Title: The mechanism of contour interaction differs in the fovea and periphery

Short title: Contour interaction differs in fovea and periphery

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Abstract

Significance: Both foveal and peripheral contour interaction are based on, as yet, unexplained neural mechanisms. Our results show that, unlike foveal contour interaction, peripheral contour interaction cannot be explained on the basis of the antagonistic structure of neural receptive fields.

Purpose: Foveal contour interaction is markedly reduced for mesopic compared to photopic targets. This finding is consistent with an explanation based on the antagonistic structure of neural receptive fields. However, no reduction was found for low-luminance targets in the periphery, possibly because the luminances used previously remained substantially above peripheral scotopic detection thresholds. In this study, we compared foveal and peripheral contour interaction for long-wavelength photopic and mesopic targets, which would be expected to significantly elevate the peripheral retinal detection threshold.

Methods: Five normal observers viewed a randomly selected Sloan letter surrounded by four flanking bars at several edge-to-edge separations (min arc). Photopic and mesopic stimuli were viewed foveally and at 6 deg peripherally through a selective red filter that ensured mesopic targets were within 1 log unit of detection threshold at both retinal locations.

Results: Whereas the magnitude of foveal contour interaction was substantially less at mesopic compared to photopic luminance (20% vs. 46% reduction of percent correct, on average), no significant difference was observed in peripheral contour interaction, which had average mesopic and photopic magnitudes of 38% and 40%. Moreover, confusion matrices representing photopic and mesopic contour interaction differed in the fovea, but not in the periphery. The extent of contour interaction did not change with luminance at either retinal location.

Conclusions: Our results indicate that although the characteristics of foveal contour interaction can be accounted for by the antagonistic structure of neural receptive fields, the same mechanism is not compatible with the characteristics of peripheral contour interaction.

Keywords contour interaction, foveal vision, peripheral vision, photopic, mesopic

The reduction of visual resolution or impairment of letter identification due to the presence of nearby flankers (bars) is known as contour interaction.[1-3] Replacing simple flanking bars with flankers more similar to the observed target (e.g., a central letter surrounded by other letters), results in crowding.[1,2] Both effects can be characterized by a lateral extent and magnitude. The lateral extent represents the largest angular separation between the flankers and central target at which a degradation of visual performance occurs. The magnitude is defined as the maximum reduction of visual performance, compared to the unflanked condition.

The mechanisms responsible for contour interaction remain a subject of study. Although other explanations have been advanced, numerous authors have proposed that the antagonistic structure of the neural receptive fields in the visual pathway is responsible for foveal contour interaction.[2,4-8] As contour interaction persists during dichoptic presentation of the target and flanking bars,[9,10] the relevant neural interactions must occur at the lateral-geniculate nucleus or, more likely, in cortical area V1 or later.

Surround antagonism within receptive fields of cells at the level of the lateral geniculate nucleus and cortex shows a significant diminution at low luminance,[11-14] especially close to the cells' absolute detection threshold.[15,16] Such a result is consistent with psychophysical data showing a reduction in magnitude of foveal contour interaction[3-5] and foveal crowding[17,18] at mesopic compared to photopic luminance, i.e., as surround antagonism is reduced, contour interaction becomes weaker. In most of these studies, the target size increased as the luminance was reduced to maintain performance under non-flanked target separation conditions. However, experiments employing low and high contrast acuity targets[19,20] demonstrated that a change in letter size *per se* does not explain the reduced magnitude of the foveal contour interaction.

Unlike the results obtained in the fovea, the magnitude of peripheral contour interaction was found to be approximately the same for targets of high and low luminance,[5] which would appear to be contrary to a possible explanation based on surround-antagonism. Nevertheless, Musilová et al.[5] cautioned that peripheral contour interaction still may be accounted for by surround antagonism. Peripheral receptive fields receive both rod and cone inputs and the lowest (scotopic) luminance used by Musilová et al.[5] was more than 2 log units above the rod absolute threshold. Surround antagonism has been shown to persist at this supra-threshold scotopic luminance level,[15,16] which Musilová et al. suggested could account for the unaltered magnitude of peripheral contour interaction in their study. An alternative explanation for the apparent luminance independence of peripheral contour interaction (also suggested by Musilová et al.[5]) is that contour interaction is mediated primarily by different mechanisms in the fovea and retinal periphery.

The purpose of this study was to test the two alternatives suggested by Musilová et al.[5], by comparing peripheral contour interaction for a photopic luminance level to the results obtained at a mesopic luminance that is not far removed from the peripheral detection threshold. One way to achieve this goal is to present mesopic stimuli that only or predominantly elicit cone signals. As the spectral sensitivity of rods is less than or equal to that of cones for wavelengths longer than 600 nm,[21-23] rod stimulation can be minimized using a suitable spectral (red) filter. When cone signals represent the predominant contribution to peripheral receptive fields, we hypothesized that surround antagonism should be reduced, both at the fovea and in the periphery, for targets of mesopic luminance. If both foveal and peripheral contour interaction are mediated by surround antagonism, then a decrease in the magnitude of interaction should be observed for mesopic peripheral and foveal long wavelength targets. However, if only the magnitude of foveal contour interaction is reduced for mesopic, long-wavelength targets, as is the case for spectrally broadband targets,[3-5] then the mechanisms that result in contour interaction likely differ in the fovea and peripherally.

Methods

Observers

Five observers (one male and four females, one experienced, four naïve, age range 25–39 years) participated in the experiment. Observers were free from ophthalmic pathology or any systematic condition known to affect vision and had normal or corrected-to-normal vision without color vision abnormalities, as assessed using Ishihara pseudo-isochromatic plates. The study met the requirements of the institutional research ethics processes. The research 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 bright background, either in isolation or surrounded symmetrically by four flanking bars. The flankers had the same contrast, length, and stroke width as the central letter. Weber contrast of the stimuli was -99%. The stimuli were generated using software developed by author FP and displayed in the center of a 22-inch LCD monitor with a resolution of 1680 x 1050 pixels and a background luminance of 208 cd/m^2. Ambient room illumination was dim and produced primarily by the luminance of the monitor. A dark cloth shroud placed over the observer's head was used to reduce this ambient light. The exposure duration of each stimulus presentation was 2 s.

In order to minimize rod activity, stimuli were viewed through a red filter that transmitted only wavelengths greater than 600 nm (see Fig. 1). Testing was performed at two luminance levels of the background field, photopic and mesopic. The luminance was measured by a LMT L 1003 luminance meter (http://www.lmt.de). The photopic luminance was 7.8 cd/m^2 and corresponded to viewing through the red filter alone. The mesopic luminance of the background field was 0.06 cd/m^2 and was achieved by combining the red filter with an additional calibrated Thorlabs glass neutral density filter (http://www.thorlabs.com) with a nominal value 2 ND. All filters were mounted in light-tight goggles, which included an opaque shield to occlude the non-viewing eye. An aperture with a horizontally oriented teardrop design of length 18 mm and maximum height 12 mm was located about 40 mm in front of the tested eye to limit its field of view. For peripheral testing, the observers viewed the fixation light (a small LED) through the narrow part of the tear-drop aperture and the letter target and flanking bars through the wider part of the aperture.

Figure 1 about here

Procedures

Testing was performed monocularly, with appropriate refractive correction as determined under photopic conditions using subjective tests (most plus sphere and Jackson cross-cylinder resulting in best visual acuity), if needed. The observer identified each presented letter verbally. The presented letter and observer's response were recorded. Stimuli were viewed foveally and peripherally under both photopic and mesopic luminance conditions. Before mesopic testing the observers underwent at least 30 min of dark adaptation. The viewing distance was 12 m for foveal testing and 1.2 m for peripheral testing. Observers were asked to fixate a red LED during non-foveal viewing of the stimuli; the center of the stimulus was located in the nasal visual field at an angular eccentricity 6 deg from the fixation light.

For each observer and combination of experimental conditions of eccentricity and luminance, the size of the stimuli on the computer monitor was adjusted to achieve approximately 80% correct identification when the letters were presented without flanking bars. Percent correct letter identification was then determined in the absence of flanking bars and for several separations between the letter target and the surrounding flanking bars (five at the fovea and seven for peripheral viewing) from a total of 100 presentations of the stimuli per viewing condition. Target-to-flanker separations were measured in min arc from the innermost edge of the flanking bar to the outer edge of the central target (edge-to-edge), in accordance with several previous studies of foveal and peripheral contour interaction.[2,4-6,20] Approximately the same angular separations in terms of min arc were used for both luminance conditions at each eccentricity. Average letter sizes and the range of target-to-flanker separations tested are shown in Table 1. Before any measurements, each observer was familiarized with the Sloan optotypes and the experimental procedure. Sufficient practice was provided using the photopic luminance without flankers to obtain consistent results.

Table 1 about here

We verified that the elevation of the mesopic stimulus background luminance above the detection threshold was roughly comparable (within 1 log unit) between the fovea and periphery. For this purpose, the observer viewed unflanked letter stimuli either at the fovea or peripherally through the combination of the red and 2-ND filter after at least 30 min of dark adaptation. The size of the letter stimuli was the same as that used during testing at the mesopic luminance condition for each eccentricity. An additional neutral density filter was added to decrease the luminance to 0.006 cd/m^2 (i.e., 1 log unit). Under these test conditions, none of the observers could distinguish the letter stimulus from the background for either retinal location.

Data analysis

The effects of separation and luminance were analysed together using a two-factor repeated-measures analysis of variance (ANOVA); ANOVA was applied separately for foveal and peripheral data. The significance level was set at 0.05. ANOVAs were performed using STATISTICA 13.0 (StatSoft, Tulsa, OK, USA). Data in the text are presented as mean [standard deviation].

Previous studies reported that letter confusions in contour interaction studies (i.e. patterns in reported letters seen) can differ between flanked (i.e. with contours) and unflanked (i.e. without contours) testing conditions.[4,24,25] Such differences may suggest differences in the underlying process. Thus, letter-confusion matrices were constructed to compare observers' responses to targets presented under photopic and mesopic luminances for two of the experimental conditions: the second smallest target-to-flanker separation, i.e., about 1 min arc foveally and 2.8 min arc peripherally, and the unflanked condition. These separations were chosen because they represent the conditions in which the measured performance of foveal and peripheral contour interaction was minimal for most of the subjects. Each confusion matrix was based on 500 letter presentations for each of the viewing conditions and constructed using the sum of letter responses across the 5 observers. In each matrix, the rows specify the letter that was presented and the columns indicate the counts of the aggregate responses per row corresponding to each of the 10 possible Sloan letters. The matrices were compared row by row; however only cells with erroneous responses were considered (i.e., diagonal cells were excluded). Further, if no data appeared in the cells of a given column when the equivalent rows of two matrices were compared, then these cells were omitted from the analysis. Thus, the comparison between pairs of matrices consisted of an analysis of ten pairs of rows, each with a maximal length of 9 cells. Each pair of response matrices was compared by a chi-square test of independence. Due to the relatively low number of many letter miscalls, the chi-square *P* value was estimated by Monte Carlo simulation based on 10,000 sampled tables.[26] The analysis was performed using MS Excel and free add-in software for MS Excel described in Slezák et al.[26] The significance level was set at 0.05.[*] A significant result indicates that the proportions of errors are different between corresponding rows of the two matrices. The matrices were considered to be different if the test was significant at least for one pair of rows. Because the number of errors was low for the unflanked condition, only the matrices for flanked targets were compared. For graphical presentation of the matrices, the counts in each row were transformed to proportions so that the sum of the proportions (including diagonal cells) in each row was equal to 1.

Results

[*] Note that implementation of a Holm-Bonferroni correction for multiple comparisons, i.e., between the ten pairs of rows in the two matrices, would increase the *P* values reported below in the Results by approximately a factor of 10.

Percent correct letter identification for each combination of luminance and eccentricity, averaged across the 5 observers, is presented in Fig. 2 as a function of the edge-to-edge separation between the flanking bars and central target, measured in min arc. An example of individual data of two naïve observers are presented in Fig. 3. The top panels show foveal and the bottom peripheral data. Contour interaction is revealed by a decrease in the percentage of correct responses for flanking-bar-to-target separations less than approximately 3 min arc in the fovea and approximately 30 min arc in the periphery and is confirmed by a significant main effect of separation in both the foveal ($F_{5, 20} = 25.93$, $P < .0001$) and peripheral ($F_{7, 28} = 12.54$, $P < .0001$) data. As the luminance was reduced, the angular size of the target letters had to be increased, from 4.9 to 13.9 min arc in the fovea and from 14.6 to 26.4 min arc at an eccentricity of 6 deg. However, at both locations in the visual field, the *extent* of contour interaction did not change markedly as a function of the luminance or letter size.

On the other hand, the *magnitude* of foveal contour interaction shows a strong dependence on luminance, which is represented by a marked difference in the percentage of correct responses for photopic vs. mesopic targets at small flanker-to-letter separations (see the top panels of Fig. 2 and 3). Specifically, the magnitude of foveal contour interaction decreases on average from 46% with a standard deviation of 15% for photopic targets to 20% with a standard deviation of 14% for mesopic targets. The reduction in the magnitude of foveal interaction at mesopic luminance is confirmed by a significant interaction between flanker separation and luminance ($F_{5, 20} = 5.63$, $P = .002$). In addition, the main effect of luminance on foveal contour interaction was marginally significant ($F_{1, 4} = 7.59$, $P = .051$). In contrast, the magnitude of peripheral contour interaction is virtually the same for both luminance levels (40% with a standard deviation of 23% and 38% with a standard deviation of 14% for the photopic and mesopic conditions, respectively). Statistical analysis indicates neither a significant main effect of luminance nor a significant interaction between luminance and flanker separation in the peripheral results ($F_{1, 4}$ = 0.117, P = .75 and $F_{7, 28}$ = .166, P = .99).

Figure 2 about here

Figure 3 about here

Letter-confusion matrices (see *Data Analysis* section) based on the aggregated data of the 5 observers are presented in Fig. 4 for flanker separations of 1 min arc (at the fovea), 2.8 min arc (in the periphery), and for the foveal and peripheral unflanked conditions. The Figure includes separate matrices for letters of photopic and mesopic luminance. As expected, the highest values generally lie on the main diagonal of each matrix, which indicates the proportion of trials on which each letter was reported correctly. Values off the main diagonal represent the proportion of letter confusions per row (each corresponding to a different letter target), and are color coded from light blue to pink to represent low vs. high proportions of letter confusions. The blank cells indicate combinations of presented letters and responses that did not occur.

Figure 4 about here

Only a few differences are apparent between the foveal and peripheral confusion matrices for the unflanked photopic vs. mesopic conditions. For example, responses of "O" when the letter D was presented increase markedly under mesopic luminance, both foveally and peripherally (compare row 2 in the top and bottom pairs of right hand matrices in Fig. 4). In addition, the legibility (indicated by the values on the main diagonal of each confusion matrix) of the unflanked letter S is lower in the fovea than peripherally (compare row 8 in the top two vs. the bottom two right hand matrices in Fig. 4). Finally, some letter confusions occur much more frequently at the fovea than peripherally, e.g., responses of "N" for R (especially under mesopic luminance) and "D" for S (compare rows 7 and 8 in the top two vs. the bottom two right hand matrices in Fig. 4). Differences in the legibility and letter confusions made in foveal and peripheral vision have been reported previously.[27]

The confusion matrices for letters with nearby flanking bars indicate more letter confusions than the matrices for unflanked letters, in accordance with the reduction of correct responses caused by the presence of contour interaction (compare the left and right hand matrices in Fig. 4). The number of confusions in the mesopic foveal flanked condition is fewer than in the photopic foveal flanked condition and, as reported previously,[4] appears to be intermediate between the numbers of confusions observed at the fovea in the mesopic unflanked and photopic flanked conditions. This outcome corresponds with the reduction in the magnitude of the foveal contour interaction for mesopic, compared to photopic, targets and is supported by statistical comparison of the matrices in the two foveal flanked conditions (significant test for C-rows, P = .0004). Specifically, when the target letter is C, the frequency of reporting “K” is higher and the frequency of reporting ”O” is lower in the photopic compared to the mesopic foveal luminance condition (compare row 1 in the top two right hand matrices in Fig. 4). In contrast, the peripheral photopic and mesopic confusion matrices in the flanked condition are very similar (comparisons were not significant for any row, all P > .08). On the other hand, there are some marked differences between the foveal and peripheral matrices for photopic flanked targets, such as responses of “H” for C and “N” for V, which occur more often at the fovea, and “R” for V, which is more common in the periphery (compare rows 1 and 9 in the top and third right hand matrices in Fig. 4). These specific differences between the foveal and peripheral confusions for flanked letters are not observed for unflanked letters. However, the comparisons between the foveal and peripheral confusion matrices under the different viewing conditions are limited by the relatively small number of trials that contribute to each row (average = 50).

Discussion

This study compared foveal and peripheral contour interaction for targets of photopic and mesopic luminance. Rod stimulation, and therefore the difference between foveal and peripheral luminance thresholds, was substantially reduced in our experiment by viewing the letter targets and flanking bars through a red filter with suitable spectral characteristics. Our results confirm the previously reported decrease in the magnitude of foveal contour interaction for targets of mesopic compared to photopic luminance.[3-5] As reported also in these previous studies, a reduction in foveal luminance resulted in little or no change in the extent of contour interaction (Bedell et al.[4] indicated an extent of approximately 3 - 4.5 min arc both photopically and mesopically; for different sets of data, Musilová et al.[5] showed extents of approximately 2 min arc photopically and mesopically and 3.5 min arc photopically vs. 4.3 min arc mesopically). Indeed, the extent of both foveal and peripheral contour interaction that is indicated by our data agrees well with previously published results.[4,5] As only cones are located in the fovea, the results that we obtained foveally in the presence of a red filter could be anticipated on the basis of previous studies and, essentially, represent a control condition. Our observation that both the magnitude and extent of peripheral contour interaction are the same for photopic and mesopic stimuli agrees with the results reported by Musilová et al.[5] for a wider range of peripheral luminances. However, unlike the stimuli used by Musilová et al.,[5] the red filter used in the current experiment ensured that the luminance of the peripheral (as well as foveal) mesopic targets was no more than 1 log unit above their detection threshold.

As luminance is reduced, the size of the target letters has to become bigger (by approximately 3x in the fovea and 2x at 6 deg in the periphery) to maintain the percentage of correct identification for unflanked letters equal to approximately 80%. Nevertheless, the lateral extent of contour interaction at each tested eccentricity remains approximately unchanged, when expressed in min arc, as the luminance is reduced from a photopic to a mesopic level. This outcome is contrary to an explanation of contour interaction based on lateral masking, which predicts that the extent should scale with the target size.[6,28-30] On the other hand, a constant lateral extent of contour interaction at each tested eccentricity is consistent with an explanation based on a receptive-field model.[6,19,31]

As noted previously, the observed reduction of foveal contour interaction with a decrease in background luminance is consistent with the reported diminution of antagonistic center-surround receptive-field interaction during dark adaptation at the level of the lateral-geniculate-nucleus[11-14] and also as seen in cortical receptive fields.[12] However, some studies indicate that the above-mentioned reduction in antagonistic receptive-field interaction is observed only for stimuli close to the absolute threshold luminance of the recorded cells.[15,16] Similar to the results reported here, Bedell et al.[4] observed a clear reduction in the magnitude of foveal contour interaction from that obtained using photopic stimuli when the target luminance was reduced to between 0.09 to 1.46 cd/m^2, a range of 1.2 log units. Both the foveal and peripheral mesopic targets used in the current experiment had a luminance of 0.06 cd/m^2, which we verified corresponds to 1 log unit or less above the detection threshold at each tested eccentricity. Therefore, if peripheral and foveal contour interaction have the same origin, we would have expected to observe a reduction of contour interaction for peripheral targets under mesopic luminance in the current experiment, even if surround antagonism is reduced only within a limited range above the luminance-detection threshold. However, as no reduction of peripheral contour interaction was observed under the mesopic luminance condition, unlike foveal contour interaction, the underlying mechanism of peripheral contour interaction is inconsistent with a model of inhibition produced by center-surround receptive field antagonism. A possible explanation is that contour interaction in the periphery may be based primarily on the integration or pooling of the flanking bars and target features, either within individual receptive fields or within the focus of attention. Such mechanisms also have been suggested to contribute to peripheral crowding.[32-38] An inappropriate integration of flanking bars and target features would not be expected to vary with the background luminance, resulting in an unchanged extent and magnitude of contour interaction, as we observed.

If both peripheral and foveal contour interaction were mediated by surround antagonism, they should presumably show similar features, i.e., a reduction in magnitude at low luminance. Such a reduction was confirmed in this study for foveal but not peripheral viewing. Further, the confusion matrices representing foveal contour interaction for different luminances are dissimilar, whereas those obtained for different peripheral luminances are similar. We conclude that although the characteristics of foveal contour interaction can be accounted for by the antagonistic structure of neural receptive fields, the same mechanism is not likely to be responsible for peripheral contour interaction.

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Figure legends

Figure 1. Spectral transmittance of the red filter used in this experiment.

Figure 2. Percentage of correct responses for contour-interaction targets presented in the fovea (top) and periphery (bottom) at 6 deg eccentricity in the nasal visual field, averaged for all observers and plotted as a function of flanker-to-target edge-to-edge separation in min arc. Photopic and mesopic luminances of the stimulus background were 7.8 cd/m^2 and 0.06 cd/m^2, respectively. All stimuli were viewed through the red filter with the characteristics shown in Fig. 1. Error bars represent ±1 standard error. Magnitudes of contour interaction, specified as the maximum decrease in percent correct letter identification from the unflanked condition, are shown by the double arrows at the right of each panel. Data at "NF" on the abscissa represent the unflanked (no flanks) condition.

Figure 3. Percentage of correct responses for contour-interaction targets presented in the fovea (top) and periphery (bottom) at 6 deg eccentricity in the nasal visual field for naïve observers NK (left) and AS (right) and plotted as a function of flanker-to-target edge-to-edge separation in min arc. Photopic and mesopic luminances of the stimulus background were 7.8 cd/m^2 and 0.06 cd/m^2, respectively. All stimuli were viewed through the red filter with the characteristics shown in Fig. 1. Data at "NF" on the abscissa represent the unflanked (no flanks) condition.

Figure 4. Letter confusion matrices for foveal and peripheral contour-interaction stimuli at photopic and mesopic luminances (7.8 cd/m^2 and 0.06 cd/m^2, respectively; all viewed through the red filter) without flanking bars (left) and with flanking bars at a separation of 1 min arc (foveally) or 2.8 min arc (peripherally). Each matrix was constructed by computing the proportions of the aggregated responses of all five observers for each of the 10 presented Sloan letters. Blank cells indicate that the specified letter-response combination did not occur. Color coding of the values in the off-diagonal cells indicates relatively low (blue) to high (pink) proportions of the individual letter confusions.

Table 1. Average value (min arc) and standard deviation of letter size and average range of flanker separations for photopic and mesopic luminance conditions and for foveal and peripheral viewing (averaged across all observers).

Luminance level	Photopic		Mesopic	
Eccentricity (deg)	0°	6°	0°	6°
Average letter size	4.9	13.9	14.6	26.4
Standard deviation of letter size (min arc)	0.6	2.7	4.7	3.5
Minimum flanker separation averaged across observers (min arc)	0.5	1.4	0.5	1.4
Maximum flanker separation averaged across observers (min arc)	4.9	27.8	4.9	27.8

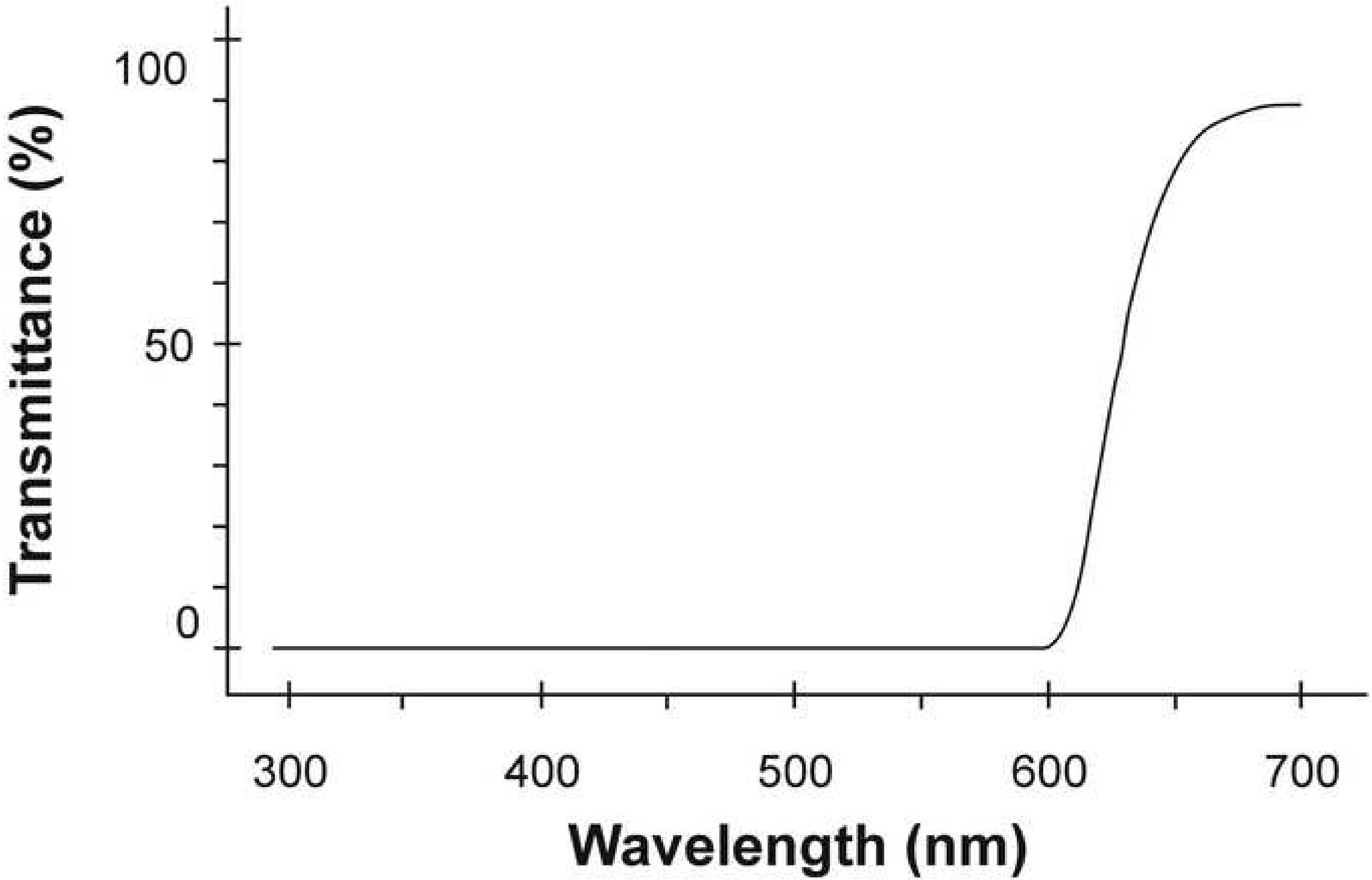

100
50
0
Transmittance (%)
300
400
500
600
700
Wavelength (nm)

Figure 4

Foveal, Photopic, No Flanks

Response (columns); Letter Presented (rows)

	C	D	H	K	N	O	R	S	V	Z
C	0.78	0.04				0.11		0.04		0.02
D	0.03	0.88				0.05	0.03			
H			0.95	0.04	0.02					
K	0.02			0.85	0.02		0.02		0.05	0.05
N		0.05	0.09		0.80	0.02	0.05			
O	0.07	0.11				0.77	0.02	0.02		
R	0.02		0.07	0.04	0.07	0.02	0.76	0.02		
S	0.05	0.19		0.02	0.05	0.02	0.05	0.55		0.07
V									1.00	
Z	0.02							0.09	0.06	0.83

Foveal, Photopic, Separation 1 min arc

Response (columns); Letter Presented (rows)

	C	D	H	K	N	O	R	S	V	Z
C	0.38	0.09	0.10	0.16	0.03	0.03	0.03	0.02	0.03	0.12
D	0.17	0.30	0.04	0.06	0.13	0.11	0.04	0.02	0.09	0.04
H	0.08	0.03	0.36	0.03	0.17	0.08	0.11		0.08	0.06
K	0.02	0.13	0.06	0.50	0.04	0.02	0.13			0.10
N	0.04	0.10	0.18		0.43	0.04	0.04	0.06	0.06	0.04
O	0.08	0.15	0.05	0.10	0.17	0.15	0.07	0.03	0.10	0.08
R	0.07	0.09	0.16	0.05	0.07		0.44	0.05	0.04	0.02
S	0.12	0.18	0.04	0.10	0.02	0.04	0.14	0.14	0.12	0.12
V	0.06	0.04	0.04	0.04	0.22		0.06		0.47	0.06
Z	0.04	0.08	0.08	0.02				0.02	0.04	0.71

Foveal, Mesopic, No Flanks

	C	D	H	K	N	O	R	S	V	Z
C	0.69	0.06				0.24				0.02
D	0.04	0.65				0.29	0.02			
H			0.96		0.02		0.02			
K				0.95			0.02	0.02		
N			0.12	0.03	0.84			0.01		
O	0.14	0.11				0.76				
R		0.04	0.02	0.02	0.20		0.69			0.02
S	0.05	0.10			0.10		0.05	0.71		
V					0.02				0.96	0.02
Z				0.02						0.98

Foveal, Mesopic, Separation 1 min arc

	C	D	H	K	N	O	R	S	V	Z
C	0.60	0.05		0.05	0.05	0.17			0.07	
D	0.13	0.33		0.05	0.03	0.31	0.02		0.05	0.08
H			0.79	0.02	0.10	0.04	0.06			
K			0.02	0.76	0.10	0.02	0.02		0.02	0.06
N		0.02	0.07	0.02	0.82	0.02	0.02		0.02	
O	0.14	0.08		0.06	0.08	0.45			0.06	0.12
R	0.02	0.04	0.15	0.02	0.21		0.42	0.06	0.04	0.04
S	0.15	0.05		0.02	0.02	0.12	0.10	0.37	0.05	0.12
V		0.02	0.02		0.04		0.02	0.02	0.88	
Z	0.04	0.02	0.02	0.04	0.02	0.02				0.83

Peripheral, Photopic, No Flanks

	C	D	H	K	N	O	R	S	V	Z
C	0.69					0.20		0.06		0.06
D		0.89				0.07		0.02		0.02
H		0.02	0.91		0.04		0.02			
K				0.91			0.04	0.02	0.02	
N			0.23		0.70		0.07			
O	0.11	0.09	0.02			0.62	0.09	0.09		
R		0.02	0.11	0.02	0.04		0.74	0.04	0.02	0.02
S		0.02					0.10	0.87		0.02
V									1.00	
Z								0.02	0.02	0.96

Peripheral, Photopic, Separation 2.8 min arc

	C	D	H	K	N	O	R	S	V	Z
C	0.22	0.13		0.15	0.09	0.24	0.09	0.04	0.02	0.02
D	0.13	0.28		0.09	0.13	0.23	0.06	0.09		
H	0.10	0.05	0.52	0.02	0.10	0.13	0.02	0.05		0.03
K	0.08	0.08		0.50	0.10	0.06	0.10	0.02	0.06	0.02
N	0.08	0.12	0.16	0.02	0.43	0.06	0.08			0.06
O	0.06	0.12	0.08	0.06	0.08	0.26	0.14	0.10	0.02	0.08
R		0.04	0.04	0.04	0.11	0.04	0.60	0.07	0.02	0.02
S	0.04	0.06	0.09	0.09	0.04	0.04	0.09	0.54		0.02
V		0.03	0.08	0.08	0.03	0.03	0.20		0.58	
Z		0.13		0.08	0.04	0.06	0.10	0.02	0.04	0.54

Peripheral, Mesopic, No Flanks

	C	D	H	K	N	O	R	S	V	Z
C	0.72	0.04				0.20	0.02	0.02		
D	0.02	0.73				0.20	0.02			0.04
H			0.83	0.04	0.13					
K				0.93			0.02		0.05	
N			0.09	0.02	0.88					
O	0.10	0.12	0.02			0.71	0.02	0.02		
R		0.05	0.14	0.05			0.70	0.05		
S	0.06	0.02		0.02		0.04	0.02	0.83		0.02
V		0.03		0.02	0.03				0.92	
Z										1.00

Peripheral, Mesopic, Separation 2.8 min arc

	C	D	H	K	N	O	R	S	V	Z
C	0.30	0.06	0.02	0.04	0.13	0.21	0.02	0.13	0.04	0.06
D	0.19	0.25	0.06	0.04	0.06	0.31	0.08		0.02	
H	0.03	0.11	0.42	0.05	0.06	0.06	0.16	0.06	0.02	0.03
K	0.05	0.11	0.05	0.45	0.05	0.03	0.13	0.03	0.05	0.05
N	0.02	0.07	0.05	0.05	0.59	0.02	0.07	0.05	0.07	0.02
O	0.04	0.13	0.02	0.09	0.13	0.36	0.02	0.08	0.06	0.08
R	0.02	0.04	0.09	0.09	0.11		0.46	0.17		0.02
S	0.06	0.06	0.02	0.10	0.04	0.04	0.02	0.55		0.10
V	0.02	0.08	0.04	0.04	0.02	0.02	0.12	0.02	0.60	0.06
Z	0.06	0.08	0.04	0.04	0.06	0.08		0.06	0.04	0.53

Color Key: 0.001 – 0.049 | 0.050 – 0.099 | 0.100 – 0.199 | 0.200 – 0.299 | 0.300 – 0.399

Figure 2

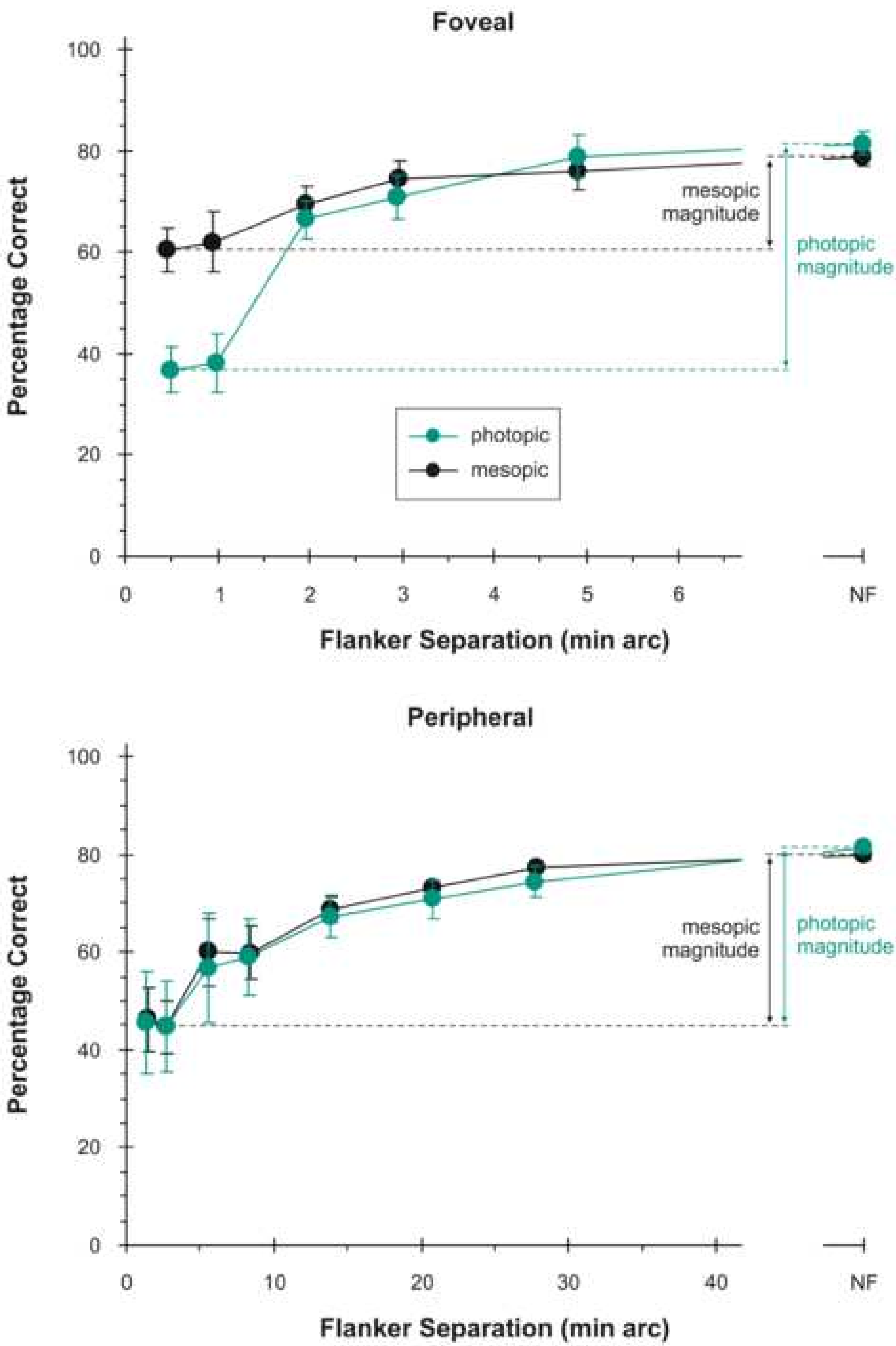
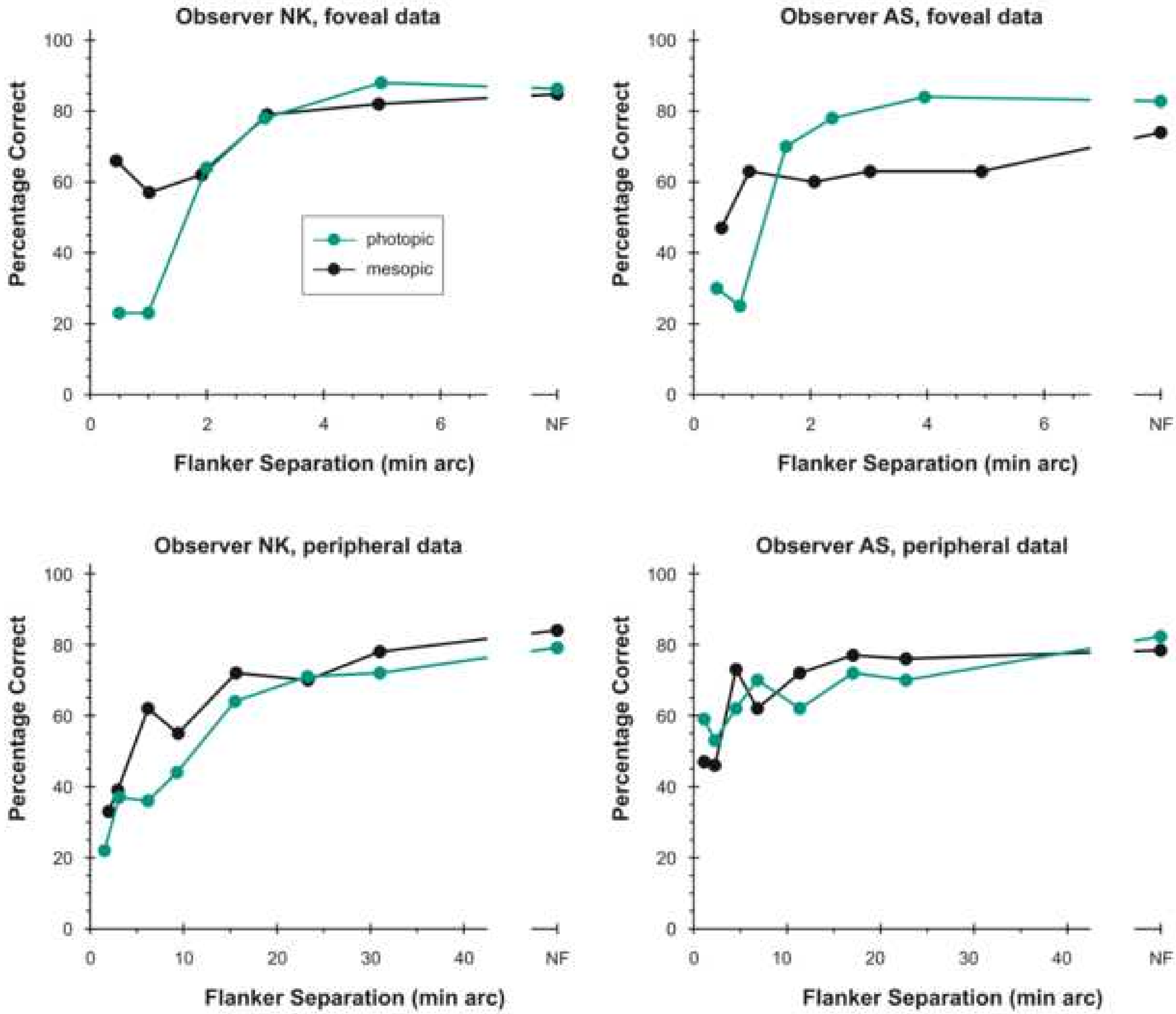

Foveal
100
80
60
40
20
0
Percentage Correct
mesopic
magnitude
photopic
magnitude
photopic
mesopic
0
1
2
3
4
5
6
NF
Flanker Separation (min arc)
Peripheral
100
80
60
40
20
0
Percentage Correct
mesopic
magnitude
photopic
magnitude
0
10
20
30
40
NF
Flanker Separation (min arc)

Figure 3


Observer NK, foveal data
Observer AS, foveal data
Observer NK, peripheral data
Observer AS, peripheral datal
Percentage Correct
Flanker Separation (min arc)
photopic
mesopic
NF
0
20
40
60
80
100
2
4
6
10
30