Wavelength dependence of the Stiles–Crawford effect explained by perception of backscattered light from the choroid

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To explain the wavelength dependence of the directional sensitivity of human foveal cones (Stiles–Crawford I effect) we extended an existing fundus reflectance model for calculation of the total absorption by visual pigment. We took experimental data from literature for both the psychophysical and the optical Stiles–Crawford effect and optimized parameters to fit the experimental data. The wavelength dependence of the Stiles–Crawford effect could be well described with the geometrical optics model. Essential elements are self-screening and the inclusion of backscattered choroidal light for perception. © 2001 Optical Society of America

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1. INTRODUCTION

The directional sensitivity of the human foveal cone system has been well known since its discovery in 1933 by Stiles and Crawford.[1] It is generally described in terms of $\eta = 10^{-\rho x^2}$, with η the retinal sensitivity relative to the peak, x the distance of beam entry with respect to the peak (in millimeters at the pupil plane), and ρ the peakedness parameter (in inverse square millimeters). A common explanation of the effect assumes that rays entering near the pupil margin pass through the outer segments of the receptor layer obliquely and so effectively miss much of the visual pigment. Thus light entering the eye near the edge of the pupil is perceived as dimmer than light entering near the center of the pupil. This was later called the Stiles–Crawford effect of the first kind (SC-I), this being in contradistinction to the Stiles–Crawford effect of the second kind (SC-II), which describes the change in hue with the position of pupil entrance. In the original study white light was used, but in 1937 Stiles measured the dependence of ρ on wavelength.[2] Since then several investigators have made new determinations.[3–8] Figure 1 gives a survey, which shows a clear common trend, albeit at different average levels; this difference may be attributed to experimental conditions differing in particular in field size. Typical characteristics are the minimum at 550 nm, the high maximum at the short-wavelength flank, and the lower maximum at the long-wavelength flank. The common explanation of the wavelength dependence of the SC-I effect given by Walraven and Bouman[9] and Walraven[10] is based on self-screening, which leads to the broadening of visual pigment extinction curves at higher concentrations. They noted that light rays with oblique incidence pass through only a thin layer of pigmented outer segment. If pigment peak optical density is high, oblique incidence has little effect on the total absorption, owing to self-screening. But at low optical densities, i.e., at the spectral flanks, the effect of oblique incidence will be large, owing to the much smaller effective pathway through the visual pigment. Consequently, high densities of visual pigment at the center of the visual spectrum should lower the SC-I effect, just as is found experimentally. Quantitative elaboration was successful insofar as a sufficiently deep dip in the middle of the visual spectrum was within the reach of a reasonable choice of parameters. Walraven and Bouman[9] estimated a visual pigment density of 0.7. Following this idea, the SC-I effect should increase when bleaching reduces the visual pigment concentration. On the other hand, at the flanks of the visual spectrum, where cone absorption is low, an absence of bleaching effects is expected. N. D. Miller[11] indeed found such an increase. The evidence, however, was weak, as Miller's data show little variation over the spectrum.[12] Walraven[13] measured the SC-I effect and found a decrease of the SC-I after applying a 650-nm bleach; however, he could not detect a significant effect with 630-nm bleach. S. S. Miller[14] isolated in dichromats the longer-wavelength-sensitive cone system. Bleaching the remaining cone system, S. S. Miller determined visual pigment densities of 0.5–0.6 for deuteranopes and 0.4–0.5 for protanopes. An effect similar to that obtained by bleaching was measured by using an entry near the pupil margin (although not always the same magnitude was reached). Burns and Elsner[15] measured the SC-II effect for different retinal illuminances. Their results show that the SC effect is due mostly to self-screening.

Walraven and Bouman[9] assumed equal optical density of the long-, middle-, and short-wavelength-sensitive (LWS, MWS, and SWS) cones. Visual pigment density decreases exponentially at the long-wavelength flank but levels off to 7% of its maximum value at the short-wavelength flank.[16] That implies that the peakedness ρ should be larger at the long-wavelength flank than at the short-wavelength flank. This is contrary to experimental evidence (Fig. 1). Walraven and Bouman[9] attributed the

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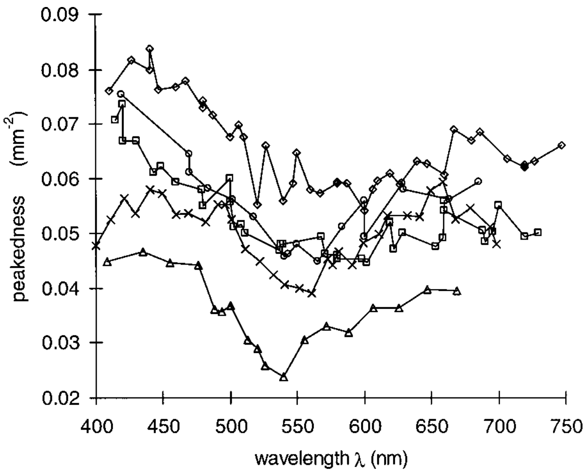

Fig. 1. Wavelength dependence of the peakedness, ρ_p, for the retinal psychophysical SC effect. Data points are taken from Stiles[2] (1-deg field size, diamonds), Stiles[3] (1-deg field size, squares), Enoch and Stiles[4] (1-deg field size, triangles), Alpern and Tamaki[7] (1-deg field size, crosses), and Wijngaard and van Kruysbergen[6] (1-deg field size, circles). Lines serve as a guide for the eye. To facilitate comparison of the data, they were each transformed to an effect at the retina, to account for changes of lens transmission with pupil position (for details see text). The different heights may be attributed to experimental conditions differing in particular in field size.

higher short-wavelength maximum to an assumed higher peakedness of the SWS cones. However, the contribution of the SWS-cone system to luminance is generally assumed to be virtually absent. Therefore, a larger SC component from the SWS cones, if existent, would hardly be noticed in terms of luminance.

In a theoretical study Snyder and Pask[12] discussed an explanation based on waveguiding. Their waveguide model predicted that minimal changes in outer-segment diameter or in relative refractive index could have a major effect on the optical properties of the receptor. Assuming that certain modes escape the outer segment at longer wavelengths, they could achieve only a limited fit to the SC-I data of Stiles and Crawford. They claimed that such a change could not be achieved with a geometrical optics approach. However, in view of variations in natural tissue, such refined model tuning hardly seems realistic. On the contrary, the virtual absence of waveguide effects in the SC effect can be regarded as a justification of geometrical optics modeling, because of the averaging over the minimal variations.

The psychophysical SC-I effect discussed above has a reflection counterpart, called the optical SC effect.[17–19] The fundus reflection model of Van de Kraats *et al.*[20] can be applied to simulate quantitatively the main spectral and directional features of the foveal fundus reflection. It uses individual estimates of parameters such as equivalent thickness of blood layers and densities of the lens, macular pigment, and melanin, together with the known spectral absorption characteristics of the various absorbers. Further, the incoming light is assumed to reflect at the sclera and at the disks in the outer segments of the photoreceptors, as well as to show some vitreous backscatter. In this model description an important difference between the optical and the psychophysical SC effect is that with the optical SC effect the entrance and exit beam angles change simultaneously, whereas in the psychophysical SC effect only the entrance beam angle changes.

In this context it is important to note that scattered light that has entered the choroid loses its original directionality.[20] As a result, cones will absorb backscattered choroidal light equally well for perpendicular and for oblique entrance. Since backscattered choroidal light is heavily filtered by blood, in the red part of the spectrum the psychophysical SC effect will be diminished compared with the case of no absorption of backscattered light.

The question to be answered, then, comes down to whether this backscattered component is sufficient to explain the attenuation of the SC effect at long wavelengths relative to short wavelengths. For that purpose we have extended the fundus reflection model of Van de Kraats *et al.*[20] for calculation of the total absorption in visual pigment.

2. EXPERIMENTAL DATA

A. Psychophysical SC-I Effect

Experimental data of the psychophysical SC-I effect as a function of wavelength were taken from the following sources: Stiles,[2,3] Enoch and Stiles,[4] Dunnewold,[5] Wijngaard and van Kruysbergen,[6] Alpern and Tamaki,[7] and Wyszecki and Stiles.[8] In these studies, different eccentric pupil positions were used, and thus different lens densities are involved.[21,22] The yellow tinted lens gets thinner for eccentric incidence, which should reduce the SC effect, in particular in the short-wavelength region. To ease comparison of the data, we converted them to an effect at the retina by correcting for this difference in lens thickness for each particular pupil position. If not indicated, the position of maximal sensitivity was taken at the pupil center. Figure 1 shows the peakedness of the psychophysical SC effect, ρ_p, as a function of wavelength from the seven sets of literature data. Data given by Dunnewold[5] and Wyszecki and Stiles[8] are based on the same experiments performed by Stiles[3] and cannot be treated independently. Therefore these data were pooled with the 1939 Stiles data points. Further, different field sizes may account for the differences in absolute value of the peakedness parameter, ρ_p. On average a 1-deg-field size was probed. To compare the data with our calculation, we made a linear spline through the data points and took the mean of these spline functions. The irregular thin curve in Fig. 2 shows the mean of these data.

B. Optical SC-I Effect

Experimental data of the optical SC-I effect as a function of wavelength were taken from a single study at two wavelengths by DeLint *et al.*[23] They probed the optical SC-I effect by changing pupil entrance and exit positions in tandem and presented mean results for five subjects for a 2.5-deg × 2.5-deg foveal field, measured at two wavelengths and several pupil entry points with a scanning laser ophthalmoscope. Fundus reflectance measurements of the SC-I effect show that the peakedness, ρ_o, is low in the central 0.5 deg, reaches a maximum at an eccentricity of 2 deg, and gradually drops with increasing

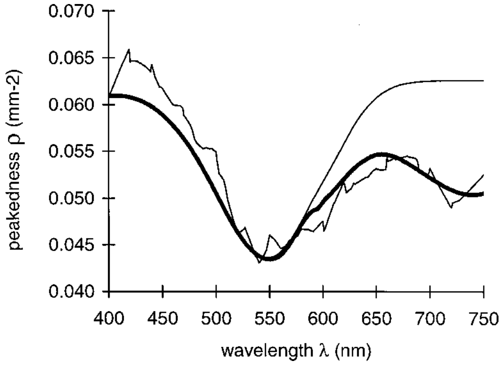

Fig. 2. Wavelength dependence of the peakedness, ρ_p, for the psychophysical SC effect. The irregular curve represents the mean of all experimental data, as determined by linear spline averaging. Error bars are inserted at several representative wavelengths, indicating how the shape as a function of wavelength of the mean deviates from the shape of the individual studies. The bold curve is calculated with inclusion of backscattered light from the choroid. The thin smooth curve is calculated in the absence of backscattered light. For details, see text.

eccentricity.[24] For comparison with the psychophysical SC effect, in which on average a 1-deg field size was probed, we used the original data of DeLint *et al.* and determined ρ_o for different field sizes. The dotted curve in Fig. 4 shows ρ_o as a function of field size for 514 nm and the solid curves for 633 nm, both in a bleached state. We found $\rho_o = 0.11$ and $\rho_o = 0.12$ averaged over a 1-deg $\times$ 1-deg foveal field for 514 nm and 633 respectively, which is 1.7 times as small as the peakedness averaged over a 2.5-deg $\times$ 2.5-deg foveal field. For the dark-adapted state we found $\rho_o = 0.05$ and $\rho_o = 0.10$ averaged over a 1-deg $\times$ 1-deg foveal field for 514 and 633 nm, respectively. Data points in Fig. 3 are for a 1-deg test field, determined from these recalculations.

3. MODEL CALCULATION

A. Psychophysical SC-I Effect

To calculate the wavelength dependence of the optical SC-I effect, we used the fundus reflection model of Van de Kraats *et al.*[20] This model describes absorption and reflection by different retinal layers and uses these and a limited number of known spectral extinctions to decompose the measured spectral reflection. To calculate the wavelength dependence of the psychophysical SC-I effect, we extended this model to calculate psychophysical consequences. No extra parameters were needed. For absorption in visual pigment there are two pathways: (1) incoming light, guided into the outer segments of the photoreceptors and (2) light reflected from layers posterior to the receptor. The first pathway shows a directional behavior. Along the photoreceptor outer segment, losses in transmission occur owing to (a) absorption by visual pigment, (b) light escaping along the outer segment for oblique angles, and (c) reflection at the outer-segment disks. Van de Kraats *et al.* assumed that for calculation of the amount of light staying in the outer segments, all losses act as homogeneously distributed optical filters.[20] The fraction absorbed, $Abs_1(x, \lambda)$, in such an optical filter is given by

$$Abs_1(x, \lambda) = \frac{D_{\mathrm{vp}}(\lambda)\{1 - 10^{-[D_{\mathrm{vp}}(\lambda) + D_{\mathrm{esc}}(x) + D_{\mathrm{disk}}]}\}}{D_{\mathrm{vp}}(\lambda) + D_{\mathrm{esc}}(x) + D_{\mathrm{disk}}}. \tag{1}$$

Here λ is the wavelength, x is the position of entrance beam in the pupil plane with respect to the peak of the SC-I effect, $D_{\mathrm{vp}}(\lambda)$ is the visual pigment density, $D_{\mathrm{esc}}(x)$ is the apparent density as a result of light leakage into the interspace between the photoreceptors, and D_{disk} is the apparent density of a single pass through the outer segment as a result of neutral reflection at the outer-segment disks. In this calculation, absorption of light re-

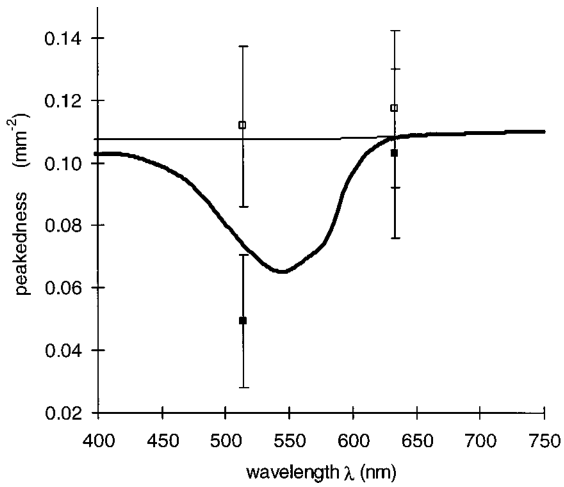

Fig. 3. Model calculation of the wavelength dependence of the peakedness, ρ_o, for the optical SC effect. Data points are the mean of five subjects from DeLint *et al.*[23] for the bleached (open squares) and the dark-adapted (solid squares) condition. The bold curve is calculated for the dark-adapted condition, the thin line for the bleached condition. Bars show standard errors.

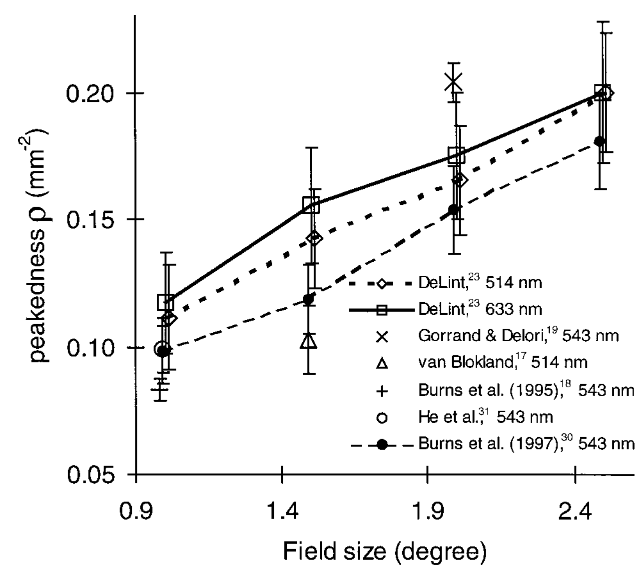

Fig. 4. Peakedness, ρ_o, of the optical SC effect as a function of field size from data of DeLint *et al.*[23] at 514 nm (diamonds, dotted curve), and 633 nm (squares, solid curve). The dashed curve (solid circles) are data points from Burns *et al.*[30] at 543 nm. The single points are from Gorrand and Delori[19] at 543 nm (cross), van Blokland[17] at 514 nm (triangle), and Burns *et al.*[18] at 543 nm (plus sign), and He *et al.*[31] at 543 nm (circle). Bars show standard errors. For additional experimental details, see text.

flected at the outer-segment disks was ignored, which is permissible if the reflectance is on the order of a few percent.

Light entering the layer posterior to the receptors consists of a fraction that has been transmitted through the outer segments and a fraction that has escaped from the outer segments. Both components traverse the retinal pigment epithelium and the choroid and partly reflect at the sclera. Reflected light that reaches the photoreceptors after a second traverse of choroid and retinal pigment epithelium can be absorbed again. This scattered light that has entered the choroid loses its original directionality.[20] As a result, cones will absorb backscattered choroidal light equally well for perpendicular and for oblique entrance, and the fraction absorbed in the visual pigment, $Abs_2(\lambda)$, is given by

$$Abs_2(\lambda) = \frac{D_{\mathrm{vp}}(\lambda)\{1 - 10^{-[D_{\mathrm{vp}}(\lambda) + D_{\mathrm{disk}}]}\}}{D_{\mathrm{vp}}(\lambda) + D_{\mathrm{disk}}}. \quad (2)$$

Equations (1) and (2) are specified for a single cone type. We summed the contributions of the MWS and LWS cones to arrive at estimates for the absorption of incoming light and the absorption of backscattered light. Their relative contributions are determined by the LWS-cone fraction. The contribution of SWS cones was neglected since they are rather sparse, especially in the fovea.[25]

The total absorption in the visual pigment, $Abs(x, \lambda)$, is the sum of the absorption of the incoming light and the absorption of backscattered light and is given by

$$Abs(x, \lambda) = T_{\text{pre-vp}}(\lambda)\{Abs_1(x, \lambda) + [T_{\mathrm{tot}}(x, \lambda) + E_{\mathrm{tot}}(x, \lambda)]R_{\mathrm{deep}}(\lambda)Abs_2(\lambda)\}. \quad (3)$$

Here $T_{\text{pre-vp}}(\lambda)$ is the transmission of the layers anterior to the photoreceptors according to Eq. (15) of Ref. 20. $T_{\mathrm{tot}}(x, \lambda)$ is the total transmission of cones and $E_{\mathrm{tot}}(x, \lambda)$ is the total escaped fraction of the cones according to Eqs. (10) and (12), respectively, of Ref. 20. Finally, $R_{\mathrm{deep}}(\lambda)$ is the reflectance of the choroidal layers, according to Eq. (3) of Ref. 20. It is determined by the density of melanin, the effective blood layer thickness, and sclera reflectance, which are all wavelength dependent, and the wavelength-independent choroidal scatter loss. Through self-screening, the SC-I effect depends on the visual pigment density, $D_{\mathrm{vp}}(\lambda)$. It appears not only in $Abs_1(x, \lambda)$ and $Abs_2(\lambda)$ but also in $T_{\mathrm{tot}}(x, \lambda)$ and $E_{\mathrm{tot}}(x, \lambda)$. In the model, the peakedness of the SC-I effect is brought in via the apparent density as a result of leakage into the interspace, $D_{\mathrm{esc}}(x)$. This $D_{\mathrm{esc}}(x)$ is the only term that depends on pupil position, x. It appears in $Abs_1(x, \lambda)$, $T_{\mathrm{tot}}(x, \lambda)$, and $Esc_{\mathrm{tot}}(x, \lambda)$. The functional form of $D_{\mathrm{esc}}(x)$ is unknown except for perpendicular angle, where $D_{\mathrm{esc}}(x = 0) = 0$. Note that when x increases, $Abs_1(x, \lambda)$ decreases, but the term in square brackets increases, causing an increase in the light intensity available for $Abs_2(\lambda)$.

The model calculation gives the total absorption, $Abs(x, \lambda)$, for one particular pupil position x, whereas data from literature (Figs. 1 and 2) give the peakedness of the SC effect, ρ_p. We converted the $Abs(x, \lambda)$ results into values of ρ_p, using

$$\rho_p = \frac{1}{x^2}\log\left[\frac{Abs(0, \lambda)}{Abs(x, \lambda)}\right]. \quad (4)$$

In all model calculations we used $x = 2$ mm. A different choice of x would result in a different parameter value for D_{esc} only.

B. Optical SC-I Effect

Application of the fundus reflection model of Van de Kraats *et al.*[20] provides the complete reflection, $R(x, \lambda)$:

$$R(x, \lambda) = T_{\mathrm{om}}(\lambda)\{R_{\mathrm{ilm}} + (1 - R_{\mathrm{ilm}})^2 10^{-2D_{\mathrm{mp}}(\lambda)} \times (R_{\mathrm{disk}}(x, \lambda) + [T_{\mathrm{tot}}(x, \lambda) + E_{\mathrm{tot}}(x, \lambda)]R_{\mathrm{deep}}(\lambda))\}. \quad (5)$$

Here $T_{\mathrm{om}}(\lambda)$ is the transmission of the ocular media, R_{ilm} is the reflectance at the inner limiting membrane (including vitreous backscatter), and $D_{\mathrm{mp}}(\lambda)$ is the density of the macular pigment. For an explanation of all other parameters see Eq. (3). In this model the main directional effect finds its origin in light reflected at the outer-segment disks. However, for oblique angles more light is transmitted to the choroid, which implies an additional effect from reflectance at the sclera, which may even be complementary to the main effect in the dark-adapted condition. DeLint *et al.*[23] separated their results on the optical SC-I effect into a directional component and a nondirectional background. The nondirectional background component in the results of DeLint *et al.*[23] is in fact the reflectance for very oblique pupil positions. Therefore we calculated the reflectance for large oblique incidence and assumed this to be the nondirectional background. For all other pupil positions, we subtracted this background from the total reflectance in order to model the peakedness found by DeLint *et al.*[23]:

$$\rho_o = \frac{1}{x^2}\log\left[\frac{R(0, \lambda) - R_{\mathrm{nd}}(\lambda)}{R(x, \lambda) - R_{\mathrm{nd}}(\lambda)}\right]. \quad (6)$$

Here $R_{\mathrm{nd}}(\lambda)$ is the nondirectional component, i.e., the reflectance for large oblique incidence. The apparent density as a result of leakage into the interspace, D_{esc}, is the only term that depends on angle of incidence. We assumed $D_{\mathrm{esc}} = 3$ to calculate $R_{\mathrm{nd}}(\lambda)$. All other parameters were the same as those used to calculate $R(0, \lambda)$.

To calculate ρ_o we used $x = 2$ mm. Again, a different choice of x would result in a different parameter value for D_{esc} only.

C. Fitting the Model to the Data

We used the χ^2 criterion to minimize the difference between the model and the data points. The psychophysical SC effect and the optical effect (the bleached and the dark-adapted data) were fitted simultaneously; i.e., the sum of their individual χ^2's was minimized. Equation (4) was fitted to the psychophysical data of Fig. 2 and Eq. (6) to the optical data of Fig. 3. Only the choroidal scatter loss and the apparent density as a result of leakage into the interspace were allowed to differ between the optical and the psychophysical SC effect, all other parameters had the same values for the two effects. Some param-

Table 1. Parameter Values Used in the Model Calculation[a]

Parameter	Model Optical	Model Psychophysical
LWS-cone fraction	0.66	0.66
D_{vp}, visual pigment density[b]	0.83	0.83
D_{esc}, apparent density as a result of leakage into the interspace[c]	0.46	0.27
D_{disk}, apparent density as a result reflection at the outer-segment disks	0.012	0.012
Melanin density (500 nm)[b]	1.25	1.25
Effective blood layer thickness (μm)	25	25
Choroidal scatter loss	0.45	0
Sclera reflectance (%) (675 nm)[b]	50	50

[a] Values for the sclera reflectance, density of melanin, effective blood layer thickness, and D_{disk} were obtained from Ref. 20. For the LWS-cone fraction we used the generally accepted mean value of 0.66 (Refs. 28–30). D_{vp}, D_{esc}, and the choroidal scatter loss vary considerably with eccentricity and were optimized to fit the experimental data.

[b] Melanin density, visual pigment density D_{vp}, and sclera reflectance are wavelength dependent. Values for melanin density and sclera reflectance are given for the wavelength indicated in the table. D_{vp} refers to the peak density.

[c] D_{esc} depends on eccentricity of the light beam in the pupil plane. Values in this table correspond to a 2-mm eccentric pupil position with respect to the position of the maximum of the SC effect. For central incidence $D_{esc} = 0$.

eters do not change much with eccentricity: sclera reflectance, density of melanin, effective blood layer thickness, and apparent density of a single pass through the outer segment as a result of reflection at the outer-segment disks. For those we took the mean derived from ten normal subjects determined in a previous paper.[20] Other parameters vary considerably with eccentricity: visual pigment density,[26] the apparent density as a result of leakage into the interspace,[24] and the choroidal scatter loss, which can be interpreted as a loss due to diffusion of light outside the detecting aperture. The relative importance of this effect increases if the field size of the retinal spot probed decreases. These three were optimized to fit the experimental data. For the LWS-cone fraction we used the generally accepted mean value of 0.66.[27–29] Changing the LWS-cone fraction resulted in only a minor shift of the position at which the SC effect has its minimum. The bold curve in Fig. 2 is the result of this fitting with inclusion of backscattered light from the choroid. For comparison, the thin curve is a calculation with the same parameters, but without inclusion of backscattered light. The bold curve in Fig. 3 was calculated for the dark-adapted conditions and the horizontal line for a completely bleached condition. Table 1 summarizes the parameters used in the model calculation.

4. DISCUSSION

The wavelength dependence of both the optical and the psychophysical SC-I effect can be calculated with a geometrical optics model. A fit with experimental data can be achieved if self-screening and backscattered choroidal light are included. Without the latter component the calculated peakedness is too high at wavelengths $\lambda > 600$ nm. This can be understood from the absorption characteristics of blood. For $\lambda < 600$ nm nearly all light that has traversed the choroid is absorbed. Hence no backscattered light is present. For $\lambda > 600$ nm blood absorption is minimal, and thus backscattered light can also contribute to the absorption by visual pigment. In the bleached case, the amount of backscattered light is independent of angle of incidence, and it will lower the peakedness of the SC effect. In the dark-adapted case it shows a complementary effect, since more light is transmitted through the photoreceptor layer for oblique angles than for normal incidence. The influence of visual pigment on the SC-I effect through self-screening accounts for the minimum in $\rho(\lambda)$ at $\sim$550 nm (see Figs. 2 and 3). Identical values were used for six out of the eight fit-parameter values in the psychophysical and optical models.[20] Only the choroidal scatter loss and the apparent density as a result of leakage into the interspace were allowed to differ in the two models. Visual pigment density, D_{vp}, apparent density as a result of leakage into the interspace, D_{esc}, and choroidal scatter loss were optimized. Visual pigment density was in the same range as assumed by Walraven and Bouman[9] but was higher than that obtained by Van de Kraats *et al.*[20] from reflectance data. This is in line with the smaller field size of 1 deg compared with the 1.6 deg in their measurements.[26]

The aim of the present paper was to study whether addition of the backscattered choroidal component can explain the attenuation of the SC effect at long wavelengths relative to short wavelengths. We wondered if this could be achieved on mean literature data by parameter values in a range predicted by other literature data. The fitting procedure was not designed to give information on errors in parameters and their possible mutual interdependencies. We also did not fit individual curves to compare parameter values and look for intersubject differences.

Experimental data of the optical SC-I effect as a function of wavelength were taken from a single study at two wavelengths by DeLint *et al.*[23] There are several studies on a single wavelength. Burns *et al.*[30] measured the optical SC effect with a 1-deg, 543-nm test field in a bleached retina. Their mean ρ_o ($N = 5$) compares well with the other results of Fig. 4. At first glance this seems peculiar, since in their study they scanned only the exit pupil, whereas in the study of DeLint *et al.*[23] entrance and exit pupil were scanned in tandem. As a consequence the latter peakedness is expected to be twice as high as that of Burns *et al.*[30] However, Burns *et al.*[30] scanned the exit pupil with a high spatial resolution, in contrast to DeLint *et al.*,[23] who used a 2-mm circular exit pupil. Convolution of the results of Burns *et al.*[30] results with a 2-mm exit pupil will decrease ρ_o to values of DeLint *et al.* With the same setup, Burns *et al.*[18] and He *et al.*[31] found similar results, also shown in Fig. 4. Gorrand and Delori[19] found a ρ_o of 0.20 ($N = 20$) for a 2-deg spot, slightly higher than measured by DeLint *et al.*[23] This may be explained by their smaller exit pupil of 1-mm diameter. Van Blokland[17] measured the optical SC effect within a 1.5-deg retinal spot at 514 nm. He found a mean peakedness of 0.10 ($N = 4$) for the absorbance diagrams, defined as the difference of the reflectance in a bleached and an unbleached state of the visual pigment.

He used an entrance pupil of 0.5 mm and exit pupil of 1.2 mm. This may explain the lower peakedness compared with the other results in Fig. 4. Recently Marcos and Burns also measured the SC-effect.[32] Their single-entry reflectometric setup is similar to the one used by Burns *et al.*[30] For one of their subjects they measured ρ_o at two wavelengths (543 and 632 nm) for a 2-deg retinal spot in a bleached situation and found ρ_o (543 nm)$>\rho_o$ (632 nm), which they attribute to scattering.[33] Their multiple-entry data show no wavelength effect. In this setting, the total amount of light guided as a function of entry pupil, which depends only on the angular tuning of the cones, is measured.[33] DeLint *et al.*[23] found no wavelength effect for the bleached situation. They used a 2-mm circular exit pupil and scanned the entrance and exit beams in tandem. This can be described as intermediate between the single-entry and the multiple-entry reflectometric setup.

In our optical setup entrance and exit pupil were scanned in tandem, whereas in the psychophysical measurements only the entrance pupil was scanned. This difference in experimental setup in itself should result in a difference in ρ. Although the model takes this into account, we still had to assume that the parameter for leakage into the interspace, D_{esc}, was much higher for the optical than for the psychophysical SC-I effect (Table 1). He *et al.*[31] recently measured the optical and psychophysical SC effects on the same subjects under identical experimental conditions. They found an average ratio of the optical and the psychophysical peakedness of 2.1 for a 1-deg test field that was comparable to the experimental data presented in this study. They suggested a number of possible factors that could contribute to this discrepancy. The most likely were (1) differences in relative number or properties of modes that are measured by reflectometry and that are available for absorption and (2) the influence of interference of light resulting from different photoreceptors at slightly different planes on the distribution of light measured in the plane of the pupil. Other, less likely, factors are differences in the absorption of the ocular media for light traversing various pupil-entry positions, differences in the orientations of groups of photoreceptors within the measurement area, differences between the effect of leakage along the outer segments for the optical and the psychophysical effect, and differences between the effect of cone-to-cone cross talk on the optical and the psychophysical effect. For an extensive discussion see He *et al.*[31]

Finally, for the psychophysical SC effect no light is lost as a result of scatter (choroidal scatter loss=0), since a large part of the retina will be used as detector. So, apart from absorption by blood and melanin, most of the backscattered light can contribute to perception. DeLint *et al.*[23] used an optical setup with a retinal conjugate aperture of 0.43 deg. Thus part of the light reflected at the sclera is lost, because it scatters out of the measurement field (choroidal scatter loss=0.45).

The choroidal scatter loss was first introduced by Delori and Pflibsen[34] to offset constraints imposed by fixed media and scalar losses. It was interpreted as spectrally neutral loss in the choroid that was due to diffusion of light outside the detection aperture and as an adjusting factor of allow for choroidal light that was missing the choroidal melanin. Van de Kraats *et al.*[20] used this factor to account for light scattered outside the detection area but also mentioned that it could account for uncertainties in the scleral reflectance spectrum. In this paper we treat the choroidal scatter loss similarly to how Van de Kraats *et al.* treated it, i.e., as a loss due to diffusion of light outside the detecting aperture. Therefore we set a limit to the fitting procedure to keep its value positive. At the same time, the scleral reflectance was fixed at 50% (at $\lambda=675$ nm), based on literature.[20,34] This could be an underestimate.[35] Changing the scleral reflectance will have the same effect as changing the choroidal scatter loss. If we were to allow the scleral reflectance to be larger than 50%, or, in other words, allow the choroidal scatter loss to be negative, it would improve the fit of the psychophysical SC effect even further.

Little spectral structure of blood is observed in the model calculations drawn in Figs. 2 and 3. This has its origin in the fact that we assumed a melanin density of 1.25. In the $\lambda=570$–580-nm wavelength region melanin is still the dominant absorber, and as a result the relative influence of blood absorption is small. Assuming a lower density will increase the structure related to blood absorption. In addition, this will lead to an increase in the contribution of the backscattered light, which will result in a further decrease of ρ_p in the long-wavelength region. Further, a large amount of stray light in the red may possibly decrease acuity. Dunnewold[5] and Van Meeteren and Dunnewold[36] measured the Campbell effect, i.e., the change in acuity with angle of incidence, and found only a small wavelength effect. For a melanin density of 1.25, the mean of ten Caucasian subjects,[20] we calculated the amount of stray light to be only 2% at 600 nm and 10% at 650 nm. A decrease to a melanin density of 0.5 would increase these percentages to 8% and 28%, respectively. Thus for low melanin densities we expect an increasing Campbell effect. Measuring ρ and the Campbell effect in subjects with low and high melanin densities could be used to further test the main idea, that the wavelength dependence of the SC effect has its origin in self-screening and the inclusion of backscattered choroidal light.

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