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Large crowding zones in peripheral vision for briefly presented stimuli

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When a target is flanked by distractors, it becomes more difficult to identify. In the periphery, this crowding effect extends over a wide range of target-flanker separations, called the spatial extent of interaction (EoI). A recent study showed that the EoI dramatically increases in size for short presentation durations (Chung & Mansfield, 2009). Here we investigate this duration-EoI relation in greater detail and show that (a) it holds even when visibility of the unflanked target is equated for different durations, (b) the function saturates for durations shorter than 30 to 80 ms, and (c) the largest EoIs represent a critical spacing greater than 50% of eccentricity. We also investigated the effect of same or different polarity for targets and flankers across different presentation durations. We found that EoIs for target and flankers having opposite polarity (one white, the other black) show the same temporal pattern as for same polarity stimuli, but are smaller at all durations by 29% to 44%. The observed saturation of the EoI for short-duration stimuli suggests that crowding follows the locus of temporal integration. Overall, the results constrain theories that map crowding zones to fixed spatial extents or to lateral connections of fixed length in the cortex.

Introduction

Everyday experience tells us that a single item is easily located and identified on an otherwise empty desk but not so easily located or identified on a cluttered desk. Similarly, the orientation of an acuity target may be easily detected when it is presented in isolation, but not so easily detected when it is surrounded by flanking stimuli (Stuart & Burian, 1962;

Flom, Heath, & Takahashi, 1963; Flom, Weymouth, & Kahneman, 1963). Discriminating the orientation of target line segments becomes more difficult in the presence of other flanking line segments, particularly when they are parallel to the target (Andriessen & Bouma, 1976). Letters that are easily identified in isolation may not be easily identified in the presence of other distracting letters (Bouma, 1970, 1973). This loss in the ability to report the orientation or identity of target items in the presence of distractors or flankers is known as crowding (for a review see Levi, 2008).

The influence of the distractors or flankers in a crowding task generally decreases as the distance between the target and distractors/flankers is increased. Several studies measured the extent of interaction (EoI) for crowding (also known as the critical spacing), which is the radius of the region around the target within which the presence of distractors interferes reliably with the identification of the target (e.g., Bouma, 1970, 1973; Toet & Levi, 1992; Kooi, Toet, Tripathy, & Levi, 1994; Chung & Mansfield, 2009). The EoI for crowding is small at the fovea and increases systematically with the retinal eccentricity of the target, with the extent being larger in the radial than the tangential direction (e.g., Bouma, 1970, 1973; Toet & Levi, 1992). Bouma proposed the following rule of thumb: The EoI is approximately $b\phi$, where b is Bouma's constant of proportionality, typically falling in the range 0.4–0.5, and ϕ represents the eccentricity of the target (Bouma, 1970, 1973; Andriessen & Bouma, 1976). Thus, the EoI is determined primarily by the eccentricity of the target and does not scale with the size of the target (Tripathy & Cavanagh, 2002; Pelli, Palomares, & Majaj, 2004). Tripathy and Levi (1994) reported that the EoI at the eccentricity of the blind spot corresponds to a distance

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of 6 mm of cortex in V1, approximately the lengths of horizontal connections in V1 (e.g., Gilbert, Hirsch, & Wiesel, 1990; Gilbert & Wiesel, 1990), suggesting that these horizontal connections might mediate the lateral interactions observed in crowding. This finding has been found to generalize across eccentricities, and it has been proposed that crowding represents a cortical constraint on the identification of letters and more generally all visual objects (Pelli, 2008; Pelli & Tillman, 2008).

One alternative to this cortical hypothesis is that crowding represents the resolution of attentional mechanisms (He, Cavanagh, & Intriligator, 1996; Intriligator & Cavanagh, 2001). According to the attentional hypothesis, crowded items can be resolved spatially but cannot be individuated and the EoI would be the region within which individual items cannot be attentionally accessed. Other possibilities are that crowding occurs when features of the target and flanking objects are either averaged or misbound (e.g., Parkes, Lund, Angelucci, Solomon, & Morgan, 2001; Pelli et al., 2004; Greenwood, Bex, & Dakin, 2009; Dakin, Cass, Greenwood, & Bex, 2010) or when the spatial locations of the target and flanking objects are confused (e.g., Strasburger, Harvey, & Rentschler, 1991; Zhang, Zhang, Liu, & Yu, 2012; Hanus & Vul, 2013).

While retinal eccentricity of the target plays a dominant role in determining the EoI for crowding, there are other stimulus factors that influence the EoI (Whitney & Levi, 2011). For example, the more similar the flankers are to the target, the larger the EoI is (Nazir, 1992; Kooi et al., 1994). Bouma's Rule provides a good estimate of the EoI when the target and flankers share similar characteristics (e.g., shape, color, contrast polarity, etc.), but can be a great overestimate when the targets and flankers are dissimilar. In particular, the EoI is reduced when target and flankers have opposite contrast-polarity (black target and white flankers, or vice versa), compared to when they have the same polarity (Kooi et al., 1994; Hess, Dakin, & Kapoor, 2000; Hess, Dakin, Kapoor, & Tewfik, 2000; Chung & Mansfield, 2009). This opposite polarity advantage (OPA) is seen also when the stimulus consists of frames of black target with white flankers that alternate with frames of white target with black flankers, compared to frames with white target and flankers that alternate with black targets and flankers (Chakravarthi & Cavanagh, 2007). However, this advantage disappears at temporal frequencies higher than 7.5 Hz, suggesting that little or no OPA might exist for stimuli of very brief duration. In addition, if misbinding of nearby features contributes to crowding, the binding of contrast-polarity information might be very weak for stimuli of very brief duration resulting in less difference

between the effects of same and opposite polarity flankers on target identification.

Several studies indicate that the stimulus duration affects the EoI, although this parameter has not been investigated in great detail. Kooi et al. (1994, figure 15) found that when stimuli were presented for 1 s at 10° eccentricity in the lower visual field the EoI was notably smaller than for stimuli presented for 150 ms. This was found to hold whether the target and flankers had the same or different colors, and whether the target and flankers had the same or opposite contrast polarity. Tripathy and Cavanagh (2002) found that the EoI at a fixed retinal eccentricity changed little for a five-fold change in target size, but for the range of target sizes tested, the EoI was notably larger for a 13- or 27-ms stimulus duration than for a 360-ms stimulus. Neither of these studies systematically varied stimulus duration.

In contrast, Chung and Mansfield (2009) reported that the EoI for lower-case letters presented at 10° in the inferior visual field increased as stimulus duration was reduced successively from 1000 to 53 ms. The EoIs in this study were defined as the distance of the flanking letters that reduced percent-correct letter identification from 100% to 62.5%, which may be problematic for the following reasons. (a) The targets and flankers were always at a fixed high contrast so performance may have saturated at longer durations. (b) EoIs can be underestimated if performance has saturated (i.e., at 100% correct identification) at larger separations (including unflanked). An example of this saturation effect can be seen in the three panels on the left-column of figure 2¹ in Danilova and Bondarko (2007), where the ascending portions of the response functions indicate smaller EoIs for highly visible targets that are at saturation. (c) This saturation effect may be contributing to the decrease of the EoI with longer durations in Chung and Mansfield's data. Finally, it remains an open question as to whether the EoI continues to get larger for durations below 53 ms, the shortest duration tested by Chung and Mansfield. Wallace, Chiu, Nandy, and Tjan (2013) plotted EoIs as a function of stimulus duration for data taken from several studies and reported a linear relationship when EoI and duration both were plotted on log axes. However, the data for this plot were taken from a range of studies and therefore neither the stimulus conditions nor the criteria for estimating the EoIs from the data were necessarily matched.

In the current study we systematically investigated the effect of stimulus duration on the EoI using a standard crowding paradigm. If the duration of the stimulus is confirmed to have a large influence on the EoI as reported by Chung and Mansfield (2009), this would indicate that Bouma's constant can be modulated even if the target and flankers have similar characteristics. In addition, this result would bring into

question whether EoIs can be mapped onto a constant cortical distance. Further, if EoIs were found to exceed approximately $0.6 \times$ eccentricity for stimuli of short duration, then, from equation 3 in Pelli (2008), the corresponding cortical distance would have to exceed the usually cited value of 6–8 mm for long-range horizontal connections in area 17 of cats and V1 of primates (Gilbert & Wiesel, 1979, 1983; Rockland & Lund, 1983; Martin & Whitteridge, 1984; Gilbert & Li, 2012). From the point of view of the attentional hypothesis, an increase in the EoI for targets of short duration could be interpreted to mean that when attention is engaged by briefly presented stimuli, attentional resources are directed over a wider area than when stimuli are presented for longer durations (e.g., Eriksen & St. James, 1986). Experiment 1 determined EoIs for different stimulus durations at a retinal eccentricity of 10° in the lower visual field, using a target and flankers with the same contrast polarity. Experiment 2 compared the EoIs for target and flankers with the same and opposite contrast polarity. As noted above, it seemed plausible that the opposite polarity advantage would disappear when the stimuli were presented for very brief durations. In both of our experiments, the EoI was found to decrease steeply and linearly with the log of the stimulus duration over the longer durations tested, but appeared to reach a plateau for the briefer durations tested. The EoI at a 10° retinal eccentricity was found to vary substantially as stimulus duration was varied, questioning the idea that the EoI corresponds to a fixed cortical distance, regardless of eccentricity. In particular, when the stimuli were presented very briefly, transformation of the measured EoIs, to cortical distances in V1 exceeded 6–8 mm, the reported extents of horizontal connections in this area.

Methods

Equipment

The stimuli were generated on an Apple G3 Macintosh computer (Apple Computer International, Cork, Ireland), running Vision Shell stimulus generation software and were displayed on a Formac, Pronitron CRT 21/650 monitor. The screen resolution was 1280 (H) \times 960 (V) and the refresh rate was 75 Hz. The background luminance was 34.4 cd/m^2 in Experiment 1 and 37.9 cd/m^2 in Experiment 2, as measured with a Minolta CS-100 Chromameter. For Experiment 1 the viewing distance was 71.6 cm, and for Experiment 2 the viewing distance was 53.7 cm. At the distances used, each pixel subtended 1.5×1.5 arcmin and 2×2 arcmin respectively, in the horizontal and vertical

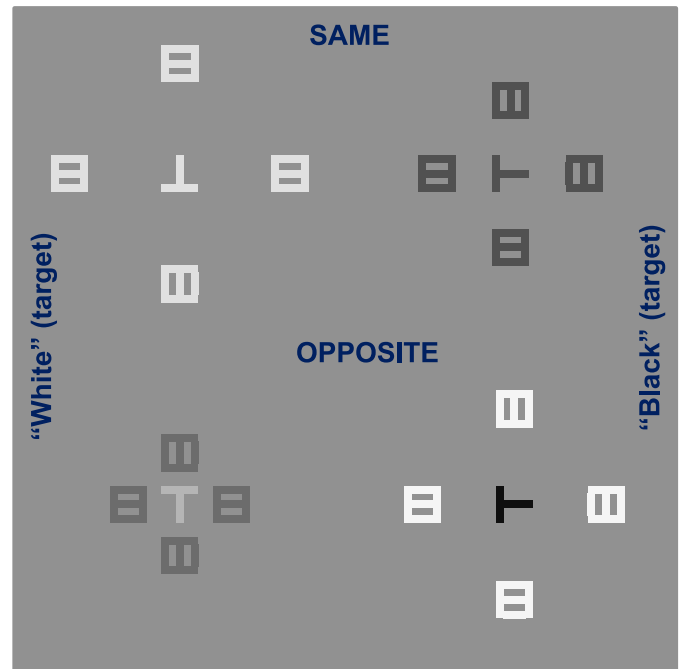


Figure 1. Stimuli used in Experiments 1 and 2. All stimuli were centered in the lower visual field at 10° eccentricity. Upper-left panel shows the stimuli used in Experiment 1. The upper panels show stimuli used in the same-polarity condition in Experiment 2, while lower panels show stimuli for the opposite-polarity condition in Experiment 2. Stimuli also included unflanked targets (letter T alone). For different stimulus durations target size and contrast were adjusted to yield approximately 90% correct identification of target orientation in preliminary unflanked trials. These adjustments determined the flanker size and contrast as well.

directions. Viewing was monocular using the observers' reported dominant eye, the fellow eye being occluded with an eye patch. A chin rest was used to stabilize the head.

Stimuli

The stimuli used in this study were very similar to those used in earlier studies (Kooi et al., 1994 with some of the modifications introduced in Tripathy & Cavanagh, 2002). A fixation spot was continuously present on the screen and the stimulus was centered at 10° eccentricity in the lower visual field. On most trials the stimulus consisted of a target surrounded by four flankers, one in each of the four cardinal directions relative to the target (Figure 1). The target consisted of a letter T rotated 0° , 90° , 180° , or 270° from vertical and the flankers were square-thetas rotated 0° or 90° . Target and flankers had the same extents, both horizontally and vertically. On flanked trials the four flankers were equidistant from the center of the target. All target-

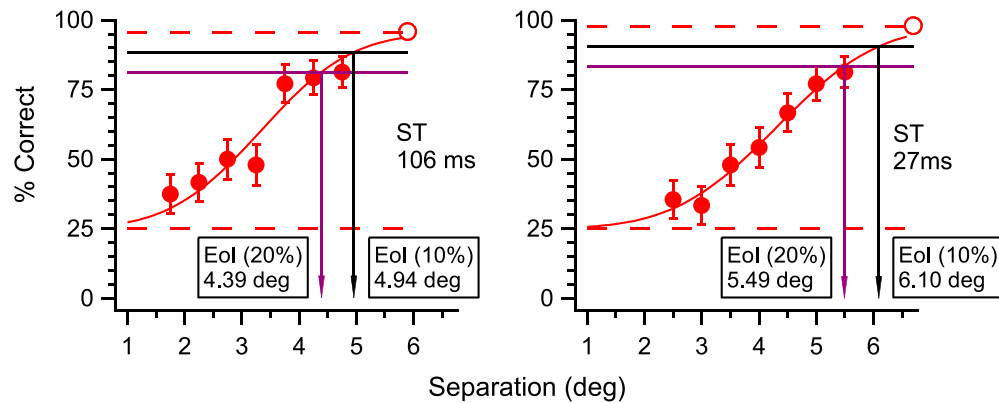


Figure 2. Estimating Eol. Data (filled symbols) are shown for observer ST for his performance for identifying the orientation of the target T as a function of target-flanker separation. The unflanked performance is also shown (open symbol). The data were fitted with a cumulative normal Gaussian function with its lower asymptote at 25% and the upper asymptote constrained by the unflanked performance and the data at the larger separations. The distance between the two asymptotes (red dashed lines) represents the amplitude of the psychometric function. Estimated Eols are shown for a 10% drop (black lines and arrow) and a 20% drop (purple lines and arrow) in performance, relative to the amplitude of the psychometric function. Data are shown for stimulus durations of 106 ms (left panel) and 27 ms (right panel).

flanker separations reported in this study refer to distances measured from the center of the target to the center of each of the four flankers. Target-flanker separations were varied between trials of a block, and unflanked trials were randomly interleaved with the flanked trials. The independent variable was the duration of the stimulus, and this was varied between 13 ms and 427 ms in Experiment 1 (1, 2, 4, 8, 16, or 32 frames of the monitor); the longest stimulation duration was not tested in Experiment 2.

In Experiment 1, only targets and flankers with positive polarity (white) were tested (Figure 1, upper left). Each block contained 16 trials for each of the seven target-flanker separations and 16 unflanked trials, all randomly interleaved. Stimulus duration was fixed within a block and three blocks were run for each of the stimulus durations.

In Experiment 2 the four contrast polarities shown in Figure 1 were tested: white target and white flankers, black target and black flankers, white target and black flankers, and black target and white flankers, all on neutral gray background. Each block contained 40 trials for each of the five target-flanker separations and 40 unflanked trials, all randomly interleaved. Stimulus duration was fixed within a block and two blocks were run for each of the stimulus durations.

Procedure

In order to compare EoIs for crowding at the different stimulus durations we needed to equate the visibility of the unflanked target at the different durations tested. For each observer and stimulus duration, preliminary practice blocks were run in order

to find the target size and contrast for which the orientation of the unflanked target was identified correctly on approximately 90% of the trials. This was done for white targets in Experiment 1 and for white and black targets separately in Experiment 2. In Experiment 1 visibility was matched for the different stimulus durations by keeping the size of the target fixed and varying the luminance, which amounted to varying the contrast since the luminance of the background was fixed. Author ST also did control experiments in which the visibility was matched for different stimulus durations by (a) keeping the luminance of the target fixed and varying the size, and (b) varying both the luminance and size of the target. In Experiment 2 both the luminance and size of the white and black targets were adjusted in order to equate visibility for the different stimulus durations. The average luminance levels and target sizes used for each stimulus duration in Experiments 1 and 2 are listed in Tables 1 and 2, respectively. The selection of 90% as the unflanked performance level ensured a large range of data (from the chance level of 25% to unflanked performance of approximately 90%) for the obtained psychometric functions, while avoiding the issue of response saturation when performance is 100%.

Once target visibility had been set to approximately 90% correct identification of the unflanked target, further practice blocks were run for each stimulus duration (and for each of the four polarity conditions in Experiment 2) to determine the range of target-flanker separations needed so that performance spanned most of the range of the psychometric function.

Data collection began following the preliminary practice blocks. Within each block of trials, the

Stimulus duration ms	DR-Constant size		GT-Constant size		ST-Constant size		ST-Constant luminance		ST-Random	
	Size arcmin	Luminance cd/m ²	Size arcmin	Luminance cd/m ²	Size arcmin	Luminance cd/m ²	Size arcmin	Luminance cd/m ²	Size arcmin	Luminance cd/m ²
13.3	52.5	103.3	60	103.3	52.5	103.3	67.5	57.3	52.5	103.3
26.7	52.5	74.2	60	56.6	52.5	68.3	60	57.3	45	103.3
53.4	52.5	43.3	60	43.3	52.5	49.7	52.5	57.3	37.5	103.3
106.7	52.5	41.7	60	41.7	52.5	40.6	45	57.3	30	103.3
213.4	52.5	40.6	60	39.5	52.5	40.6	37.5	57.3	30	57.3
426.8	52.5	40.6	60	39.5	52.5	40.0	30	57.3	30	57.3

Table 1. Stimulus size and luminance for the different targets and flankers used in Experiment 1. *Note:* DR, GT, ST = observers.

stimulus duration was fixed, the size and luminance of the target were fixed at the levels determined for the selected duration, and performance was measured for identifying the target’s orientation as a function of the different target-flanker separations (the unflanked target being assigned a separation of infinity) using the method of constant stimuli. For each stimulus condition in Experiment 1, three blocks were run yielding 384 trials (3 blocks × 8 separations [including infinity] × 16 repetitions) per psychometric function. The corresponding number for Experiment 2 was 480 trials (2 blocks × 6 separations × 40 repetitions). The different stimulus durations were tested in random order. In Experiment 2, for each duration, the different polarity conditions also were tested in random order.

The data for a given duration were plotted with proportion of correct identification (%) on the ordinate and target-flanker separation on the abscissa. A cumulative normal psychometric function was fitted to these data (see below) and the EoI was estimated for this duration. To evaluate the effect of duration on EoI, the EoIs obtained in the different conditions were plotted as a function of stimulus duration.

Observers

Three observers (DR, GT, and ST) participated in Experiment 1 and four observers (DR, MG, NV, and ST) participated in Experiment 2. Observers DR, GT,

and ST were experienced psychophysical observers, while observer NV had no prior experience as an observer in a psychophysical experiment. One of the observers (MG) did not complete the experiment and his data are not reported. The corrected foveal visual acuity for each observer was 6/6 or better. Observers gave informed consent in adherence to the Declaration of Helsinki.

Estimating EoI

The procedure for estimating EoI was similar to that used in Tripathy and Cavanagh (2002) and is illustrated in Figure 2. The proportion of correct responses was plotted against the target-flanker separation, with the unflanked performance assumed to correspond to a large target-flanker separation (2000 arcmin—the actual value used here has little influence on estimated EoIs). A cumulative normal Gaussian with three free variables (amplitude, mean, and standard deviation) was fitted to the data. The lower asymptote of the fit was at 25% (chance performance—lower dashed line in Figure 2) and the upper asymptote (typically close to 90%—upper dashed line in Figure 2) was constrained by the data at the larger separations and the unflanked performance. The EoI corresponded to the target-flanker separation for which the performance (measured along the cumulative fit) dropped from the upper asymptote of the fit by 10% of the amplitude of the fit (black arrow in Figure 2).

Stimulus duration ms	DR			NV			ST		
	Size arcmin	Lum (Wh) cd/m ²	Lum (Bl) cd/m ²	Size arcmin	Lum (Wh) cd/m ²	Lum (Bl) cd/m ²	Size arcmin	Lum (Wh) cd/m ²	Lum (Bl) cd/m ²
13.3	60	78.0	22.1	60	69.9	20.9	60	74.2	18.4
26.7	50	56.6	27.0	50	79.6	17.4	50	70.5	20.9
53.4	40	58.6	22.8	40	62.0	20.9	40	59.3	25.3
106.7	30	65.5	20.9	30	59.9	18.4	30	64.0	19.8
213.4	30	56.6	27.0	30	56.6	20.9	30	58.6	20.2

Table 2. Stimulus size and luminance for the different white (Wh) and black (Bl) targets and flankers used in Experiment 2. *Note:* DR, NV, ST = observers.

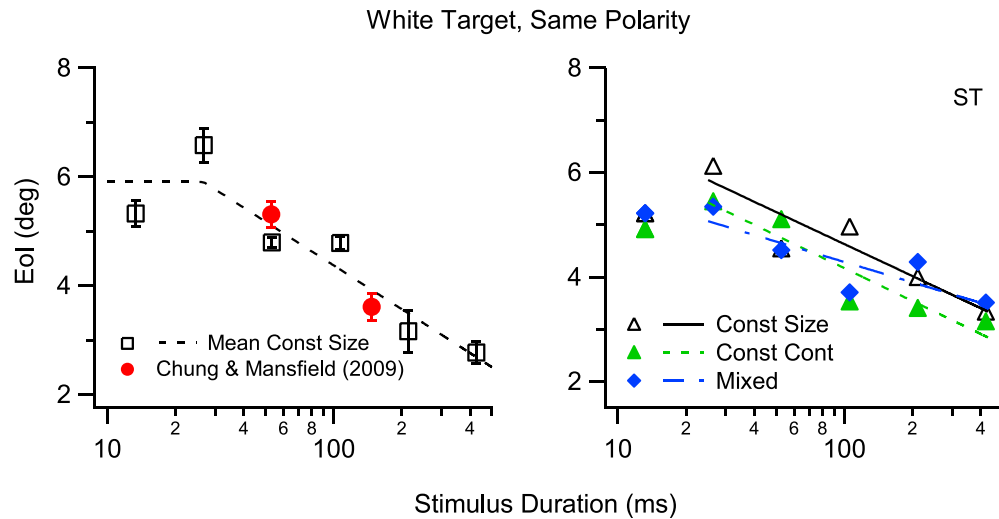


Figure 3. Effect of stimulus duration on EoI in Experiment 1. Left panel: Average EoIs (± 1 SEM, $n = 3$) are shown for different stimulus durations when contrast of the target was adjusted to equate its visibility for the different durations. Also shown for comparison are data reported by Chung and Mansfield (2009) for their same polarity condition. Right panel: Data for observer ST are shown for conditions in which visibility was equated by varying contrast alone, by varying size alone, and by varying both size and contrast. Bilinear fits in the left panel and straight-line fits in the right panel show the linear relationship between EoI and $\log(\text{stimulus duration})$ over the range of larger durations. The break, which was a free parameter in the bilinear fitting routine used for the data in the left panel, occurred at 27 ms.

EoIs were also estimated for a drop of 20% of the amplitude from the upper asymptote (purple arrow in Figure 2), but these yielded no qualitative differences in the results and are not reported.

In Experiment 2 we found an asymmetry in performance for white targets compared to black targets (see Lu & Sperling, 2012). For example, when the Weber formula was used, the contrast needed to get an observer's performance to 90% correct for a white unflanked target was typically greater than that needed for a black target; the two contrasts were more comparable when the Michelson formula was used. Therefore in the same-polarity and the opposite-polarity conditions, we report the EoIs for white targets and for black targets separately. We also report the combined same-polarity EoIs and opposite-polarity EoIs. For example, to determine the combined EoIs in the same-polarity condition a cumulative normal Gaussian was fit to the average of the performances for white and black targets (as opposed to estimating EoIs separately for black and white targets and averaging them).

Results and discussion

Experiment 1

The left panel of Figure 3 shows mean EoI as a function of stimulus duration for three observers with

EoIs estimated from a drop of 10% from the upper asymptote of the psychometric function. The EoIs increased systematically as the duration of stimulus presentation decreased, except for a few of the briefer durations tested. This pattern of responses was consistent across observers in both Experiments 1 and 2. The EoIs in the left panel were fitted with a bilinear function with three free variables: the y -intercept, the duration that corresponded to the break in the bilinear fit, and the slope of the line fitted to the data for the longer durations—the slope of the line fitted to the briefer durations was constrained to zero. The break-point produced by the fitting algorithm was at 27 ms. Over the range 27–427 ms the EoI decreased linearly with the \log of stimulus duration, going from an average of 6.6° at 27 ms to 2.8° at 427 ms. This drop corresponds to a 2.7° drop in EoI per log unit increase in duration. Also shown in this panel are data (red circles) from the experiment investigating the effect of duration on crowding by Chung and Mansfield (2009, same polarity data in their figure 3); only the data that lie within the range of durations tested in the current study are shown. Although there were methodological differences between Chung and Mansfield (2009) and the current study, both sets of data fall close to the fitted line. However, the current study extends the findings of Chung and Mansfield (2009) to stimulus durations briefer than 53 ms and shows that EoIs do not increase in size indefinitely as the stimulus duration is reduced. Rather, when the stimulus duration is less than approximately 27 ms the resulting EoIs no longer

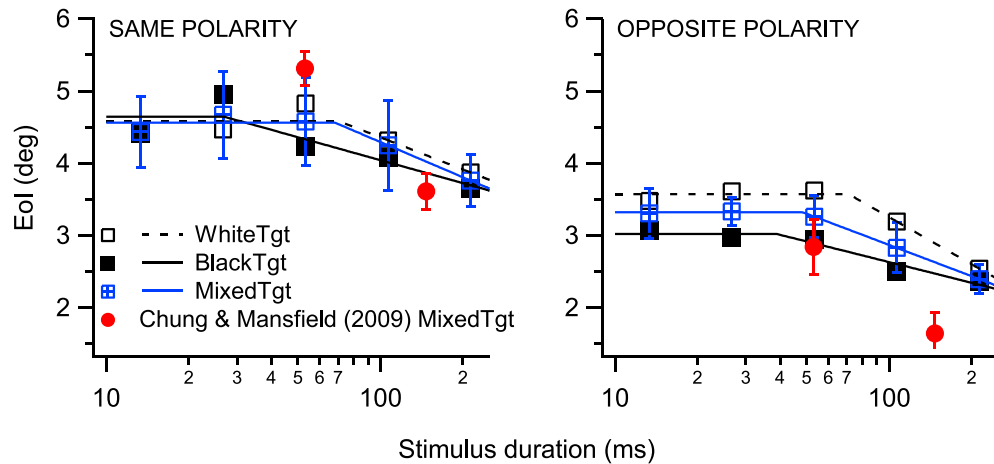


Figure 4. Effect of stimulus duration on EoI in Experiment 2. The average EoIs for three observers are shown for different stimulus durations in the same polarity conditions (left panels) and in the opposite polarity conditions (right panels). EoIs are shown separately for white targets and black targets and for EoIs estimated from the combined raw data. Lines were fitted to the data as in Experiment 1. The filled circles replot the average data from Chung and Mansfield (2009) for their same- (left) and mixed-polarity (right) conditions.

follow a linear-log relationship but appear to attain a plateau.

In addition to the constant size condition, author ST also provided data in a constant contrast condition, in which only size was varied to equate unflanked performance across the different stimulus durations, and in a mixed condition in which both the size and the contrast were varied to equate unflanked performance. The right panel of Figure 3 presents ST's performance for the three conditions. The bilinear nature of the average EoIs in the left panel is also seen in ST's individual data in the right panel, with the data in both panels showing a linear-log relationship for stimulus durations longer than approximately 27 ms. Differences between ST's performance under the three conditions were small and were mostly quantitative. ST's EoIs were on average approximately 0.25° smaller in the constant contrast and mixed conditions. For a stimulus duration of 13 ms, the results in the constant contrast and mixed conditions for observer ST were essentially identical to those in the constant size condition. Because performance in the three conditions was qualitatively highly similar, in Experiment 2 both target size and target contrast were varied in order to equate target visibility for the different stimulus durations and for the two contrast polarities.

Experiment 2

Several asymmetries were found with regard to performance for white and black targets (see Lu & Sperling, 2012). Quite frequently the contrast needed to identify the orientation of a white target 90% of the

time was higher than the contrast needed for a black target when the Weber formula for contrast was used. Further, the EoI estimated for a white target in the same-polarity or opposite-polarity condition was sometimes different from that for a black target in the corresponding condition. For this reason, EoIs in Experiment 2 have been presented for both white targets and black targets and for the average of the two polarities.

The left panel of Figure 4 show average EoIs of three observers as a function of stimulus duration in the same-polarity condition and the right panel shows the corresponding average EoIs in the opposite-polarity condition. In each panel data are shown for white targets, black targets, and for the average of the two.

The pattern of results for the same-polarity condition is similar to that seen in Experiment 1 and the data again were fitted with bilinear functions. However, the average EoIs seen for the briefer durations were smaller than those seen in Experiment 1, resulting in a shallower slope for the line fitted to the data for the longer stimulus durations. For the fit to the combined data (blue line) average EoI decreased by 1.62° per log unit increase in stimulus duration for durations longer than 68 ms. The breaks in the fits ranged from 71 ms (white target) to 27 ms (black target). Experiment 2 involved over 15 hrs of data collection for each observer, including several hours of pilot experiments to determine the appropriate target size and contrast and the correct range of target-flanker separations. It is likely that this practice contributed to the reduction in the average EoIs compared to Experiment 1 (see Chung, 2007; Huckauf & Nazir, 2007; Hussain, Webb, Astle, & McGraw, 2012). For example, observer DR

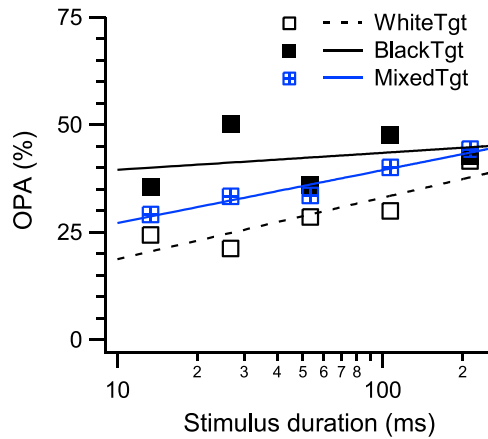


Figure 5. Effect of stimulus duration on the OPA. The data in Figure 4 were transformed to normalized OPAs (see text) and replotted. Normalized OPAs are shown separately for white and black targets and for the combined raw data.

participated in both experiments but had not participated in a crowding experiment before. The largest EoI measured for DR in Experiment 1 was 7.2° when the stimulus duration was 27 ms; the corresponding EoI in Experiment 2 was 4.0° . A similar drop in DR's EoIs occurred also for the other stimulus durations. On the other hand, observer ST had participated in many previous crowding experiments using stimuli similar to those in current study and showed no change in EoI across the two experiments. The effects of practice may be seen also by comparing the data from Chung and Mansfield (2009) that are included in Figure 4 (red circles). Unlike Experiment 1, the lines in each panel that are fit to the data from the current experiment are too shallow to describe the results from Chung and Mansfield (2009).

A comparison of the average EoIs in the opposite-polarity condition with those in the same-polarity condition (right panel vs. left panel in Figure 4) shows that the patterns of results are similar, with a bilinear relationship between EoI and log-duration. However, the EoIs in the opposite-polarity condition are systematically smaller than those in the same-polarity condition. The slope of the best fitting line to the combined data for durations longer than 48 ms is 1.43° per log unit of duration for the opposite-polarity condition. The breaks in the bilinear fits ranged from 39 ms (black target) to 71 ms (white target). The right panel also shows, for purposes of comparison, the corresponding data (red circles) from the mixed-polarity condition in Chung and Mansfield (2009). The EoIs in the opposite-polarity condition in the current study are larger than those in Chung and Mansfield (2009). While we do not know the origin of this difference, it cannot be a consequence of practice

during our pilot experiments, as that would predict that our EoIs should be smaller rather than larger.

In order to quantify the OPA we combined the same-polarity EoIs and the opposite-polarity EoIs to obtain:

Normalized OPA(%)

$$= \frac{\{EoI[SamePolarity] - EoI[OppositePolarity]\}}{\{Average(EoI[SamePolarity], EoI[OppositePolarity])\}}$$

Normalized OPAs were calculated and plotted for performance using white targets, black targets, and as the average of the performance for black and white targets. The average OPAs of the three observers are shown in Figure 5. The normalized OPAs, averaged for the different contrast polarities (blue symbols and blue line), range from 29% at a duration of 13 ms to 44% for a duration of 427 ms. Thus, the OPA persists across the range of stimulus durations tested.

General discussion

A bilinear relationship between EoI and stimulus duration

We asked how the duration of stimulus presentation influences the EoI for crowding. In Experiment 1, we found that EoI is approximately constant for stimuli of short duration and decreases linearly with the logarithm of the stimulus duration over the range 27–427 ms for stimuli consisting of white targets and white flanks. We confirmed a similar bilinear relationship between EoI and log duration for both Same- and Opposite-Polarity stimuli in Experiment 2. The duration at which the break in the fits occurred ranged from 27 ms to 71 ms across the different conditions of target-flanker polarity, with an average duration of 54 ms. Although the relationship between EoIs and duration that we found is similar to that reported by Chung and Mansfield (2009) over the longer range of durations, we find deviations from this relationship when stimulus durations fall below 27 ms in Experiment 1 and about 54 ms in Experiment 2. When the stimuli are briefer than these critical durations the resulting EoIs remain roughly constant.

Opposite polarity advantage and duration

We suggested in the Introduction that the OPA might be reduced or disappear for briefly presented stimuli as the binding of features, such as polarity, might be less robust under these conditions. The EoIs in Experiment 2 are smaller on average by about 30%

when target and flankers have opposite contrast polarities (see also Kooi et al., 1994; Chakravarthi & Cavanagh, 2007; Chung & Mansfield, 2009), and the OPA was found to persist across stimulus durations ranging from 13–213 ms, with the normalized OPA ranging between 29% and 44%, including the plateau region of durations shorter than about 70 ms. This OPA is smaller in magnitude than the value of about 70% reported by Chung and Mansfield (2009), but they, too, reported that it remains approximately constant in terms of percent advantage across the range of durations that they tested.

Large EoIs for briefly presented stimuli

EoIs at a stimulus duration of 27 ms in Experiment 1 exceed $0.5 \times$ eccentricity (discussed further below). EoIs in excess of $0.5 \times$ eccentricity have been reported previously in the context of super-crowding, where a weakly masked target is surrounded by remote flankers (Vickery, Shim, Chakravarthi, Jiang, & Luedeman, 2009). Studies investigating the role of grouping in crowding also have reported influences on target identification from outside of Bouma's window (Manassi, Sayim, & Herzog, 2013). While these two studies found target-flanker interactions over long distances, the current study used only traditional crowding stimuli, with no additional stimuli either between the target and flankers (Vickery et al., 2009) or beyond the first set of flankers (Manassi et al., 2013). In general, large EoIs, such as those reported here, constrain current models of crowding, as they would seem to require longer lateral connections in the cortex, more extended cortical feedback loops, reduced attentional resolution, or more extended grouping mechanisms.

Implications for proposed explanations for crowding

According to Bouma's Rule, the EoIs for crowding measured using similar targets and flankers extend to approximately 0.5 of the retinal eccentricity of the target, which corresponds to an extent of approximately 6 mm of V1 at any given eccentricity (Tripathy & Levi, 1994; Pelli, 2008; Pelli & Tillman, 2008). Therefore, one proposed explanation for crowding is that it reflects a cortical constraint on individuation. The current findings pose several problems for such an explanation. When the stimulus duration was varied in Experiment 1, the average of the EoIs at 10° eccentricity ranged from 2.8° to 6.6° , yielding a range of Bouma's constants from 0.28 to 0.66 and corresponding cortical extents from 4.1 mm to 8.5 mm, as estimated from Equation 3 in Pelli (2008). The largest

EoI we measured was for observer DR for a stimulus duration of 27 ms; her EoI of 7.2° would correspond to a cortical extent of 9.0 mm. These cortical distances are beyond the upper limit for the reported extent of horizontal connections in primary visual cortex. In addition, the EoIs for observer DR were reduced in Experiment 2, after extended practice. Any hard-wired cortical explanation for the EoI would have difficulty accounting for the effects of duration and practice on the EoI.

According to the attentional hypothesis discussed in the Introduction, the resolution of attention places a constraint on individuation that results in crowding (He et al., 1996; Intriligator & Cavanagh, 2001). If crowding reflects the spatial resolution of attention, then the current findings suggest that attentional resolution changes with the duration of the stimulus in the crowding task, consistent with the zoom-lens metaphor proposed for attention (Eriksen & St. James, 1986). Intriligator and Cavanagh (2001) determined that attentional access to individual items should be possible when about 60 items are laid out within the central 30° of the visual field. The current study suggests that the number of items that can be individually accessed would be much fewer when the stimulus presentation is brief.

However, no current crowding proposal can account readily for the saturation in the EoI size in Figures 3 and 4 for durations below 27 to 70 ms. Because the unflanked performance was equated in all stimulus durations by adjusting the contrast and/or the size of the target, the deviation from log linearity at the shortest duration cannot be attributed to a difference in visibility. One possible explanation for this deviation is that crowding follows an earlier site of temporal integration such that stimuli briefer than a certain duration, equated for visibility, have equivalent neural responses. Specifically, durations less than 50 to 70 ms having equal visibility all give rise to equivalent neural responses at stages following the temporal integration.

Keywords: crowding, peripheral vision, spatial vision, temporal vision, lateral interactions

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Footnote

¹ Figure 2 in the pdf version of Danilova and Bondarko (2007) is Figure 3 in the html version of this article.

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