# <sup>1</sup> Critical resolution: a superior measure of

# <sup>2</sup> crowding

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- 7 Declaration of interest: None

# 8 Abstract

9 Visual object recognition is essential for adaptive interactions with the environment. 10 It is fundamentally limited by crowding, a breakdown of object recognition in clutter. The 11 spatial extent over which crowding occurs is proportional to the eccentricity of the target 12 object, but nevertheless varies substantially depending on various stimulus factors (e.g. 13 viewing time, contrast). However, a lack of studies jointly manipulating such factors precludes 14 predictions of crowding in more heterogeneous scenes, such as the majority of real life 15 situations.

16 To establish how such co-occurring variations affect crowding, we manipulated 17 combinations of 1) flanker contrast and backward masking, 2) flanker contrast and 18 presentation duration, and 3) flanker preview and pop-out while measuring participants' 19 ability to correctly report the orientation of a target stimulus. In all three experiments, 20 combining two manipulations consistently modulated the spatial extent of crowding in a way 21 that could not be predicted from an additive combination. However, a simple transformation 22 of the measurement scale completely abolished these interactions and all effects became 23 additive. Precise quantitative predictions of the magnitude of crowding when combining 24 multiple manipulations are thus possible when it is expressed in terms of what we label the 25 'critical resolution'. Critical resolution is proportional to the inverse of the smallest flanker 26 free area surrounding the target object necessary for its unimpaired identification. It offers a 27 more parsimonious description of crowding than the traditionally used critical spacing and may thus constitute a measure of fundamental importance for understanding object 28 29 recognition.

Keywords: Object recognition, visual crowding, psychophysics, critical spacing, critical
 resolution, visual perception, flanker interference

# 32 1. Introduction

33 Object recognition is essential for visually guided adaptive behaviour. For example, while driving on a rainy evening, timely recognition of a pedestrian about to cross the street 34 may be essential to avoiding an accident. Our ability to recognise an object in the periphery 35 36 as a pedestrian would be impaired if she were standing next to an object of similar size and 37 shape, such as for example, a road sign. This reduction in the ability to identify objects in 38 clutter is called visual crowding (Bouma, 1970; Levi, 2008; Pelli & Tillman, 2008; Pelli, 39 Palomares, & Majaj, 2004; Whitney & Levi, 2011). Crowding fundamentally limits our ability 40 to process visual scenes as diverse as driving, reading or searching for a particular object. In most situations crowding, rather than visual acuity, is the limiting factor on visual perception. 41 42 In recent years, substantial efforts have been undertaken to uncover the limits of object recognition, using crowding as a tool (Chung, Levi, & Legge, 2001; Harrison & Bex, 2015; He, 43 44 Cavanagh, & Intriligator, 1996; Herzog & Manassi, 2015; Herzog, Sayim, Manassi, & Chicherov, 45 2016; Pelli et al., 2004).

46 The Bouma Law (coined by Pelli & Tillman, 2008) describes one of the most 47 fundamental properties of crowding. It states that the distance between a target and its 48 flankers below which the flankers start to interfere with the identification of the target is 49 proportional to the target's eccentricity, i.e. its distance from fixation (Bouma, 1970). This 50 distance between target and flankers is known as the 'critical spacing' and is considered to be 51 the measure that best characterises the interference between nearby objects. It was initially 52 reported to be approximately half the target's eccentricity (Bouma, 1970). There is evidence 53 that the Bouma Law holds true for a large variety of objects and features, such as orientation, 54 hue, lightness, size (van den Berg, Roerdink, & Cornelissen, 2007), spatial frequency (Chung 55 et al., 2001), letters (Bouma, 1970; Kooi, Toet, Tripathy, & Levi, 1994; Pelli et al., 2004; 56 Wolford & Chambers, 1984), faces (Farzin, Rivera, & Whitney, 2009), real-world objects 57 (Wallace & Tjan, 2011) and natural scenes (Wallis & Bex, 2012). This consistency has led some researchers to propose the Bouma Law as a general principle of object recognition (Pelli & 58 59 Tillman, 2008) that has implications for the neural mechanisms of feature integration. 60 According to this idea, neurons (in say V1) responding to object features will pool their 61 responses if they are within a certain distance (6 mm in the radial direction) of each other in 62 the cortex (Pelli, 2008), leading to crowding.

63 However, this notion seems inconsistent with studies that have revealed large 64 variations in the proportionality constant that links critical spacing and eccentricity. For 65 example, critical spacing is reduced (less target-flanker interference) if target and flankers 66 differ in some property such as colour (Andriessen & Bouma, 1976; Chung et al., 2001; Kennedy & Whitaker, 2010; Kooi et al., 1994; Nazir, 1992; Põder, 2007; Scolari, Kohnen, 67 Barton, & Awh, 2007) or if the flankers are previewed (Scolari et al., 2007; Watson & 68 69 Humphreys, 1997). On the other hand, critical spacing is increased, and indeed can be much 70 larger than half the eccentricity, if the flankers' luminance contrast is higher than that of the 71 target (Rashal & Yeshurun, 2014), if the target is mildly masked, (Vickery, Shim, Chakravarthi, 72 Jiang, & Luedeman, 2009), or if display duration is reduced (Kooi et al., 1994; Tripathy, 73 Cavanagh, & Bedell, 2014), whereas masking the flankers reduces critical spacing 74 (Chakravarthi & Cavanagh, 2009; Wallis & Bex, 2011).

75 These findings suggest substantial variability in the distance over which features are 76 integrated, depending on stimulus properties. Thus, the amount of crowding may differ vastly 77 between dissimilar scenes or even objects within the same scene. To understand how 78 crowding limits visual perception, it is, therefore, necessary to know how various stimulus 79 manipulations affect crowding and what the combined effect of such manipulations is. The 80 latter is especially important for two reasons. First, real-world scenes combine multiple object 81 properties in a variety of ways. For example, a flanker might differ from the target in contrast, 82 spatial frequency, and orientation, simultaneously. In addition, effective viewing durations 83 might vary a lot due to movements of eyes, observers, or objects. Masking can occur when 84 an object or its flankers are occluded by other (perhaps moving) objects. In order to move 85 towards an understanding of the limitations of object recognition in the real world, it is 86 therefore necessary to understand the effects of combinations of stimulus properties. Second, the magnitude of the effects of different stimulus properties on crowding can only 87 be compared across studies if they are either independent of each other or if the way in which 88 89 these effects are combined is exactly understood. For example, doubling the contrast of 90 flankers (while keeping target contrast constant) approximately doubled the critical spacing 91 in a previous study (Rashal & Yeshurun, 2014). Would such a surprisingly large effect also have 92 been observed if stimuli had not been presented very briefly and with a backward mask? It 93 could even be the case that the effect of one manipulation is contingent upon a certain

combination of other factors. If this were the case, manipulating flanker contrast might only
have a (detectable) effect when measured under these specific conditions. Perhaps
surprisingly, previous studies have typically tested the effects of manipulating stimulus
properties on crowding in isolation (e.g., Kooi et al., 1994; Rashal & Yeshurun, 2014; Scolari
et al., 2007). It is therefore unknown what the combined effect of such manipulations is and
whether it follows a regular pattern across different manipulations.

100 The present study examined how the effects of stimulus properties that affect object 101 recognition in a cluttered scene are combined. We manipulated flanker contrast together 102 with backward masking (Experiment 1) and display duration (Experiment 2). Additionally, we 103 manipulated flanker preview and target-flanker similarity in a third experiment (Experiment 104 3). We employed full-factorial designs in order to assess both main effects and interactions of 105 these manipulations on critical spacing. This allows us to determine whether the effects of 106 combining two properties can be predicted from the extent of visual crowding observed when 107 manipulating these properties separately.

## 108 **2.** Methods

## 109 2.1. Participants

110 All participants were students at the University of Aberdeen. Experiment 1 had fifteen participants (11 female; 13 right-handed; mean age = 22.2 years; age range: 18 – 25 years), 111 112 Experiment 2 had ten participants (6 female; all right-handed; mean age = 22.6 years; age 113 range: 19 – 27 years) and Experiment 3 had twelve participants (8 female; 11 right-handed; mean age = 24.1 years; age range: 20 - 26). In all experiments, participants had normal or 114 corrected to normal visual acuity. Participants gave written informed consent prior to 115 participation. They received either £5 or course credits as compensation for their 116 117 participation. All experiments were approved by the University of Aberdeen Psychology Ethics Committee (Project number: PEC/3146/2014/10) and the work was carried out in accordance 118 119 with the Code of Ethics of the World Medical Association (Declaration of Helsinki).

## 120 2.2. Experiment 1

121 2.2.1. Materials

122 Stimuli were generated and presented using Matlab (The MathWorks, Natick, MA) 123 with the Cogent Graphics toolbox (developed by John Romaya, Laboratory of Neurobiology,

124 Wellcome Department of Imaging Neuroscience) on a 19 inch CRT monitor set to a resolution 125 of 1024x768 pixels and a refresh rate of 60 Hz, viewed from a distance of 60 cm. The target 126 was the letter 'T' (1.3° of visual angle) and was presented 9° from fixation in either the left or 127 right visual field along the horizontal meridian in one of four cardinal orientations: upright, inverted, rotated 90° right or 90° left. The target letter appeared either in isolation or was 128 129 surrounded by three flanking stimuli (above, below and on the outer side of the target). No 130 flanker was presented on the inner side of the target as such a flanker would have approached or intersected fixation at large target-flanker distances. Flankers were letter 'H's (same size 131 132 as the target stimulus), presented either upright or rotated 90°. Flankers, when present, could 133 be at one of seven possible distances from the target measured centre to centre: 1.5°, 2°, 134 2.5°, 3°, 4°, 5° and 7° of visual angle. The experiment manipulated the presence of backward 135 masking and flanker contrast. The backward mask was a rectangle of size 8.2° x 26.7°, created 136 by tiling patches of size 0.2° x 0.2°. Each individual patch of the mask had a random grey scale 137 luminance value sampled from a uniform distribution between 0.02 and 57.44  $cd/m^2$ .

138 The Weber Contrast of stimuli was calculated as follows:

$$contrast = \frac{I - I_b}{I_b} \tag{1}$$

where *I* is the luminance of the stimulus and  $I_b$  is the luminance of the background. Targets had a luminance of 19.6 cd/m<sup>2</sup> corresponding to a contrast of 0.25 against the grey background (15.7 cd/m<sup>2</sup>). The flankers either had the same contrast as the target or had a luminance of 39.5 cd/m<sup>2</sup> corresponding to a contrast of 1.5 from the background.

# 144 2.2.2. Procedure

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145 The sequence of events during Experiment 1 are depicted in Figure 1A. Each trial 146 started with a fixation cross presented for 1000 ms. Then, the target and three flankers were 147 presented for 100 ms. In half the trials, a noise mask was presented for 300 ms after the offset 148 of the target display (target-mask SOA of 100 ms). Flanker contrast was the same as the 149 target's in half the trials and higher in the other half. Target and flanker orientations were 150 randomly chosen for each trial. Participants were instructed to report the target orientation 151 by pressing the corresponding arrow key (left, right, up or down) on a keyboard. Auditory 152 feedback was provided on each trial; percentage correct averaged over all the trials within a 153 block was displayed at the end of that block.

Participants underwent training for 1 to 3 blocks of 32 trials each, at the beginning of 154 155 the experiment. The main experiment consisted of a total of 1024 trials. There were 256 156 different types of trials: 2 sides (L/R) x 2 flanker contrasts (equal/higher) x 2 masking conditions (yes/no) x 8 flanker distances (1.5°, 2°, 2.5°, 3°, 4°, 5°, 7° and no flankers) x 4 target 157 orientations. Each type of trial was repeated 4 times and all trials were presented in random 158 order. After every block of 128 trials, participants were given a self-paced break during which 159 they received written feedback on their average accuracy in the preceding block. For purposes 160 161 of analysis, data was averaged over sides and target orientations, leaving 32 conditions with 162 32 trials each.



**Figure 1. (A & B)** The sequence of events in a single trial in Experiment 1 **(A)** and Experiment 2 **(B)**. A fixation cross was presented in the middle of the screen throughout the experiment. The target and flankers were presented either to the right or left of the fixation (9° eccentricity). Targets ('T') were either presented in isolation or surrounded by equal contrast (Weber contrast of 0.25) or higher contrast (Weber contrast of 1.5) flankers ('H') at one of seven different target-flanker distances (closest spacing depicted in the figure). In Experiment

170 1, the target display was followed by a backward mask (same side as stimulus display) or no 171 mask. In Experiment 2, target display was presented for either 20 ms or 200 ms (no masking). 172 The next trial started immediately after participants had responded to the target orientation 173 (up, down, left or right) by a key press. (C) The sequence of events in a single trial in Experiment 174 3. While participants fixated on the central cross, bilateral place-holders or flankers were presented for 150 ms at one of nine flanker distances (closest spacing depicted in the figure) 175 176 and with positive or negative contrast polarity. Subsequently, a target with the same or 177 opposite polarity was presented for 50 ms along with flankers that matched the place-holders' 178 contrast polarity or in isolation. The following trial started 1000 ms after participants had 179 reported the orientation of the target.

180 2.2.3. Analysis

181 Exponential curves were fit to the accuracy of target orientation discrimination responses as a function of target-flanker distance for each condition and each participant 182 183 separately. The no flanker condition, which is virtually an infinite target-flanker distance 184 condition, was included in these fits by assigning it the very large target-flanker distance of 185 20°. This particular choice of where to insert the no flanker condition on the x-axis did not 186 affect the resulting fits noticeably as verified by re-running the analysis with other values (9 187 to 100°). The no flanker conditions are physically identical in the equal and higher flanker contrast conditions in Experiment 1 and 2, and in all conditions in Experiment 3. Accuracy was 188 189 averaged across all physically identical conditions for the no-flanker condition prior to fitting 190 (plotted separately for illustration).

The exponential function (Rashal & Yeshurun, 2014; Scolari et al., 2007; Strasburger,
2001), used to fit the data was:

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$$y(x) = \propto (1 - e^{(-s(x-t))})$$
 (2)

194 where y is target-identification accuracy,  $\propto$  is the upper asymptote, s is the scaling 195 factor, x is the target-flanker distance and t is the x-intercept of the curve. Lower bound for 196 parameter  $\propto$  was guessing chance (i.e. 0.25) and parameters t & s were restricted to be non-197 negative ( $\geq$  0). The upper bounds were 1 (100% performance) for  $\propto$  and 10 for s, which 198 corresponds to an almost impossibly steep slope. There was no upper bound for t. The critical 199 spacing  $x_c$  is commonly defined as the distance, at which performance reaches 90% of the 200 asymptote, and was computed as follows:

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$$x_c = t - \log(0.1)/s \tag{3}$$

202 Critical spacing was calculated using equation (3) for each participant and condition 203 separately, and the results were subjected to a 2x2 repeated measures ANOVA. Bonferroni-204 Holm correction was used for post hoc analysis. To verify that our results were not specific to 205 the particular choice of fitting function we reran analyses with fits to cumulative Gaussian and 206 Weibull curves, both of which yielded qualitatively identical results. In two of our 207 experiments, the critical spacing, defined as 90% of the asymptote, was sometimes beyond 208 the furthest stimulus spacing, i.e. we extrapolated. However, the results were qualitatively 209 the same with a 75% of asymptote criterion, for which such extrapolation did not happen. We 210 can, therefore, exclude the possibility that our findings were qualitatively influenced by such 211 extrapolation.

## 212 2.3. Experiment 2

The design of Experiment 2 was identical to that of Experiment 1, except that we manipulated flanker contrast (equal/higher) and display duration (20 ms / 200 ms). No mask was used in this experiment. Monitor refresh rate was set to 100 Hz. The sequence of events during Experiment 2 are depicted in Figure 1B.

# 217 2.4. Experiment 3

218 The design of Experiment 3 was the same as the previous two experiments, except 219 that here we manipulated flanker preview (preview/no preview) and target-flanker similarity 220 (pop-out/no pop-out). We also employed backward masking, as the performance was near 221 ceiling without it. The background was set to 24.8 cd/m<sup>2</sup> light grey and the red fixation cross 222 was isoluminant to the background. Targets and flankers were either black (luminance 14.9 223  $cd/m^2$ ) or white (luminance of 34.6  $cd/m^2$ ), both of which had a Weber contrast of ± 0.4 relative to the background. The mask was identical to Experiment 1, except that it was 224 225 presented on both sides of fixation.

The sequence of events in Experiment 3 was slightly different from the previous two experiments and is depicted in Figure 1C. After a fixation interval of 1000 ms, placeholders at the flanker locations (three on each side of fixation) were presented for 150 ms. The target 229 was then presented for 50 ms on one side of fixation. The symmetrical location on the other 230 side remained unoccupied. Flankers replaced the placeholders for the same duration. 231 Flankers appeared on both sides. Immediately after the offset of the stimuli, masks were 232 presented on both sides for 300 ms. In flanker preview conditions, flankers were presented instead of placeholders. That is, flankers were presented for 200 ms and the target was 233 234 presented only during the last 50 ms of that interval. Since the preview also reduces position 235 uncertainty of the flankers (participants will know how far the flankers will be on that trial), we presented the placeholders in the no-preview condition (Scolari et al., 2007). Hence, the 236 237 only difference in the latter, relative to the preview condition, is not having previewed the 238 flankers.

239 In the pop-out condition, flankers and targets had opposite contrast polarities (i.e. a 240 black target surrounded by white flankers or a white target surrounded by black flankers) and 241 in the no pop-out condition, flanker and target contrast polarities were the same (i.e. a black 242 target surrounded by black flankers or a white target surrounded by white flankers). The 243 previewed flankers and place-holders had the same contrast polarity as the subsequent 244 flanker display. Pilot data revealed that the spatial extent of crowding was smaller than in the 245 two previous experiments. To obtain the full range of performance as a function of target-246 flanker distance, a ninth flanker distance was added and the tested target-flanker distances 247 were restricted to 1°, 1.25°, 1.5°, 2°, 2.5°, 3°, 4° and 5.5°. Target and flanker size was reduced 248 to 0.7° visual angle. Due to including nine target flanker distances while retaining the same 249 number of trials per condition (32 trials), the total number of trials increased to 1152. Before 250 fitting exponential curves, accuracy in no-flanker conditions was averaged across all 251 manipulations.

# 252 **3.** Results

## 253 3.1. Experiment 1: Backward masking and contrast

We independently manipulated the visibility of objects (by either presenting a subsequent mask or no mask) and flanker contrast (equal or high, relative to target contrast) while measuring the accuracy with which participants reported the orientation of a peripheral target 'T'. We estimated critical spacing for each condition using exponential fits to accuracy

performance as a function of target-flanker distance (Figure 2A). The fit of the exponential curves to the data was excellent (mean  $r^2 = 0.92$ ; range: 0.73 – 0.99).

260 The critical spacing data were subjected to a repeated measures two-way (masking x 261 flanker contrast) ANOVA. Critical spacing (Figure 2B) was greater when the stimuli were 262 backward masked (6.69° ± 0.41° of visual angle) compared to when they were not masked  $(4.66^{\circ} \pm 0.23^{\circ})$ ; main effect of masking: F(1,14) = 39.37, p < 0.001,  $\eta^2 = 49.98\%$ ). Critical spacing 263 264 was also greater when flanker contrast was higher than target contrast  $(6.36^{\circ} \pm 0.46^{\circ})$ 265 compared to when they had the same contrast (4.99° ± 0.23°; main effect of flanker contrast: 266 F(1,14) = 22.23, p < 0.001,  $\eta^2 = 19.61\%$ ). Importantly, critical spacing for the combination of masking and higher contrast flankers was greater than would be expected from the sum of 267 268 the individual main effects (interaction between masking and flanker contrast: F(1,14) = 9.30, 269 p = 0.009,  $\eta^2 = 3.91\%$ ). That is, increasing flanker contrast had a much larger effect on critical 270 spacing when the stimuli were backward masked (post hoc pairwise comparisons between 271 the four conditions are shown in Table 1). This becomes evident when considering the effects 272 in relative terms: flankers with higher contrast than the target increased critical spacing by 273 18% without backward masking, but in the presence of masking, this effect almost doubled (34% increase). Thus, the surprisingly large effect of the contrast manipulation previously 274 275 observed (Rashal & Yeshurun, 2014) was in part due to the combination with backward 276 masking, although the effect persists to a diminished extent even in the absence of masking.



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Figure 2. Results of experiment 1, 2 and 3. Mean accuracy as a function of the target-flanker 278 distance (plus the No flanker condition) for each condition in experiments 1 (A), 2 (C) and 3 (E) 279 with exponential fits for each condition. Critical spacing for each condition is computed by 280 281 determining the target-flanker distance at which performance is at 90% of asymptotic performance. These are depicted by the vertical lines, drawn where the horizontal lines (90% 282 of asymptote) intersect with the psychometric curves. (B, D, & F) Mean and standard error of 283 284 the mean of the critical spacing overlaid on Violin plots (smoothened histogram with normal 285 Kernel). Black dots depict individual participants' critical spacing.

#### 286 3.2. Experiment 2: Display duration and contrast

287 The findings of Experiment 1 show a pronounced, and larger than expected, increase 288 in critical spacing when combining two manipulations. To test whether this super-additive 289 interaction is specific to the particular manipulations in the first experiment (backward 290 masking and flanker contrast) or whether it is of a more general nature, we combined the 291 previous contrast manipulation with a manipulation of presentation duration (Figure 1B), 292 which is also known to affect critical spacing (Kooi et al., 1994; Tripathy et al., 2014). 293 Experiment 2 was identical to Experiment 1, except that stimuli were presented at two 294 different display durations (20 ms or 200 ms) without backward masking.

295 Critical spacing for each of the four conditions was determined as in Experiment 1. Excellent fits to the data (Figure 2C) were obtained (mean  $r^2 = 0.92$ ; range: 0.79 – 0.99). A 296 297 repeated measures two-way (flanker contrast x display duration) ANOVA revealed that critical 298 spacing (Figure 2D) was larger when stimuli were presented for a shorter duration (20 ms, 299  $6.36^{\circ} \pm 0.54^{\circ}$ ) than for a longer duration (200 ms,  $3.23^{\circ} \pm 0.16^{\circ}$ ; main effect of display duration: F(1,9) = 51.36, p < 0.001,  $\eta^2 = 57.90\%$ ). Higher contrast flankers (relative to target 300 301 contrast), once again, increased critical spacing (5.59° ± 0.65°) compared to equal contrast flankers (4.00° ± 0.30°; main effect of flanker contrast: F(1,9) = 25.32, p < 0.001,  $\eta^2 = 14.92\%$ ). 302 303 The combination of short stimulus display and higher contrast flankers resulted in the highest 304 critical spacing, which was larger than would have been predicted from the main effects (interaction: F(1,9) = 19.67, p = 0.002,  $\eta^2 = 8.05\%$ ). Thus, as in the first experiment, the 305 306 combination of two manipulations non-additively affected critical spacing (Table 1).

307 In Experiment 1, we tested critical spacing at a display duration of 100 ms. The two 308 conditions without masking in that experiment can be directly compared to the results from 309 Experiment 2, which presented stimuli for 20 and 200 ms while manipulating flanker contrast. 310 Although participants in the two experiments were not the same, a consistent pattern emerged: the shorter the display duration, the larger the effect of the flanker contrast 311 manipulation. Higher contrast flankers increased critical spacing by 55% when presentation 312 313 duration was 20 ms (Experiment 2), 33% at 100 ms (Experiment 1), and 14% at 200 ms. Thus, the effect of flanker contrast is substantially modulated by other factors, such as stimulus 314 315 duration and visibility. This further confirms that combining manipulations of two stimulus 316 properties leads to pronounced non-additive interactions in critical spacing.

- 317 **Table 1.** Critical spacing with proportion of eccentricity in brackets (e = eccentricity = distance
- of the target from fixation at 9°), pairwise comparisons of critical spacing and mean change
- in each condition in degrees of visual angle in each experiment separately. Significant p-values
- $(\alpha < 0.05)$  indicated in bold (Bonferroni-Holm correction was used for post hoc analysis).

Experiment 1: Masking and flanker contrast					
Condition	Critical spacing	Equal contrast, no mask	High contrast flankers, no mask	Equal contrast, mask	High contrast flankers, mask
Equal contrast,	4.28°		+0.76°	+1.42°	+3.40°
no mask	(0.48 e)				
High contrast	5.04°	t(14) = -3.74,		+0.66°	+2.64°
flankers, no mask	(0.56 e)	<i>p</i> = 0.002			
Equal contrast,	5.70°	t(14) = -5.76,	t(14) = 2.43,		+1.98°
mask	(0.63 e)	<i>p</i> < 0.001	<i>p</i> = 0.029		
High contrast	7.68° (0.85 a)	t(14) = -6.16,	t(14) = -5.52,	t(14) = 4.34,	
nankers, mask	(0.85 e)	p < 0.001	<i>p</i> < 0.001	p < 0.001	
	Experiment	2: Display dura	ition and flank	er contrast	
Condition	Critical spacing	Equal contrast, 200ms	Higher contrast flankers, 200ms	Equal contrast, 20ms	Higher contrast flankers, 20ms
Equal contrast,	3.01°		+0.43°	+1.97°	+4.73°
200ms	(0.33 e)				
Higher contrast	3.44°	t(9)=-3.09,		+1.54°	+4.30°
flankers, 200ms	(0.38 e)	<i>p</i> = 0.014			
Equal contrast,	4.98°	<i>t</i> (9) = 7.72,	t(9) = 8.15,		+2.76°
20ms	0.55 e	<i>p</i> < 0.001	<i>p</i> < 0.001		
Higher contrast	7.74°	t(9) = -6.39,	t(9) = 6.37,	t(9) = -4.88,	
flankers,	0.86 e	p < 0.001	<i>p</i> < 0.001	<i>p</i> < 0.001	
201115	_				
	Experiment	3: Target pop-	out and flanke	r preview	
Condition	Critical spacing	Target pop-out, flanker preview	No pop-out, flanker preview	Target pop-out, no preview	No pop-out, no preview
Target pop-out,	1.58°		+0.39°	+1.19°	+3.15°
flanker preview	(0.18 e)				
No pop-out,	1.97°	t(11) = -2.06,		+0.80°	+2.76°
tlanker preview	(0.22 e)	p = 0.063			1.00
larget pop-out,	2.//č	t(11) = 5.22,	t(11) = -2.86,		+1.96°
No preview	(U.31 e) 1 72°	<i>µ</i> < 0.001 t(11) = 7.26	μ = 0.016 t(11) - 5 54	t(11) - 5 34	
no preview	(0.53 e)	<i>p</i> < 0.001	p < 0.001	p < 0.001	

#### 322 3.3. Experiment 3: Flanker preview and pop-out

323 Experiments 1 and 2 show super-additive effects on critical spacing when two 324 properties are combined. This raises the question of whether such an effect of property 325 combinations might be a general rule in crowding. However, some caution is warranted 326 before generalising these findings to other manipulations. Both experiments shared one 327 manipulation, flanker contrast, and in both cases, the second manipulation affected the 328 overall visibility of the stimulus display (backward masking in Experiment 1, display duration 329 in Experiment 2). Therefore, we cannot exclude the possibility that the pattern of our results 330 is limited to specific manipulations or combinations thereof. To test the generality of our 331 findings we conducted a third experiment in which we chose two manipulations that both 332 differed from the ones employed in Experiments 1 & 2, and which did not affect visibility of the entire stimulus display. It has been extensively documented that target-flanker 333 334 dissimilarity ('pop-out') decreases the spatial extent of crowding (Andriessen & Bouma, 1976; 335 Kooi et al., 1994; Põder, 2007) and so does previewing flankers prior to the onset of the target 336 (Scolari et al., 2007; Watson & Humphreys, 1997). Here, we tested whether the combination 337 of flanker preview and pop-out leads to a similar nonlinear interaction (Figure 1C).

In this experiment, the contrast polarity of target and flankers was varied, i.e. these stimuli could either be lighter or darker than the background. Thus flankers could either have the same (no pop-out) or opposite (pop-out) contrast polarity as that of the target and be presented in advance of (preview) or simultaneously with (no preview) the target. Once again, we fitted exponential curves to the accuracy data as a function of target-flanker spacing (Figure 2E, mean  $r^2 = 0.86$ ; range: 0.51 - 1.00) to estimate the critical spacing in each of these conditions.

345 As expected, critical spacing (Figure 2F) was reduced when flankers were previewed 346 (1.78° ± 0.11°) as compared to when only placeholders were presented in the flanker locations 347 prior to flanker onset  $(3.75^{\circ} \pm 0.34^{\circ})$ ; main effect of flanker preview: F(1,11) = 39.45, p < 0.001,  $\eta^2$  = 49.12%). It was also smaller when flankers had the opposite contrast polarity relative to 348 the target (pop-out: 2.18° ± 0.19°; no pop-out: 3.35° ± 0.38°; main effect of pop-out: 349 F(1,11) = 40.39, p < 0.001,  $\eta^2 = 17.50\%$ ). The combination of flanker preview and pop-out 350 351 further reduced the critical spacing than what each factor considered independently would 352 predict (interaction flanker preview and pop-out: F(1,11) = 12.12, p = 0.005,  $\eta^2 = 7.83\%$ ), i.e.

the combination of target pop-out and flanker preview non-additively affects critical spacing(post hoc pairwise comparisons between the four conditions are shown in Table 1).

# 4. Effects of combined manipulations are additive when crowding is quantified

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# by means of 'critical resolution'

357 The three experiments indicate that the combination of multiple stimulus properties 358 generally affects critical spacing in a nonlinear super-additive manner. That is, knowing just 359 the effects of individual manipulations of properties on critical spacing, it is not possible to 360 predict the effect of their combination by simple addition. However, the observed 361 interactions followed a regular pattern across all the three experiments. This suggests that 362 there might be a general rule that explains the magnitude of the interaction between two 363 properties as a function of the two main effects. In other words, such a general rule should 364 allow us to predict the effect of two simultaneously varying properties on crowding given the 365 effect of each property separately.

366 If such a general rule exists, then the magnitudes of each of the main effects should 367 be correlated with the magnitude of the interaction for each experiment. This is indeed the 368 case: participants with larger main effects also displayed larger interactions (correlations with 369 95% confidence intervals<sup>1</sup>: Experiment 1:  $r_1 = 0.65 (0.21 - 0.87)$ ,  $r_2 = 0.72 (0.32 - 0.90)$ ; Experiment 2:  $r_1 = 0.85$  (0.47 - 0.96),  $r_2 = 0.91$  (0.64 - 0.98); Experiment 3: 370 371  $r_1 = 0.70 (0.20 - 0.91), r_2 = 0.59 (0.03 - 0.87))$ . These strong correlations between both main 372 effects and the interaction in all three experiments suggest that, indeed, the interaction might 373 directly be a function of the main effects.

The attempt to discover the quantitative relationship between the main effects and 374 the interaction in our data can be formalised as the search for a transformation  $F(x_c)$  of the 375 376 critical spacing data  $x_c$  that minimises (or entirely removes) the interaction. Thus we ask the 377 question what transformation of the critical spacing data would explain all the data in terms of additive main effects with no interaction effects. Towards this end, we considered the 378 family of power functions  $F(x_c) = x_c^{\gamma}$  (see Fig. 3A). Relationships in which one variable is 379 380 proportional to some power of another variable are very common in many fields of 381 technology and science. Additionally, power functions yield monotonic transformations of the

<sup>&</sup>lt;sup>1</sup> Computed using the 'corrcoef' function in Matlab

data which are commonly utilised to enhance symmetry and normality of the data for statistical purposes (Box & Cox, 1964). Variation of a single parameter,  $\gamma$ , yields a wide variety of shapes. For  $\gamma = 1$ , the power function is simply the identity, thus the untransformed data is explicitly included in the search space.

In order to determine an exponent  $\gamma$  which meets the condition of minimising the 386 interaction, we computed the transformed critical spacing data  $x_c^{\gamma}$  for all values of  $\gamma$  in the 387 interval from -4.0 to +4.0 in steps of 0.01 for each participant (Fig. 3B). We computed the 388 interaction term from  $x_c^{\gamma}$  for the four conditions of each experiment and subjected the results 389 to a one-sample t-test against zero to obtain the p-values of the null-hypothesis  $H_0$  of no 390 interaction across all participants for each experiment separately<sup>2</sup>. The resulting functions 391  $p_e(H_0|\gamma)$  for each experiment *e* reflect the significance of the interaction after 392 393 transformation of the critical spacing data (Fig. 3B) and can be interpreted as the likelihood  $L_e(\gamma|H_0)$  of  $\gamma$  given the Null-hypothesis  $H_0$  of the interaction. Accordingly, the maximum 394 395 likelihood estimates of  $\gamma$  are indicated by the peaks of these functions, which were located at -1.44, -1.98, and -2.01 for experiments 1, 2, and 3, respectively (Fig. 3B). All three experiments 396 397 converged on similar values for  $\gamma$ , indicating that the same transformation of the critical 398 spacing data might abolish the interaction in all three experiments and thus allow to explain all data in terms of main effects of the transformed data. The combined likelihood  $L(\gamma|H_0)$ 399 400 of the parameter  $\gamma$  given  $H_0$  across all three experiments is given by the product of the three 401 probability functions  $p_e(H_0|\gamma)$ :

402

$$L(\gamma|H_0) = \prod_{e=1}^{3} p_e (H_0|\gamma)$$
(4)

This yields a maximum likelihood estimate of  $\gamma = -1.98$  with a 14.7% likelihood 403 region (confidence interval) from -2.60 to -1.33 (Fig. 3B). This is remarkably close to  $\gamma = -2.0$ . 404 405 This particular estimate of  $\gamma$  was obtained for the definition of the critical spacing as 90% of the asymptotic performance (equation 3). As the 90% criterion is arbitrary, we computed the 406 maximum likelihood  $\gamma$  for a range of criteria (60% of asymptote to 90%) (Fig. 3C). The 407 408 parameter  $\gamma$  exhibited little dependency on the particular percentage of the asymptote used 409 to calculate the critical spacing. Importantly, for all tested values the confidence interval for  $\gamma$  included -2.0. 410

<sup>&</sup>lt;sup>2</sup> The interaction of a factorial 2x2 ANOVA is equivalent to a t-test of  $x_{11} + x_{22} - x_{12} - x_{21}$  against zero, where x denotes the dependent variable and the indices denote the levels of the two factors. A significant interaction thus indicates a departure from an additive combination of the two main effects.



412 Figure 3. (A) Examples of power functions for different values of parameter y. The functions 413 are monotonically increasing for y>0 and monotonically decreasing for y<0. (B) Likelihood of different values of the exponent y under the null hypothesis of no interaction. The combined 414 likelihood was obtained by multiplying the three likelihoods of the separate experiments. The 415 416 black bar at the bottom indicates the 14.7% likelihood region for y. (C) The combined 417 maximum likelihood y as a function of the criterion (percentage of the asymptote) used to calculate the critical spacing. (D) Estimated proportion of all neurons of receptive field size r 418 419 processing a target stimulus which are subject to biased competition by a flanker stimulus at 420 distance d (see discussion for details). The displayed receptive field sizes may roughly correspond to neurons in V1 (0.5° and 1.0°), V2 (2.0°) and V4 (4.0°) (Kastner et al., 2001). 421 422 Although the individual functions for neurons of the same receptive field size are almost linear 423 for d<2r, the function resulting from averaging over neurons of different receptive field sizes

424 is strongly convex. Thus, a change in distance affects the extent of biased competition much
425 more at smaller distances than at larger distances.

For  $\gamma = -2.0$ , the transformation has a straightforward interpretation: the squared critical distance is proportional to the area around the target which has to be flanker-free for there to be no crowding<sup>3</sup>. One divided by this area is thus proportional to the highest density of objects beyond which crowding occurs under the given circumstances. We can therefore define the *critical resolution* as follows:

431

436

443

$$\rho_c = \frac{1}{\chi_c^2} \tag{5}$$

Expressed in terms of this critical resolution, as opposed to the critical spacing, all effects in
our three experiments become independently additive (Fig. 4), such that the combined effect
of varying different stimulus properties is simply the sum of their individual effects (see Table
2 and Fig. 4 A-C).



Figure 4. Critical resolution in Experiment 1, 2 and 3. Mean and standard error of the mean
critical resolution for each of the four conditions are overlaid on Violin plots (smoothened
histogram with normal Kernel). Black dots depict individual participants' critical resolution. (A)
Experiment 1, (B) Experiment 2 and (C) Experiment 3.

441 This analysis can also be extended to the Bouma Law. The law states that the critical 442 spacing  $x_c$  is proportional to the eccentricity e:

$$x_c = be \tag{6}$$

<sup>&</sup>lt;sup>3</sup> The squared critical distance is only proportional, but not equal, to the area: if e.g. we assume a circular shape, then the actual area of that circle would be obtained by further multiplying by  $\pi$ .

444 The proportionality constant *b* depends on a variety of factors and generally ranges between

445 0 and 1. Applying our definition of the critical resolution (equation 2), we can write the Bouma

- Law using the critical resolution  $\rho_c$  rather than the critical spacing as follows:
- 447

$$o_c = \frac{1}{b^2 e^2} = \frac{c}{e^2}$$
(7)

- 448 The constant *c* is given by
- 449

$$c = \frac{1}{b^2} \tag{8}$$

450 **Table 2.** Critical resolution (one divided by the squared critical spacing) ANOVA results. 451 Significant p-values ( $\propto < 0.05$ ) indicated in bold.

Critical resolution ANOVA results					
Experiment 1	Masking:	Flanker contrast:	Interaction:		
	F(1,14) = 33.12, <b>p &lt; 0.001</b> ,	F(1,14) = 34.88, p < 0.001,	F(1,14) = 0.24, p = 0.63,		
	η <sup>2</sup> = 52.84%	$\eta^2$ = 11.65%	$\eta^2 = 0.14\%$		
Experiment 2	<b>Display duration:</b>	Flanker contrast:	Interaction:		
	F(1,9) = 61.72, <b>p &lt; 0.001</b> ,	F(1,9) = 69.12, <b>p &lt; 0.001</b> ,	F(1,9) = 0.97, p = 0.97,		
	η <sup>2</sup> = 78.60%	η <sup>2</sup> = 7.46%	η <sup>2</sup> < 0.001%		
Experiment 3	<b>Preview:</b>	<b>Pop-out:</b>	Interaction:		
	F(1,11) = 73.40, <b>p &lt; 0.001</b> ,	F(1,11) = 9.28, <b>p = 0.01</b> ,	F(1,11) < 0.001, p = 0.99,		
	η <sup>2</sup> = 59.97%	η <sup>2</sup> = 9.70%	$\eta^2 < 0.001\%$		

452

## 453 **5.** Discussion

We investigated the effect of combined manipulations of stimulus properties on 454 455 object recognition in the visual periphery and obtained highly consistent results across three 456 experiments: manipulation of flanker contrast and masking (Experiment 1), flanker contrast 457 and display duration (Experiment 2) and pop-out and flanker preview (Experiment 3) all led 458 to super-additive interactions in critical spacing, i.e. when combining two properties, the 459 critical spacing was not predicted by the sum of the individual main effects. This has two 460 important consequences: first, the spatial extent of visual crowding can vary vastly between 461 situations in which multiple stimulus properties differ. When favourable properties are 462 combined, crowding might be minimal or practically non-existent, whereas the combination 463 of multiple unfavourable properties can lead to crowding across very large distances. Second, 464 predicting the critical spacing across scenes in which parameters vary heterogeneously is 465 difficult because the magnitude of the effect of any manipulation depends on all other 466 stimulus properties that it is combined with. More precisely, any observed effect of a given property (say, flanker contrast) is valid for the specific set of other stimulus parameters tested 467

468 in that experiment, such as stimulus duration. Changing those parameters might strongly 469 change the magnitude of the observed effect. However, we found that when crowding was 470 measured as the critical resolution (one divided by the squared critical spacing) the effects of 471 qualitatively very different manipulations were combined additively, i.e. without interaction. This finding is remarkable as it allows prediction of the extent of crowding under 472 473 heterogeneous viewing conditions provided that the effects of individual manipulations are 474 known. It also allows for better comparability of the magnitude of effects obtained under 475 different conditions, because the magnitude of any manipulation becomes independent of 476 other manipulations when quantified by the critical resolution. This may be of particular value 477 when comparing critical spacing effects across dissimilar experiments in the literature. We 478 obtained qualitatively identical results when rerunning our analyses with fits to cumulative 479 Gaussian and Weibull curves, thus our conclusions seem to be independent of the particular 480 analytical approach used to determine the critical spacing.

481 We propose that measuring crowding in terms of critical resolution is advantageous 482 relative to the traditionally used critical spacing because it allows for a straightforward 483 prediction of the effects of multiple varying stimulus properties. Although we here obtained 484 the critical resolution directly by transformation of the critical spacing, these two measures 485 are conceptually different. Critical spacing is the target-flanker distance beyond which 486 flankers do not interfere with target identification. On the other hand, critical resolution is 487 proportional to the inverse of the smallest area of the visual field surrounding a target 488 stimulus that needs to be flanker free for the brain to resolve this target without interference. 489 It is thus a measure of the brain's capacity to extract information from a given area of the 490 visual field or retina and, like critical spacing, is a function of eccentricity and stimulus 491 properties. For any given area of the visual field, a specific number of neurons' receptive fields 492 will intersect that area. Thus, critical resolution is inversely related to the amount of cortical 493 'real estate' necessary to extract information without interference. Considering the 494 conceptual differences between critical spacing and critical resolution, it might be possible to 495 derive direct measurement techniques of the critical resolution without recourse to critical 496 spacing in the future.

497 We observed very similar interactions between combinations of dissimilar 498 manipulations and the same transformation of the measurement scale abolished all of these

499 interactions. The most parsimonious explanation for these results is that the interactions 500 observed in critical spacing are largely or entirely due to non-linear properties of critical 501 spacing as a measurement scale. The underlying principle of all three experiments was to 502 manipulate properties that increase or decrease the strength of crowding and measure how 503 much the spacing between targets and flankers must be changed to compensate for these 504 effects. The interactions in our data (Figure 2) are such that the larger the spacing needed for 505 unimpaired target identification under a given set of conditions already is, the more the 506 spacing needs to be further increased to compensate for a further manipulation that 507 increases crowding. In other words: the larger the spacing, the less effective any additional 508 increase in spacing.

509 In the following, we will derive a hypothetical explanation for this pattern based on 510 principles of biased competition models (Bundesen, 1990; Desimone & Duncan, 1995; 511 Reynolds & Heeger, 2009). The central idea of such models is that stimuli compete for 512 neuronal representation when multiple stimuli fall into the receptive field of the same neuron 513 (Moran & Desimone, 1985). This approach has previously been used to derive a quantitative 514 explanation of crowding data (Kyllingsbaek, Valla, Vanrie, & Bundesen, 2007) based on the 515 idea that crowding results from such competitive interactions between stimuli. The extent of 516 competition for processing resources depends on how many neurons have both stimuli within 517 their receptive fields. An estimate of the proportion of such neurons as a function of the 518 spatial separation between stimuli can be derived as follows:

519 The centres of the receptive fields of all neurons that process a given stimulus lie 520 within a circle of a radius equal to their receptive field size r around that stimulus. The area 521 of a circle of radius r is given by

522

$$A = \pi r^2 \tag{9}$$

If we assume that neurons are distributed fairly homogenously within the part of the visual field of interest, the number of neurons with receptive field size r processing this stimulus will be proportional to this area. If we now consider two stimuli placed at a distance d, then the receptive field centres of all neurons with both stimuli within their receptive fields lie within the intersection of two circles of equal radius r whose centres are separated by d. This area is given by equation (10):

529 
$$A = 2r^2 \cos^{-1}\left(\frac{d}{2r}\right) - \frac{d}{2}\sqrt{4r^2 - d^2}$$
(10)

530 Thus we can estimate the proportion p of all neurons of receptive field size r that process a 531 target stimulus and which also have a flanker stimulus at distance d within their receptive 532 fields by dividing equation (10) by equation (9):

533 
$$p(d) = \frac{2}{\pi} \cos^{-1}\left(\frac{d}{2r}\right) - \frac{d}{2\pi r^2} \sqrt{4r^2 - d^2}$$
(11)

534 The function p(d) estimates the fraction of all neurons of receptive field size r processing a target stimulus which are subject to biased competition by a flanker stimulus at distance d 535 536 (Figure 3D). Thus p(d) is an estimate of the competition for processing resources between 537 two stimuli. If one considers only neurons of one specific receptive field size r, then the 538 competition for neuronal processing between the two stimuli decreases fairly linearly as the separation d between the stimuli increases, until it reaches zero for d > 2r. If, however, we 539 540 consider a mixture of neurons with very different receptive field sizes ('average' in Figure 3D), 541 then further increasing the distance between objects reduces competition drastically at small 542 spacings but only has very little effect at larger spacings. These simple<sup>4</sup> geometric ideas thus 543 yield an explanation for non-linear effects of changes in object spacing consistent with the pattern of interactions observed in our data. From this perspective, the transformation to 544 545 critical resolution with  $\gamma = -2.0$  (Figure 3A) compensates for non-linear effects of changes in 546 object spacing, such as those derived here (Figure 3D) and potentially others related to information integration across neurons and decision making. Therefore, independent 547 548 manipulations yield independent (additive) effects when measured in terms of critical 549 resolution, but not critical spacing. In agreement with our ideas above, the biased competition 550 model (Desimone & Duncan, 1995) assumes that competition for neuronal representation occurs at many levels of the visual processing system and thus involves neurons with very 551 552 different receptive field sizes. This is also consistent with the large variability of critical spacing across conditions observed in our data. 553

<sup>&</sup>lt;sup>4</sup> The presented derivation is for illustration of underlying principles. Many aspects are highly simplified, e.g. we ignore anisotropies of the distribution of neurons across the visual field, the preponderance of neurons with different receptive field sizes and their functional specialisations, etc.

554 There is considerable debate regarding the locus of crowding in the visual system (e.g., 555 Levi, 2008). Findings from recent imaging studies disagree, but generally point to crowding 556 occurring at multiple stages of visual processing (Anderson, Dakin, Schwarzkopf, Rees, & 557 Greenwood, 2012; Freeman, Donner, & Heeger, 2011; Kwon, Bao, Millin, & Tjan, 2014; also see Chen et al., 2014). Similarly, several behavioural experiments have argued for 558 559 interference at different stages of the visual hierarchy (Blake, Tadin, Sobel, Raissian, & Chong, 560 2006; Chakravarthi & Cavanagh, 2009; Dakin, Greenwood, Carlson, & Bex, 2011; Farzin et al., 561 2009; Louie, Bressler, & Whitney, 2007; Wallis & Bex, 2011). These lend credence to our 562 hypothetical explanation that neurons with receptive fields of different sizes contribute 563 towards target-flanker interactions, which can in turn explain the interactions found in our 564 study.

565 Interestingly, it has been posited that objects must be separated by a certain distance 566 on the cortical surface (6 mm in the radial direction and 1 mm in the tangential direction in 567 V1) to be resolved without interference (Motter & Simoni, 2007; Pelli, 2008). That is, objects 568 must be cortically separated to avoid crowding. This has been interpreted to suggest that 569 pooling occurs over a fixed set of neurons and if more than one object activates these 570 neurons, their features are pooled, leading to crowding. Note that this conceptualisation of 571 pooling does not require pooling to occur in V1, but can occur in any one (or more) of the 572 retinotopic areas. Our proposal modifies this hypothesis by suggesting that the ability to 573 resolve an object is inversely related to the cortical *area* necessary to extract information 574 without interference. One crucial difference with the former proposal is that we do not 575 suggest that there is a fixed number of neurons that pool information. The critical resolution, 576 and hence the cortical area required for identification, varies according to stimulus properties 577 (duration, masking, contrast, etc.). A larger area is needed to resolve an object under some 578 circumstances, compared to others. This variability might be a consequence of varying attentional recruitment of neurons (Chen et al., 2014; He et al., 1996) or simply competition 579 for resources between objects (Scalf & Beck, 2010) under different circumstances. For 580 581 example, an object presented with low contrast or for a short duration might need the 582 recruitment of a larger number of neurons to process it with a high signal-to-noise ratio. 583 Hence such objects need a larger flanker-free area to avoid crowding, whereas at higher 584 contrast or longer duration a smaller area would suffice for appropriate behavioural

performance. Similarly, attention (or grouping mechanisms) might aid segmentation of targets that are dissimilar to the flankers or when presented among previewed flankers, and hence reduce the number of neurons necessary for processing their identity. Whatever the mechanism that renders critical resolution sensitive to stimulus properties, our findings suggest that this resolution is additively (independently) affected when multiple stimulus properties are manipulated.

591 A key observation in our experiments is that the magnitude of the effect of one 592 manipulation on object recognition is dependent on other stimulus parameters when 593 expressed in terms of the critical spacing. This helps understand some previous findings, such 594 as for example, the very large effect of a contrast manipulation on critical spacing in one study 595 (Rashal & Yeshurun, 2014). This study employed both backward masking and very short 596 display durations, both of which should have increased the effect of the contrast 597 manipulation on critical spacing. The opposite pattern emerges when multiple favourable 598 stimulus properties are combined. In this case, the effect of any manipulation is reduced 599 which may make it harder to detect reliably. For example, in Experiment 3 the well-known 600 effect of pop-out on critical spacing (Põder, 2007; Scolari et al., 2007) was only marginally 601 significant when comparing the two conditions with preview (Table 1). Taken out of context, 602 one could have concluded that the effect of pop-out is abolished when combined with 603 preview. The incorrectness of this conclusion becomes easily apparent when the same data 604 is expressed in terms of the critical resolution (Table 2, Figure 4C). As can be seen from these 605 examples, quantifying crowding in terms of critical resolution instead of the critical spacing 606 enhances comparability across conditions and experiments because the magnitude of effects 607 becomes independent of other manipulations.

608 Critical resolution, as a tool, is agnostic about the underlying mechanism of crowding. 609 We argue that it is simply a better measure of crowding. Our ideas were presented in the context of the biased competition model above, but the utility of critical resolution is 610 611 independent of whether one adopts this particular theoretical explanation. The idea of a 612 limited resolution is similar to the attentional hypothesis of crowding (He et al., 1996), which 613 posits that crowding arises when the resolution of selective attention is insufficient to focus 614 on the target stimulus. However, it is also compatible with bottom-up models of crowding 615 such as pooling, averaging (Greenwood, Bex, & Dakin, 2009; Parkes, Lund, Angelucci,

Solomon, & Morgan, 2001), and flanker substitution (Ester, Klee, & Awh, 2014; Nandy & Tjan,2007).

618 Some recent studies have determined that the effects of grouping on crowding 619 challenge long-standing conclusions about crowding, such as the Bouma Law; these findings might also question the general validity of critical resolution as a measure of crowding. For 620 621 example, it has been shown that flankers presented at distances far exceeding half the target 622 eccentricity can alleviate crowding if they group with each other (Herzog, Sayim, Chicherov, 623 & Manassi, 2015, but see Van der Burg, Olivers, & Cass, 2017). In other words, manipulating 624 objects outside the critical spacing modulates crowding. On the face of it, this conclusion 625 appears to contradict the notion underlying critical spacing and thus critical resolution. 626 However, one way to reconcile these opposing findings is to consider that grouping might 627 occur before the resolution bottleneck comes into play. That is, segmentation of feature sets 628 occurs first, via grouping. This segmentation renders the neurons that represent these 629 grouped feature sets functionally non-overlapping, allowing them to escape mutual 630 interference. Hence the critical resolution for identifying the target will be high. According to 631 this explanation, the pop-out manipulation in our third experiment reduced crowding by 632 segmenting the target and flankers into separate feature sets.

633 We found a highly consistent pattern of additive effects on critical resolution across 634 three experiments testing different combinations of flanker contrast, backward masking, 635 display duration, pop-out and preview, all of which were previously known to affect the 636 critical spacing (Andriessen & Bouma, 1976; Chakravarthi & Cavanagh, 2009; Chung et al., 637 2001; Kennedy & Whitaker, 2010; Kooi et al., 1994; Nazir, 1992; Põder, 2007; Rashal & Yeshurun, 2014; Scolari et al., 2007; Vickery et al., 2009; Wallis & Bex, 2012; Watson & 638 639 Humphreys, 1997). However, we cannot exclude the possibility that the regularity we 640 observed here does not extend to any combination of properties that affect the critical 641 distance. Although we tested a variety of manipulations, other manipulations can also affect 642 the critical distance, for example, attention (Põder, 2006; Strasburger, 2007; Yeshurun & 643 Rashal, 2010). Attention is conceptually distinct from the other manipulations as it affects an 644 internal variable rather than the stimulus display. It remains for future work to assess whether 645 our pattern of results holds up for all of these factors and their combinations.

# 646 6. Conclusion

647 Manipulating different properties of stimuli in peripheral vision leads to non-additive 648 interactions on the spatial extent of crowding (critical spacing). These interactions are 649 quantitatively similar across different combinations of manipulations and become additive 650 when crowding is quantified in terms of critical resolution. We propose that the critical 651 resolution is a superior measure of crowding which facilitates understanding the limits of 652 visual object recognition in the visual periphery across heterogeneous scenes.

## 653 Author Contributions

654 Conceptualization, L.S., R.C. and S.K.A.; Methodology, L.S., R.C. and S.K.A.; Software,

L.S. and S.K.A; Formal Analysis, L.S. and S.K.A.; Investigation, L.S.; Writing – Original Draft, L.S.;

656 Writing – Review & Editing, L.S., R.C. and S.K.A.; Visualization, L.S.; Funding Acquisition, L.S.,

657 R.C. and S.K.A.; Supervision, R.C. and S.K.A.

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# 663

## References

- Anderson, E. J., Dakin, S. C., Schwarzkopf, D. S., Rees, G., & Greenwood, J. A. (2012). The
- 665 neural correlates of crowding-induced changes in appearance. *Current Biology*, 22(13),
- 666 1199-1206. doi:10.1016/j.cub.2012.04.063
- Andriessen, J., & Bouma, H. (1976). Eccentric vision: Adverse interactions between line
  segments. *Vision Research*, *16*(1), 71-78.
- Blake, R., Tadin, D., Sobel, K., Raissian, T., & Chong, S. (2006). Strength of early visual
- 670 adaptation depends on visual awareness. *Proceedings of the National Academy of*

- 671 Sciences of the United States of America, 103(12), 4783-4788.
- 672 doi:10.1073/pnas.0509634103
- Bouma, H. (1970). Interaction effects in parafoveal letter recognition. *Nature, 226*, 177-178.
- Box, G. E., & Cox, D. R. (1964). An analysis of transformations. *Journal of the Royal Statistical*
- 675 Society.Series B (Methodological), , 211-252.
- 676 Bundesen, C. (1990). A theory of visual attention. *Psychological Review*, 97(4), 523.
- 677 Chakravarthi, R., & Cavanagh, P. (2009). Recovery of a crowded object by masking the
- flankers: Determining the locus of feature integration. *Journal of Vision, 9*(10), 4.1-9.
- 679 doi:10.1167/9.10.4 [doi]
- 680 Chen, J., He, Y., Zhu, Z., Zhou, T., Peng, Y., Zhang, X., & Fang, F. (2014). Attention-dependent
- 681 early cortical suppression contributes to crowding. *The Journal of Neuroscience : The*
- 682 *Official Journal of the Society for Neuroscience, 34*(32), 10465-10474.
- 683 doi:10.1523/JNEUROSCI.1140-14.2014 [doi]
- Chung, S. T., Levi, D. M., & Legge, G. E. (2001). Spatial-frequency and contrast properties of
  crowding. *Vision Research*, 41(14), 1833-1850.
- 686 Dakin, S. C., Greenwood, J. A., Carlson, T. A., & Bex, P. J. (2011). Crowding is tuned for
- 687 perceived (not physical) location. *Journal of Vision, 11*(9), 2. doi:10.1167/11.9.2
- Desimone, R., & Duncan, J. (1995). Neural mechanisms of selective visual attention. *Annual Review of Neuroscience, 18*(1), 193-222.

690	Ester, E. F., Klee, D., & Awh, E. (2014). Visual crowding cannot be wholly explained by
691	feature pooling. Journal of Experimental Psychology-Human Perception and
692	<i>Performance, 40</i> (3), 1022-1033. doi:10.1037/a0035377

- Farzin, F., Rivera, S. M., & Whitney, D. (2009). Holistic crowding of mooney faces. *Journal of Vision, 9*(6), 18-18.
- Freeman, J., Donner, T. H., & Heeger, D. J. (2011). Inter-area correlations in the ventral
  visual pathway reflect feature integration. *Journal of Vision*, *11*(4), 15.

697 doi:10.1167/11.4.15

- 698 Greenwood, J. A., Bex, P. J., & Dakin, S. C. (2009). Positional averaging explains crowding
- 699 with letter-like stimuli. *Proceedings of the National Academy of Sciences of the United*

700 States of America, 106(31), 13130-13135. doi:10.1073/pnas.0901352106 [doi]

Harrison, W. J., & Bex, P. J. (2015). A unifying model of orientation crowding in peripheral

vision. *Current Biology*, 25(24), 3213-3219. doi:10.1016/j.cub.2015.10.052

He, S., Cavanagh, P., & Intriligator, J. (1996). Attentional resolution and the locus of visual

704 awareness. *Nature, 383*(6598), 334-337. doi:10.1038/383334a0

- Herzog, M. H., & Manassi, M. (2015). Uncorking the bottleneck of crowding: A fresh look at
  object recognition. *Current Opinion in Behavioral Sciences*, *1*, 86-93.
- Herzog, M. H., Sayim, B., Manassi, M., & Chicherov, V. (2016). What crowds in crowding? *Journal of Vision, 16*(11), 25-25.

709	Herzog, M. H., Sayim, B., Chicherov, V., & Manassi, M. (2015). Crowding, grouping, and
710	object recognition: A matter of appearance. <i>Journal of Vision, 15</i> (6), 5.
711	doi:10.1167/15.6.5

- 712 Kastner, S., De Weerd, P., Pinsk, M., Elizondo, M., Desimone, R., & Ungerleider, L. (2001).
- 713 Modulation of sensory suppression: Implications for receptive field sizes in the human
- visual cortex. *Journal of Neurophysiology*, *86*(3), 1398-1411.
- 715 Kennedy, G. J., & Whitaker, D. (2010). The chromatic selectivity of visual crowding. *Journal*

716 of Vision, 10(6), 15-15.

- 717 Kooi, F., Toet, A., Tripathy, S., & Levi, D. (1994). The effect of similarity and duration on
- spatial interaction in peripheral-vision. *Spatial Vision*, *8*(2), 255-279.
- 719 doi:10.1163/156856894X00350
- 720 Kwon, M., Bao, P., Millin, R., & Tjan, B. S. (2014). Radial-tangential anisotropy of crowding in
- the early visual areas. *Journal of Neurophysiology*, *112*(10), 2413-2422.
- 722 doi:10.1152/jn.00476.2014
- 723 Kyllingsbaek, S., Valla, C., Vanrie, J., & Bundesen, C. (2007). Effects of spatial separation
- between stimuli in whole report from brief visual displays. *Perception & Psychophysics,*
- 725 *69*(6), 1040-1050. doi:10.3758/BF03193942
- Levi, D. M. (2008). Crowding—An essential bottleneck for object recognition: A mini-review.
- 727 Vision Research, 48(5), 635-654.

728	Louie, E. G., Bressler, D. W., & Whitney, D. (2007). Holistic crowding: Selective interference
729	between configural representations of faces in crowded scenes. Journal of Vision, 7(2),
730	24. doi:10.1167/7.2.24
731	Moran, J., & Desimone, R. (1985). Selective attention gates visual processing in the
732	extrastriate cortex. Science, 229(4715), 782-784. doi:10.1126/science.4023713
733	Motter, B. C., & Simoni, D. A. (2007). The roles of cortical image separation and size in active
734	visual search performance. <i>Journal of Vision, 7</i> (2), 6. doi:10.1167/7.2.6
735	Nandy, A. S., & Tjan, B. S. (2007). The nature of letter crowding as revealed by first- and
736	second-order classification images. <i>Journal of Vision, 7</i> (2), 5. doi:10.1167/7.2.5
737	Nazir, T. A. (1992). Effects of lateral masking and spatial precueing on gap-resolution in
738	central and peripheral vision. Vision Research, 32(4), 771-777.
739	Parkes, L., Lund, J., Angelucci, A., Solomon, J. A., & Morgan, M. (2001). Compulsory
740	averaging of crowded orientation signals in human vision. Nature Neuroscience, 4(7),
741	739-744. doi:10.1038/89532
742	Pelli, D. G., & Tillman, K. A. (2008). The uncrowded window of object recognition. Nature
743	Neuroscience, 11(10), 1129-1135.
744	Pelli, D. G., Palomares, M., & Majaj, N. J. (2004). Crowding is unlike ordinary masking:
745	Distinguishing feature integration from detection. <i>Journal of Vision, 4</i> (12), 1136-1169.
746	doi:10:1167/4.12.12 [doi]

- Pelli, D. G. (2008). Crowding: A cortical constraint on object recognition. *Current Opinion in Neurobiology*, *18*(4), 445-451. doi:10.1016/j.conb.2008.09.008
- Põder, E. (2006). Crowding, feature integration, and two kinds of "attention". *Journal of Vision, 6*(2), 7-7.
- 751 Põder, E. (2007). Effect of colour pop-out on the recognition of letters in crowding
- conditions. *Psychological Research*, *71*(6), 641-645.
- 753 Rashal, E., & Yeshurun, Y. (2014). Contrast dissimilarity effects on crowding are not simply
- another case of target saliency. *Journal of Vision, 14*(6) doi:10.1167/14.6.9
- Reynolds, J. H., & Heeger, D. J. (2009). The normalization model of attention. *Neuron, 61*(2),
  168-185. doi:10.1016/j.neuron.2009.01.002
- 757 Scalf, P. E., & Beck, D. M. (2010). Competition in visual cortex impedes attention to multiple
- 758 items. Journal of Neuroscience, 30(1), 161-169. doi:10.1523/JNEUROSCI.4207-09.2010
- 759 Scolari, M., Kohnen, A., Barton, B., & Awh, E. (2007). Spatial attention, preview, and popout:
- 760 Which factors influence critical spacing in crowded displays? *Journal of Vision*, 7(2), 7.
- 761 doi:10.1167/7.2.7
- 762 Strasburger, H. (2001). Converting between measures of slope of the psychometric function.
   763 *Perception & Psychophysics, 63*(8), 1348-1355.
- Strasburger, H. (2007). Unfocussed spatial attention underlies the crowding effect in indirect
  form vision. (vol 5, pg 1024, 2005). *Journal of Vision*, 7(3), 7. doi:10.1167/7.3.7

766	Tripathy, S., Cavanagh, P., & Bedell, H. E. (2014). Large crowding zones in peripheral vision
767	for briefly presented stimuli. <i>Journal of Vision, 14</i> (6), 11. doi:10.1167/14.6.11
768	van den Berg, R., Roerdink, J. B. T. M., & Cornelissen, F. W. (2007). On the generality of
769	crowding: Visual crowding in size, saturation, and hue compared to orientation. Journal
770	of Vision, 7(2), 14.1-1411. doi:10.1167/7.2.14
771	Van der Burg, E., Olivers, C. N. L., & Cass, J. (2017). Evolving the keys to visual crowding.
772	Journal of Experimental Psychology-Human Perception and Performance, 43(4), 690-
773	699. doi:10.1037/xhp0000337
774	Vickery, T. J., Shim, W. M., Chakravarthi, R., Jiang, Y. V., & Luedeman, R. (2009).
775	Supercrowding: Weakly masking a target expands the range of crowding. Journal of
776	<i>Vision, 9</i> (2), 12.1-15. doi:10.1167/9.2.12 [doi]
777	Wallace, J. M., & Tjan, B. S. (2011). Object crowding. <i>Journal of Vision, 11</i> (6), 19-19.
778	Wallis, T. S. A., & Bex, P. J. (2011). Visual crowding is correlated with awareness. Current
779	<i>Biology, 21</i> (3), 254-258. doi:10.1016/j.cub.2011.01.011
780	Wallis, T. S. A., & Bex, P. J. (2012). Image correlates of crowding in natural scenes. Journal of
781	<i>Vision, 12</i> (7), 6. doi:10.1167/12.7.6
782	Watson, D. G., & Humphreys, G. W. (1997). Visual marking: Prioritizing selection for new
783	objects by top-down attentional inhibition of old objects. Psychological Review, 104(1),
784	90.

- 785 Whitney, D., & Levi, D. M. (2011). Visual crowding: A fundamental limit on conscious
- perception and object recognition. *Trends in Cognitive Sciences*, *15*(4), 160-168.
- 787 Wolford, G., & Chambers, L. (1984). Contour interaction as a function of retinal eccentricity.
- 788 Attention, Perception, & Psychophysics, 36(5), 457-460.
- 789 Yeshurun, Y., & Rashal, E. (2010). Precueing attention to the target location diminishes
- rowding and reduces the critical distance. *Journal of Vision, 10*(10), 16.
- 791 doi:10.1167/10.10.16