensemble coding of an average location (Alvarez & Oliva, 2008). The location reports in the simultaneous experiment might thus be biased towards the mean location of the array. On the other hand, ensemble coding seems unlikely in the sequential experiment due to the long delays between items (500 ms presentation plus 500 ms blank interval). Moreover, were ensemble coding playing a role in the sequential experiment, its impact would be less clear than for the simultaneous experiment because temporal summation of spatial features presented sequentially

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[2] Since the orientation report errors were lower overall for the simultaneous experiment, one might think that, when the orientation report task is less demanding, it frees up resources for location task performance, and that might explain the lower location-report errors for the simultaneous experiment compared to sequential experiment. Were such a resource trade-off hypothesis correct, the less difficult orientation conditions (tangentially configured) should also free resources for location task (compared to the more difficult radial orientation conditions). Thus, separately in each experiment, we compared the location-report errors across radial (orientation-difficult) and tangential (orientation-easy) configurations. In the sequential experiment, the Bayes factor was equivocal (BF01 = 0.945, t(23) =-1.937, p = 0.065), neither providing evidence for or against the null hypothesis. In the simultaneous experiment, the evidence was inconsistent with the resource trade-off hypothesis (BF01 = 3.682, t(22) =-0.692, p = 0.496), suggesting that location errors were equivalent across easy and difficult orientation trials. We also reasoned that, with middle targets being more difficult for orientations, we might see differences between middle and edge targets for locations. When we compared the location errors across middle and edge targets for the tangential configurations, again there was no difference (sequential experiment: BF01 = 1.928, t(23) = -.1.146, p = 0.170; simultaneous experiment: BF01 = 2.916, t(22) = -.1.003, p = 0.327). However, when we compared the location errors across middle and edge targets for the radial configurations, middle targets had lower location report errors than edge targets (sequential experiment: BF01 = 0.173, t(23) = -2.897, p = 0.008; simultaneous experiment: BF01 = 0.651, t(22) = -2.167, p = 0.041). These results are contrary to the above defined resource trade-off hypothesis, though any location analysis must be interpreted with caution since, unlike orientations, locations are dependent among items in the present experiments.

has been shown to be biased towards the earlier items of the sequences (Hubert-Wallander & Boynton, 2015). In the sequential experiment, if there is ensemble encoding, location reports might be more erroneous due to reliance on the first item presented. Two thirds of the time, the first item is an edge item, which, at least on radial trials, is at a different eccentricity from the middle item. On the other hand, location reports of the simultaneous arrays can utilize the mean position of the array items as a whole, encouraging precision.

Discussion

In this study, we aimed to investigate whether VWM crowding might reflect cumulative effects during encoding and maintenance. To accomplish this, we measured VWM crowding using simultaneously presented arrays and then compared the obtained VWM crowding to previously collected data where we presented the VWM items sequentially (Yörük et al., 2020). We expected to observe higher crowding errors in the simultaneous experiment due to the additional opportunity for competition between items during the perceptual encoding stage (versus during VWM maintenance alone for the sequential experiment).

Similar to the previous sequential VWM crowding experiment, we observed both crowding anisotropy and the overall crowding effect (more error for middle than edge items) for simultaneous arrays. However, comparison of crowding anisotropy between simultaneous and sequential experiments revealed no main effect of the presentation type, and the comparison of overall crowding effects across experiments revealed that the presentation method did not affect crowding errors when the arrays were radially configured. While there was a tendency to show higher crowding errors for sequential presentations than the simultaneous presentations when the arrays were configured tangentially, this trend ran counter to the predicted direction (and also to a potential expectation for reduced performance in the simultaneous experiment due to the overall shorter stimulus presentation time in that experiment). Because we expected cumulative effects of crowding at encoding and during maintenance, these results were surprising.

The similarity between VWM crowding errors for sequential and simultaneous displays points out a methodologically important aspect of VWM crowding studies. Because simultaneous presentations are enough to evoke similar VWM crowding to sequential displays, future VWM crowding experiments may not necessarily need to use the sequential approach. This is advantageous because sequential approaches introduce an additional factor to the experimental design—the temporal presentation order of the items in the arrays. The addition of this factor increases the number of trials needed in the design and complicates analysis as well. Even so, the sequential approach could still be preferred when examination of order effects is needed. Such order effects are central to some VWM studies (Pratte, 2020; Vergauwe et al., 2016). Relatedly, it is sometimes assumed that sequential presentations reflect a more pure measure of interactions between items in VWM because they lack potential encoding effects (Harrison & Bays, 2018; Yörük et al., 2020). However, the more complicated sequential presentation method may not measure only interactions between stably maintained items after all, because the sequential method entails temporal order and recency effects (Zhang & Luck, 2009; Vergauwe et al., 2016).

It is possible that the similar results for sequential and simultaneous arrays reported here actually reflect a complex interplay between sources of error and information. Specifically, it is possible that there is more relational or holistic encoding in the simultaneous than sequential arrays—in other words, participants may encode the array in a holistic manner when all items are simultaneously available, while they may avoid such holistic or relational encoding when only one element is presented at a time. On this speculative account, tasks with simultaneously presented arrays may be able to overcome a portion of the crowding error by encoding not just each array element but also relations between elements and/or the entire array as a unit. Thus, the present results would be explained by offsetting sources of error (additional crowding during encoding for sequential compared to simultaneous arrays) and information (greater reliance on holistic/relational representations for simultaneous compared to sequential arrays). It is also possible that this balance between increased information and increased error could be shifted by task-specific or trial-specific requirements and factors (e.g., individual representation of the target items might be biased towards to or away from the summary information of the features of the whole array; Brady & Alvarez, 2011), or even participant factors; this poses an interesting topic for further investigation. However, this speculative account needs to be considered in light of previous research that suggests that *competition* between items in simultaneously presented arrays is typically higher than that between items in sequential arrays (e.g., Kastner et al., 1998), and sequential presentation generally increases performance for accurately reporting each item compared to simultaneous presentations (Ihssen, Linden & Shapiro, 2010; also see Ahmad et al., 2017). In this alternative explanation, it is possible that one source of crowding error in the simultaneous experiment stems from the spatial competition between the items in stimulus array, while this competition is more limited in the sequential arrays (at least sometimes—relational or holistic encoding is possible even for sequential presentations, considering the research that brought evidence for temporal crowding effect; Tkacz-Domb & Yeshurun, 2021). Considering the alternative explanations discussed here, the possibility of offsetting sources of error and information for simultaneous arrays remains a topic for future investigation.

Another interpretation of the present results is that crowding could occur either during encoding or VWM maintenance, but crowding errors do not gradually accrue. Instead, VWM crowding either happens or does not, and once it happens, it cannot happen further. This either/or (i.e., either during encoding or maintenace, but not both) interpretation is consistent with previous findings that working memory and perceptual crowding share the same spatial resolution limitations, but that the nature of errors differed across these phenomena (Tamber-Rosenau et al., 2015). In that research, perceptual errors were based on both substitution of flankers for targets and imprecision (which was associated with pooling of flanker and target features). On the other hand, that research demonstrated that VWM crowding specifically stemmed from substitution errors alone (Tamber-Rosenau et al., 2015). Therefore, in the sequential experiment (Yörük et al., 2020), VWM items could have initially been encoded and maintained individually without pooling, with the crowding errors stemming primarily from swaps. Future studies should directly examine the potential gradual accrual of crowding by manipulating the duration of the maintenance period in order to determine if longer maintenance leads to more crowding.

Relatedly, one limitation of the present study is we did not identify the sources of VWM crowding errors: array item swaps, uninformed guesses, or mere representational imprecision (c.f., Zhang & Luck, 2008; Bays, Catalao, & Husain, 2009). Similar amounts of error for sequential and simultaneous conditions might stem from different mechanisms (Emrich & Ferber, 2012; Tamber-Rosenau et al., 2015). The present research could not evaluate the sources of error because neither the previous data from the sequential experiment nor the novel data from the simultaneous experiment (see footnote 1) were reliably fit by the required mixture model (Yörük et al., 2020).

One consideration for the present results is the observation of a temporal order effect in the form of a recency advantage for the third item compared to the first two items in the sequential experiment. Importantly, the presence of an especially low-error ("easy") condition—final item targets—in the sequential experiment is unlikely to explain the key result of the present study: that sequential presentation does not lead to the predicted reduction in VWM crowding compared to simultaneous presentation. This is because the simultaneous experiment led to (numerically) less crowding than the sequential experiment; were the "easy" third items in the sequential experiment removed from the analysis, sequential crowding would increase, not decrease. Nevertheless, the interaction of recency with VWM crowding should be investigated in future research.

Another limitation of the current study is that the sequential vs simultaneous presentation manipulation was between subjects, while all the other parameters were manipulated within-subjects. However, both samples were drawn from the same population, which makes it unlikely that the results were driven by overall different VWM or visual perceptual capabilities among samples. However, it is possible that participants in each experiment adopted distinct strategies that were better suited to the array presentation approach of that experiment. While the use of distinct strategies is certainly a limitation, it is not at all clear that shifting to a within-subjects manipulation would overcome this limitation. This is because seeing an individual target vs. the whole array during the initial stimulus presentation on each trial could cue the participants to adopt a certain strategy on even a trial-to-trial basis in a hypothetical within-subjects experiment.

Nevertheless, future research should examine simultaneous vs. sequential VWM crowding using a within-participants design.

Conclusion

Past research has assumed that VWM crowding occurs during encoding, maintenance, or both. Past research has not resolved if crowding can accumulate across both stages. The present research shows that it does not—both for the mechanisms of crowding strongly associated with retinotopic early visual cortex (crowding anisotropy) and for overall crowding effects. Future research should directly examine the accumulation of VWM crowding over time, not just stages of information processing.

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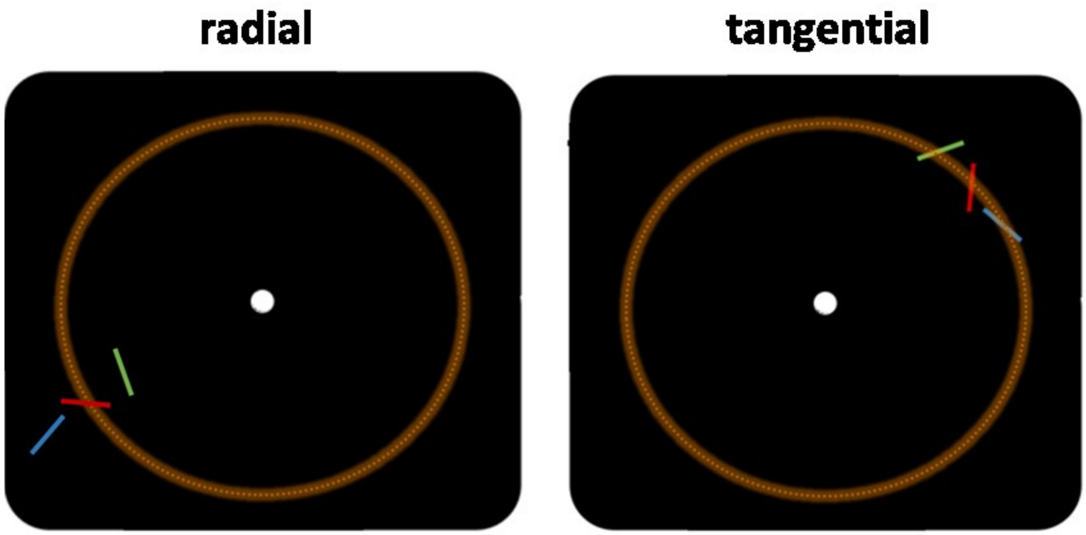

Figure 1. Cartoon examples of a radial (left panel) and a tangential (right panel) configuration. The orange circle is the imaginary circle that the middle targets were positioned on, and it was not present in the experimental displays.

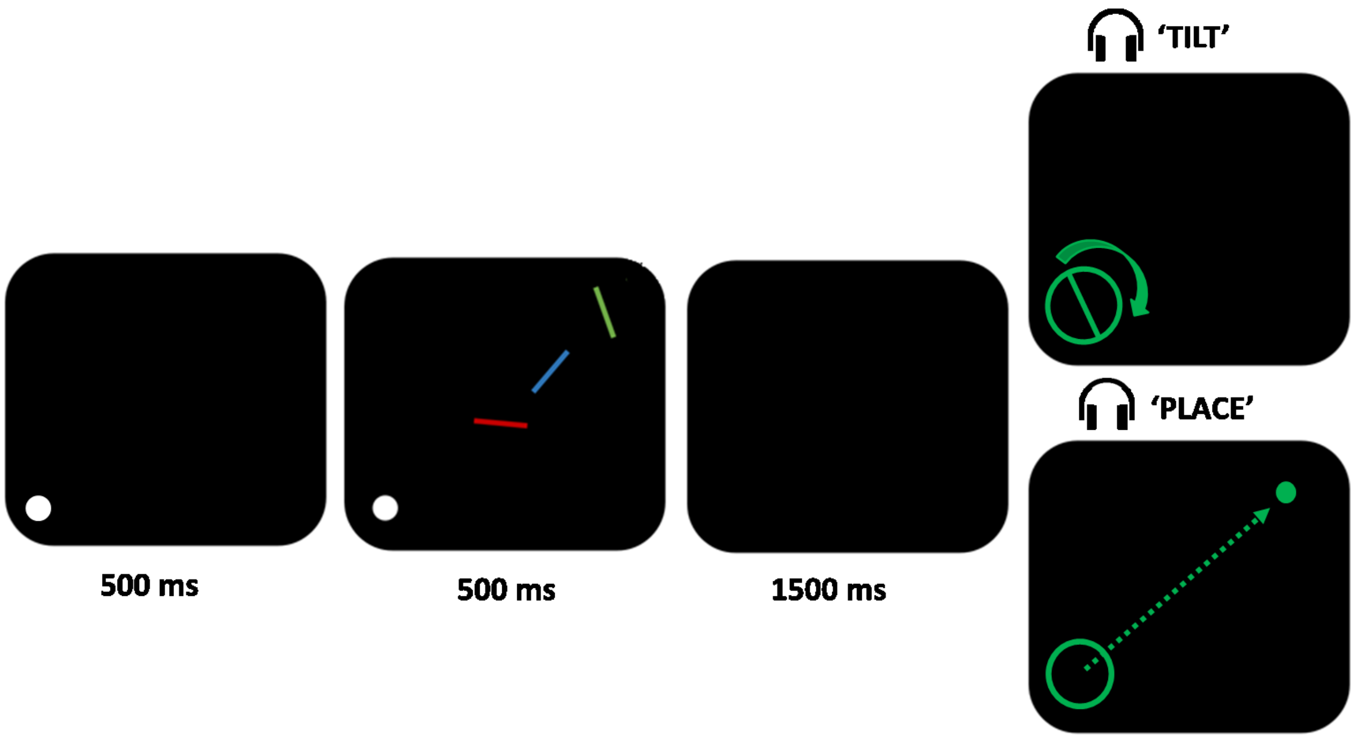

Figure 2. Cartoon example of a single trial procedure, representing the right upper quadrant of the screen. Stimuli not presented to scale. Each trial began with a 500 ms fixation screen. During the stimulus presentation, the stimulus arrays was presented 500 ms, followed by a 1500 ms fixation-only delay screen. At the response phase, the participants either rotated the response probe to indicate the orientation of the color-cued target if they heard the auditory cue 'tilt', or they indicated the location of the target if they heard 'place'. (See online article for a color version of this figure.)

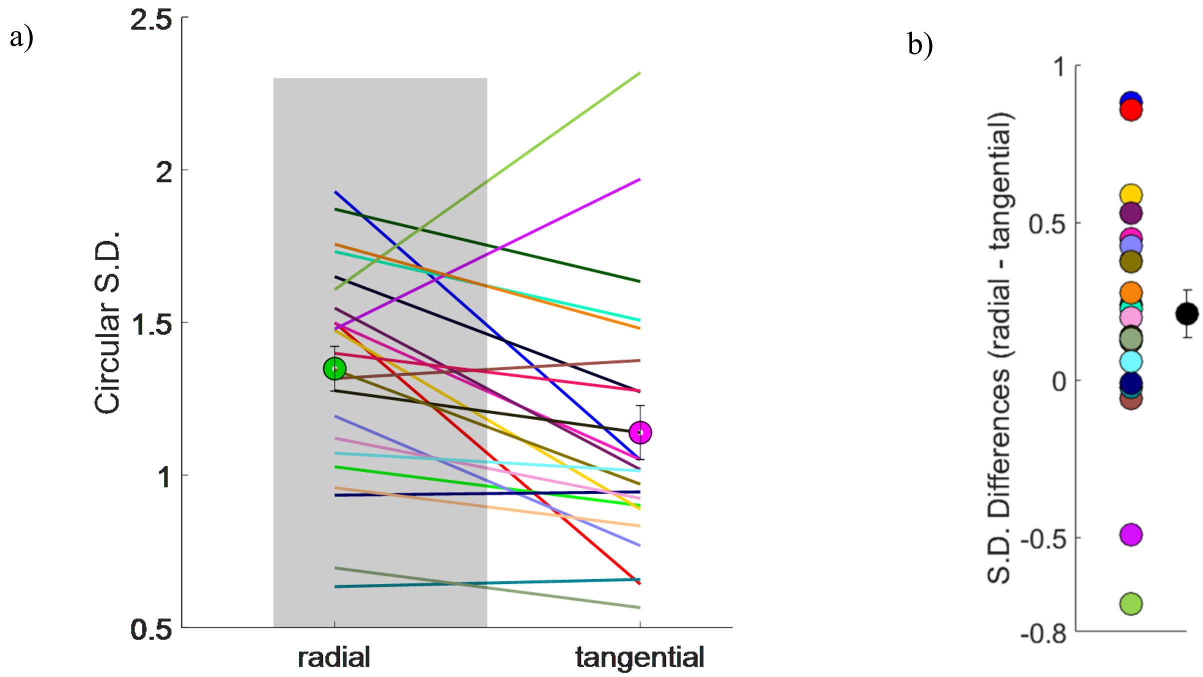

Figure 3. Comparison of circular S.D. across radial and tangential conditions in the simultaneous experiment. Error bars indicate +-1 SE. (a) Each colored line indicates performance from an individual participant. Dots indicate condition means. (b) Subtraction between errors in radial and tangential conditions. Colored dots indicate difference for each participant. Black dot indicates group difference. (See online article for a color version of this figure.)

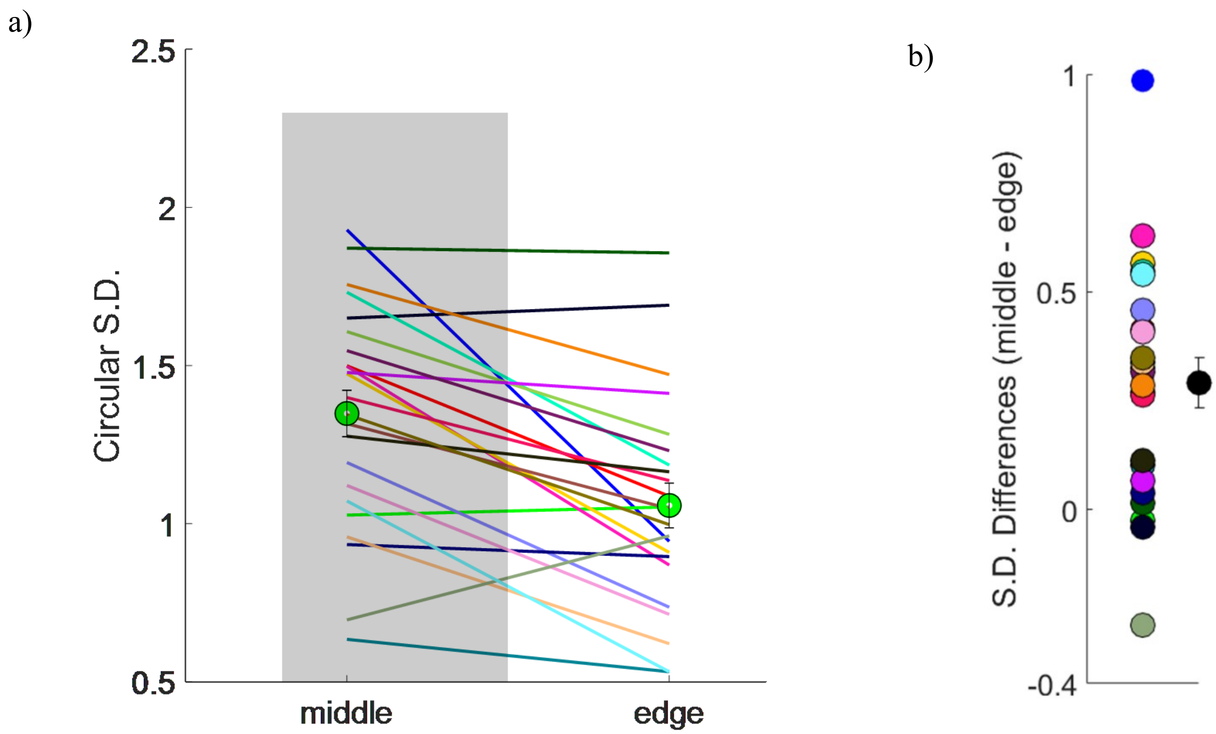

Figure 4. Comparison of circular S.D. across middle and edge targets for radially configured arrays in the simultaneous experiment. Error bars indicate +-1 SE. (a) Each colored line indicates performance from an individual participant. Dots indicate condition means. (b) Subtraction between errors in each participant. Black dot indicates group difference. (See online article for a color version of this figure.)

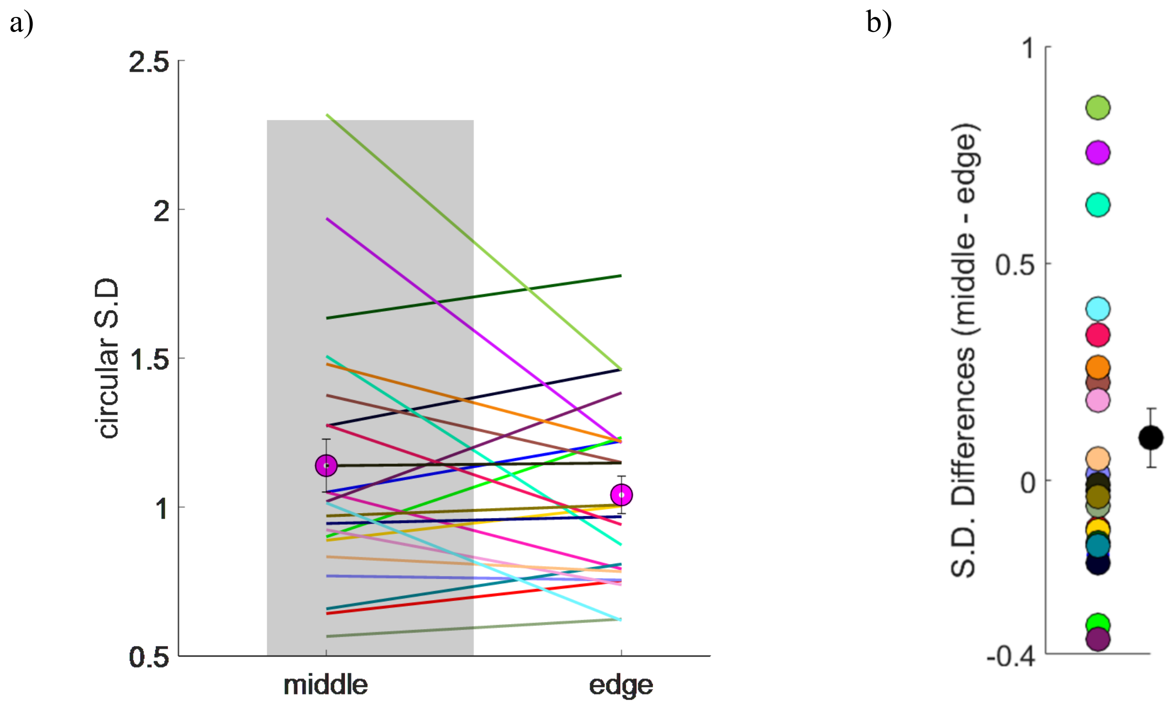

Figure 5. Comparison of circular S.D. across middle and edge targets for tangentially configured arrays in the simultaneous experiment. Error bars indicate +-1 SE. (a) Each colored line indicates performance from an individual participant. Dots indicate condition means. (b) Subtraction between errors in each participant. Black dot indicates group difference. (See online article for a color version of this figure.)

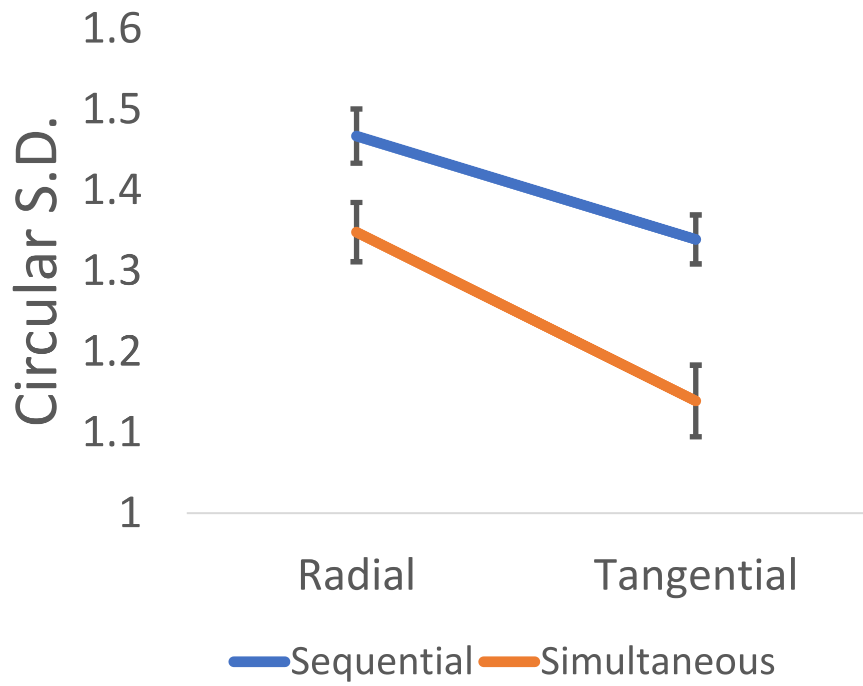

Figure 6. Comparison of crowding anisotropy through the errors for middle targets across sequential and simultaneous experiments. Error bars indicate +-1 SE. (See online article for a color version of this figure.)

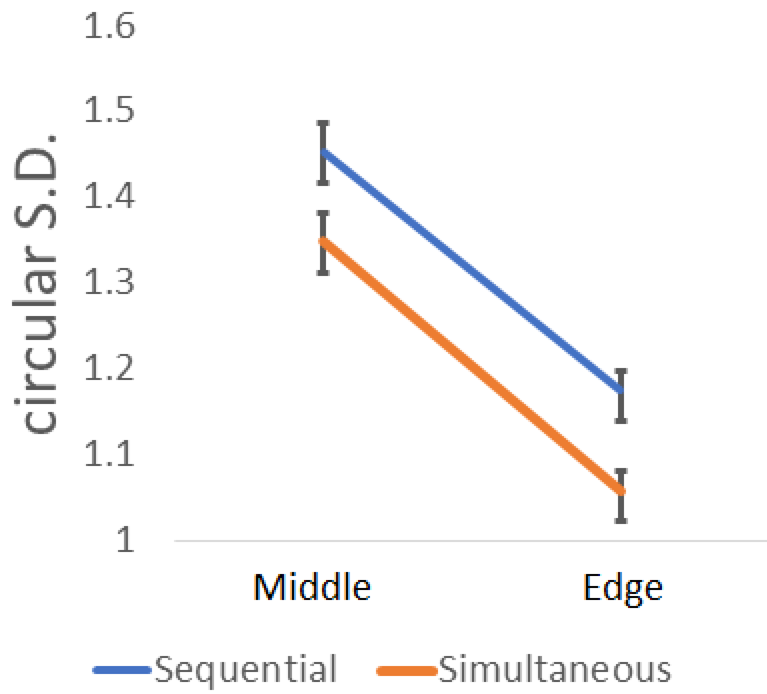

Figure 7. Comparison of crowding errors for the radially configured arrays across sequential and simultaneous experiments. Error bars indicate +-1 SE. (See online article for a color version of this figure.)

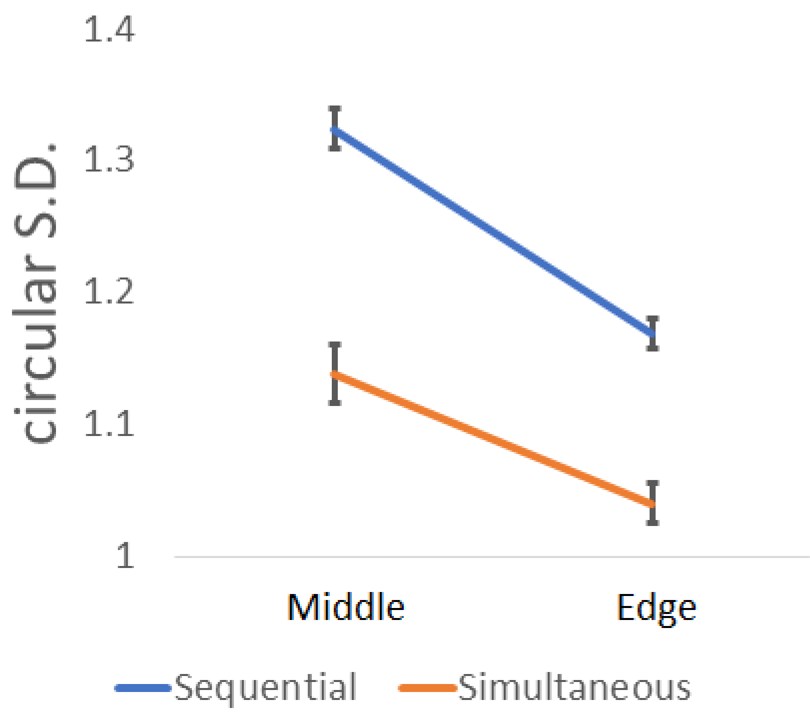

Figure 8. Comparison of crowding errors for the tangentially configured arrays across sequential and simultaneous experiments. Error bars indicate +-1 SE. (See online article for a color version of this figure.)