This manuscript is now published in the “Vision Research” journal. The updated published version can be found at:

<https://doi.org/10.1016/j.visres.2021.07.012>

Encoding perceptual ensembles during visual search in peripheral vision

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The data from the experiments reported in this paper and the scripts for statistical analyses are available at <https://osf.io/ckpyu/>.

Abstract

Observers can learn complex statistical properties of visual ensembles, such as their probability distributions. Even though ensemble encoding is considered critical for peripheral vision, whether observers learn such distributions in the periphery has not been studied. Here, we used a visual search task in order to investigate how the shape of distractor distributions influences search performance and ensemble encoding in peripheral and central vision. Observers looked for an oddly oriented bar among distractors taken from either uniform or Gaussian orientation distributions with the same mean and range. The search arrays were either presented in the foveal or peripheral visual fields. The repetition and role reversal effects on search times revealed observers' internal model of distractor distributions. Our results showed that the shape of the distractor distribution influenced search times only in foveal, but not in peripheral search. However, role-reversal effects revealed that the shape of the distractor distribution could be encoded peripherally depending on the inter-item spacing in the search array. Our results suggest that while peripheral vision might rely heavily on summary statistical representation of feature distributions, it can also encode information about the distributions themselves.

There are large differences in the processing of visual information between the central and peripheral visual fields. This reflects the fact that a much higher percentage of neural structures in both retina and primary visual cortex are devoted to the foveal region (e.g. Curcio & Allen, 1987; Daniel & Whitteridge, 1961; Hubel & Wiesel, 1974; Drasdo, 1977; see Jóhannesson, Tagu & Kristjánsson, 2018 for review). Resolution, acuity and contrast sensitivity are higher for foveal than peripheral vision (Anstis, 1974; Virsu & Rovamo, 1979). However, only a small central region of our visual field corresponds to the fovea, whereas the bulk of it is processed peripherally. This means that a significant amount of our daily visual perception depends on our peripheral vision. In order to have a complete picture of our visual capabilities, it is crucial to understand how processing differs between central and peripheral vision.

Apart from diminished resolution and acuity, one of the main reasons why visual performance is degraded in peripheral vision is crowding, which occurs when similar items (i.e. distractors, or “flankers”) are present nearby a target item (Stuart & Bruian, 1962; Bouma, 1970; Levi, Klein & Aitsabaomo, 1985; Wilkinson, Wilson & Ellemberg, 1997). Recent work on crowding has suggested that peripheral visual information is encoded as visual ensembles, which are represented in terms of summary statistics (Levi, 2008; Pelli & Tillman, 2008; Balas, Nakano, & Rosenholtz, 2009; Rosenholtz, Huang, Raj, Balas & Ilie, 2012; Ehinger & Rosenholtz 2016). This would enable peripheral vision¹ to process a large area of the visual field very quickly to detect any potentially informative visual items or events. This would then guide consequent eye movements made to project informative parts of the visual scene onto the fovea for further processing. Therefore, examining how visual ensembles are encoded in peripheral vision could increase our understanding of how the visual scene is processed.

While the visual system can represent a distribution of features (e.g. orientation, color, size, facial expression) across many objects as ensembles, and can accurately and efficiently extract the summary statistics of these ensembles (for reviews, see Haberman & Whitney, 2011; Alvarez, 2011; Whitney & Leib 2018), foveal information is not needed for this (Wolfe, Kosovicheva, Leib, Wood & Whitney, 2015). Furthermore, it has even been argued that summarizing information in the peripheral visual field as ensembles is

¹ Throughout this article, the term “peripheral” visual field is used to refer to all the areas outside of the fovea, which includes parafoveal and peripheral regions (i.e. might also be referred to as extra-foveal)

an automatic compulsory process, which, in turn, explains why crowding becomes stronger with increasing eccentricity (Parkes, Lund, Angelucci, Solomon, & Morgan, 2001; Fischer & Whitney, 2011; but see also Livne & Sagi, 2007; Bulakowski, Post & Whitney 2011). While crowding can be seen as a limiting factor for object recognition in the periphery, this compulsory averaging might facilitate scene perception as it has been shown that peripheral processing is more useful for recognizing the gist of a scene than foveal processing (Larson & Loschky, 2009; Ehinger & Rosenholtz, 2016).

Given this strong link between peripheral processing and ensemble perception, the effects of eccentricity in encoding visual ensembles have not received the attention they deserve. In particular, little work has focused on how ensemble encoding differs between central and peripheral vision. Ji, Chen, & Fu (2014) presented participants with sets of faces where certain faces appeared in the foveal visual field, and others in the periphery. Participants judged whether the overall emotion of the set was positive or negative. They found that faces in the foveal region were given more weight than those in the periphery in participants' judgments. On the other hand, by using gaze-contingent displays, Wolfe et al. (2015) demonstrated that participants were equally accurate in reporting the mean emotion of a set of faces when there was a foveal occluder and when there was not.

Both of these studies required explicit judgments about the mean value of a set of features. These explicit judgments on statistical parameters of a feature distribution might have limited power in revealing how accurately feature distributions in an ensemble are encoded by the visual system. Recently, Chetverikov, Campana & Kristjánsson (2016, 2017a, 2017b, 2017c) used a novel method to demonstrate that observers can encode the probability density function underlying the distractor distribution in an odd-one-out visual search task for orientation (2016, 2017a) and color (2017b). Instead of using explicit judgments of distribution statistics, they measured observers' visual search times varying target similarity to previously learned distractors, which revealed observers' expectations of distractor feature distributions. This was achieved by using role-reversal effects between the target and distractors, which occur when feature values of target and distractors used on previous search trials are swapped on the next trial (Kristjánsson & Driver, 2008; Becker, 2010). This causes search times to increase due to the similarity between the current target and the previous distractors, compared to a case where current target and previous distractor features are dissimilar. In this study, we use this implicit method and manipulate this

116 similarity between the target and the previous distractors to assess whether observers
117 encode orientation distributions differently with central and peripheral vision. In this way,
118 we can examine observers' internal representations of ensembles, rather than their
119 explicit summary-statistics judgements that may in fact rely on these ensemble
120 representations.

121 Another goal of our study is to examine the effect of ensemble encoding on odd-one-out
122 visual search performance. Ensemble encoding can strongly influence visual search for
123 outliers (Cavanagh 2001; Alvarez, 2011; Whitney, Haberman & Sweeny, 2014).
124 Detecting outliers among a set of items by comparing each item to all others would
125 require complex calculations. However, creating ensemble statistics of the relevant
126 feature distribution over the items would make outlier detection much simpler.
127 Rosenholtz et al. (2012) have shown that a model that represents the visual search area
128 by dividing it into patches and then analyzing these patches with respect to their
129 statistical summaries successfully predicts performance on classical visual search tasks.
130 When the difference between the statistical summary of the patch that includes both the
131 target and distractors and of the patch that only includes distractors increases, the
132 search becomes easier, even when the target-distractor confusability is the same at an
133 individual item level (e.g. search for 'O' among 'Q's vs. search for 'Q' among 'O's). In this
134 study, we will examine whether this influence of ensemble encoding on visual search
135 performance changes between the central and peripheral visual fields. More importantly,
136 previous studies have typically focused on the effect of target-distractor discriminability
137 (Duncan & Humphreys, 1989, Palmer, Verghese & Pavel, 2000), segmentability of
138 distractor features (Utochkin & Yurevich, 2016; Cho & Chong, 2019), or of summary
139 statistics (Rosenholtz et al. 2012) on visual search performance. In contrast, our
140 methodology allows us to investigate the effect of the shape of the distractor distribution
141 while keeping all those other factors as constant as possible.

142 In Experiment 1 we assessed observers' encoding of the orientation distribution of the
143 distractor set in an odd-one out visual search task, as well as its effect on search
144 performance. The search array was presented either in the central or the peripheral
145 visual field. In Experiment 2, we increased the spacing of the oriented bars as well as
146 their size in the peripheral condition, while decreasing their size in the central condition,
147 in order to make the two conditions more comparable in terms of processing capacity
148 and partly accounting for the cortical magnification factor.

To summarize, our aim was to study search for targets among distractors with different distributions to answer the question of performance differences between the periphery and the center, as well as to measure feature distribution learning as described above (and in Chetverikov et al., 2016; 2017a) as a function of retinal eccentricity.

Experiment 1

Method

Participants

Fourteen participants (seven males, age $M = 32.14$) took part in the study. All had normal or corrected-to-normal visual acuity. All participants signed an informed consent form before participating. Four were paid for their participation, whereas the other ten, who were staff or students at the University of Iceland, participated voluntarily. The experiment was run in accordance with the Declaration of Helsinki and the requirements of the ethics committee of the University of Iceland.

Stimuli

The display included a search array of 36 white lines arranged in a 6 by 6 invisible grid extending to $9 \times 9^\circ$ on a grey background (Figure 1). For the central condition, the search array was placed at the center of the screen, whereas for the peripheral condition it was centred 9° to the right or left of the center of the screen. The length of each line was 1° , and their position in the grid was jittered by randomly adding a value between $\pm 0.25^\circ$ to their horizontal and vertical coordinates. A red fixation dot with a radius of 5 pixels was placed at the center of the screen.

Design

The details of the methodology we used in this study have been described in Chetverikov, Hansmann-Roth, Tanrikulu & Kristjánsson (2019). Here, we followed the same design except for the addition of the peripheral condition and eye-tracking to make sure that participants were fixating at the center of the screen.

175

189 *Figure 1: A. Example search array for the central condition in experiment 1. B. Example search array for the*
 190 *peripheral condition in experiment 1. In half of the peripheral trials, the search array was placed 9° to the*
 191 *right of center (red fixation dot) of the screen, and to the left of it in the other half.*
 192

193 The experiment included streaks of learning and test trials. Each learning streak
 194 included five or six search trials in which the orientations of the distractors were sampled
 195 either from a uniform (range = 60°) or a truncated Gaussian ($SD = 15^\circ$) distribution. The
 196 Gaussian distribution was truncated at $2*SD$ away from the mean so that the range for
 197 the uniform and the Gaussian distribution was equal. This was additionally ensured by
 198 setting the orientation of two distractor lines to the minimal and maximal values of a
 199 given range and mean for both distributions. The mean orientation of the distractor
 200 distribution was determined randomly for each learning streak and kept fixed during that
 201 streak. The orientation of the target line was randomly determined with the restriction
 202 that the target to mean-distractor distance in feature space was at least 60°.

A single test trial followed the learning trials. The main variable that was manipulated in the test trial was the distance between the target orientation on the current test trial and the mean distractor orientation on the previous learning streak. This CT-PD (Current Target – Previous Distractor) distance determines the extent of the role reversal effects. In order to have a uniform distribution of CT-PD values, we divided the orientation space into 12 bins where each bin covered a range of 15° . Then for each test trial, a CT-PD value was randomly chosen from the bins ensuring that at the end of the experiment we had equal numbers of CT-PD values from each bin. Given the chosen CT-PD value for that test trial, the target orientation was determined to yield the chosen CT-PD distance (Figure 2). The orientations of the distractors in the test trial were sampled from a truncated Gaussian ($SD = 10^\circ$) distribution. The mean orientation of the distractors was randomly determined with the restriction that the target to mean-distractor distance in feature space was at least 60° .

Each participant completed 1872 search trials, which corresponds to a total of 288 (learning + test) streaks – i.e. 2 (search location: central or peripheral) $\times 2$ (distractor distribution: Gaussian or uniform) $\times 12$ (CT-PD bins) $\times 2$ (learning streak length: 5 or 6) $\times 3$ (repetition).

Figure 2: An example of a learning streak and a test trial. On the left, the distractor distribution and the target orientation is shown for a learning streak. The distractor orientations are sampled from the same distribution throughout the learning trials, however, the target orientation is randomly chosen given that it is at least 60° away from the distractor distribution mean. On the test trial, the target orientation is chosen to yield different CT-PD values. In the example shown here, the distance between the current target orientation (80°) and the previous distractor distribution mean (60°) yields a CT-PD value of $+20^\circ$.

227 *Procedure and Materials*

228 Participants sat 100 cm away from a 24-inch LCD monitor (1920 x 1080) connected to a
229 Windows 7 PC. An EyeLink 1000 Plus eyetracker was used to track participants'
230 fixations. The experiment was presented using the Psychtoolbox (Brainard, 1997;
231 Kleiner, Brainard & Pelli 2007) and EyeLink (Cornelissen, Peters & Palmer, 2002)
232 toolbox extensions in MATLAB. We recorded eye movements from observers' right eye,
233 while their head was stabilized with a chin rest. **The experiment included 8 blocks of**
234 **trials, and at the beginning of each block a 5-point calibration was performed. The**
235 **average calibration error for the participants was 0.37°**

236 Participants were asked to find the oddly oriented line among the 36 oriented lines, and
237 indicate whether the oddly oriented line was in the upper three rows or in the bottom
238 three rows of the search array by pressing the up and down arrow keys accordingly.
239 Target position in the search array was randomized. Participants were asked to respond
240 as quickly and correctly as possible while keeping fixation on the red dot centred on the
241 screen. The next search trial was shown immediately after the participants responded,
242 except when an error was made. In that case, the word "Error" appeared in the middle of
243 the screen in a red font for 1 s. In order to motivate subjects, a score was calculated for
244 each trial based on the participant's accuracy and response time (For correct response:
245 $score = 10 + (1 - RT) * 10$; for errors: $score = -|10 + (1 - RT) * 10| - 10$; where RT is
246 response time in seconds). The accumulated current score was shown to participants
247 during the breaks.

248 The experiment was completed in 8 blocks, split into 2 sessions. Each block consisted of
249 36 learning + test streaks. Participants took as much resting time as they needed
250 between the blocks. At the beginning of each block, the participants were told in which
251 location on the screen the search array would appear (left, right or center) relative to the
252 fixation point. The location of the search array was kept fixed throughout a block, but
253 alternated across blocks. All conditions were counterbalanced, and trials were
254 randomized for each subject separately. The order in which participants performed trials
255 with different search array locations was also counterbalanced across subjects. **For all**
256 **fourteen participants, the first session included** 72 practice streaks (roughly 400 search
257 trials, where half of them in the central, other half in a peripheral location), which was
258 followed by three blocks of experimental trials. The second session included 24 practice

streaks (i.e. 130 search trials) and five experimental blocks. The four participants who were inexperienced with the search task were given a full practice session (i.e. 5 blocks which corresponds to 180 streaks) before they started the two experimental sessions. This was done to acquaint these participants with the search task, since their response times were exceptionally high (> 3 s) when they were first introduced to the task. The other ten participants were already experienced with similar visual search tasks, and since their overall search times were already lower than 1 s they did not perform separate practice sessions (but they still completed the practice trials embedded in the experimental sessions). On average, each session took 50 min. to complete.

Results and Discussion

In the central condition, trials where participants made an eye-movement outside of the search array grid were excluded. In the peripheral condition the trials where participants made an eye movement into the search area were excluded (overall 10% of all trials). If such an eye movement occurs during the learning streak, the learning process can potentially be interrupted. That is why we used longer learning streaks with five or six trials, rather than two trials, which has been found to be enough for observers to encode the distractor distribution with this method (Chetverikov et al., 2017a). Therefore, even if the learning streak is interrupted by such an eye movement, this would only shorten the length of the effective learning streak, but there would still be enough learning trials on average to encode the distractor distribution. Therefore, exclusion of test trials was independent of exclusion of learning trials.

Trials where RTs were too high (> 3 s) or too low (< 150 ms) were also excluded (less than 0.1% of remaining trials). Trials where participants made an error were excluded from RT analyses (9% of the remaining trials). RTs were log-transformed for all analyses.

Visual search performance

Figure 3 shows visual search performance in the different conditions. Participants were fastest when the distractor orientations were sampled from the Gaussian with $SD = 10^\circ$ ($M = 648$ ms, $SD = 81$ ms), followed by the Gaussian with $SD = 15^\circ$ ($M = 666$ ms, $SD =$

98 ms) and they were slowest when sampled from a Uniform distribution ($M = 688$ ms, $SD = 118$ ms). A two-way repeated measures ANOVA yielded a significant effect of distribution type on RT ($F(2,26) = 10.91, p < 0.001, \eta_G^2 = 0.02$), as well as a significant interaction between distribution type and search location ($F(2,26) = 3.87, p < 0.05, \eta_G^2 = 0.003$). However, search location alone did not have a significant effect on RTs ($F(1,13) = 0.81, p > 0.05$). When the two search locations were analysed separately, an effect of distribution type was only observed in the central condition ($F(2,26) = 12.71, p < 0.05, \eta_G^2 = 0.03$), while in the peripheral condition distribution type had little influence on RTs ($F(2,26) = 3.35, p > 0.05$).

Participants were most accurate when the distractor orientations were sampled from the Gaussian with $SD = 10^\circ$ ($M = 0.95, SD = 0.02$), followed by the Gaussian with $SD = 15^\circ$ ($M = 0.91, SD = 0.03$) and they were least accurate when sampled from a Uniform distribution ($M = 0.89, SD = 0.04$). A two-way repeated measured ANOVA revealed a significant effect of distribution type on accuracy. ($F(2,26) = 54.15, p < 0.001, \eta_G^2 = 0.37$). There was no significant main effect of location ($F(1,13) = 0.26, p > 0.05$), nor an interaction between the two factors ($F(2,26) = 2.28, p > 0.05$).

Figure 3: Visual search performance in Experiment 1. Error bars represent 95% confidence intervals. "Gaussian with $SD = 10^\circ$ " (denoted by black) corresponds to the results obtained from the test trials, and the other two distractor distribution types (Gaussian with $SD = 15^\circ$ and uniform, which are denoted by red and blue respectively) correspond to the results obtained from learning trials.

Overall, search was faster and more accurate when the variance of the distractor distribution was lower. While this finding is in line with previous studies, there was one interesting exception to this general trend. When the search array was presented in the periphery, the distractor distribution did not have a significant effect on search times, even though the accuracy was similar for the central and peripheral conditions.

Encoding of distractor distributions

Figure 4 shows the CT-PD curves (response times on the test trials as a function of CT-PD distance), which reflect the effect of role reversals between target and distractor orientations. Since the distributions we used were symmetric, absolute values of CT-PD distances were used in the following plots and analyses. Test trials following an error were excluded from the analyses, because participants tend to slow down on a trial following an error, which overrides the role-reversal effects.

In order to assess to what extent participants encoded the distractor distribution, we compared these CT-PD curves to the corresponding type of the distractor distribution used in the learning streak. Given that absolute values of CT-PD were used here, following a learning streak in which distractors were sampled from a Gaussian distribution, it would be expected that the search times in test trials would monotonously decrease with increasing CT-PD values. Whereas, for the test trial following a learning streak with uniform distribution of distractors with a range of 60° , the search times would be expected to be roughly constant within the 30° range, but then decrease outside of that range.

Figure 4: Role reversal effects in Experiment 1. Search times on test trials are plotted as a function of the distance (in orientation space) between the current target orientation in the test trials and the mean distractor orientation of the preceding learning streak (CT-PD: Current Target – Previous Distractor). Shaded area indicates 95% confidence intervals of the local (loess) regression fit.

To test this, we fit several possible distribution models to the CT-PD curves we obtained from the test trials (Figure 5). These models included a null model (i.e. constant RT over CT-PD values), a linear model (i.e. RT linearly depends on CT-PD), a half-Gaussian model (i.e. RT as a function of CT-PD described by a half-Gaussian with $SD = 15^\circ$), a uniform model (i.e. constant RT but with different baselines within and outside of the 30° CT-PD range) and a uniform-with-decrease model (i.e. constant RT within the 30° CT-PD range, then linear decrease outside of that range). More formal descriptions of the models used in these analyses can be found in Chetverikov et. al. (2017b). Table 1 shows the fit quality for the two best models among all models for each search array location, with accompanying Bayesian Information Criteria (BIC) of relevant model comparisons.

Figure 5: Fitted models and the CT-PD curves obtained from the test trial RTs in Experiment 1

Table 1: Model fits to the search times as a function of CT-PD distances in Experiment 1.

Distractor Distribution	CENTER		PERIPHERY	
	Gaussian	Uniform	Gaussian	Uniform
Best Model	Uni. w/ decrease	Linear	Linear	Uni. w/ decrease
2 nd Best Model	Linear	Uni. w/ decrease	Uni. w/ decrease	Linear
Δ BIC: Best vs. Null	10.42	17.86	27.21	30.79
Δ BIC: Best vs. 2 nd	0.41	0.92	4.58	3.69

Note: Δ BIC > 2 indicates "positive" evidence, Δ BIC > 6 indicates "strong" evidence, while Δ BIC > 10 corresponds to "very strong" evidence (Kass & Raftery, 1995).

Uniform distractor distributions were considerably better ($\Delta BIC > 10$) than the null model. However, the best fits for both conditions were not better than the second best fits ($\Delta BIC < 1$). This suggests that when the search array was in the center, participants were able to encode certain summary statistics (e.g. mean orientation) of the distractor distributions, but notably, they were not able to encode the shape of that distribution. The two best models, uniform with decrease and linear, fit the CT-PD curves obtained from the Gaussian or Uniform distractor distribution condition equally well.

When the search array was presented in the periphery, the two best fits were considerably better than the null model ($\Delta BIC > 25$). Not only that, the best fit for the Gaussian condition (linear model) was better than the second best fit (uniform with decrease model) ($\Delta BIC = 4.58$). This indicates that when the distractor distribution was Gaussian, the search times linearly decreased as CT-PD value increased. When the distractor distribution was Uniform, the best fit (uniform with decrease model) was better than the second best fit (linear model) ($\Delta BIC = 3.69$), meaning that the RTs stayed roughly constant for a certain range but then decreased outside of that range. This suggests that participants were able to encode **more** details about the distractor distribution (such as shape) when the search array appeared in the periphery. However, this was not observed to the same extent when the array appeared centrally.

Whether the distractor distribution was encoded beyond its summary statistics was assessed by the demonstration of a statistically meaningful shape correspondence between the CT-PD curves and the physical distractor distribution. However, due to noise in the visual system, a representation of a distribution would be expected to involve certain approximations. For example, comparison of observers' priors and natural statistics reveals important similarities but not an exact match between the two (Girshick, Landy & Simoncelli, 2011). This can explain why the best fit for the Gaussian distractor distribution was a linear model rather than a half-Gaussian model for the periphery condition. Both the linear and the half-Gaussian model involve a strict² decrease in RT as CT-PD increases, which was the expected shape feature of a CT-PD curve obtained following a Gaussian distractor distribution. However, this strict decrease is not expected following a Uniform distractor distribution. Accordingly, the best model

² We use "strictly decreasing" to refer to a function that is always decreasing and does not remain constant (i.e. cannot include a plateau). We use "monotonic decrease" to refer to a function that is always decreasing or remaining constant (i.e. can include a plateau).

for the uniform distractors in the periphery condition was the “Uniform with decrease” model, which does not involve a strict decrease in RT as CT-PD increases.

Item heterogeneity (for example, from variance) is known to influence judgments of visual ensembles (e.g. Marchant, Simons & de Fockert, 2013). In our experiment, there was a slight variance difference between the Gaussian and the uniform distribution as their ranges were equal. Notably, however, in a previous study using the same implicit methodology we used here, Chetverikov et al. (2016) showed that the shape correspondence between CT-PD curves and distractor distributions cannot be explained by this variance difference.

Experiment 2

In Experiment 2, we changed the spacing between the oriented lines, as well as their lengths. For the peripheral condition, we increased both the spacing between the lines and their length. Since effects of crowding increase with increasing eccentricity, these changes will partly compensate for crowding in the periphery, as well as for the cortical magnification factor. In addition, we decreased both the spacing between the lines and their length in the central condition. These changes ensured that all the lines of the search array in the central condition fell within the foveal region. These changes made the two search array location conditions more comparable in terms of general processing capacity.

Method

Participants

Fourteen participants (seven males, age $M = 29.93$) took part in the study. Ten had previously participated in Experiment 1. All had normal or corrected-to-normal visual acuity. All participants signed an informed consent form before participating. Four were paid for their participation, whereas the other ten, who were staff or students at the University of Iceland, participated voluntarily. The experiment was run in accordance with the Declaration of Helsinki and the requirements of the ethics committee of the University of Iceland.

Stimuli and Procedure

The search display was the same as in Experiment 1, except that the size of the search field and of the oriented lines were scaled differently for the peripheral and central conditions. In the central condition, the 36 oriented lines of the search array were arranged in a grid extending only to $4^\circ \times 4^\circ$ and centred on the screen. The length of each line was 0.5° and their position was jittered randomly by adding a value between $\pm 0.1^\circ$ to their horizontal and vertical coordinates. For the peripheral condition, the search array extended $13^\circ \times 13^\circ$, and was placed 11° to the right or left of the fixation point. In this way, the distance between the fixation point and the oriented line that was closest to the fixation point (4.5°) was the same in the peripheral conditions of Experiment 1 and 2. The length of each line in the periphery condition was increased to 1.4° , and their position was jittered randomly between $\pm 0.3^\circ$. A red dot with a radius of 5 pixels was again used as a fixation point.

The equipment, procedure and the design of the experiment were exactly the same as in Experiment 1. A 5-point eye-tracking calibration was again performed before each experimental block. Average calibration error was 0.39° .

Results and Discussion

In the central condition, trials in which participants made an eye movement outside of the search array grid were excluded; whereas in the peripheral condition trials where participants made an eye movement into the search array were excluded from the analysis (overall 10% of all trials). Trials in which RTs were more than 3 s, less than 150 ms, and where participants made an error were also excluded from the RT analyses (11% of the remaining trials). RTs were log-transformed for all analyses.

Visual search performance

Figure 6 shows the RT and search accuracy for each of the conditions. A two-way repeated measures ANOVA yielded a significant effect of distractor distribution type on RT ($F(2,26) = 10.5$, $p < 0.001$, $\eta_G^2 = 0.03$). Similar to the results of Experiment 1, participants were fastest when the distractor distribution was Gaussian with $SD = 10^\circ$ ($M = 613$ ms, $SD = 50$ ms), followed by the Gaussian $SD = 15^\circ$ ($M = 619$ ms, $SD = 59$ ms), and they were slowest when the distractor distribution was uniform ($M = 644$ ms, $SD = 77$ ms). Similar to what we observed in Experiment 1, there was no significant effect of search array location on RT ($F(1,13) = 3.23$, $p > 0.05$), however there was a significant

interaction between search location and distribution type ($F(2,26) = 22.25$, $p < 0.001$, $\eta_G^2 = 0.03$).

A repeated measures ANOVA on accuracy yielded a significant effect of distribution type ($F(2,26) = 22.74$, $p < 0.001$, $\eta_G^2 = 0.22$), as well as a significant effect of search location ($F(1,13) = 6.86$, $p < 0.05$, $\eta_G^2 = 0.07$). Participants were most accurate when the distractor distribution was Gaussian with $SD = 10^\circ$ ($M = 0.94$, $SD = 0.03$), followed by Gaussian with $SD = 15^\circ$ ($M = 0.9$, $SD = 0.03$), and were least accurate with uniformly distributed distractors ($M = 0.89$, $SD = 0.03$). Overall, participants were more accurate in the central condition ($M = 0.91$, $SD = 0.04$), than the peripheral condition ($M = 0.89$, $SD = 0.04$). There was no significant interaction between the two factors ($F(2,26) = 2.13$, $p > 0.05$).

Figure 6: Visual search performance in Experiment 2. Error bars represent 95% confidence intervals. "Gaussian with $SD = 10^\circ$ " (denoted by black) corresponds to the results obtained from the test trials, and the other two distractor distribution types (Gaussian with $SD = 15^\circ$ and uniform, which are denoted by red and blue respectively) correspond to the results obtained from learning trials.

As in Experiment 1, participants in Experiment 2 were overall more accurate and faster when the distractor distribution had lower variance. Effects of distribution type on search times were, however, not observed in the peripheral condition. Overall average accuracy was similar between the two experiments. Average RT in Experiment 2 was 43 ms lower

than the one obtained in Experiment 1. This difference was likely due to those observers in Experiment 2 who previously participated in Experiment 1 becoming slightly faster in their response as they performed more sessions.

Encoding of distractor distributions

Figure 7 shows the CT-PD curves obtained from Experiment 2. The curves were calculated in the same way as in Experiment 1. In the central condition, when the distractor distribution was Gaussian, the search times monotonously decreased as CT-PD increased. However, when the distractor distribution was uniform, search times stayed roughly constant but then steadily decreased when the CT-PD exceeded the range of the uniform distribution. These observations were confirmed by the model comparisons done by fitting possible distribution models to RTs from the test trials (Table 2 and Figure 8). The best fit for the Gaussian distractor distribution was the linear model, whereas the best fit was the uniform-with-decrease model for the uniform distractor distribution. Both of these best fits were better than the second best fit models ($\Delta BIC > 2$), and better than the null model ($\Delta BIC > 8$).

Figure 7: Role reversal effects in Experiment 2. Search times on test trials are plotted as a function of the distance (in orientation space) between the current target orientation in the test trials and the mean distractor orientation of the preceding learning streak (CT-PD: Current Target – Previous Distractor), separately for each search array location. Shaded area indicates 95% confidence intervals of the local (loess) regression fit.

Table 2: Model fits to the search times as a function of CT-PD distances in Experiment 2.

Distractor Distribution	CENTER		PERIPHERY	
	Gaussian	Uniform	Gaussian	Uniform
Best Model	Linear	Uni. w/ decrease	Linear	Linear
2 nd Best Model	Uni. w/ decrease	Linear	Uni. w/ decrease	Uni. w/ decrease
Δ BIC: Best vs. Null	8.92	11.41	65.00	34.11
Δ BIC: Best vs. 2 nd	2.11	2.01	11.04	4.30

Note: Δ BIC > 2 indicates “positive” evidence, while Δ BIC > 6 indicates “strong” evidence, whereas Δ BIC > 10 corresponds to “very strong” evidence (Kass & Raftery, 1995).

Figure 8: Fitted models and the CT-PD curves obtained from the test trial RTs in Experiment 2.

For the peripheral condition, CT-PD curves did not change depending on the preceding distractor distribution type. As shown on the right side of Figure 7, search times in the periphery condition linearly decreased as CT-PD distance was increased, regardless of the preceding distractor distribution type. This was also confirmed by the model fit comparisons (Table 2). The best fit for both distractor distribution types was the linear model, which had a considerably better fit than the second best models ($\Delta BIC > 4$), and better than the null model ($\Delta BIC > 34$).

Contrary to what was observed in Experiment 1, participants in Experiment 2 were better at encoding the shape of the distractor distribution when the search array was presented in the center, compared to in the periphery. However, role reversals with CT-PD distance around 0° had a bigger influence on RTs in the periphery regardless of the preceding distractor distribution. Response times decreased sharply and monotonously as CT-PD increased, as seen from the high negative slopes obtained in the CT-PD curves of the peripheral condition. For example, the estimated slope of the best fit model for the Gaussian distractor distribution in the peripheral condition ($B = -0.03$, $SE = 0.0003$, $z = -8.67$, $p < .001$) was highly negative, whereas that level of steepness was not observed for the best fit model for the Gaussian distractor distribution in the central condition ($B = -0.01$, $SE = 0.0003$, $z = -3.97$, $p < .001$)³. This indicates that even though participants did not encode the shape of the preceding distractor distribution in the periphery condition, it is clear that the mean of the distractor distribution was specifically encoded.

General Discussion

In two experiments, we investigated similarities and differences in visual search performance and ensemble encoding of distractor sets between the central and peripheral visual fields. A crucial part of our experimental design involved investigating the effects of distractor distributions with the same mean and range, but with different shapes (Gaussian or uniform). Firstly, **in both experiments**, we found that the shape of the distractor distribution strongly affected visual search times when the search was performed in the foveal region, but we did not observe its effect in the periphery. **In the first experiment, more details of the shape of the distractor distribution were found to be encoded in the peripheral condition than the central condition. In the second experiment,**

³ Note that analyses were done on log-transformed reaction times.

we scaled down the search array for the central condition, but scaled it up for the peripheral condition. This time, encoding of the shape of the distractor distributions was found to be better in the central than the peripheral condition. Overall, we conclude that in addition to summary statistics, detailed information (e.g. shape) about distractor distributions can be encoded with peripheral vision, depending on the scale (or the inter-item distance) of the search array.

In what follows, we speculate what these findings are likely to reflect.

Search times in central vs. peripheral vision

The influence of distractor distribution type on search times in the central condition of our experiments is in line with previous studies. Distractor heterogeneity is known to have negative effects on search performance (Duncan & Humphrey, 1989; Rosenholtz, 2001). In the central condition, the lower the variance of the distractor distribution, the faster and more accurate participants were. Search times in the center differed even though only the shape of the distractor distribution was changed while their summary statistics were kept similar. However, this was not observed when the search array was presented in the periphery. To our knowledge, this differential effect of distractor distribution on search times in the center and periphery has not been observed before in the literature.

Eccentricity effects on search performance have been well established (Carrasco, Evert, Chang & Katz, 1995; Carrasco & Yeshurun, 1998). Even though crowding increases with increasing eccentricity, these eccentricity effects were found to be independent of crowding (Carrasco & Frieder, 1997; Madison, Lleras & Buetti, 2018). However, other researchers have also found effects of peripheral crowding on visual search performance (Vlaskamp, Over & Hooge, 2005). In our experiments, regardless of the influence of eccentricity and crowding, the overall search times in the central and peripheral conditions did not differ. This result was not surprising since the influences of eccentricity and crowding are not as strong in pop-out search as in other types of visual search tasks (Wertheim, Hooge, Krikke & Johnson, 2006; Gheri, Morgan & Solomon, 2007). In contrast with previous studies, however, we found that certain characteristics of the distractor distribution had no influence on the search times in the periphery, even though this influence was observed in foveal search. These characteristics include the variance (or range) and the shape of the distractor distribution. This result was observed

in both experiments, in other words, even when the spacing between the search items, as well as their size, were manipulated to account for the cortical magnification factor. Moreover, this difference between central and peripheral regions was observed even though the overall search times and accuracy did not differ between the two regions. We propose that this interaction between distractor distribution type and search array location is consistent with the summary statistical account of visual search times of Rosenholtz et al. (2012). According to this view, what determines search times is the difference in summary statistics of a “feature pooling” region that contains the target feature and a region that does not (i.e. only distractor features). The size of these feature-pooling regions increases with eccentricity. This view can account for the search times observed in our experiments. The summary statistics of the different distractor distributions used in our study were very similar to each other. The mean of the distractor distribution was equally distant (in orientation space) from the target on all trials of the experiment. Gaussian $SD = 15^\circ$ and uniform distractor distributions had the same range, which made their variance very similar. The only slightly different distribution (with respect to its summary statistics) was the low variance for Gaussian $SD = 10^\circ$. The reason why peripheral search times with the Gaussian $SD = 10^\circ$ were not lower than the other two distribution type conditions could be due to role reversal effects, since the Gaussian $SD = 10^\circ$ distribution was only used in the test trials. However, it should be noted that the search times observed with Gaussian $SD = 10^\circ$ in the central condition were lower than the other two distribution conditions, even in Experiment 1, where the overall amount of slowing due to role reversals was fairly similar in the center and periphery.

In contrast to peripheral search, response times in the central condition were sensitive to the different types of distractor distributions even though the differences between their summary statistics were small. This contrast between foveal and peripheral search times provides evidence for the view that summary statistical representations in peripheral vision account for visual search times.

Ensemble coding with central vs. peripheral vision

Notably, our results go beyond the summary statistical account of peripheral vision. We used the methods introduced by Chetverikov et al (2016, 2017) to assess any feature

distribution learning in the periphery and in the center. Chetverikov et al. have shown that observers can extract more detailed information about feature distributions within visual ensembles than previous studies on ensemble perception have indicated. In Experiment 1, when the search array was presented in the periphery, search times on test trials with respect to CT-PD distance revealed that participants were able to encode more than just the summary statistics of the distractor distribution. The shape of the CT-PD curves observed on the test trials of Experiment 1 depended on the shape of the distractor distribution used in the preceding learning trials. However, the effect of the shape of the distractor distribution was not observed in the periphery when the spacing of the search items was increased in Experiment 2. This observation is in line with other studies demonstrating that crowding facilitates ensemble coding (Parkes et al., 2001; Fischer & Whitney, 2011). Since the peripheral search array was more crowded (low inter-item spacing) in Experiment 1 than Experiment 2, this increased crowding might have facilitated a more efficient process, perhaps akin to texture segmentation (Julesz, 1981), which, in turn, can explain why the shape of the distractor distribution was encoded **in more detail** for the periphery **condition** in Experiment 1 but not Experiment 2.

However, in Experiment 2, when the target orientation on test trials was set to the mean orientation of the distractor distribution on the preceding learning trials (i.e. CT-PD = 0), the effect of role reversal was stronger in the periphery than in the center (Figure 7). Not only that, RTs decreased linearly with a relatively high negative slope as soon as CT-PD increased. This suggests that the visual system relied heavily on the mean orientation of the distractor distribution for finding the target in the periphery condition of Experiment 2, rather than encoding other details of the distractor distribution.

What factors **could** have facilitated the encoding of information about the shape of the distribution as opposed to its summary statistics? **Apart from the effect of crowding mentioned above**, another reason could be the increase in inter-item spacing in Experiment 2, which made a significant part of the search array appear at even higher eccentricity. This could have made the encoding of the distractor distributions more difficult. In fact, participants made more mistakes in the periphery condition than the central condition in Experiment 2. This could force peripheral vision to rely on the summary statistics of the distractor distribution, rather than encoding the distribution itself. However, further empirical evidence is needed to confirm such an explanation.

Overall, we suggest that the difference in results between the two experiments reflect performance differences of the ensemble encoding mechanism in peripheral vision due to the changes introduced to the visual stimuli, rather than two different encoding mechanisms (e.g. summary statistics vs. distribution). In other words, we argue that the peripheral visual system constructed a representation of the distractor distribution in both experiments, however, this representation was less precise in Experiment 2, where more weight was given to the mean of the distribution in building the representation of the distribution, rather than its other features. Such an explanation is consistent with a distribution-based framework of visual attention (see Chetverikov et al., 2017c for a review).

The display used in the central condition in Experiment 1 was very similar to the ones used in previous studies, which demonstrated that participants encode the shape of the distractor distribution (Chetverikov et al. 2016, 2017a). However, in this study we did not observe distribution shape learning in Experiment 1. The CT-PD curves obtained in this study were noisier than those obtained in previous studies. One of the main differences between our study and those previous ones was that we asked observers to maintain fixation while they performed the search while in the previous studies participants were free to move their eyes. Even though the size of the search array in Experiment 1 was smaller than the ones used previously by Chetverikov et al. (2016, 2017a), when participants fixated at the center of the array, the lines at the outer part of the array still fell outside of the foveal region. Some participants in our study reported that in the central condition when they saw a candidate line that they thought was the target, they sometimes struggled with inhibiting their eye movements towards that candidate line. It is possible that this inhibition of eye movements influenced the encoding of the shape of the distractor distribution. Our results from Experiment 2 support this interpretation because when the search array was scaled down so that almost all the oriented lines fell within 2° around the fixation point, more details about the shape of the distractor distribution were encoded. However, further studies are needed in order to understand the influence of eye movements on the learning of distractor distribution shape.

The main difference between the two experiments was the scaling of the search array and the difference in results might also be explained by the degree of mismatch between

the size of the spatial filters in the periphery (or fovea) and the spatial resolution of the search array. Such a mismatch can influence performance in texture segmentation tasks. The task and the stimuli used in our study have parallels with texture segmentation tasks. However, the effect of spatial resolution on texture segmentation has been observed in explicit performance measures such as accuracy (Yeshurun & Carrasco, 1998). In our study, the pattern of results obtained for such performance measures did not essentially differ between the two experiments. Therefore, if our method had only relied on such explicit measures, then it could not have revealed any differences in how scaling of the search array influences encoding of the distractor feature distributions. This highlights an urgent need in the literature for implicit experimental methods similar to the one used in this study. For example, future studies can use our implicit method for novel insights into texture processing mechanisms, eschewing the limitations of explicit experimental measures.

Conclusion

Our results showed that the shape and variance of the distractor distribution in a pop-out search for an oddly oriented line did not influence search performance when the search was performed with peripheral vision, whereas they had a significant effect when the search was performed around the foveal region. This result is in line with the view that visual information in the periphery is represented in terms of the summary statistics of the scene. However, our results also showed that beyond summary statistics, **more details about the** distractor distribution can be encoded with peripheral vision depending on the spacing between the search items (or the overall size of the search array). When the inter-item spacing was increased (in Experiment 2), participants tended to encode the mean of the distractor distribution rather than details about its shape.

Our study also suggests that visual search studies of ensemble summary statistics should be interpreted with caution. The visual search times were not sensitive to the different distractor distributions when the summary statistics of those distributions were roughly the same. This could suggest that peripheral vision relies mostly on summary statistics. However, our implicit method revealed that, under certain conditions, participants' peripheral vision encoded more detailed information about the distractor distribution than only the summary statistics. These results call for the increased use of

implicit experimental methods for a deeper understanding of what information is encoded from visual ensembles.

References:

- Alvarez, G. A. (2011). Representing multiple objects as an ensemble enhances visual cognition. *Trends in Cognitive Sciences*, 15(3), 122–131. doi:10.1016/j.tics.2011.01.003.
- Anstis, S. M. (1974). Letter: A chart demonstrating variations in acuity with retinal position. *Vision Research*, 14, 589–592.
- Balas, B. J., Nakano, L., & Rosenholtz, R. (2009). A summary-statistic representation in peripheral vision explains visual crowding. *Journal of Vision*, 9(12):13, 1–18, doi:10.1167/9.12.13.
- Becker, S. I. (2010). The role of target-distractor relationships in guiding attention and the eyes in visual search. *Journal of Experimental Psychology: General*, 139(2), 247–265. <http://dx.doi.org/10.1037/a0018808>.
- Bouma, H. (1970) Interaction effects in parafoveal letter recognition. *Nature* 226, 177-178.
- Brainard D. (1997). The Psychophysics Toolbox. *Spatial Vision*, 10 (4), 433–436.
- Bulakowski PF, Post RB & Whitney D. (2011). Dissociating crowding from ensemble percepts. *Atten. Percept. Psychophys.* 73(4):1003–9
- Carrasco, M., Evert, D. L., Chang, I., & Katz, S. M. (1995). The eccentricity effect: Target eccentricity affects performance on conjunction searches. *Perception & Psychophysics*, 57, 1241–1261.
- Carrasco, M. & Frieder, K. S. (1997). Cortical magnification neutralizes the eccentricity effect in visual search. *Vision Research*, 37(1), 63–82.
- Carrasco, M., & Yeshurun, Y. (1998). The contribution of covert attention to the set-size

- 724 and eccentricity effects in visual search. *Journal of Experimental Psychology: Human*
725 *Perception and Performance*, 24, 673–692.
- 726 Cavanagh, P. (2001) Seeing the forest but not the trees. *Nat. Neurosci.* 4, 673–674
- 727 Chetverikov, A., Campana, G., & Kristjánsson, Á. (2016). Building ensemble
728 representations: How the shape of preceding distractor distributions affects visual
729 search. *Psychological Science*. <http://dx.doi.org/10.1177/0956797617713787>.
- 730 Chetverikov, A., Campana, G., & Kristjánsson, Á. (2017a). Rapid learning of visual
731 ensembles. *Journal of Vision*, 17(21), 1–15. <http://dx.doi.org/10.1167/17.2.21>.
- 732 Chetverikov, A., Campana, G., & Kristjánsson, Á. (2017b). Representing color
733 ensembles. *Psychological Science*. <http://dx.doi.org/10.1177/0956797617713787>.
- 734 Chetverikov A, Campana G, & Kristjánsson Á (2017c) Learning features in a complex
735 and changing environment: A distribution-based framework for visual attention and
736 vision in general, In: *Progress in Brain Research*, pp. 97–120 Elsevier.
737 DOI: 10.1016/bs.pbr.2017.07.001
- 738 Chetverikov, A., Hansmann-Roth, S., Tanrikulu, O.D. & Kristjánsson, Á. (2019). Feature
739 Distribution Learning (FDL): a new method to study visual ensembles with priming of
740 attention shifts. *Neuromethods*, Springer
741
- 742 Cho, J., & Chong, S. C. (2019). Search termination when the target is absent: The
743 prevalence of coarse processing and its intertrial influence. *Journal of Experimental*
744 *Psychology: Human Perception and Performance*, 45(11), 1455-1469.
- 745 Cornelissen, F.W., Peters, E., Palmer, J. (2002). The Eyelink Toolbox: Eye tracking with
746 MATLAB and the Psychophysics Toolbox. *Behavior Research Methods, Instruments &*
747 *Computers*, 34, 613-617.
- 748 Curcio, C.A., Sloan, K.A, Packer, O., Hendrickson, A.E. & Kalina, R.E (1987).
749 Distribution of cones in human and monkey retina: individual variability and radial
750 asymmetry. *Science*, 236(4801), 579-582.
- 751 Daniel, P. M., & Whitteridge, W. (1961). The representation of the visual field on the

- 752 cerebral cortex in monkeys. *Journal of Physiology*, 159, 203–221.
- 753 Drasdo, N. (1997) *The neural representation of visual space*. *Nature* (Lond.) 266, 554-
754 556
- 755 Duncan, J., & Humphreys, G. W. (1989). Visual search and stimulus similarity.
756 *Psychological Review*, 96, 433–458.
- 757 Ehinger, K. A. & Rosenholtz R. (2016) A general account of peripheral encoding also
758 predicts scene perception performance. *Journal of Vision* 16(2):13, 1–19
- 759 Fischer, J., & Whitney, D. (2011). Object-level visual information gets through the
760 bottleneck of crowding. *Journal of Neurophysiology*, 106(3), 1389–1398.
761 doi:10.1152/jn.00904.2010.
- 762 Gheri, C., Morgan, M. J., & Solomon, J. A. (2007). The relationship between search
763 efficiency and crowding. *Perception*, 36, 1779–1787.
- 764 Girshick, A.R., Landy, M.S., Simoncelli, E.P., 2011. Cardinal rules: visual orientation
765 perception reflects knowledge of environmental statistics. *Nature Neuroscience*. 14 (7),
766 926–932. [http:// dx.doi.org/10.1038/nn.2831](http://dx.doi.org/10.1038/nn.2831).
- 767 Haberman, J., & Whitney, D. (2011). Ensemble perception: Summarizing the scene and
768 broadening the limits of visual processing. In J. Wolfe & L. Robertson (Eds.), *From*
769 *perception to consciousness: Searching with Anne Treisman*. New York: Oxford
770 University Press.
- 771 Hubel, D. H., & Wiesel, T. N. (1974). Uniformity of monkey striate cortex: A parallel
772 relationship between field size, scatter, and magnification factor. *Journal of Comparative*
773 *Neurology*, 158, 295–306.
- 774 Ji, L., Chen, W., and Fu, X. (2014). Different roles of foveal and extrafoveal vision in
775 ensemble representation for facial expressions. *Engineering Psychology and Cognitive*
776 *Ergonomics Lecture Notes in Computer Science*, 8532, 164–173.
- 777 Jóhannesson, Ól, Tagu, J, & Kristjánsson, Á. (2018) Asymmetries of the visual system
778 and their influence on visual performance and oculomotor dynamics. *European Journal*
779 *of Neuroscience*, 48: 3426– 3445. <https://doi.org/10.1111/ejn.14225>

- 780 Julesz, B. (1981). Textons, the elements of texture perception, and their interactions.
781 *Nature*, 290 (12), 91–97.
- 782 Kass, R. E., & Raftery, A. E. (1995). Bayes factors. *Journal of the American Statistical*
783 *Association*, 90(430), 773–795. <http://dx.doi.org/10.1080/01621459.1995.10476572>.
- 784 Kleiner M., Brainard D. H., Pelli D. G. (2007). What's new in Psychtoolbox-3?
785 *Perception*, 36, ECVF Supplement 14.
- 786 Kristjánsson, Á., & Driver, J. (2008). Priming in visual search: Separating the effects of
787 target repetition, distractor repetition and role-reversal. *Vision Research*, 48(10), 1217–
788 1232. <http://dx.doi.org/10.1016/j.visres.2008.02.007>.
- 789 Larson A. M. Loschky L. C. (2009). The contributions of central versus peripheral vision
790 to scene gist recognition. *Journal of Vision*, 9(10):6, 1–16
- 791 Levi, D. M. (2008). Crowding: An essential bottleneck for object recognition: A mini-
792 review. *Vision Research*, 48, 635–654.
- 793 Levi, D., Klein, S. & Aitsabaomo, A. P. (1985) Vernier acuity, crowding and cortical
794 magnification factor. *Vision Research* 25, 963-967.
- 795 Livne, T., & Sagi, D. (2007). Configuration influence on crowding. *Journal of Vision*,
796 7(2):4, 1–12
- 797 Madison, A., Lleras, A. & Buetti, S. (2018). The role of crowding in parallel search:
798 Peripherap pooling is not responsible for logarithmic efficiency in parallel search.
799 *Attention, Perception & Psychophysics* 80(2), 352 - 373
- 800 Palmer, J., Verghese, P., & Pavel, M. (2000). The psychophysics of visual search. *Vision*
801 *Research*, 40, 1227–1268.
- 802 Parkes, L., Lund, J., Angelucci, A., Solomon, J. A., & Morgan, M. (2001). Compulsory
803 averaging of crowded orientation signals in human vision. *Nature Neuroscience*, 4, 739–
804 744.
- 805 Pelli, D. G., & Tillman, K. A. (2008). The uncrowded window of object recognition. *Nature*
806 *Neuroscience*, 11, 1129–1135.

- 807 Rosenholtz, R. (2001). Visual search for orientation among heterogeneous distractors:
808 Experimental results and implications for signal-detection theory models of visual
809 search. *Journal of Experimental Psychology: Human, Perception and Performance*, 27,
810 985–999.
- 811 Rosenholtz, R., Huang, J., Raj, A., Balas, B. J., & Ilie, L. (2012). A summary statistic
812 representation in peripheral vision explains visual search. *Journal of Vision*, 12(4), 1–17.
- 813 Stuart, J., & Burian, H. (1962). A study of separation difficulty: Its relationship to visual
814 acuity in the normal amblyopic eye. *American Journal of Ophthalmology*, 53(471), 163–
815 169.
- 816 Utochkin, I. S., & Yurevich, M. A. (2016). Similarity and heterogeneity effects in visual
817 search are mediated by “segmentability”. *Journal of Experimental Psychology: Human*
818 *Perception and Performance*, 42(7), 995-1007.
- 819
- 820 Virsu, V., & Rovamo, J. (1979). Visual resolution, contrast sensitivity, and the cortical
821 magnification factor. *Experimental Brain Research*. 37,475–494.
- 822 Vlaskamp, B. N. S., Over, E. A. C., & Hooge, I. T. C. (2005). Saccadic search
823 performance: The effect of element spacing. *Experimental Brain Research*, 167, 246–
824 259.
- 825 Wertheim, A. H., Hooge, I. T. C., Krikke, K., & Johnson, A. (2006). How important is
826 lateral masking in visual search. *Experimental Brain Research*, 170, 387–401.
- 827 Whitney D, Haberman J, Sweeny T. (2014). From textures to crowds: multiple levels of
828 summary statistical perception. In *The New Visual Neuroscience*, ed. JS Werner, LM
829 Chalupa, pp. 695–710. Cambridge, MA: MIT Press
- 830 Whitney, D., & Leib, A. Y. (2018). Ensemble perception. *Annual Review of Psychology*,
831 69, 12.1-12.25.
- 832 Wilkinson, F., Wilson, H. R. & Ellemberg, D. (1997) Lateral interactions in peripherally
833 viewed texture arrays. *J Opt Soc Am A* 14, 2057-68.

- 834 Wolfe, B. A., Kosovicheva, A. A., Leib, A. Y., Wood, K. & Whitney, D. (2015) Foveal
835 input is not required for perception of crowd facial expression. *Journal of Vision* 15, 11.
836
- 837 Yeshurun, Y., & Carrasco, M. (1998). Attention improves or impairs visual performance
838 by enhancing spatial resolution. *Nature*, 396(6706), 72.
839