Contour interaction under photopic and scotopic conditions

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In the present study, we asked whether contour interaction undergoes significant changes for different luminance levels in the central and peripheral visual field. This study included nine normal observers at two laboratories (five at Palacky University Olomouc, Czech Republic and four at the University of Houston, USA). Observers viewed a randomly selected Sloan letter surrounded by four equally spaced bars for several separations measured edge-to-edge in min arc. Stimuli were viewed foveally under photopic and mesopic luminances and between 5° and 12° peripherally for four different background luminances of the display monitors, corresponding to photopic, mesopic, scotopic, and dim scotopic levels. The extent of the contour interaction in the fovea is approximately 20 times smaller than in the periphery. Whereas the magnitude of foveal contour interaction markedly decreases with decreasing luminance, no consistent luminance-induced change occurs in peripheral contour interaction. The extent of contour interaction does not scale with the size of the target letter, either in the fovea or peripherally. The results support a neural origin of contour interaction consistent with the properties of center-surround antagonism.

Introduction

Contour interaction is a reduction of visual resolution or an impairment of single-letter identification in the presence of nearby flanking contours (Flom, 1991; Flom, Weymouth, & Kahneman, 1963; Takahashi, 1968). If the flanking stimuli are not simple bar targets, but are more similar to the acuity target (e.g., a central letter target surrounded by other letters), the more general crowding phenomenon is observed (Flom, 1991; Flom, Weymouth, & Kahneman, 1963). It has been proposed that contour interaction contributes to the crowding effect, together with unstable and imprecise fixational eye movements and inaccurate attention (Flom, 1991). Both contour interaction and crowding can be characterized by a lateral *extent* (or critical spacing), within which the identification of acuity targets is reduced, and by the *magnitude* of this reduction. The lateral extent represents the angular distance at which the surrounding flankers begin to produce a criterion degradation of visual performance. The magnitude of contour interaction or crowding can be defined as the maximal decrease in visual performance compared to the condition with no flanking targets. The distance (separation) between the flankers and target stimulus is often defined from the center of the stimulus to the center of the flanker, particularly for peripheral crowding (center-to-center separation; e.g., Bouma, 1970; Toet & Levi, 1992; Tripathy & Cavanagh, 2002), whereas the flanker-to-target distance for contour interaction is defined more frequently from the edge of the stimulus to the innermost edge of the flanking target (edge-to-edge separation; e.g., Bedell et al., 2013; Danilova & Bondarko, 2007; Flom, Weymouth, & Kahneman, 1963; Siderov, Waugh, & Bedell, 2014; Takahashi, 1968).

A main goal of many studies of crowding or contour interaction is to quantify precisely the lateral extent and magnitude and to explain the basis of these effects. The extent of contour interaction does not scale with the

target size if the location of the target remains unchanged (for contour interaction see, e.g., Danilova & Bondarko, 2007; Siderov, Waugh, & Bedell, 2013; Simunovic & Calver, 2004; for crowding, e.g., Pelli, Palomares, & Majaj, 2004, Tripathy & Cavanagh, 2002). In peripheral viewing, the contrast of the stimulus does not change the extent of crowding, provided the contrast of the target and distractors are matched (Kooi, Toet, Tripathy, & Levi, 1994; Rashal & Yeshurun, 2014). Similar observations were reported for foveal contour interaction (Siderov et al., 2013). With an increasingly peripheral eccentricity of the target, the extent of contour interaction or crowding increases. Bouma (1970) reported that the extent of crowding is roughly 0.5 times the target eccentricity (for a detailed review see Pelli & Tillman, 2008). Recent work indicates that the presence of flankers outside Bouma's "window" can markedly influence the effect of flankers within the window (e.g., Herzog & Manassi, 2015). However, when peripheral crowding and contour interaction are compared, contour interaction has a more limited extent (e.g., compare Levi, Hariharan, & Klein, 2002, and Wolford & Chambers, 1984, for contour interaction vs. Chung, Levi & Legge, 2001, Pelli et al., 2004; and Tripathy & Cavanagh, 2002 for crowding). A direct comparison between peripheral crowding and contour interaction also shows a smaller magnitude of contour interaction (Marten-Ellis & Bedell, 2015).

The majority of previous studies have investigated crowding or contour interaction under photopic conditions; significantly fewer have done so for mesopic or scotopic luminance levels (Bedell et al., 2013; Matteucci, Maraini, & Peralta, 1963; Simunovic & Calver, 2004; Takahashi, 1968). Bedell et al. (2013) and Takahashi (1968) reported that the magnitude of foveal contour interaction decreases systematically as the stimulus and background luminance of the acuity target are reduced. A similar result was obtained by Matteucci et al. (1963) for crowding in amblyopic eyes. On the other hand, Bedell et al. (2013) showed that the extent of contour interaction remains more or less constant over a 3-log unit range of foveal luminances. The systematic reduction in magnitude and the approximately constant extent of foveal contour interaction as luminance decreases is analogous to the luminance-dependent properties of the antagonistic receptive-field surround of neurons in the retina (Barlow, Fitzhugh, & Kuffler, 1957; Cleland & Enroth-Cugell, 1968; Derrington & Lennie, 1982; Muller & Dacheux, 1997; Peichl & Wässle, 1983; Rodieck & Stone, 1965) and the lateral-geniculate nucleus (Kaplan, Marcus, & So, 1979; Ramoa, Freeman, & Macy, 1985; Virsu, Lee, & Creutzfeldt, 1977; Wróbel, 1981), consistent with a neural rather than physical origin (Hess, Dakin & Kapoor, 2000) of the contour-interaction effect.

Only one previous study (Simunovic & Calver, 2004) assessed peripheral contour interaction using targets of scotopic luminance. For Landolt C targets presented at a luminance of 0.001 cd/m^2 and an eccentricity of 10°, Simunovic & Calver (2004) reported that the extent of scotopic contour interaction does not scale with the size of the acuity target. These authors also concluded that the spatial extent of contour interaction for their scotopic targets was significantly less (about 0.6°) than the extent of crowding reported for photopic viewing at a similar eccentricity (e.g., Bouma, 1970; Tripathy & Cavanagh, 2002). This counter-intuitive conclusion—that the extent of peripheral contour interaction is larger under photopic than scotopic conditions—may have resulted from (in our opinion) Simunovic and Calver's inappropriate comparison of their scotopic results to crowding data from the literature, rather than to the measured extent of photopic contour interaction at the same retinal location. A major goal of our investigation was to provide clarification of this issue.

To do so, the present study compared contour interaction measured foveally and at different retinal eccentricities for targets of photopic, mesopic and scotopic luminance. Similar experiments were conducted concurrently at Palacky University, Olomouc, Czech Republic (PU) and the University of Houston, Houston, USA (UH). The PU experimenters used peripheral targets that were displaced horizontally from the fixation point, whereas a vertical target displacement from fixation was used in the laboratory at UH.

Methods

Observers

A total of nine observers took part in the study. Five trained observers (FP, JL, KK, LM, and PL; two males and three females, age range 25–39 years) participated in the experiment at PU and four (DL, HEB, PV, SME; three males and one female, age range 22–66 years) at UH. Observers were free from ophthalmic pathology or any systematic condition known to affect vision and had normal or corrected-to-normal vision. The research at both universities was conducted in accordance with the tenets of the Declaration of Helsinki, and written informed consent was obtained from each observer before participating.

Stimuli

Dark Sloan letters (C D H K N O R S V Z) were presented one at a time on a white background, either in isolation or surrounded symmetrically by four

flanking bars. The flanking bars had the same contrast, length and stroke width as the central letter. Weber contrasts of the stimuli were −97% at PU and −98% at UH. The stimuli were generated using custom software developed by one of authors (FP) and displayed on a PC monitor. The monitor at PU measured 22 in. diagonally, with $1,680 \times 1,050$ pixel resolution and a background luminance of 208 cd/m^2. A 13-in. monitor was used at UH, with $1,600 \times 900$ pixel resolution and background luminance of 200 cd/m^2. Ambient illumination in both laboratories was dim and produced primarily by luminance from the display monitor. Ambient light was reduced using a dark cloth shroud at PU and by having the observers view the display monitor from inside a blackened box at UH. The exposure duration of each stimulus was 2 s at PU and unlimited at UH.

To vary the luminance of both the stimuli and the background, the observers at PU viewed the computer monitor through calibrated Thorlabs glass neutral density filters (http://www.thorlabs.com). The filters were mounted in a pair of light-tight goggles, which included an opaque shield to occlude the nonviewing eye. An aperture with a horizontally oriented teardrop design of length 18 mm and height 12 mm was located about 40 mm in front of the tested eye to limit the field of view of the tested eye. For peripheral testing conditions, the observers viewed the fixation light through the narrow part of the tear-drop aperture and the target and flanking bars through the wider part of the aperture. At UH, luminance was controlled using calibrated Tiffen neutral density filters (http://tiffen.com/neutral-density/) mounted in a filter holder in front of the tested eye. A 3-mm pinhole controlled the retinal illuminance but was close enough to the eye (~10 mm) that the observers could view simultaneously the test stimuli on the computer monitor and (for nonfoveal testing) the fixation LEDs. As noted above, the unattenuated luminance of the background field under the photopic luminance condition was 208 cd/m^2 at PU and 200 cd/m^2 at UH. The mesopic, scotopic, and dim scotopic background luminances were 0.150 cd/m^2, 0.0014 cd/m^2, and 0.00026 cd/m^2, respectively, at PU and 0.5 cd/m^2, 0.008 cd/m^2, and 0.00036 cd/m^2, respectively, at UH. These luminances represent attenuation of the background and target luminances by 3.1, 5.2, and 5.9 log units at PU and 2.6, 4.4, and 5.7 log units at UH.

Procedure

Testing was performed monocularly, with appropriate refractive correction determined under photopic testing, if needed. The observer identified each presented letter verbally. Stimuli were viewed peripherally under all four luminance conditions and foveally for just the photopic and mesopic luminance levels. Before scotopic and dim scotopic testing began, subjects underwent 45 min of dark adaption.

Measurements using foveal stimuli were done to compare with the results obtained in a previous experiment (Bedell et al., 2013). Two of the observers at PU and all four observers at UH underwent these control measurements. The viewing distance for foveal stimuli was 12 m at PU and, depending on the luminance condition, ranged from 2.0 to 5.5 m at UH.

Observers were asked to fixate on either one or two LEDs during nonfoveal viewing of the stimuli. The center of the stimulus was located in the nasal visual field at angular eccentricities of 6° and 12° from the fixation light at PU and in the inferior visual field at eccentricities of 5° and 10° at UH. Viewing distances for the peripheral measurements were 1.2 m (PU) and 2 m (UH). At PU, both eccentricities (6° and 12°) were tested for the photopic, mesopic, and scotopic luminance conditions. For the dim scotopic luminance condition, only the 12° stimulus eccentricity was used. At UH, all four background luminance conditions were tested at both the 5° and 10° eccentricities. Pilot experiments as well as previously published observations (e.g., Simunovic & Calver, 2004) indicated that perception of the test stimuli rapidly fades in the peripheral low-luminance conditions. To overcome this, the stimuli in the scotopic and dim scotopic conditions at the PU laboratory changed position vertically within a small range of 30 min arc between successive presentations. To prevent fading in the UH laboratory, from one target presentation to the next the observers switched fixation between two LEDs that subtended angles of 11° clockwise and anticlockwise with respect to the vertical meridian.

For each combination of eccentricity and luminance, the size of the stimuli on the computer monitor was adjusted to achieve approximately 80% correct identification responses, when the letters were presented without flanking bars. Percent correct letter identification was then determined in the absence of flanking bars and for several edge-to-edge separations between the letter and the surrounding flanking bars (at least five flanker-to-target separations at the fovea and at least seven for peripheral viewing). Approximately the same angular separations were used for the photopic and mesopic luminance conditions at each eccentricity. Similarly, approximately the same angular separations were tested for the scotopic and dim scotopic luminance conditions at each eccentricity. Details about the letter sizes and separations tested are provided in Table 1. For each observer, percent correct letter identification was determined from a total of at least 100 presentations per viewing condition both at PU and UH. Before any measurements, each observer was

Luminance level	Photopic			Mesopic			Scotopic		Dim scotopic	
Eccentricity (°)	0	6	12	0	6	12	6	12	6	12
PU										
Average letter size (min arc)	3.8	12.8	24.0	16.2	18.3	28.4	67.6	67.6	—	122.1
Minimum gap size (% letter size)	10	10	10	3	7	9	10	10	—	6
Maximum gap size (% letter size)	100	200	200	24	146	172	200	200	—	112
Luminance level	Photopic			Mesopic			Scotopic		Dim scotopic	
Eccentricity (°)	0	5	10	0	5	10	5	10	5	10
UH										
Average letter size (min arc)	3.6	21.2	30.1	8.1	25	30.1	42.2	44.0	80.1	87.0
Minimum gap size (% letter size)	10	10	10	5	9	10	10	10	5	5
Maximum gap size (% letter size)	100	200	200	45	169	200	200	200	88	101

Table 1. Average letter size and minimum and maximum flanker separations (gaps) for each of the luminance condition and eccentricity for two groups of observers. *Notes*: Peripheral data were measured in the nasal visual field at PU and the inferior visual field at UH.

familiarized with the optotypes and the experimental procedure. Practice was provided using the photopic luminance condition with no flankers.

The percentages of correct letter identification, $p(s)$, were considered as a function of the flanker-to-target separation, s, in the form of a cumulative normal density curve with modified range (Tripathy & Cavanagh, 2002) in the form

$$p(s) = \gamma + (1 - \lambda - \gamma) \frac{1}{\sigma\sqrt{2\pi}} \int_{-\infty}^{s} e^{\frac{-(t-s_0)^2}{2\sigma^2}} dt,$$

where e is Euler's number ($e \approx 2.718$), s_0 and σ are the mean and standard error of the cumulative normal density function, and γ and $(1 - \lambda)$ are its lower and upper asymptotes. For all peripheral data, the lower limit γ was set equal to 0.1, i.e. the likelihood of guessing correctly, which is 10%.

To compare the results obtained under the different testing conditions, the *magnitude* of contour interaction is defined as the decrease of the percentage correct from the no-flanker condition (i.e., from the upper limit $1 - \lambda$) to the extrapolated percentage correct at zero edge-to-edge separation, as computed using the fitted curve. Because the value of λ can differ for each condition, the magnitude of contour interaction is expressed as a percentage of the interval (amplitude A) from 0.1 to $(1 - \lambda)$. This definition is independent of the units used to define the edge-to-edge separation; i.e., the calculated magnitude is the same whether the separation is expressed in min arc or as a percentage of the letter size.

The spatial *extent* of contour interaction was defined as the separation at which the percentage of correct responses decreases from $(1 - \lambda)$ to $(1 - e^{-3})$, corresponding to ~0.95 of the above defined magnitude (Figure 1). Tripathy and Cavanagh (2002) defined

the extent as the separation at which the percentage of correct responses decreased to $(1 - e^{-1}) \approx 0.632$ of the fitted curve's amplitude, which can underestimate the extent or even be negative if the curve decreases very slowly. Our modification precludes these effects.

All required basic parameters (i.e., s_0, σ, λ, and γ for foveal data; s_0, σ, and λ for peripheral data), the derived magnitudes and extents of contour interaction, as well as the 95% confidence intervals for each condition were determined from the pooled data within each lab using bootstrapping (Davison & Hinkley, 2003). We considered at least 1000 bootstrap iterations of samples taken with replacement from the original pooled data set. Each sample was equal in size to that of the original data set. The basic curve parameters were fitted using a least-squares criterion (Gauss-Newton numerical method) for each bootstrap sample.
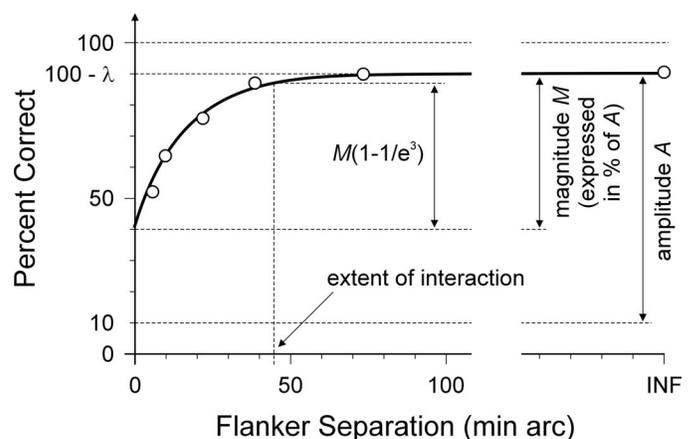

Figure 1. Specification of the amplitude A, magnitude M (expressed as a percentage of A) and extent of contour interaction, derived from the smooth curve (bold solid line) fitted to illustrative experimental data (circles).
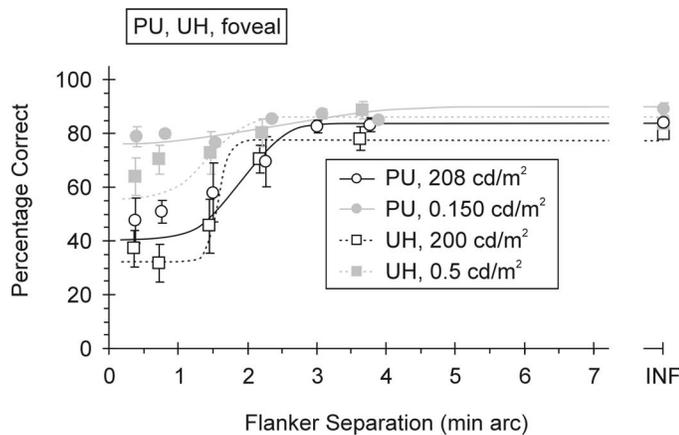
Figure 2. Percentage of correct responses for foveal contour interaction for two luminance levels, averaged separately for the observers at PU and UH and plotted as a function of flanker separation measured edge-to-edge in min arc. Error bars represent ± 1 SE. Data at "INF" on the abscissa represent the unflanked condition.

For each fit, we considered only the first 1000 samples for which the fitting algorithm converged properly. All computations were realized by using MATLAB 6.5 with statistical toolbox.

The statistical analysis of the estimated magnitudes and extents of contour interaction were based on comparing the 95% CI, i.e. with a significance level of 5%. Because of the differences in the testing conditions, the data from the laboratories at PU and UH were analyzed separately.

Results

Figures 2 through 4 present the average values of percentage correct letter identification obtained at PU and UH, plotted as a function of the edge-to-edge flanker-to-target separation expressed in terms of min arc. Each data set was fitted with a smooth curve. The foveal data in Figure 2 reveal lower values of percent correct for photopic than for mesopic luminance conditions when the flanker-to-target separations are small, i.e. the magnitude of foveal contour interaction is greater at a photopic compared to a mesopic luminance level. In contrast to foveal viewing, the peripheral contour interaction data from PU and UH in Figures 3 and 4, respectively, do not show any marked dependence on luminance level. Moreover, the plots seem similar for both eccentricities in each data set.

The extent and magnitude of contour interaction were computed using bootstrapping as described above in Section 2.3. The mean values and 95% CI for the estimates of extent and magnitude of contour interac-
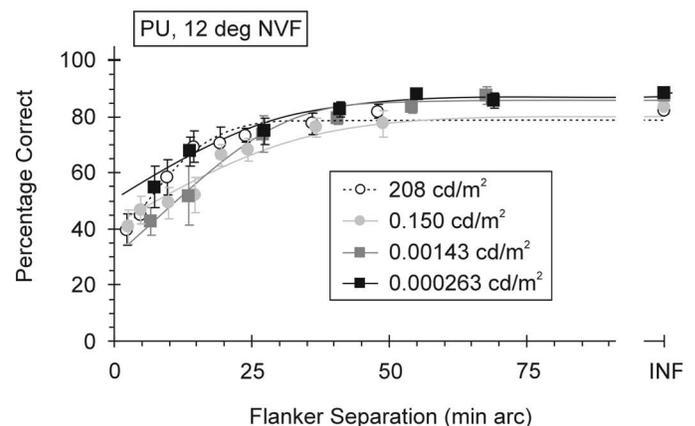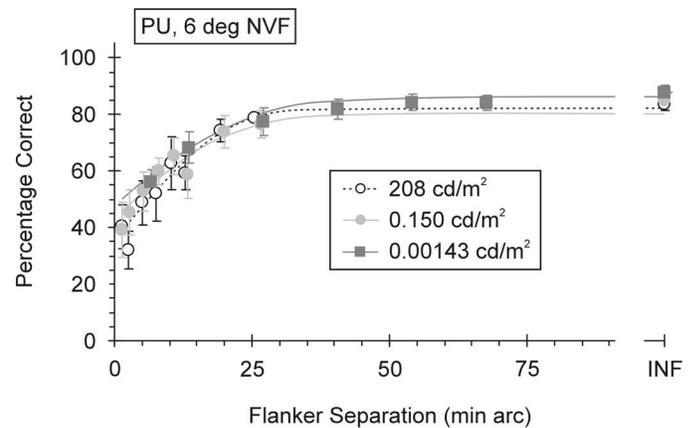

Figure 3. Percentage of correct responses for peripheral contour interaction at 6° (top) and 12° (bottom) eccentricity in the nasal visual field (NVF), averaged for the observers at PU and plotted as a function of flanker edge-to-edge separation in min arc. Error bars represent ± 1 SE. Data at "INF" on the abscissa represent the unflanked condition.

tion at each tested eccentricity are presented in Figures 5, 6, and 7 as a function of luminance.

For foveal viewing, the extent of contour interaction (in min arc) is roughly the same with small insignificant differences between the photopic and mesopic luminance conditions (see the upper panel in Figure 5). In contrast, the magnitude of contour interaction decreases significantly at the fovea when the stimulus and background luminances are reduced (see the lower panel in Figure 5). The weakening of contour interaction at mesopic luminance is most evident at the smaller flanker-to-target separations (see Figure 2).

The estimated mean angular extent of peripheral contour interaction ranges between 22.5 and 110.6 min arc for all of the eccentricities and luminance levels tested (see the upper panels in Figures 6 and 7). The mean PU data yield relatively consistent estimates of extent at the two peripheral eccentricities (from 27.5 to 37.2 min arc at 6° and from 24.3 to 51.6 min arc at 12°).
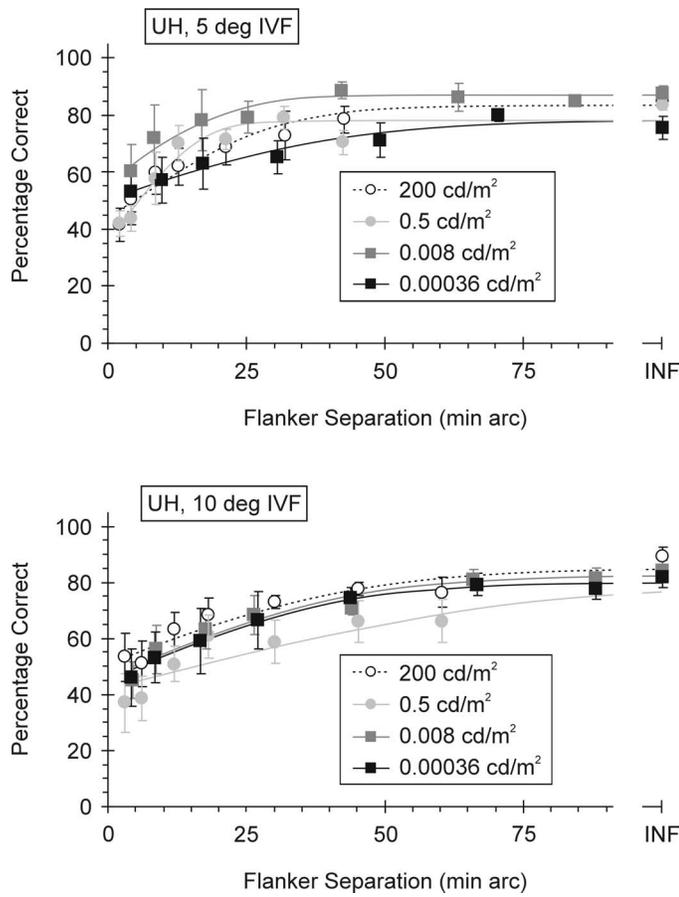
Figure 4. Percentage of correct responses for peripheral contour interaction at 5° (top) and 10° (bottom) eccentricity in the inferior visual field (IVF), averaged for the observers at UH and plotted as a function of flanker edge-to-edge separation in min arc. Error bars represent ±1 *SE*. Data at "INF" on the abscissa represent the unflanked condition.

The mean peripheral extents of contour interaction estimated from the mean UH data range from 22.5 to 68.3 min arc at 5° and from 63.7 to 110.6 min arc at 10°. Comparisons of the confidence intervals do not show any significant differences in extent among conditions in the data from either laboratory. According to these results, there is no marked relationship among eccentricity, luminance, and the extent of contour interaction for the conditions tested in this study.

The magnitude of peripheral contour interaction (lower panels in Figures 6 and 7) does not exhibit the distinct luminance-related reduction, as occurs in foveal viewing (Figure 2; see also Bedell et al., 2013). The comparison of confidence intervals does not show any significant differences in magnitude as a function of either luminance or eccentricity, either in the PU or UH data. Thus, the effect of luminance and eccentricity on the magnitude of peripheral contour interaction seems unimportant.
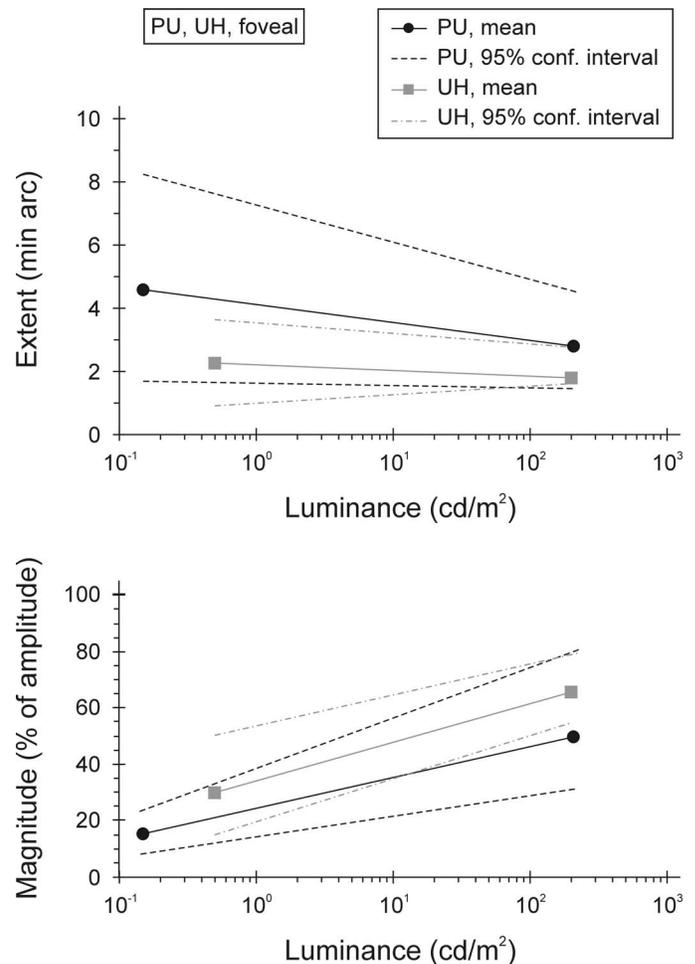

Figure 5. Mean values (symbols and solid lines) and 95% CI (dashed lines) for the extent (top) and magnitude (bottom) of foveal contour interaction for the observers at PU and UH, plotted as a function of luminance.

Discussion

Our results confirm the few previous reports that the magnitude of foveal contour interaction decreases substantially between photopic and mesopic luminances (Bedell et al., 2013; Takahashi, 1968). In contrast, the extent of contour interaction expressed in min arc does not change significantly at the fovea when the stimulus and background luminances are reduced, i.e., as the target letters become bigger (by approximately 2×–4×, in our study). On the other hand, we found similar magnitudes of contour interaction for targets presented in the peripheral visual field at photopic, mesopic, scotopic, and dim scotopic luminances. When compared to the fovea, the extent of peripheral contour interaction is, on average, approximately twenty times larger for targets presented between 5° and 12°. The average extents of contour interaction for stimuli shown at 5°, 6°, 10°, and 12°
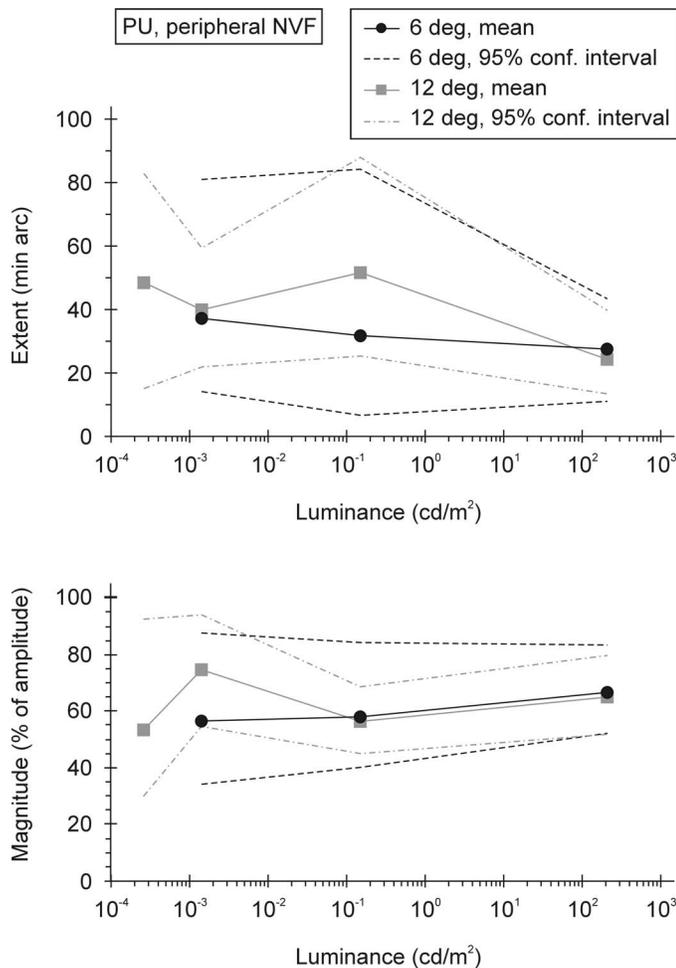
Figure 6. Mean values (symbols and solid lines) and 95% CI (dashed lines) for the extent (top) and magnitude (bottom) of peripheral contour interaction at 6° and 12° in the nasal visual field (NVF) for the observers at PU, plotted as a function of luminance.
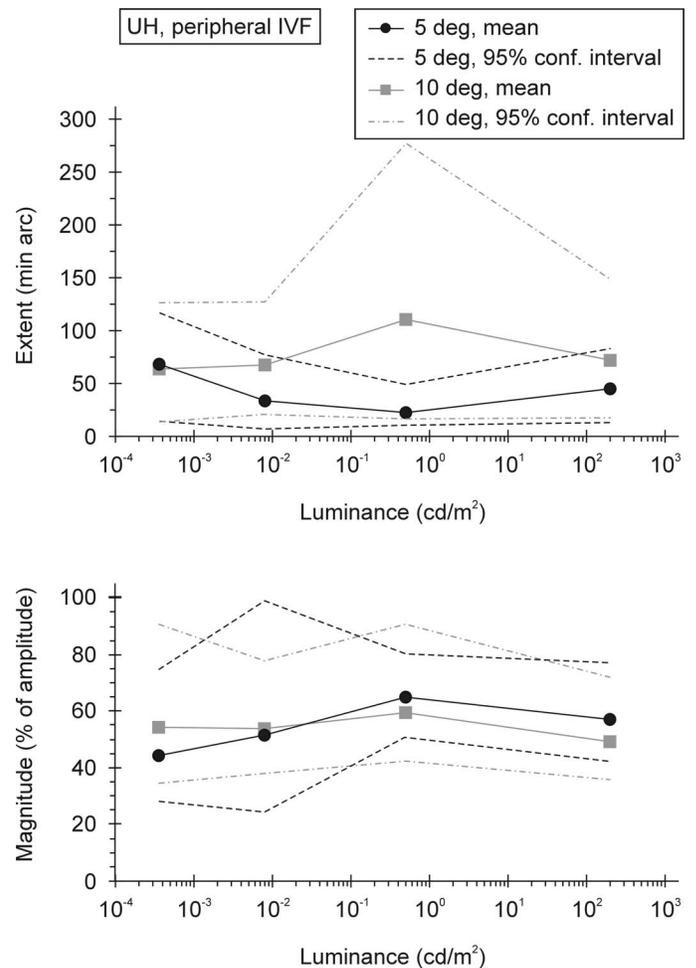
Figure 7. Mean values (symbols and solid lines) and 95% CI (dashed lines) for the extent (top) and magnitude (bottom) of peripheral contour interaction at 5° and 10° in the inferior visual field (IVF) for the observers at UH plotted as a function of luminance.

eccentricities are 42, 32, 78, and 41 min arc, respectively. However, statistical analysis showed no significant influence of eccentricity. The effect of luminance on the extent of peripheral contour interaction also was either insignificant or very small.

As the stimulus and background luminances are reduced, larger letters are required to achieve the fixed criterion value of percent correct letter identification in the absence of any flanking contours. As our results show that the extent of both foveal and peripheral contour interaction (expressed in min arc) exhibits no dependence on the luminance, our study indicates that contour interaction does not scale with the size of the stimulus letter, in agreement with previous studies of contour interaction at the fovea (Bedell et al., 2013; Danilova & Bondarko, 2007; Siderov et al., 2013) and in the periphery (Simunovic & Calver, 2004), as well as with studies of peripheral crowding (Chung et al., 2001; Hariharan, Levi, & Klein, 2005; Pelli et al., 2004;

Tripathy & Cavanagh, 2002). Thus, our results support the contention that, like peripheral crowding, neither foveal nor peripheral contour interaction can be explained on the basis of lateral masking, which would predict that the extent of contour interaction should scale with the target size (Chung et al., 2001; Danilova & Bondarko, 2007; Ehrt & Hess, 2005; Nandy & Tjan, 2007). Moreover, if the extent of contour interaction were to scale with the target size, then the extent expressed as a percentage of the letter size should remain approximately the same. Our results, recomputed in terms of a percentage of the target-letter size, show a mean peripheral extent of contour interaction that varies from 40% to 216% of letter size for the PU data and from 73% to 368% of the letter size for the UH data.

As discussed above, most crowding studies specified the flanker-to-target separation as center-to-center, whereas most contour-interaction studies, including

ours, expressed separation as edge-to-edge. Because the extent of peripheral crowding and contour interaction remain approximately constant across target size only when the appropriate metric (center-to-center and edge-to-edge, respectively) is used to express the flanker-to-target separation (e.g., Tripathy & Cavanagh, 2002; Simunovic & Calver, 2004), the measure of separation appears to be closely linked with the basic mechanism of each phenomenon. This observation suggests, in agreement with other data (Marten-Ellis & Bedell, 2015), that different neural mechanisms underlie peripheral crowding and peripheral contour interaction.

A number of authors suggested that contour interaction results from the antagonistic neural interactions between stimuli that are imaged within a common neural receptive field (Bedell et al., 2013; Danilova & Bondarko, 2007; Flom, Weymouth, & Kahneman, 1963; Latham & Whitaker, 1996; Wolford & Chambers, 1984). Based on psychophysical data that contour interaction persists for dichoptically presented targets and flanking bars (Flom, Heath, & Takashi, 1963), it is assumed that the relevant neural interaction occurs at the lateral-geniculate nucleus or, more likely, in cortical area V1 or later. Some neurophysiological studies showed a significant diminution of surround antagonism in receptive fields at the level of the lateral-geniculate nucleus (Kaplan et al., 1979; Ramoa et al., 1985; Virsu et al., 1977; Wróbel, 1981) under low luminance. Other studies of the lateral-geniculate nucleus and visual cortex found persistence of the antagonistic surround at low luminance levels (Bisti, Clement, Maffei, & Mecacci, 1977; Maffei & Fiorentini, 1972; Wiesel & Hubel, 1966). The apparent disagreement between these reports may be explained by the observation that the surround effect falls off only with respect to a cell's absolute detection threshold, but remains present for suprathreshold conditions (Duffy & Hubel, 2007; Wiesel & Hubel, 1966). This explanation corresponds with our results[1] as elaborated in the following paragraph.

Retinal ganglion and lateral geniculate cells as well as the neurons in area V1 at small eccentricities (up to ~2°) receive the majority of their input from cones, whereas peripheral receptive fields receive both rod and cone inputs, with the contribution of rods rising sharply with eccentricity (Duffy & Hubel, 2007; Wikler, Williams, & Rakic, 1990). Because the cone threshold corresponds to a mesopic light level, the antagonistic mechanism of foveal receptive fields should be diminished at low mesopic luminances and the magnitude of foveal contour interaction should decrease, as we observed (see also Bedell et al., 2013; Takahashi, 1968). On the contrary, as all of the luminances tested in our experiment represent suprathreshold conditions for rods (more than 2 log units above the absolute scotopic

threshold of 10^{-6} cd/m^2), we can suppose that the antagonistic surround of peripheral receptive fields persists for the luminances used in this study. Persistence of the antagonistic receptive field surround as the luminance of a nonfoveal target decreases from photopic to a dim scotopic level would be consistent with the only minor changes in the magnitude of contour interaction that we observed for peripheral viewing.

Whereas the magnitude of surround antagonism is reduced at near-threshold light levels, the basic architecture of lateral geniculate and cortical neural receptive fields, including their diameter, has been reported to remain unchanged during dark adaptation (e.g., Bisti et al., 1977; Duffy & Hubel, 2007; Wiesel & Hubel, 1966). This observation is in agreement with the roughly unchanged extent of contour interaction that we observed for the wide range of foveal and peripheral luminances tested in this study. Moreover, the substantial difference between the foveal and peripheral extent of contour interaction corresponds with properties of the receptive fields in the primary visual cortex, as reported for example by Duffy and Hubel (2007).

According to Bouma (1970), the extent of interaction in crowding should be approximately one half of the tested eccentricity. Hence, Bouma's "law" implies that the extent of crowding should be 2.5°–3° at eccentricities of 5° and 6°, and 5°–6° at eccentricities of 10° and 12°. However, the maximum extent of contour interaction that we observed is on the order of 1.3°. A similar departure from Bouma's law was reported by Wolford and Chambers (1984), who reported that the mean extent of contour interaction was approximately 0.24° at an eccentricity of 2° and 0.8° at an eccentricity of 5°. The differences between the extent of interaction reported by Bouma (1970) and our observations may be attributable to the different interaction effects that were studied—contour interaction in our case and crowding in Bouma's investigation. Comparison of our results with those obtained in studies of peripheral crowding (Chung et al., 2001; Pelli et al., 2004; Tripathy & Cavanagh, 2002) indeed shows that the extent of peripheral crowding is much larger than the extent of contour interaction. For example, Tripathy and Cavanagh (2002) reported that the extent of crowding is about 3° (center-to-center) at an eccentricity 9.2°. If we apply the same definition used by Tripathy and Cavanagh (2002) to define the extent of interaction for eccentricities of 10° and 12°, the mean extent (averaged across subjects) of contour interaction based on our data does not exceed 80 min arc (center-to-center) or 24 min arc (edge-to-edge).

A recent study by Marten-Ellis and Bedell (2015) reported that the extent of contour interaction is approximately 4× smaller than the extent of crowding at 5° in the inferior field. In this study, edge-to-edge separation was used to quantify the flanker-to-target

separations for both types of interaction. Based on the results of Levi, Hariharan and Klein (2002), peripheral contour interaction (i.e., using bar-like flankers) should have an extent of 0.1-fold of eccentricity at 5° and 10°. In contrast, our results show no significant dependence on eccentricity. In the Levi, Hariharan, et al. (2002) study, flanker-to-target separation was measured from the center of the flanker to the center of the adjacent limb of the central letter target. If we consider our results in terms of the separation between the center of the flanker and the center of the adjacent limb of the central letter target, the extents of contour interaction that we measured for different eccentricities should change relatively little, due to the relatively small width of the flanking bars and the letter strokes our stimuli (e.g., the extent of contour interaction in the PU photopic data for 6° and 12° would change from 28 and 24 min arc to 30 and 29 min arc, respectively). Thus, the measure of flanker-to-target separation is not the reason for the difference in extents found by Levi, Hariharan, et al. (2002) and the present study. A relevant factor could be the design of flanking bars and letter strokes. Whereas we used compact bars and letter strokes, both of high contrast, Levi, Hariharan, et al. (2002) constructed their stimuli from more distributed Gabor or Gaussian patches.

The only previous study to investigate contour interaction using scotopic targets reported a *maximum* extent of interaction (edge-to-edge, using Tripathy & Cavanagh's formula to determine the extent) of 0.6°, or 36 min arc, at an eccentricity of 10° (Simunovic & Calver, 2004). The *average* extent reported by Simunovic and Calver (2004) was approximately 0.2°, or 12 min arc. For comparison (using Tripathy's & Cavanagh's definition of extent), we obtained an average scotopic extent of 12 min arc at 10° and 16 min arc at 12° eccentricity. Simunovic and Calver (2004) compared their scotopic results to data from studies of photopic peripheral crowding (see above) and concluded that the extent of interaction is substantially reduced by dark adaptation. Our data show that the extent of peripheral contour interaction exhibits little variation over a 6-log unit change in background luminance, suggesting that the difference in extent noted by Simunovic and Calver (2004) resulted from an unfortunate comparison between (scotopic) contour interaction and (photopic) crowding.

Keywords: contour interaction, crowding effect, luminance, scotopic, photopic, mesopic, peripheral vision

Acknowledgments

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Footnote

[1] An alternative explanation is that the mechanism of contour interaction differs in the fovea and periphery. For example, whereas foveal contour interaction may result from the antagonistic receptive-field mechanism discussed above, the unchanged magnitude of peripheral contour interaction as luminance decreases could signify the operation of a different, or an auxiliary mechanism.

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