Optometry and Vision Science

Changes in Ricco's Area with Background Luminance in the S-cone Pathway
--Manuscript Draft--

Abstract:	Purpose: The area of complete spatial summation (Ricco's area) for achromatic stimuli has previously been shown to decrease with increased background luminance. A popular hypothesis is that such a phenomenon reflects increased centre-surround antagonism within the receptive field of the retinal ganglion cell. We wished to investigate if similar changes in Ricco's area occur with blue background luminance for the S-cone pathway, guided by the knowledge that the retinal ganglion cells with S-cone input do not display S-cone mediated centre-surround antagonism (S+/S-). Methods: Spatial summation functions were measured for four young healthy observers under S-cone pathway isolation by presenting blue test stimuli on a background consisting of intense fixed yellow (600cd/m2) component in combination with a variable blue component (background range: 1.78 - 2.82 log S-Td). Ricco's area was estimated by two-phase regression analysis. Results: All subjects demonstrated a notable decrease in Ricco's area with increasing blue background luminance. On average, Ricco's area decreased in size by 0.39 log units per log unit increase in blue background luminance. Conclusions: The change in Ricco's area with the blue background component is not what one would initially expect given the known organization of S-cone driven cells at the retinal level. Spatial re-organization by the suppressive surround of the receptive fields at a cortical level and a reduction in the contribution from S-cones with the lowest weights in the retinal receptive field periphery are among the possible mechanisms of the summation changes observed. These findings have implications for the design of clinical tests of the S-cone pathway.

Synopsis of manuscript

A decrease in Ricco's area with increasing background luminance under achromatic conditions have previously been attributed to increased centre-surround antagonism in the receptive fields of retinal ganglion cells. Here, we show a decrease in Ricco's area with increasing blue background luminance in the S-cone pathway, despite spatial antagonism of the form S+/S- not having been observed at the retinal level. It is possible that these changes arise at the level of the visual cortex where both spatial and S-cone antagonistic receptive fields are known to exist.

Title for 'OVS Announces'

Changes in Ricco's area with blue background luminance

Changes in Ricco's Area with Background Luminance in the S-cone Pathway

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Short title: Changes in Ricco's Area in the S-cone Pathway

2 tables; 5 figures

ABSTRACT

Purpose. The area of complete spatial summation (Ricco's area) for achromatic stimuli has previously been shown to decrease with increased background luminance. A popular hypothesis is that such a phenomenon reflects increased centre-surround antagonism within the receptive field of the retinal ganglion cell. We wished to investigate if similar changes in Ricco's area occur with blue background luminance for the S-cone pathway, guided by the knowledge that the retinal ganglion cells with S-cone input do not display S-cone mediated centre-surround antagonism (S+/S-). **Methods.** Spatial summation functions were measured for four young healthy observers under S-cone pathway isolation by presenting blue test stimuli on a background consisting of intense fixed yellow ($600cd/m^2$) component in combination with a variable blue component (background range: 1.78 – 2.82 log S-Td). Ricco's area was estimated by two-phase regression analysis. **Results.** All subjects demonstrated a notable decrease in Ricco's area with increasing blue background luminance. On average, Ricco's area decreased in size by 0.39 log units per log unit increase in blue background luminance. **Conclusions.** The change in Ricco's area with the blue background component is not what one would initially expect given the known organization of S-cone driven cells at the retinal level. Spatial re-organization by the suppressive surround of the receptive fields at a cortical level and a reduction in the contribution from S-cones with the lowest weights in the retinal receptive field periphery are among the possible mechanisms of the summation changes observed. These findings have implications for the design of clinical tests of the S-cone pathway.

Key words: spatial summation; background luminance; Ricco's area; S-cone pathway; adaptation perimetry

Ricco's law of spatial summation,[1] states that, for sufficiently small stimuli, stimulus area and intensity are inversely proportional at threshold (*Intensity × Area = k, where k = constant*). During a response to such a stimulus, the visual system is said to be operating under conditions of complete spatial summation. For larger stimuli, the threshold signal response is governed by incomplete levels of spatial summation. The limit to complete spatial summation is known as Ricco's area or the area of complete spatial summation. The schematic in Fig.1 illustrates these concepts.

While the exact physiological basis for Ricco's area is a subject of ongoing debate, it has been found to differ with different experimental conditions including retinal illuminance[2-5] and locus,[6-8] chromatic pathway,[7, 9, 10] the temporal profile of the stimulus[2] and optical correction.[11] Ricco's area has also been shown to increase with age under scotopic conditions[12] but not under photopic conditions for achromatic stimuli or under S-cone selective conditions.[13] Using achromatic stimuli, Barlow[2] and Glezer[4] demonstrated an increase in the achromatic Ricco's area with a decrease in background adaptation level down to scotopic levels. Glezer[4] hypothesised that Ricco's area represented the size of ganglion cell receptive field centre mechanisms, a proposition discussed further by subsequent investigators.[5, 8, 14, 15] Glezer reported that decreased involvement of the receptive field OFF-surround at low adaptation levels caused an enlargement of the effective size of Ricco's area. Davila and Geisler[3] also found that the area of complete spatial summation enlarged under low background adaptation levels and suggested that this was due to a change in the neuron population that detects the stimulus under dark adaptation conditions, namely, an increased contribution from the magnocellular cells with large receptive fields. While it is clear from the studies of Davila and Geisler[3] and Dalimier and Dainty[11] that

optical factors also influence the size of Ricco's area, the presence of a region of complete summation after correction with adaptive optics[11] indicates that it is first and foremost a neural phenomenon.

No study to date has purposefully examined the effect of background luminance on Ricco's area in the S-cone pathway. The S-cone driven ganglion cells, namely small bistratified cells,[16-18] which likely constitute the main route of S-ON signals to the brain, have no identified S-cone antagonistic (S+/S-) centre-surround organization[18] and no such antagonism is known to exist at the pre-LGN level.

In this study, we investigate changes in Ricco's area for different levels of blue background under S-cone isolating conditions. If any previously observed decrease in Ricco's area as a function of background luminance results solely from increased centre-surround antagonism in the retinal receptive field, one could expect Ricco's area to remain constant with increasing blue background luminance in the human S-cone pathway. Any change in the area of complete spatial summation with blue background illumination must owe to some other cause.

Knowledge of the way in which Ricco's area changes with background luminance is important clinically, particularly in the design of psychophysical tests of the visual field for conditions such as glaucoma. Short-Wavelength Automated Perimetry (SWAP), employing blue stimuli superimposed on a yellow adapting field, is used clinically to uncover damage to the S-cone pathway in early glaucoma. However, high response variability with SWAP in glaucoma patients[19] likely limits the performance of the technique in measuring visual field damage. There

is no blue component to the adapting field in SWAP, thus for the isolated S-cone pathway, the task is detection of blue stimuli on a dark background. Felius and Swanson[20] point out that response variability in SWAP may be reduced by increasing S-cone adaptation. If Ricco's area changes with blue background luminance in the S-cone pathway, it may be appropriate to scale the perimetric stimulus size to Ricco's area under the altered conditions, in order to improve the sensitivity of the test to glaucomatous damage.[21, 22]

METHODS

Subjects

Four young healthy subjects ranging in age from 20 to 27 years took part in the experiment, including one of the authors (TR). The right eye was used as the test eye in all cases. Subjects were refracted both centrally and peripherally (at 10 deg), using retinoscopy prior to the experiment. There was no measurable difference in refraction between the central and peripheral location for these subjects. All subjects achieved a best-corrected visual acuity of 6/4 and did not demonstrate any visual field defects (Humphrey HFA II, SITA-Standard, 24-2 strategy; Carl Zeiss Meditec, Dublin, CA, USA). None was found to have any ocular abnormality as determined by an eye examination including binocular indirect fundoscopy. Each subject had clear media. No colour vision defects were found using an Ishihara plate test and a Farnsworth D-15 test. In order to permit high retinal illuminance and to control it throughout the tests, a drop of Tropicamide hydrochloride (1%) was instilled in the test eye. Each pupil measured 8mm in diameter after mydriasis. The pupil diameter remained unchanged throughout the experiment. The refractive error found during the initial refraction was refined subjectively (post-mydriasis) for a working distance of 60cm using full-aperture trial lenses and a peripheral blue sinusoidal

grating stimulus, projected to the same retinal location as the test stimulus. The lens that gave the optimum subjective peripheral acuity was used in all tests for each individual. Only one of the subjects (subject DG) was inexperienced at psychophysical observing, however two extra clinical visual field tests (Humphrey HFA II, SITA-Standard, 24-2 strategy; Carl Zeiss Meditec, Dublin, CA, USA) were performed as a practice session in peripheral spot stimulus detection before the commencement of experiments. Informed consent was obtained from each observer and the study conformed to the tenets of the Declaration of Helsinki. Ethical approval was granted by the University of Ulster research ethics committee.

Apparatus and Stimuli

In order to study the effect of blue background adaptation level on Ricco's area under S-cone isolation conditions, we used Stiles' "two-colour threshold" method[23, 24] whereby a blue background was added to an intense yellow adapting field. The experimental set-up was similar to that previously described by Anderson *et al*[25] and is demonstrated in Fig. 2. Stimuli and the blue background component were generated on the blue gun of a gamma-corrected 21" SONY GDM-F500 monitor (SONY Corp., Tokyo, Japan; Pixel resolution 1280 x 965, frame rate 73Hz) using a Visual Stimulus Generator VSG 2/3 card (Cambridge Research Systems, Rochester, UK). The CIE coordinates of the blue phosphor were x = 0.147, y = 0.07. The monitor was placed at 60cm from the test eye and the screen subtended 37.2 deg. A chin-rest and forehead bar were used to keep the viewing distance constant and to assist better alignment. The yellow adapting field was produced by passing white light from a projection system through a glass long-wavelength pass filter (Schott OG530, 530nm half-height) and a diffuser screen. The spectrum of the yellow component of the background is shown in Fig. 2. CIE coordinates were x

= 0.521, y = 0.474. A luminance level of 600cd/m^2 was employed. This level was chosen after determining threshold-versus-luminance (TvL) functions (see the paragraph below and Fig. 3). A beam splitter (Edmund Optics Ltd, York, UK) angled at 45 deg was used to superimpose the yellow light and the blue light from the monitor. Luminance and chromaticity coordinates were measured before and after each experiment using a calibrated SpectraScan PR-650 Spectra Colorimeter® (Photo Research Inc., Chatsworth, CA, USA) and no variation was found. Stimuli were presented at an eccentricity of 10 deg in the nasal field at a meridian of 175 deg (as shown in Fig. 2). This meridian was specifically chosen so that thresholds for the largest stimulus would not be influenced by the anatomical midline separating the superior and inferior retina. Two increment squares separated vertically by 0.2 degrees and of the same chromaticity as the blue background field served as a fixation target. The size of each stimulus was regularly measured at the monitor surface using a compound magnifier containing a 0.1mm increment graticule scale to more accurately describe the on-screen stimulus size. Blue background components employed in this study ranged from 0cd/m^2 to 2.2cd/m^2. Background luminance levels were subsequently considered in terms of retinal illuminance. In particular, we wished to assess the S-cone quantal catch from the composite background, therefore S-cone retinal illuminance was calculated and expressed in S-cone Trolands (S-Td), where 1 S-Td equates to 1 Troland of an equal-energy white.[26] The blue and yellow light spectra were measured in 4nm steps using the SpectraScan PR650 at the eye position. The calculations are based on the Judd luminosity function[27] and Smith and Pokorny fundamentals.[28] Since we tested retinal locations virtually free from macular pigment, we used modified Smith and Pokorny fundamentals with the macular pigment spectrum removed. The resulting values were corrected for the Stiles-Crawford directional effect using the Le Grand formula.[29] The calculated retinal illuminance in photopic Td and S-Td (for a standard

observer) is shown in Table 1. The increment threshold data were also expressed in S-Td units.

TvL Curves

In order to ensure that S-cone pathway isolation had been achieved, it was necessary to carry out an initial experiment investigating the relationship between detection thresholds for our stimuli and the luminance of the yellow adapting field. TvL functions (increment threshold ΔL versus luminance L) were determined for subject TR. Using the same experimental setup as described above, thresholds were measured for our smallest (-1.22 log deg^2; 0.28 deg diameter) and largest (0.92 log deg^2; 3.25 deg diameter) stimuli using a black (0cm/m^2) background adaptation field and a high (4.5cd/m^2) blue background adaptation field and yellow light of various luminance levels (13cd/m^2 – 1203cd/m^2). Varying intensities of yellow light were achieved by placing a series of neutral density filters in front of the projector emitting the yellow light. The subject was allowed to dark-adapt initially for 20 minutes and then for 3 minutes to each yellow background level, starting with the lowest level. Increment threshold values were determined using a 2-alternative forced choice paradigm for each level of yellow background luminance and are shown in Fig. 3. Background adaptation level was expressed in photopic Trolands (Td) and corrected for the Stiles-Crawford effect, for an 8 mm pupil. Two distinct branches were initially evident under all conditions. The data points were fitted using the equation

$$\Delta L = A*(1 + L/L_e)^n$$

as used by Kalloniatis and Harwerth[30], where ΔL represents increment threshold, A represents the intercept on the ordinate, L_e characterises the horizontal position of the TvL function and n is the slope of the function. The second branch was demonstrated for both small and large stimuli,

indicating that S-cone isolation was achieved under these conditions.[31] The value of the yellow background at the intersection of the two branches is typical for the point at which the signal response becomes predominantly mediated by the S-cone pathway. We have previously shown[6] that under similar background conditions, the threshold for detection of small blue stimuli changes in accordance with the known distribution of S-cones (foveal tritanopia and maximal sensitivity at 1.5 deg eccentricity) and its variation with wavelength resembles the spectral curve of Stiles's π_1 mechanism, with a maximum at 440nm.[10] It was also noticed by the observer that the colour appearance of the test stimuli shifted at that point to a violet/white colour with non-distinct edges, typical of S-cone vision. The yellow luminance value of 600cd/m^2, chosen to isolate the S-cone pathway in the current study is represented by the vertical dotted line in Fig. 3. This background gave rise to a retinal illuminance of 4.3 log Td (for an 8mm pupil), which exceeds the background level below which rod involvement is known to contribute to threshold measurements.[31]

Psychophysical Procedure

Threshold was measured for 8 stimuli of varying size (and in random order) under different blue background levels, between 1.78 and 2.82 log S-Td. The non-test eye was occluded. A temporal 2-alternative forced choice (AFC) procedure was used for all subjects. The stimulus was presented in one of two intervals marked by tones. The subject was required to decide whether the stimulus presentation was made during the first or second interval and respond accordingly by pressing one of two buttons on a response box. No feedback was given and the subject was encouraged to guess if unable to see the stimulus. Stimulus duration was 200ms with a square temporal profile. A 3-up/1-down staircase method was employed, with contrast reducing by

0.8dB after three correct responses and rising by 0.8dB after each incorrect answer. Under these conditions the staircase would converge towards a threshold corresponding to 79% correct responses.[32] Threshold was recorded after six reversals. Three sessions were undertaken under each blue background level (each chosen at random) and detection thresholds were averaged accordingly. To avoid subject fatigue, only one session (i.e. generation of one spatial summation curve) was performed each day.

Prior to the commencement of the psychophysical experiments, a short practice session was given using a circular incremental stimulus, the diameter of which was chosen at random. This practice session lasted until two reversals were reached.

RESULTS

Fig. 4 shows log increment threshold as a function of log stimulus area for each participant and at each blue background level expressed in S-Td. Increment thresholds for all stimuli increased with higher blue background luminance and the difference in increment threshold between low and high levels of blue background luminance was larger for large stimuli. It is also noticeable on inspection of the data points alone that complete spatial summation is limited to smaller stimuli under high blue background conditions (i.e. Ricco's area is smaller). In order to quantify this, two-phase regression analysis (Levenberg-Marquardt estimation) was performed on each data set, using the method of Seber and Wild,[33] and regression lines were plotted accordingly. The slope of the first line segment was constrained to -1 (obeying Ricco's Law) while its intercept, the slope of the second line segment and the point of intersection of the two segments were allowed to vary. The intersection of the two line segments was taken to represent the area

of complete spatial summation (Ricco's area). This method has been well accepted in published literature as a means of estimating spatial summation characteristics.[7, 10-13, 22, 34] The coefficient of determination (r^2) exceeded 0.95 in all cases. Values for the slope of the second line (as determined by the software) are given in Table 2. Fig. 4 shows that, for each subject, the spatial summation curve undergoes an upward shift along the threshold axis and a leftward shift along the area axis as the blue background luminance is increased. Fig. 5 summarizes the changes in Ricco's area with blue background luminance. The area of complete spatial summation becomes notably smaller with increased background luminance in each subject. On average, Ricco's area decreased in size by 0.39 log units per log unit increase in blue background luminance. Subject DG displayed the largest change; a 0.53 log decrease in Ricco's area following a 1.04 log increase in background retinal illuminance. Subject LMI demonstrated the least change over the same change in background; a 0.31 log unit decrease in Ricco's area. Values for Ricco's area under low background conditions in the current study are typical of those found for subjects of similar age for similar background conditions.[13]

DISCUSSION

While changes in Ricco's area with background adaptation level have previously been shown for achromatic stimuli, the current study is the first to report a reduction in Ricco's area with background luminance in the S-cone pathway. The difference in vertical separation of TvL curves for large and small stimuli with background luminance supports these findings.

What mechanism subserves the changes in S-cone spatial summation with the level of adaptation? A long-held belief is that the change in the achromatic Ricco's area with background

adaptation level is a result of centre-surround antagonism at the level of the retinal ganglion cells. The main difficulty with this hypothesis for the current study is the absence of physiological data supporting the existence of retinal receptive fields with antagonistic S-cone inputs to their centre and surround. The receptive fields of ganglion cells with S-cone ON input in the primate retina have spatially coextensive excitatory blue-on and inhibitory yellow-off fields.[17, 35] Although more recent studies on the primate retina and LGN have shown that S-ON cell receptive fields can demonstrate center-surround antagonism,[36-38] this is $S/(L+M)$ antagonism[39] rather than S+/S- antagonism. Such receptive fields should not be capable of producing the changes in Ricco's area observed in the present study. An alternative hypothesis is that changes in Ricco's area occur at a post-LGN site, where both spatial and S-cone antagonistic receptive fields exist. So-called 'double-opponent cells', have been found in the primate visual cortex,[40-42] including those with spatial S+/S- antagonism.[40, 43] It is therefore possible that these cells are involved in the changes in Ricco's area that we have seen here. Other studies also point to double-opponent cortical cells as a possible neural substrate for a range of S-cone mediated phenomena. Monnier and Shevell[44] demonstrated that the colour shifts created by a background of concentric circles, distinguished by S-cones only, are predicted by receptive field organization observed in cortical neurones – an S-cone antagonistic centre-surround (S+/S-) receptive field. The ability to demonstrate Westheimer functions under S-cone isolation under both monoptic and dichoptic conditions[45, 46] is suggestive of spatial and S-cone antagonism that occurs after the merging of signals from both eyes.

Nonetheless, the notion that the observed effect occurs at a retinal level is not inconceivable. Dacey *et al*[47] (their Fig. 4c) indicate variation in local dendritic tree size of small bistratified

cells, and it is likely that similar variation exists in their receptive field size. It may be that under low levels of background luminance, ganglion cells with large receptive fields are more sensitive and become the dominant responders in an S-cone driven task while summing light over a larger area. Chichilnisky and Baylor[48] reported considerable variation in the strength of input from individual S-cones to the receptive fields of blue-ON ganglion cells in the macaque and attributed this to differences in gain arising from synaptic connections. During a 75ms impulse response from the ganglion cell, they estimated that around 700 additional S-cone photo-isomerizations added 1 extra cell spike to a 1-spike maintained discharge rate and there was some evidence of a quantized S-cone input. In our experiment, if at some point the isomerization level of those S-cones affording a weaker input dropped below the required level to elicit a response, and those cones input to the periphery of the receptive field, the field would appear to shrink. Thus a sophisticated feedback mechanism may not be necessary to alter the area of complete spatial summation for the more primitive S-cone pathway.

Regardless of the mechanism underlying the changes that we report here, the fact that the size of Ricco's area depends on the state of adaptation of the S-cone system and this has implications for visual function. A smaller Ricco's area under higher levels of blue background adaptation level can be seen as an effective means of increasing S-cone mediated spatial resolution while decreasing the extent of S-cone signal pooling, similar to the effect observed for achromatic vision between scotopic and photopic levels. Indeed, Stiles[23] and other investigators[49-52] have shown that acuity for blue stimuli increases with blue background luminance.

Our findings have implications for clinical testing of the visual field. Under achromatic

conditions in the normal eye (as employed in conventional perimetry), the relationship between sensitivity to the stimulus and local ganglion cell number depends on the size of the stimulus relative to the achromatic Ricco's area;[53] specifically, the stimulus size should be closely scaled to the normal Ricco's area in order to maximise spatial summation and the sensitivity of the test to conditions such as glaucoma[21, 22]. Here we have shown that, when the background contains no blue component, as is the case in SWAP, Ricco's area at our test locations (mean: -0.01 log deg^2; 1.11 deg diameter) is already smaller than the Goldmann V stimulus (0.36 log deg^2; 1.7 deg diameter) used in SWAP. Although the addition of a blue component to the adapting background should reduce threshold variability,[20] Ricco's area would only shrink further, relative to the stimulus size. Thus, in order to boost the sensitivity of the test, it may also be appropriate to scale the SWAP stimulus size to equate to Ricco's area under increased background adaptation conditions at each test location in the normal visual field.[21, 22]

In conclusion, spatial re-organization by the suppressive surround of the receptive fields (most probably at a cortical level), a change in the population of the most sensitive neurons with different receptive field sizes, reduction in the contribution from S-cones with the lowest weights (in the retinal receptive field periphery) might all be among the possible mechanisms of spatial summation changes observed under selective S-cone stimulation.

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Table 1. Adaptation conditions created by the composite background.

L (cd/m^2)	Log Photopic Td	Log S-Td
0	4.158	1.78
1.2	4.159	2.58
2.2	4.160	2.82

Table 2. Values for the slope (M) of the second line for all conditions, as determined by two-phase regression analysis. The 2.5% and 97.5% confidence limits (CL) for the slope determination are also given.

I (log S-Td)	1.78		2.58		2.82	
Subject	M	± CL	M	±CL	M	±CL
TR	-0.66	0.13	-0.55	0.07	-0.54	0.10
LMI	-0.53	0.12			-0.61	0.10
DG	-0.74	0.35			-0.76	0.08
LD	-0.86	0.25			-0.70	0.17

FIGURE LEGENDS

Figure 1. Schematic diagram of a spatial summation curve. Intensity and area are inversely proportional for stimuli smaller than Ricco's area. On a log-log scale, data points in this region may be joined by a line with a slope of -1. Beyond Ricco's area, spatial summation is incomplete. A color version of this figure is available online at www.optvissci.com.

Figure 2. Experimental apparatus. Chromatic spectra for the blue test light and the yellow adapting field are also shown. A color version of this figure is available online at www.optvissci.com.

Figure 3. Threshold-versus-Luminance (TvL) functions for subject TR, with a pupil diameter of 8mm, for A) a large stimulus (0.92 log deg^2; 3.25 deg diameter) and B) a small stimulus (-1.22 log deg^2; 0.28 deg diameter). Open diamonds represent thresholds measured without a blue background component and filled diamonds represent those measured with a blue background component of 4.5cd/m^2.

Figure 4. Spatial summation curves for each subject under different levels of S-cone retinal illuminance (thresholds expressed in S-Td). Dotted lines indicate the size of Ricco's area. Error bars represent the standard error of the mean for each point. Goldmann sizes (with diameter in degrees) are shown on the upper abscissa, for reference.

Figure 5. Changes in Ricco's area for each subject as a function of S-cone retinal illuminance (expressed in S-Td). Error bars represent the standard error of the breakpoint estimate by two-phase regression analysis. Goldmann sizes (with diameter in degrees) are also given, for reference.

Figure 1
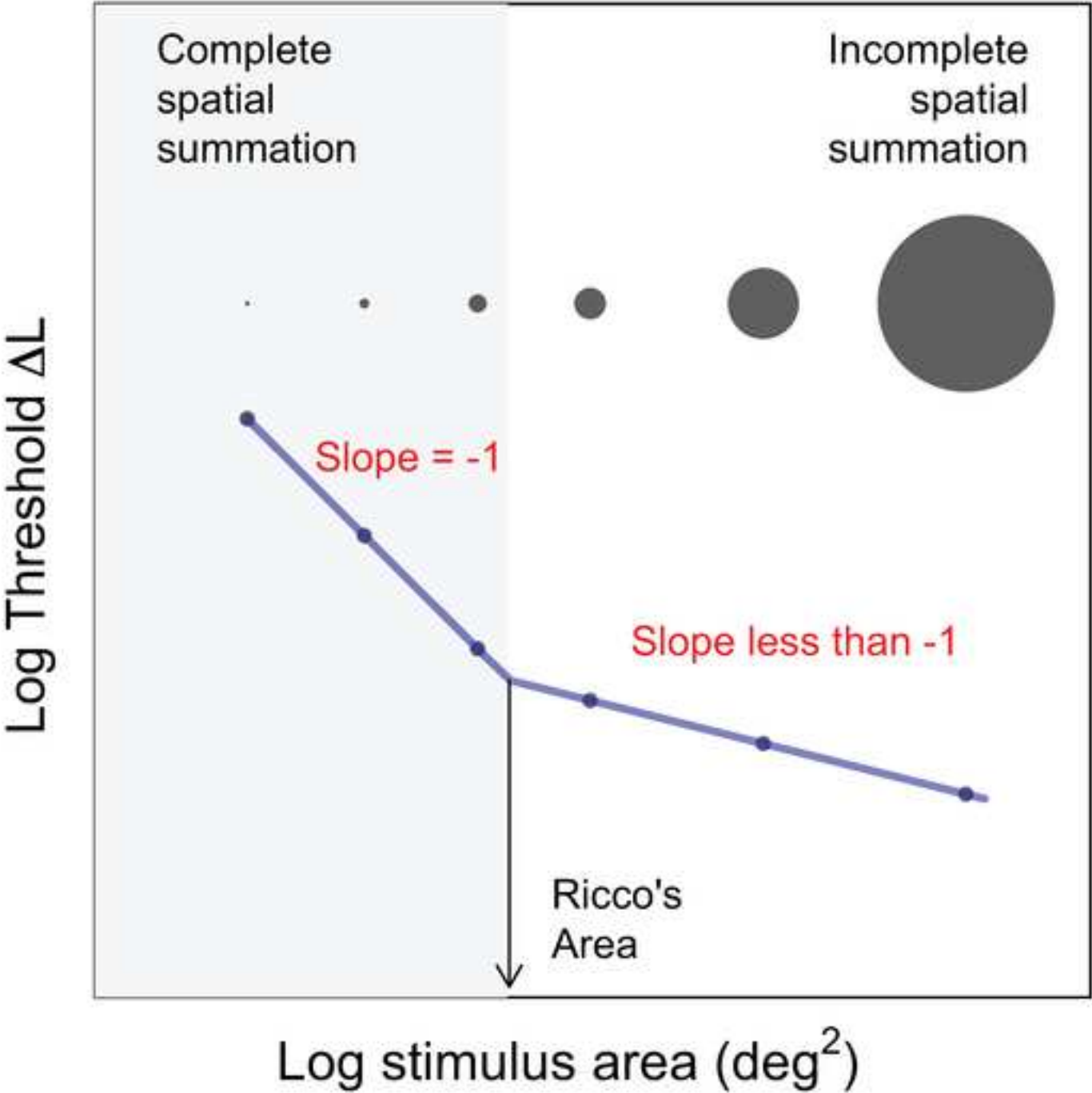
Figure 1. Complete spatial summation. Incomplete spatial summation. Slope = -1. Slope less than -1. Ricco's Area. Log Threshold ΔL. Log stimulus area (deg^2).

Spectra: test and background
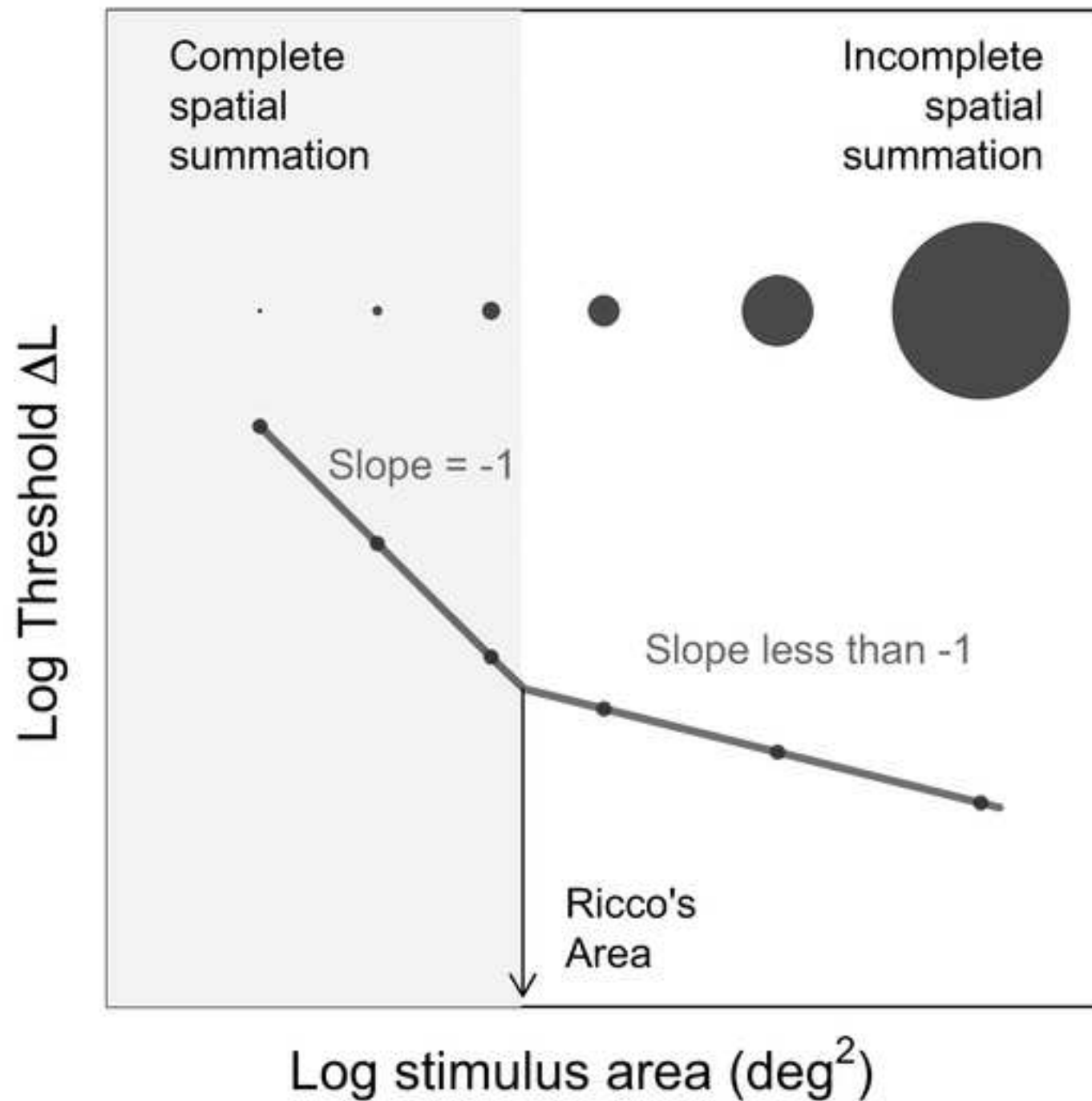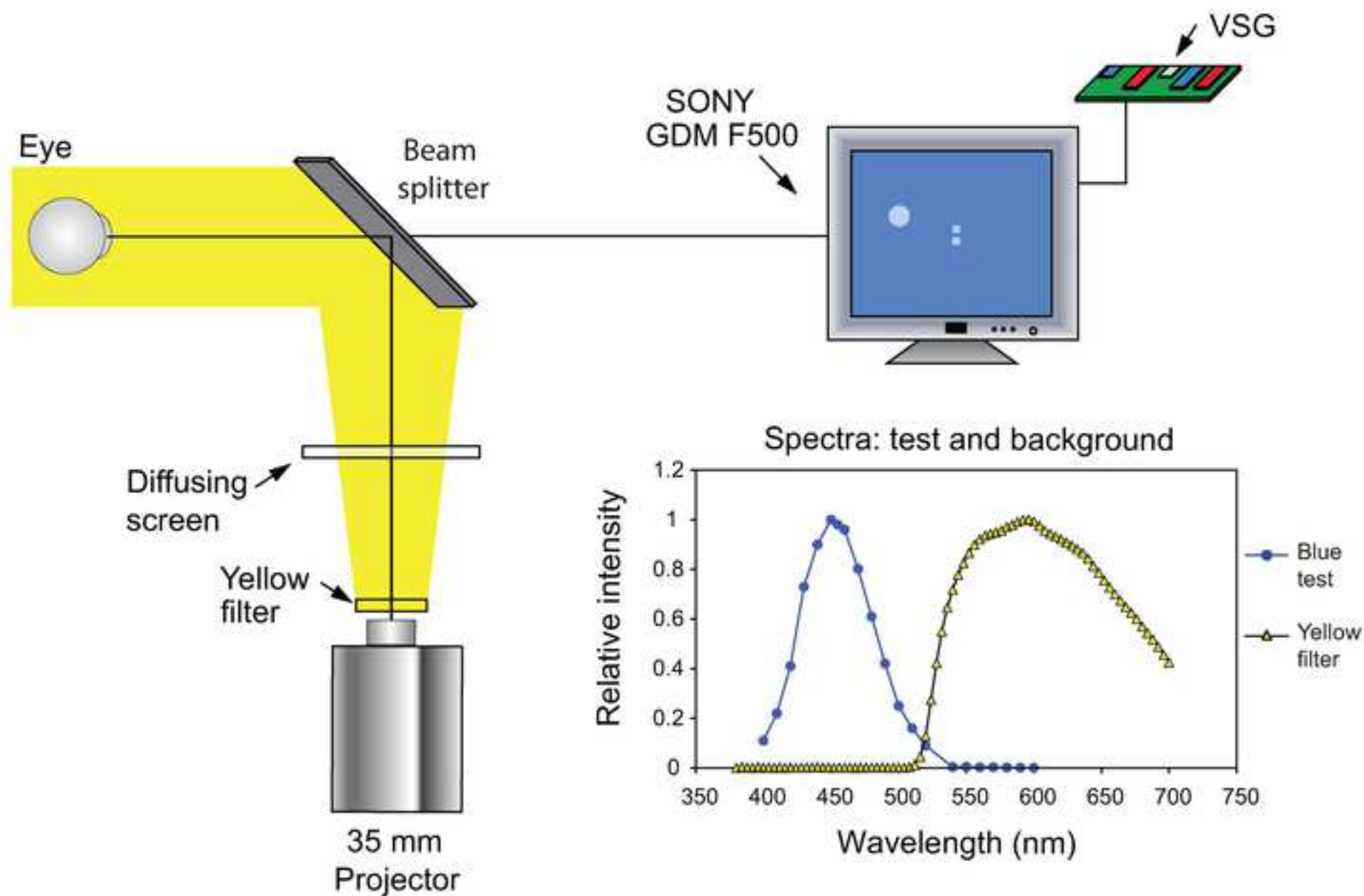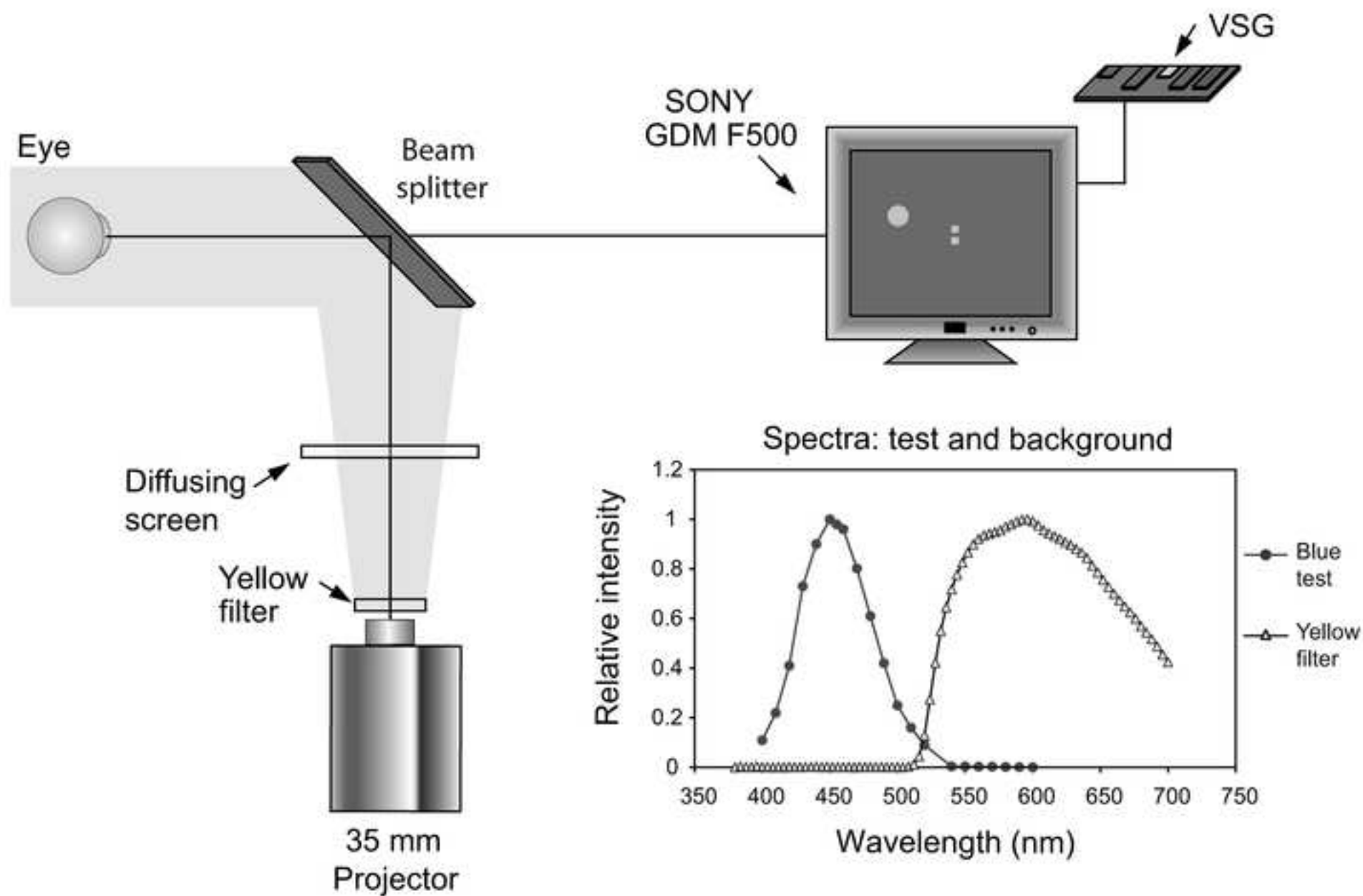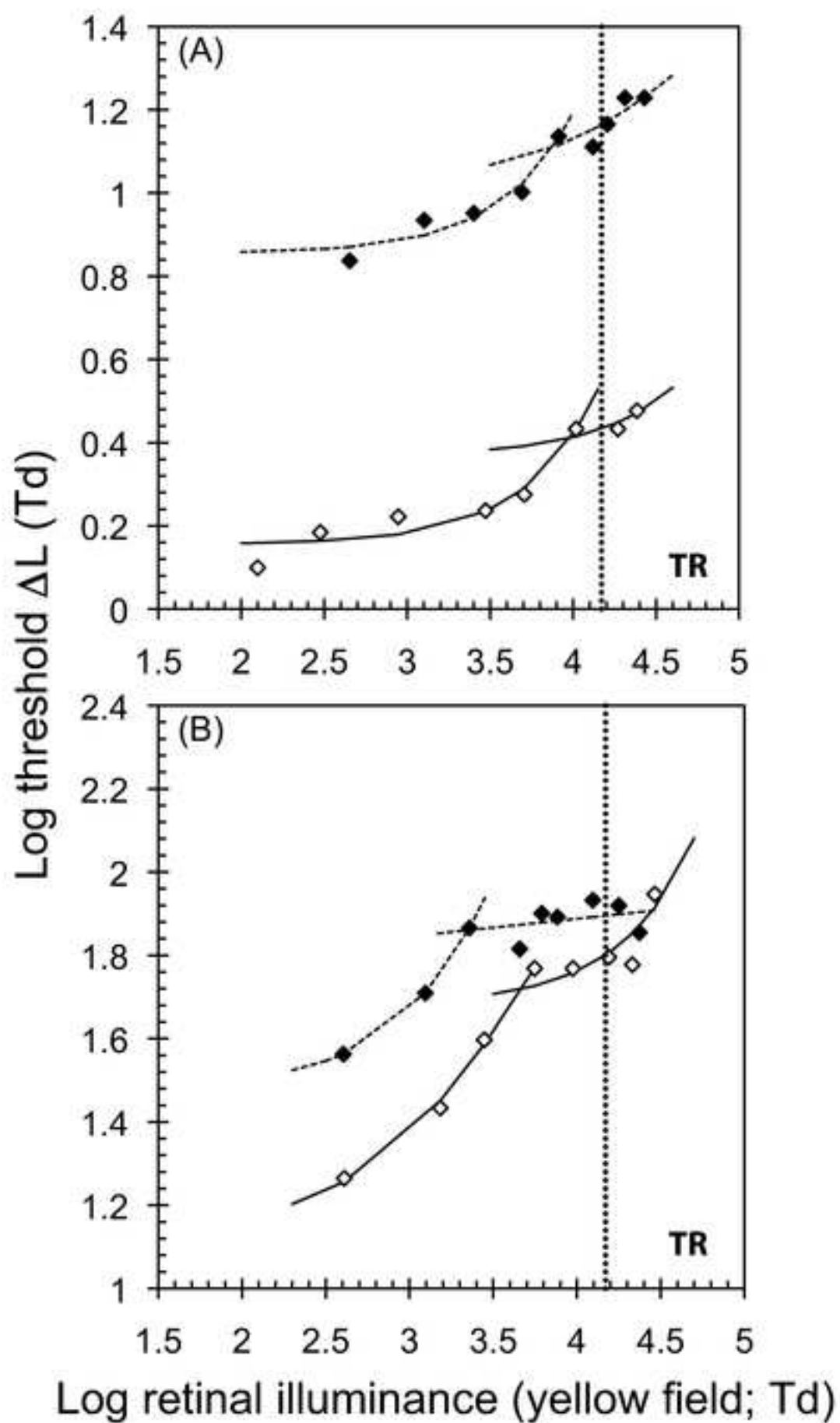
Figure 4 finalKAZ
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Goldmann size
Stimulus diameter (deg)

Figure 5 finalKAZ
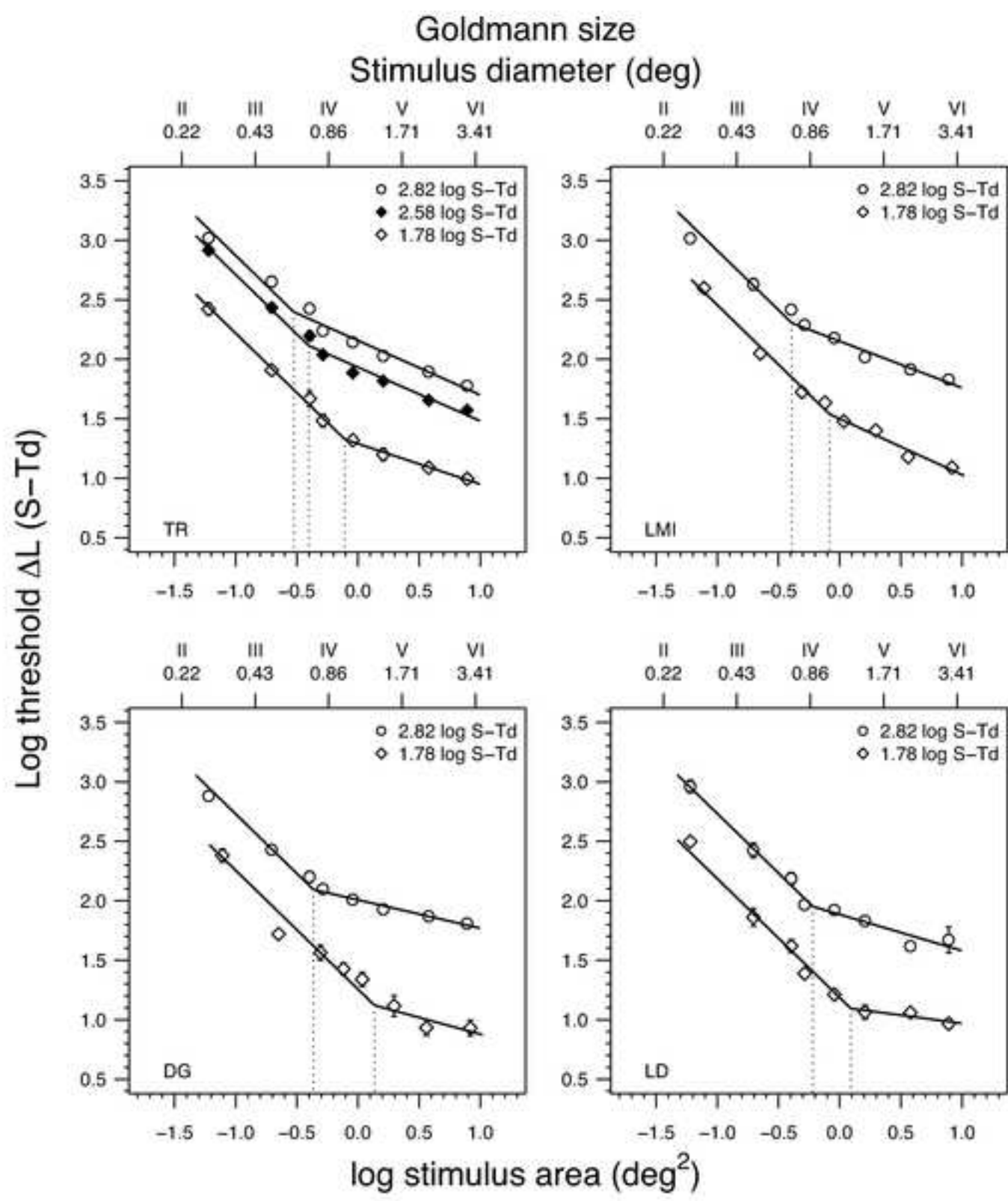Click here to download high resolution image