

Visual crowding is a combination of an increase of positional uncertainty, source confusion, and featural averaging

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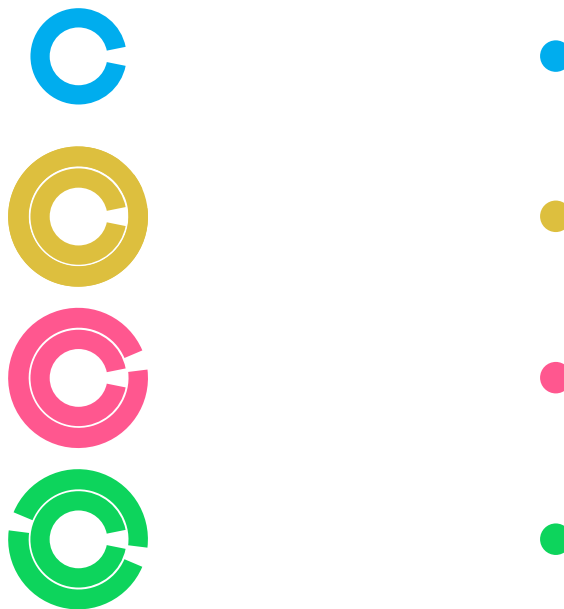
1 **Although we perceive a richly detailed visual world, our ability to identify individual objects**
2 **is severely limited in clutter, particularly in peripheral vision. Models of such crowding have**
3 **generally been driven by the phenomenological misidentifications of crowded targets:**
4 **using stimuli that do not easily combine to form a unique symbol (e.g. letters or objects),**
5 **observers typically confuse the source of objects and report either the target or a**
6 **distractor, but when continuous features are used (e.g. orientated gratings or line**
7 **positions) observers report a feature somewhere between the target and distractor. To**
8 **reconcile these accounts, we develop a hybrid method of adjustment that allows detailed**
9 **analysis of these multiple error categories. Observers reported the orientation of a target,**
10 **under several distractor conditions, by adjusting an identical foveal target. We apply new**
11 **modelling to quantify whether perceptual reports show evidence of positional uncertainty,**
12 **source confusion, and featural averaging on a trial-by-trial basis. Our results show that**
13 **observers make a large proportion of source-confusion errors. However, our study also**
14 **reveals the distribution of perceptual reports that underlie performance in this crowding**
15 **task more generally: aggregate errors cannot be neatly labelled because they are**
16 **heterogeneous and their structure depends on target-distractor distance.**

17
18 Throughout the entire visual field, vision is constrained by multiple bottlenecks in visual processing
19 that limit the information reaching our awareness. Initially, information is lost to physiological
20 factors such as the eyes' optics and retinal nerve fiber density, and neural selective sensitivity to
21 spatio-temporal patterns^{1,2}. However, our ability to identify even a simple object, such as a letter
22 or an oriented grating, is far worse than predicted from these factors when the object is surrounded
23 by clutter^{3,4}. These identification failures, referred to as "crowding", occur even though adaptation
24 after-effects demonstrate that the object's features have been encoded, at least in primary visual
25 cortex⁵⁻⁷. Thus, our ability to consciously access the identity of an object is constrained by
26 information processing capacity, not simply by retinal physiology or sensitivity limitations of the
27 visual system.

28
29 Crowding, the inability to recognise an object in visual clutter, influences many aspects of vision. It
30 is generally agreed to occur across the entire visual field⁸, although it is markedly more difficult to
31 measure at the fovea⁹. As discussed in a review by Pelli and Tillman⁴, crowding affects all basic
32 object recognition tasks, predicts reading speed and dyslexia, and is diagnostic of foveal deficits
33 present in amblyopia¹⁰. Furthermore, it limits visibility of naturalistic images¹¹⁻¹³, and interacts with
34 saccadic and smooth pursuit eye movements in non-trivial ways¹⁴⁻¹⁹. There have been several
35 recent reviews of crowding that summarize very well its ubiquity^{4,20-22}, as well as examples in
36 which object recognition is seemingly unaffected by parameters that cause crowding in other
37 instances^{e.g. 23}.

38
39 The spatial extent of crowding is quite similar across paradigms. Perceptual errors increase with
40 eccentricity and decrease as the distance between target and distractor increases. The precise
41 target-flanker distance at which crowding is alleviated at a given eccentricity, often referred to as
42 Bouma's constant, is somewhat variable across studies⁸, and changes dynamically according to
43 the duration and relative timing of target and distractors^{19,24-28}. Despite this variability, the term
44 "crowding" is typically taken to refer to any target identification interference that depends on target-
45 distractor proximity²⁹.

46 Although there are many fascinating aspects of crowding, we focus on fundamental findings. By
47 viewing Figure 1, the reader can experience firsthand three phenomenal aspects of crowding that
48 arise with stimuli similar to those used in our experiments. Following standard convention, we term
49 these phenomena: 1) positional uncertainty^{30,31}, 2) feature averaging³², and 3) source confusion^{33,34}.
50 In this figure we present the same target stimulus, a Landolt C¹, in a series of distractor
51 conditions. An observer's goal is to locate the orientation of the gap section as accurately as
52 possible. If the reader fixates the spots in succession from top to bottom, they may note that the
53 apparent clarity of the correspondingly-coloured target orientation is affected differently in each
54 condition. The target gap is clearest in the top row, but its position is less clear when fixating the
55 yellow spot below, perhaps because the solid ring distractor adds noise to the positional
56 mechanisms encoding the target orientation³⁵. When fixating the pink spot, the target and
57 distractor gaps may perceptually blend together, shifting the perceived target orientation toward
58 the distractor orientation^{e.g. 36}. When fixating the green spot, it is not immediately clear which of the
59 multiple gaps is the target, and it may be easy to confuse a distractor gap for a target gap³⁷. The
60 changes in target visibility while viewing the yellow, pink, and green stimuli demonstrate, in order,
61 positional uncertainty, feature averaging, and source confusion.



62
63 **Figure 1. Examples of stimuli in our experiments that produce qualitatively different**
64 **perceptual outcomes. From top to bottom, rows represent the unflanked, no-gap flanker,**
65 **one-gap flanker, and two-gap flanker conditions. Stimuli are drawn to scale, but were white**
66 **on a grey background in the experiment. Data in later figures follow the colour conventions**
67 **shown here.**

68
69 The perceptual phenomena experienced in cluttered displays are typically revealed across studies
70 employing different methodologies. Changes in positional uncertainty and feature averaging are
71 found in experiments in which an observer is required to make a spatial judgment about a
72 continuous property of the target, such as its orientation or relative position, for examples, see^{36,38}.
73 Feature substitutions – mistaking a distractor element for a target – are mostly found in paradigms
74 in which the observer is required to report the categorical identity of target such as a letter; trials in
75 which the observer reports a distractor identity instead of the target reveal source confusions^{33,34,39},
76 which may be independent of an increase in positional uncertainty⁴⁰⁻⁴².

¹ Note that our target is a modified version of a Landolt C. A true Landolt C has a gap section formed by parallel lines, whereas the gap section in our stimulus is formed by non-parallel lines.

77 It is important to note that distinct categories of errors, such as *averaging* and *substitution* errors,
78 are descriptors of results, not descriptors of a mechanism per se. Indeed, even the term crowding
79 refers to the result of some visual process and not a mechanism. The underlying cause of
80 crowding has previously been explained by various computational models^{11,22,36-38,43-45} and higher-
81 level mechanistic hypotheses^{23,46}. Population code models, in which all visual features
82 probabilistically contribute to perceptual reports, can produce a wide variety of data⁴⁷, including
83 so-called averaging and substitution errors³⁷. We have thus argued that the different classes of
84 errors reported across the crowding literature are actually arbitrary categories of the output of a
85 single mechanism. In the present report, therefore, we use the terms “substitution” and “averaging”
86 as a convenient way to describe patterns in our data, but not to indicate hypothesised
87 mechanisms. Our aim in the present study is to shed further light on the cause of crowding using a
88 single paradigm that produces multiple perceptual phenomena. Here we use experiment and
89 modelling to quantify changes in positional uncertainty, averaging, and source confusions in visual
90 clutter.

91

92 **Methods**

93 This experiment accorded with the protocols reviewed and approved by our local institutional
94 review board. We tested three highly experienced psychophysical observers, including the two
95 authors, all of whom gave informed consent. In figures, we refer to the participant naïve to the
96 specific purposes of this experiment as N1, and to the authors as A1 (PJB) and A2 (WJH). All
97 observers previously participated in two similar crowding experiments³⁷.

98

99 An observer sat 57 cm from the display with their head stabilised by a chin and headrest. The
100 display was a CRT monitor (1280 x 1024 resolution, 85 Hz). We programmed the experiment with
101 the Psychophysics Toolbox Version 3^{48,49} in MATLAB (MathWorks). Stimuli were white (100
102 cd/m²) on a gray (50 cd/m²) background. The target was centered 10° to the right of the fixation
103 spot, had a 2° diameter, and a line width of 0.4°. The gap width, measured at the midpoint of the
104 line width, was 0.4°. In the one-gap and two-gap flanking conditions, the size of the gaps remained
105 constant across flanker diameters. For all flanking conditions, the line width remained constant
106 (0.4°). A flankers' outer edge was separated from the target's outer edge by 0.4°, 0.92°, 1.62°,
107 2.58°, 3.9°, or infinity (ie. no flanker). We express flanker size as the flanker radius as a proportion
108 of the eccentricity of its centre, giving 0.14 ϕ , 0.19 ϕ , 0.26 ϕ , 0.36 ϕ and 0.49 ϕ , where ϕ is the
109 flanker eccentricity (10°). The flanker condition was selected randomly from trial-to-trial.

110

111 The orientations of flankers were constrained in the following way to produce maximal crowding
112 effects³⁷. In the one-gap and dual-gap flanker conditions, the flanker orientation was drawn from a
113 normal distribution, centred on the target orientation and with a standard deviation of 22.5°. Within
114 this range, we expect maximum levels of crowding. For the dual-gap flanker condition, a second
115 flanker gap was drawn from a normal distribution centred 180° from the first flanker gap, with a
116 standard deviation of 22.5°.

117

118 Each trial began when an observer pressed the space bar, which triggered the display of a small
119 spot in the centre of the screen and the target (with or without flanks) for 500 ms. Immediately
120 following the offset of the target, a Landolt C was presented in the centre of the display, and
121 observers could rotate this clockwise or anti-clockwise by pressing the right or left arrow key
122 respectively. To report an orientation, they pressed the space bar, and the next trial would begin.
123 Observers were instructed to be as accurate as possible without rushing. They could take a break
124 at any time by withholding a report. All observers completed 320 trials per session (20 repetitions
125 of each target-flanker combination), for five sessions, giving a total of 1600 trials, or 100 trials per

126 target-flanker condition. Each session took approximately 15 – 20 minutes.

127

128 Results

129 For all conditions, report error is defined as the difference between the reported orientation and the
130 target orientation, with positive errors indicating a report that was more clockwise than the target.

131 Because in our experiments increasing the flanker size increases target-flanker separation, we use
132 the terms “flanker size” and “target-flanker separation” interchangeably.

133

134 *No-gap flanker condition*

135 Because the no-gap flanker has no features that could be substituted or averaged with the target,
136 results from this condition allow us to examine clearly changes in positional uncertainty. In the no-

137 gap flanker condition, observers’ report errors clustered around 0° for all target-flanker separations
138 (Fig. 2A). We used the Circular Statistics Toolbox² to find the circular standard deviation of

139 observers’ reports. We refer to this measure as perceptual error, which is plotted in degrees
140 separately for each observer in Figure 2B-D as a function of the flanker size. Consistent with the

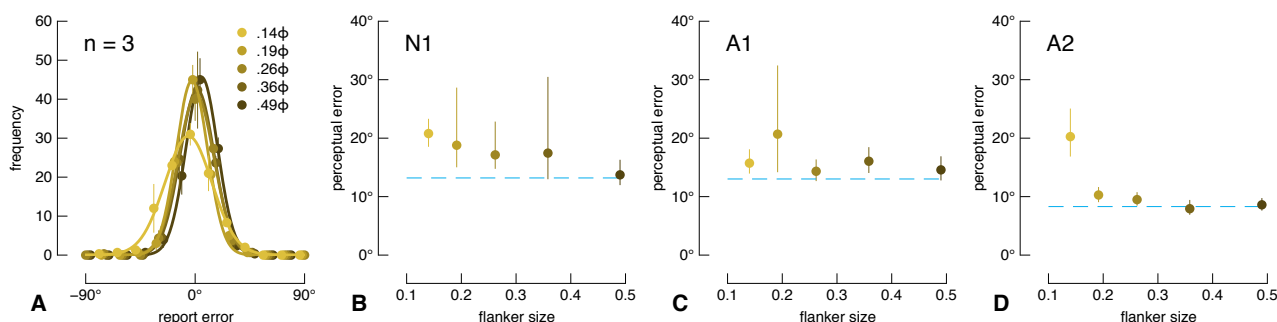
141 crowding literature, all participants’ perceptual error was higher than the unflanked condition
142 (dashed lines) for the two smallest flanker sizes. Observers N1 and A2 in particular show the

143 characteristic, approximately linear improvement in performance with increasing flanker size.

144 Performance in the largest flanker condition was similar to unflanked performance for all

145 observers.

146



147

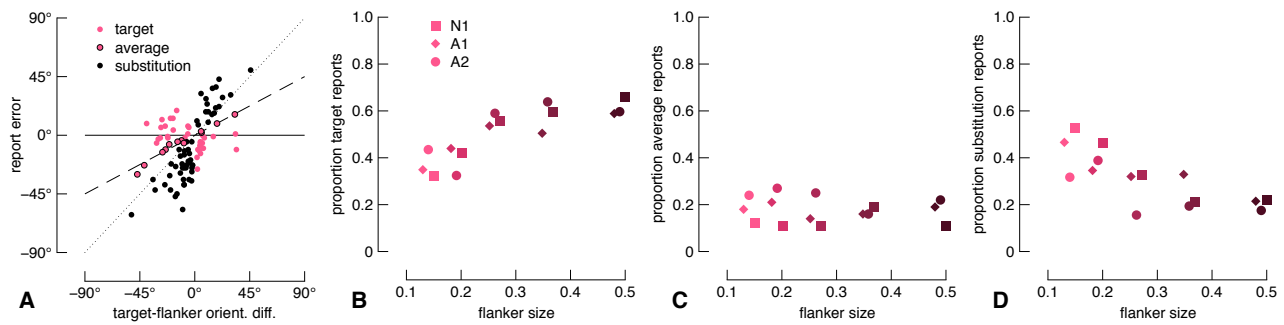
148 **Figure 2. Results from the no-gap flanker condition. A)** Average frequencies of each report
149 error size (25 bins; bin width = 15°), fit with circular distributions. To improve visibility, the
150 data have been offset slightly along the x-axis, and the x-axis has been truncated to $\pm 90^\circ$.
151 Only a total of 4 errors greater than $\pm 90^\circ$ were made by all observers across all no-gap
152 flanker conditions. The inset legend shows the target-flanker separation condition. Error
153 bars show one standard error. B – D) Perceptual error (the circular standard deviation of
154 report errors) plotted as a function of flanker size for each participant. Flanker size is
155 expressed as flanker radius divided by the eccentricity of its centre (i.e. in units of Bouma’s
156 constant). The dashed line indicates perceptual error for the unflanked condition. Error bars
157 show 95% bootstrapped confidence intervals.

² <http://uk.mathworks.com/matlabcentral/fileexchange/10676-circular-statistics-toolbox--directional-statistics->

158 *One-gap flanker condition*

159 In the one-gap flanker condition, we have previously shown that observers' reports correspond to
160 the distribution of weighted responses to the target and flanker orientations³⁷. Thus, reports may
161 include a proportion of responses at the target orientation, the flanker orientation and their mean
162 orientation. Quantifying reports with a unimodal circular standard deviation measure as used for
163 the no-gap flanker condition above, is inappropriate in such a case. For a detailed explanation from
164 the working memory literature, see⁵⁰. We express report errors as a function of target-flanker
165 orientation difference (see Fig. 3A and Appendix Figure A1A). Under a first analysis (see Appendix
166 A), we fit linear models to the data: reports at the target orientation have a slope of zero, reports at
167 the flanker orientation fall on the diagonal with unity slope, and reports at the average orientation
168 fall on the diagonal with a slope of 0.5. For all observers for the two most crowded conditions, the
169 slopes were close to 0.5 and reduce to 0 at larger target-flanker separations. However, if these
170 data were composed of noisy target and noisy flanker reports as described above and as has been
171 argued previously⁴¹, the slope of a linear fit to crowded data may give a spurious interpretation
172 favoring the averaging model. We further applied maximum likelihood mixture modelling as
173 described by Bays et al⁵⁰, as well as Monte Carlo simulations, but these alternative analyses failed
174 to return the true proportions of underlying report types of simulated data with known distributions.
175 We thus used a simplified approach that labels each datum according to its distance from each
176 model prediction, as described below.

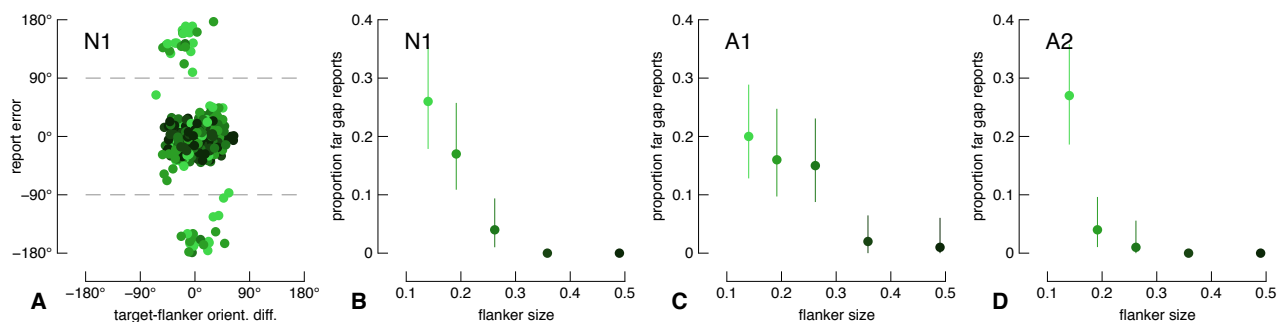
177
178 To quantify report errors in the one-gap flanker condition, we measured the distance of all report
179 errors from each of three underlying model predictions that correspond to target reports, averaged
180 reports, or substitution reports, and labelled each datum according to the nearest model (see Fig.
181 3A). We then quantified report types as a proportion of all trials from each condition. These
182 proportions are shown for all target-flanker separations in Figure 3B-D with symbols indicating
183 observers as per the legend. The ordinate labels on the different panels correspond to different
184 model predictions. Note that this analysis fits data simultaneously to all model predictions, and so
185 summing across panels for one flanker size for a single observer gives 1. The pattern is very
186 similar for all observers: with increasing flanker size, the proportion of target reports increases, the
187 proportion of average reports is relatively stable, and the proportion of substitution reports
188 decreases. Note that this pattern of results indicates that the response distribution is multi-modal,
189 since the proportions of data for each error type changes non-monotonically. Although the
190 proportion of target reports saturates around 0.6 (Fig. 3B), this is likely an underestimate due to a
191 limitation of our analysis for distributions when the response standard deviation is large and the
192 target-flanker orientation difference is small: our simulations revealed that the modelled proportion
193 of target reports is accurate when the proportion of other model components is high (greater than
194 ~0.3), but the proportion of target reports is underestimated when the contribution from other
195 model components is minimal. For small flanker sizes, the conditions under which we expect
196 relatively poor performance, the proportion of each report type is likely more accurate than for
197 larger flanker sizes. Based on our previous work and the crowding literature, it is likely that
198 observers' reports are barely, if at all, influenced by the flanker for the largest flanker condition (for
199 example, see Fig. 2).



200
201 **Figure 3. Results from the one-gap flanker condition. A) Raw report errors from the naïve**
202 **participant. Solid, dashed, and dotted lines show target, averaging, and substitution**
203 **models, respectively. Data are attributed to each model according to proximity. B-D)**
204 **Proportion of report type as a function of flanker size for all observers. Report type is**
205 **shown on the ordinate across panels. Data for different observers have been horizontally**
206 **offset slightly for clarity.**

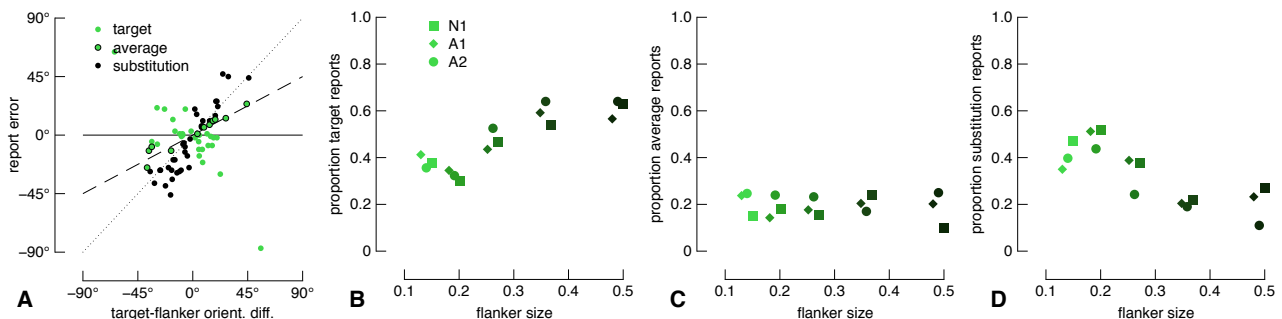
207
208 *Two-gap flanker condition*

209 In the two-gap flanker condition, one flanker gap orientation was normally distributed around the
210 target orientation (“near gap”; s.d. = 22.5°) and the second flanker gap orientation was distributed
211 180° from the first flanker gap (“far gap”; s.d. = 22.5°). Because of the relatively narrow report error
212 distributions even in the presence of a single flanker gap (e.g. Fig. 3A), we can with some
213 confidence delineate which errors are associated with the near gap and which with the far gap. In
214 Figure 4A, we show the raw report errors for the naïve observer. Report errors form two clusters:
215 one cluster centred on the y-axis at approximately 0° and another at approximately ±180°. We
216 arbitrarily defined reports with an absolute error greater than 90° as far-gap reports. These reports
217 are shown above and below the top and bottom dashed lines, respectively, of Figure 4A. The
218 proportion of far gap reports for each flanker size and each observer are shown in Figure 4B-D.
219 For all observers, the proportion of far-gap flanker errors is greatest for the smallest flanker size,
220 and gradually decreases as the flanker size increases.



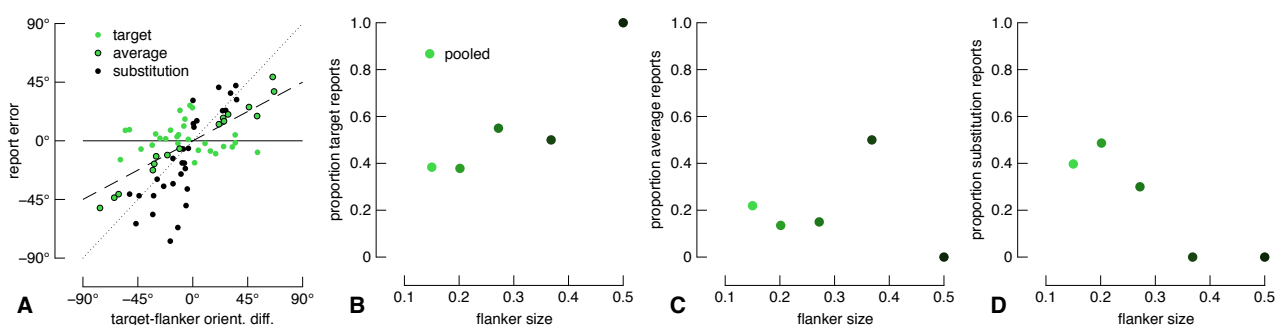
222
223 **Figure 4. Report errors in the two-gap flanker condition. A) Raw report errors from the naïve**
224 **participant. Report errors greater than 90° or less than -90° (dashed lines) were classified as**
225 **trials in which observers misreported the far-flanker gap rather than the target or near-**
226 **flanker gap. B-D) The proportion of such far gap reports as a function of flanker size for all**
227 **observers. Errors bars are 95% confidence intervals.**

228 We next divided the two-gap flanker condition data into two subsets for further analysis. First, we
 229 examined only those report errors within 90° of the target orientation. We performed the same
 230 analysis as we did for the one-gap flanker condition. Results are shown in Figure 5, and are highly
 231 similar to the results from the one-gap flanker condition in Figure 3. We also performed simple
 232 linear fits to the raw data, the results of which (misleadingly) favour an averaging model (see
 233 Appendix Fig. A2).
 234



235 **Figure 5. Results from the one-gap flanker condition. Data are shown as per Figure 3. A)**
 236 **Raw report errors from the naïve participant, focusing on only those errors within 90° of the**
 237 **target. B-D) Proportion of report type as a function of flanker size.**
 238

239 Second, we performed the same modelling on report errors that were greater than 90° from the
 240 target orientation. Due to the small number of observations in this analysis (Fig. 4), we pooled
 241 observers' data. We re-centered this subset of data by subtracting 180° from the orientation
 242 difference between the target gap and far flanker gap, as well as from the report error. The pooled
 243 errors corresponding to the far flanker gap are shown in Figure 6A. Because we re-centered these
 244 data, an error of 0° corresponds to a report of the target's polar opposite orientation, whereas data
 245 falling on the line of unity are reports following the far flanker gap orientation. As in the results
 246 above, with increasing flanker size, the proportion of target reports increases, the proportion of
 247 average reports is relatively stable, and the proportion of substitution reports decreases. In
 248 contrast to the results above, the proportion of target reports reached at the largest flanker size.
 249 However, there was only a single trial that had an error greater than 90° for the largest flanker
 250 condition, so this proportion necessarily had to be one or zero. Similarly, there were only two trials
 251 in the condition with the second largest flanker size, greatly restricting the possible proportions of
 252 report types.
 253



254 **Figure 6. Results from the two-gap flanker condition for report errors greater than 90° from**
 255 **the target with re-centered data (see text). Data are shown as per Figure 3. A) Raw report**
 256 **errors pooled across observers. B-D) Proportion of report type as a function of flanker size.**
 257

258 Discussion

259 We used a method of adjustment to quantify perceptual error in peripheral vision under novel
260 crowded conditions. In all conditions, performance depended on the distance between the target
261 and flanker, in line with the vast crowding literature⁴. Based on the phenomenological responses
262 and appearance of crowded stimuli, three general classes of mechanism have been advanced to
263 account for crowding: 1) positional uncertainty³⁰, 2) feature averaging³², and 3) source confusion
264³³. These models are not necessarily mutually exclusive and image processing based approaches
265 have been advanced that incorporate elements of each of these mechanisms (refs 11 & 13), but it
266 has been difficult to reconcile which best accounts for the data because of the use of different
267 methodologies and stimuli across studies supporting each account. Furthermore, with image
268 processing based models that produce foveal performance deficits with synthetic images that
269 simulate peripheral vision, it is not clear which combinations of these underlying processes
270 accounts for perceptual performance^{11,51,52}. The experimental design and complementary
271 modelling employed here provides a novel way to classify the frequency of each error type with the
272 same stimuli and observers. Our results reveal that all error types characterise crowding with
273 Landolts, but their proportions vary with the distance between the target and flanking stimuli.
274

275 In the no-gap flanker condition, the crowding we observed at relatively small target-flanker
276 separations is likely caused exclusively by an increase in orientation uncertainty (for example, ref
277³⁰). In this condition, there are no flank features for averaging or substitution to occur, yet, as
278 shown in Figure 2, we found a reliable increase in the circular standard deviation of perceptual
279 errors with decreasing target-flanker separation, see also³⁷. This result is unlikely due to a form of
280 classical masking, such as meta-contrast masking, because perceptual reports were not randomly
281 distributed in the presence of close flankers⁵³. It is also difficult to account for these errors with an
282 attentional account of crowding, in which observers' attentional resolution is too coarse to
283 individuate the target gap⁵: even in the smallest flanker condition, observers' reports cluster
284 around the actual target position, indicating that they could indeed attend to the target gap, albeit
285 with greater perceptual error that is directly attributable to an increase in orientation variance (Fig.
286 2). We suggest that this orientation noise can be attributed to the solid flanking ring increasing the
287 bandwidth of a population code that encodes the target orientation (see below and ref³⁷).
288

289 The results of the one-gap and two-gap flanker conditions also support recent proposals that
290 crowding may best be accounted for by a population code. Rather than conforming neatly to a
291 single report error type, we found errors could be accurate, follow the flanker gap, or some
292 average of the two. These data are thus difficult to reconcile with simple averaging or substitution
293 models. Van den Berg et al⁴⁷ showed that many hallmarks of crowding can be explained by a
294 biologically inspired model that simulates the responses of populations of neurons tuned to
295 orientation within a fixed region of space (ie. a receptive field). Crowded stimuli create systematic
296 shifts in the population code, so that when the population code is decoded, the decoded signal is
297 prone to error. We further showed that an idealised population code can, for a given crowded
298 stimulus, produce accurate, averaged, or substituted report errors in a probabilistic fashion³⁷. We
299 thus argued that there is no averaging or substitution mechanism per se, but instead that
300 perceptual reports are drawn from the population response to the stimuli. Such a process is distinct
301 from any single phenomenon such as source confusion, averaging or substitution but instead
302 results from the broad spatial bandwidth of early stage filters.
303

304 Critically, the results from the present study show that averaging of features is not compulsory, in
305 contrast to previous work³². On a number of trials in which a flanker gap is present, observers can
306 recover the target orientation with a precision similar to that observed with no flanker gap (Fig. 3).
307 With only a single report, it is impossible to know if, on a single trial, an observer perceived both

308 the target orientation and the flanker orientation, their average, or if the frequencies of these
309 percepts varied across trials. We previously asked participants to report both the target and flanker
310 orientations in an experiment similar to the present report, and found that participants were
311 generally capable of reporting both elements, though they often reversed feature positions³⁷.
312 Taken together, these data reveal that perceptual reports in clutter are probabilistic, but relatively
313 fine detail can be recovered.

314

315 It is clear from our data that observers often report an orientation closer to the flanker orientation
316 instead of the target orientation (Fig. 4). However, our findings suggest the proportion of
317 substitution-type errors is substantially greater than the proportion of substitution errors that occur
318 when whole letter stimuli are used³⁹. It is likely that this discrepancy can be explained by the task
319 differences. Letter report paradigms limit the response range and so the observer is forced to
320 select the most similar letter, even if the perceived stimulus does not match any of the possible
321 responses. Our response method does not suffer from this limitation.

322

323 Our results thus provide new evidence revealing that the component features of visual objects can
324 be individuated even far in the periphery, although their relative positions and orientations may
325 appear noisy and confusable across trials. The level of detail made available by the visual system
326 has been heavily debated both within the crowding literature and more generally. Our data suggest
327 one possible reason for this apparent conflict in the literature. Note that our analyses suggest all
328 observers have very high rates of substitution-type reports under crowded conditions: combining
329 the proportion of far-flanker gap substitutions (Fig. 4) and proportion of near-gap errors (Fig. 5),
330 observers made approximately 50% - 70% substitution-type errors in the most crowded conditions.
331 Such performance may be misinterpreted in alternative forced choice experiments (AFC), a more
332 common psychophysical paradigm in which an observer is forced to categorise a target as being
333 one of usually two to four alternatives. In these experiments, such a high proportion of substitution-
334 type reports could render performance at or close to chance, leaving it unclear if a participant was
335 randomly guessing, reporting an average stimulus or reporting what they thought was the target on
336 some trials and the flanker on other trials. This is especially true in experiments with simple stimuli
337 such as lines or Gabors, though it is less problematic with letter stimuli^{e.g. 34,39}.

338

339 In conclusion, our findings show that relatively fine featural detail is not necessarily lost during
340 early visual processing, but the precision of each perceptual report is corrupted. The aggregate of
341 errors made when viewing crowded displays cannot be characterised as simply being accurate,
342 averaged or substituted. The variety of report error types that occur within the same paradigm, as
343 demonstrated here, provides a continued challenge to models of visual crowding.

Author Contributions

Both authors designed the experiments and analyses. WJH collected the data and wrote the manuscript. PJB and WJH analysed the data, and PJB revised the manuscript.

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The authors declare no competing nancial interests.

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Appendix A – Supplementary Analyses

Prior to the mixed-model analyses for the one-gap and two-gap flanker conditions presented in the Results section, we performed the following linear analyses.

One-gap flanker condition

Shown in Figure A1A are the naïve observer's report errors and linear fits as a function of target-flanker orientation difference. Note that a linear fit with a slope of 1 would indicate the observer's reports followed the flanker gap closely, a slope of 0 would indicate the observer's reports were not influenced by the flanker, and a slope of 0.5 conforms to the average of target and flanker orientations. In Figure A1B-D we plot the slope parameter for all conditions from all observers for the one-gap flanker condition. Slope parameters were close to 0.5 for the two smallest flanker sizes, and generally decreased as the flanker size increased. For all observers, the slopes were approximately 0 for the largest flanker condition. However, these analyses do not describe the data in full (see Results).

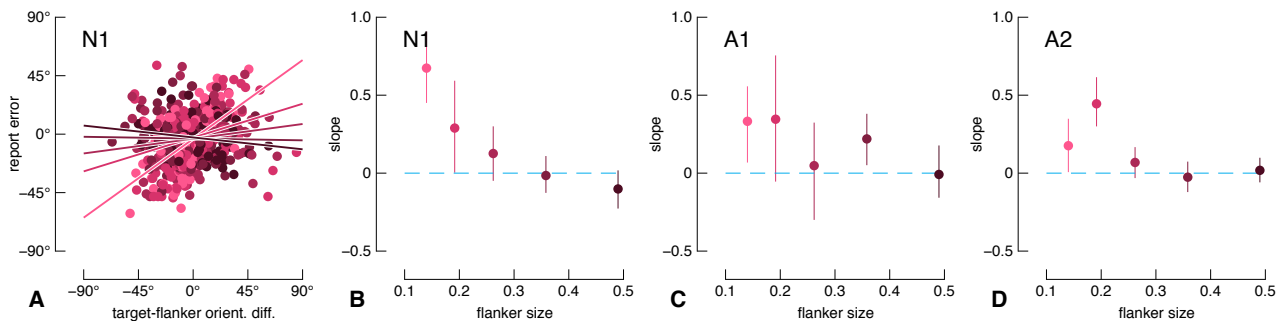


Figure A1. Results from linear fits in the one-gap flanker condition. A) Example raw data from the naïve participant. Lines show linear fits for each target-flanker separation, with colour shading indicating conditions as in Fig. 2A. To improve visibility, we have truncated the x-axis and y-axis. B-D) Slope parameters as a function of flanker size for all observers. Errors bars are 95% confidence intervals.

Two-gap flanker condition (near-gap)

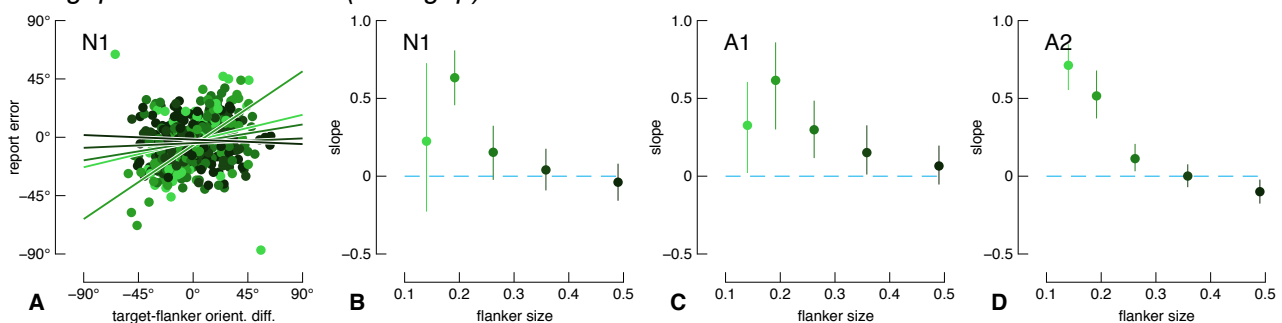


Figure A2. Results from the two-gap flanker condition for report errors less than 90° from the target. A) Raw data from the naïve participant. The x-axis indicates the orientation difference between the target gap and the nearest flanker gap. Data presented as in Fig. A1A. B-D) Slope parameters as a function of flanker size for all observers. Errors bars are 95% confidence intervals.