The directionality of photoreceptors in the human retina

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ABSTRACT

The directional sensitivity of photoreceptors is a result of their structure that make them act as optical fibers. Therefore measurement of photoreceptor directionality is a tool for testing the physical properties of photoreceptors in vivo. Clinical studies of photoreceptor directionality are limited by the fact that psychophysical methods for measuring the Stiles-Crawford effect are time consuming and require excellent co-operation from the subject. Thus different reflectometric techniques have been developed recently. This paper describes such methods, that allow to characterize the optical properties of photoreceptors, i.e. their orientation and directionality. Mechanisms likely to explain the discrepancy between the directionality factor values given by these techniques are discussed. Finally the functional advantages of photoreceptor optics are considered.

KEYWORDS

Stiles-Crawford, directionality, alignment, reflectometry, fovea, photoreceptor

RÉSUMÉ

La sensibilité directionnelle des photorécepteurs est une conséquence de leur structure de guide d'ondes. La mesure de la directivité des photorécepteurs constitue donc un outil pour tester leurs caractéristiques physiques in vivo. Malheureusement la mesure psychophysique de l'effet Stiles-Crawford est peu adaptée à la routine clinique car elle est longue et exige une excellente coopération du sujet. Aussi différentes méthodes réflectométriques ont-elles été développées récemment. Cet article décrit les réflectomètres qui permettent de caractériser les propriétés optiques des photorécepteurs, en particulier leur orientation et leur directivité. Les mécanismes physiques susceptibles d'expliquer les valeurs singulières des facteurs de directivité données par chacune de ces méthodes sont discutés. Enfin les avantages fonctionnels de la structure optique des photorécepteurs sont développés.

MOTS-CLÉS

Stiles-Crawford, directivité, alignement, réflectométrie, fovéa, photorécepteur

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INTRODUCTION

The finding of directional sensitivity by Stiles and Crawford [41] in 1933 represented the first phenomenon which could be attributed to the optical properties of human retinal photoreceptors. The photoreceptors are typically more sensitive to light coming from the centre of the pupil than to light coming from the edge of the pupil. This change in the relative luminous efficiency as a function of pupil location is called the Stiles-Crawford effect of the first kind (SCE-I). The photoreceptors at the posterior pole are oriented toward the centre of the pupil. The directional sensitivity of the photoreceptors is a result of their physical properties (shape, diameters, indices of refraction) that make them act as optical fibers.[17-18,31,42] These waveguides collect light from an acceptance cone centred around their axis, and guide light to the photopigment inside the outer segment. Therefore measurement of photoreceptor directionality is a tool for testing the physical properties of photoreceptors in vivo.

This ideal arrangement of photoreceptors was shown to be disturbed in numerous clinical situations, including retinitis pigmentosa,[5-6] central serous choroidopathy,[36] gyrate atrophy, [47] fibrous scars,[33] trauma [11] and age-related macular changes.[20,37] But measurement of the psychophysical Stiles-Crawford function is time-consuming, requires excellent co-operation from the subject, and is therefore limited to a restricted number of patients. To address these limitations, reflectometric techniques [9,13,21-23,26,29,34,44,48] have been developed recently. In the optical assessment of photoreceptor directionality, the retina is illuminated from a region of the subject's pupil and the angular distribution of light exiting the eye is measured.

This paper will describe the different reflectometric methods that have been developed to characterize the optical properties of photoreceptors, i.e. their orientation and directionality, and the corresponding results. The mechanisms likely to explain the discrepancy between the directionality factor values given by these techniques will be discussed. Finally the functional advantages of photoreceptor optics will be considered. They include a decreased total volume of photopigment needed for the same effective optical density, a decreased sensitivity of the photoreceptors to stray light, and a decreased effect of aberrations of the eye optics upon visual performance.

DETERMINATION OF THE PHOTORECEPTOR DIRECTIONALITY

Psychophysics (method SCE)

A lightbeam carrying the radiant flux Φ enters the subject's pupil through the point J and falls upon the retinal area A (Fig. 1). The visual sensation induced by this beam depends on the co-ordinates x and y of J. On normal eyes there exists a pupillary point I (co-ordinates x_0, y_0) such that this sensation be maximal. The relative directional sensitivity η of the photoreceptors inside the test field is defined as:

$$\eta = \Phi(x_0, y_0) / \Phi(x, y)$$

such that the radiant flux $\Phi(x, y)$ induces the same visual sensation as $\Phi(x_0, y_0)$.
Stiles [40] showed that η was well fitted to a gaussian function:

$$\eta \approx 10^{-\rho_x (x-x_0)^2} \text{ (horizontal pupil traverse)}, \quad \eta \approx 10^{-\rho_y (y-y_0)^2} \text{ (vertical pupil traverse)} \quad (1)$$

The co-ordinates x_0 and y_0 give the orientation of photoreceptors' axes within the sample field. The directionality factors ρ_x and ρ_y characterize the angular tuning of photoreceptors along the directions O_x and O_y, respectively. The higher ρ_x and ρ_y, the more narrowly tuned are photoreceptors.

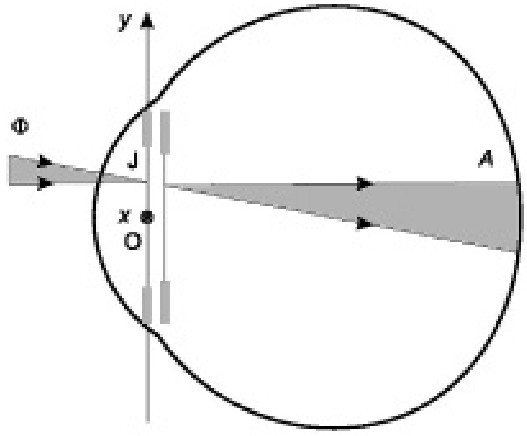

Fig. 1. Directional sensitivity. A lightbeam carrying the radiant flux Φ enters the subject's pupil through the point J (co-ordinates *x*, *y*) and falls upon the retinal area *A*. This beam induces a visual sensation, which depends on the co-ordinates *x* and *y*.

Reflectometry

Krauskopf [26] showed a direct correspondence between the psychophysical Stiles-Crawford effect and changes in reflectivity when the entry and exit pupils are moved. He pointed out that no simple theory of retinal reflectivity can account for the data quantitatively.

Moving entry and exit pupils (method ENEX)

In this method the directional properties of photoreceptors are determined by changing the angles of incidence and reflection at the retina in tandem. Such a principle was applied in the design of the photoreceptor alignment reflectometer[22-23] (PAR) and of a custom-built SLO.[13]
The principle of the PAR is illustrated in figure 2. A lightbeam at 543 nm enters the eye through the entry pupil P_i (dia < 0.1 mm) and illuminates a retinal field R_i (dia: 3 deg). The reflected light is sampled from a field R_r (dia: 2 deg) and is collected through the exit pupil P_r (dia: 1 mm). The entry pupil P_i and the exit pupil P_r are moved jointly inside the subject's pupil. This is accomplished with stationary retinal fields. The distance between the two pupil centres is set at 1.2 mm. The position of H, the midpoint between the centres of P_i and P_r, is defined by the co-ordinates *x* (horizontal axis) and *y* (vertical axis). A test sequence (4 s duration) consists in moving H across the subject's pupil along five horizontal lines 1 mm apart (dotted path in figure 2 A). The radiant flux Φ_m passing through P_r is measured by a photomultiplier as a function of the coordinates *x* and *y* of H.
The experimental data consist of the radiant flux values Φ_m at different positions (*x*, *y*) in the pupil. These data are fitted to the function:

$$\Phi(x,y) = C + B\,10^{-\left[\zeta_x (x-x_0)^2 + \zeta_c (x-x_0)(y-y_0) + \zeta_y (y-y_0)^2\right]} \qquad (2)$$

This function is the sum of a constant *C* and a directional component, the height of which is *B*. The co-ordinates x_0 and y_0 give the orientation of photoreceptors' axes within the sample field. The directionality factors ζ_x and ζ_y describe the sharpness of $\Phi(x, y)$ along the directions O_x and O_y, respectively; the higher ζ_x and ζ_y, the steeper Φ.
The mean directionality factor ζ is:

$$\zeta = \frac{\zeta_x + \zeta_y}{2} \qquad (3)$$

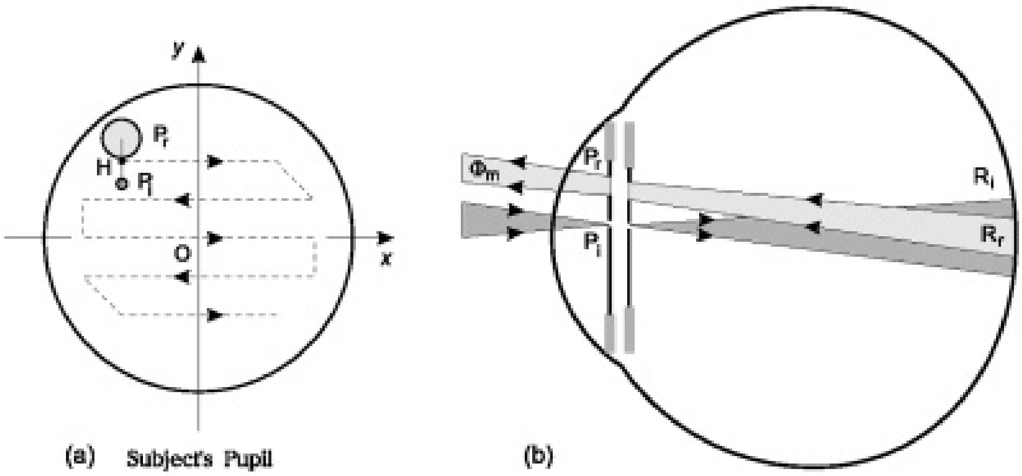

Fig. 2. Principle of the PAR. Light enters the eye through the entry pupil P_i. The field R_r determines the photoreceptor population which is tested. The radiant flux Φ_m collected by the exit pupil P_r is measured by a photomultiplier.

This factor ζ depends on the angular tuning of photoreceptors, but also on other parameters that will be considered in the section "Discussion".

An optical diagram of the PAR is given in figure 3. The measuring beam is provided by a 543 nm He-Ne laser, yielding a retinal irradiance of 0.8 mW/cm^2 (safe time [1] of 10 min). Fixation is provided by a 633 nm He-Ne laser. The fixation beam is combined with the measuring beam through beam splitter T_1, and both beams are directed toward the eye by reflection on beam splitter T_2. Light reflected from the fundus is transmitted by beam splitter T_2, then collected by the optical system with accurate control of both the pupillary (eyepiece EP1) and retinal focus (eyepiece EP2). The radiant flux is measured by the photomultiplier PMT.

The circular diaphragms P_i and P_r are conjugate with the entry pupil P_i and the exit pupil P_r, respectively. The circular diaphragms R_i, R_r and R_f are focused on the retina. The diaphragm R_i defines the retinal area R_i which is illuminated by the green light. The diaphragm R_r defines the retinal area R_r from which light is collected by the PMT. The diaphragm R_f defines the fixation target (5 arcmin in diameter); the operator selects the retinal eccentricity (0 - 8 deg, in any direction) by rotating mirror M_1.

The objectives L_5 and L_{12} are mounted on a plate which is moved transversally in steps of 10 μm by the stepping motors X and Y. This allows the entry pupil P_i and exit one P_r to scan the subject's pupil according to the path depicted in figure 2 A.

The head of the subject is stabilised by a bite bar which is fixed on a three-dimensional positioner. The components inside the dotted lines in figure 3 are mounted on a single plate which can be shifted longitudinally, thus allowing focus adjustment from -12 D to +12 D of ametropia. A computer controls the shutter Sh (green light), the two stepping motors, and receives input from the PMT. The electric signal collected by the PMT is sampled at every horizontal step, converted into a digital signal, then stored in the computer memory. A map of the measured flux Φ_m is created by the computer within seconds after data acquisition, allowing immediate inspection of the data.

The alignment parameters from a population of 20 normal subjects (age: 20-60) were measured by Gorrand and Delori.[23] All subjects were in good health, free of ocular pathology, and provided with a visual acuity correctable to 20/20 or better. They gave written informed consent to the protocol approved by the Institutional Review Board, then their pupil was dilated by application

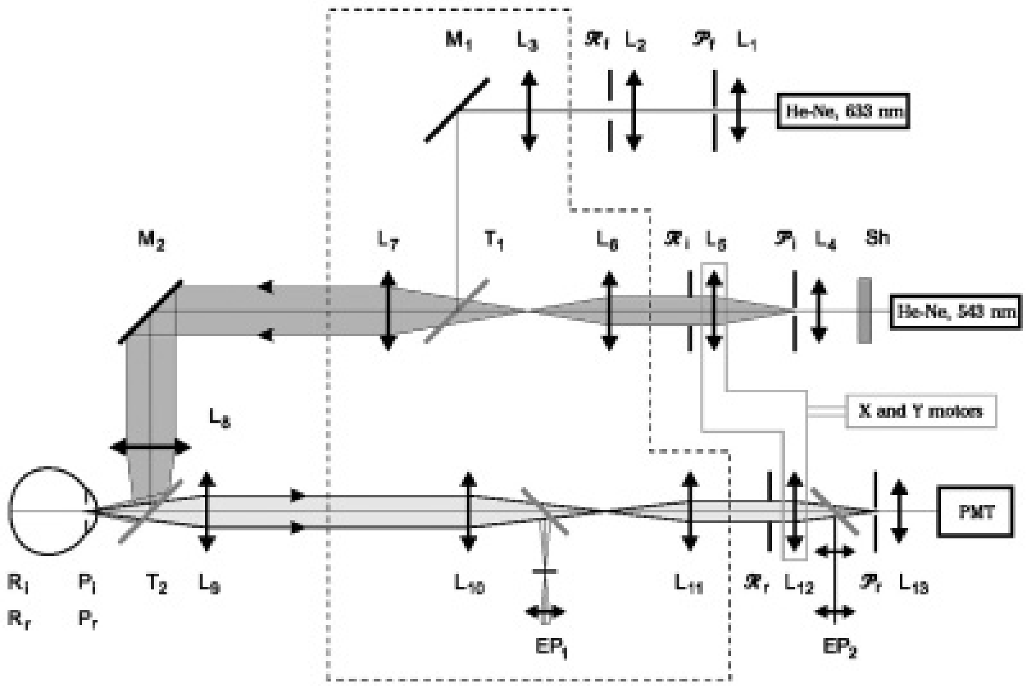

Fig. 3. Optics of the PAR. The fixation beam (red He-Ne laser) is combined with the measuring beam (green He-Ne laser) through dichroic beam splitter T_1. The reflected light is separated from the incident by beam splitter T_2. PMT : photomultiplier. P_f, P_i and P_r: circular diaphragms conjugate to the subject's pupil. R_f, R_i and R_r: circular diaphragms conjugate to the retina. L_1 to L_{13}: objectives. EP_1 and EP_2: eyepieces.

of 1 % Mydriacyl to a minimum diameter of 7 mm. The retinal test site (hereafter the foveola) was bleached at 95 % for 10 s before the scan sequence of the subject's pupil.
As mentioned above, the same principle was applied by De Lint et al.,[13] who developed a custom-built scanning laser ophthalmoscope to determine the directionality of photoreceptors. Entry and exit pupils were moved jointly in the horizontal meridian over the subject's pupil, thus simultaneously altering the retinal angles of entrance and exit beams.

Moving exit pupil (method EX)

The directional properties of photoreceptors are determined by measuring the bidirectional reflectance distribution function (BRDF) of the retina. In such a configuration the entry pupil remains fixed. Such a principle was applied in the design of the reflectometers of van Blokland and van Norren, and Burns et al.
Van Blokland and van Norren [43-44] built a set-up where light enters the eye via an 0.5 mm entry pupil P_i. Light reflected from the retina is collected through a 1.2 mm exit pupil P_r and analysed in term of intensity as a function of the position of the exit pupil. The entry pupil can be either central, or 3 mm into the temporal or nasal side. The exit pupil scans the horizontal axis.
Burns et al.[9-10] improved this method by measuring the spatial distribution of light remitted from the retina in the plane of the subject's pupil (Fig. 4). The position of the entry pupil J is chosen such that it be aligned with photoreceptor axes. The image of the pupil is then formed on a cooled CCD camera.

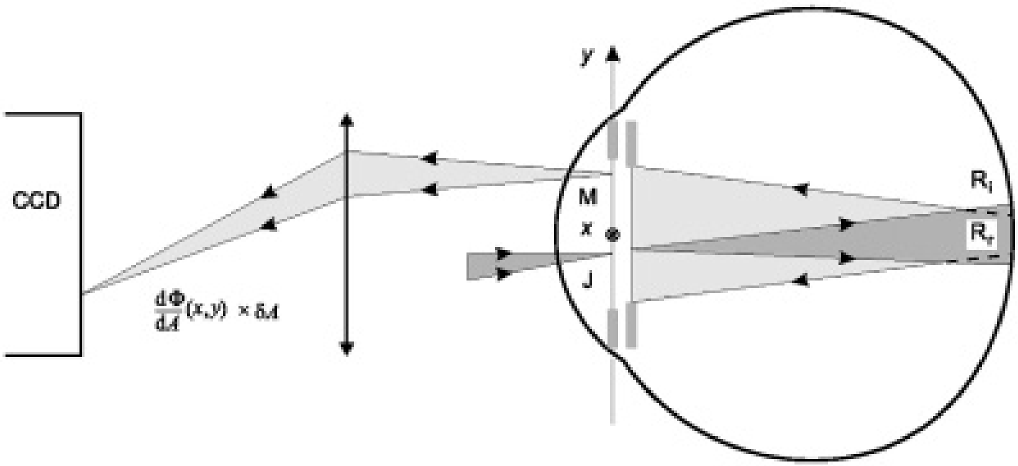

Fig. 4. Measurement of the bidirectional reflectance distribution function of the retina. The cooled CCD camera is conjugate with the subject's pupil.

The experimental data from the above authors consist of the distribution of light in the subject's pupil (Fig. 4). They are fitted to the function:

$$d\Phi / dA = C + B\,10^{-\rho_s\left[(x-x_0)^2+(y-y_0)^2\right]} \qquad (4)$$

Parameters have the same meaning as in equation 2. Contrary to the shape factor ζ, which takes into account a double passage through photoreceptors, the shape factor ρ_s corresponds to a single passage in reverse direction. Thus the letter ρ is used by analogy with the shape factor of the psychophysical Stiles-Crawford function (equation 1).

Moving entry pupil (method EN)

The third reflectometric method consists in moving the entry pupil J (Fig. 4). Marcos et al.[29] measured the total guided light Φ_g radiated from photoreceptors as a function of the co-ordinates (x, y) of J and refer their method as multiple-entry reflectometric measurements since it is derived from multiple images.
The total guided light is fitted to the function:

$$\Phi_g = B\,10^{-\rho_m\left[(x-x_0)^2+(y-y_0)^2\right]} \qquad (5)$$

The directionality factor ρ_m corresponds to a single passage through photoreceptors inwards. Roorda and Williams [34] could apply this method to sample fields as small as a single cone by means of the Rochester adaptive optics ophthalmoscope.

RESULTS

All results presented hereafter were obtained in conditions where the subject maintained a fully bleached state, so that the directional component be maximal.

Photoreceptor orientation

The orientation of photoreceptor axes within the sample field is given by the co-ordinates x_0 and y_0 in the subject's pupil (derived from equations 1, 2, 4 or 5, according to the method). Gorrand

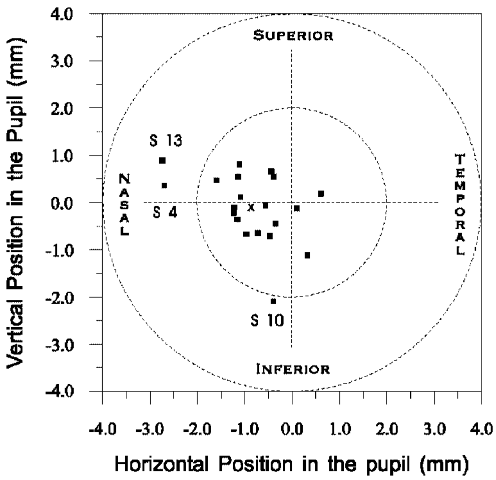

Fig. 5. Orientation of foveolar photoreceptors (20 subjects). The diameters of the two dotted circles are 4.0 mm and 8.0 mm.

and Delori [23] measured the alignment parameters from a population of 20 normal subjects with the PAR. Figure 5 gives the co-ordinates x_0 and y_0 for the twenty subjects. Each point represents the average of three measurements (SD < 0.2 mm). The mean horizontal peak location is 0.86 mm nasal (SD: 0.84 mm), and the mean vertical peak location is 0.09 mm inferior (SD: 0.73 mm). The results for most subjects are clustered within a 4 mm diameter circle around the centre of the pupil. However 3 subjects have photoreceptors with a pronounced tilt: two in the nasal direction and one in the inferior direction. OI was defined as the distance from the centre of the subject's pupil to the point of co-ordinates (x_0, y_0). The mean value of OI is 1.22 mm (SD: 0.69 mm). No correlation was found between OI and age ($r = -0.127$, $p = 0.59$).
Applegate and Lakshminarayanan [2] formed a normative database for the normal variation of photoreceptor alignment, as determined by the psychophysical Stiles-Crawford function. Their database included 53 eyes with horizontal pupil traverses, and 49 eyes with vertical ones. The mean horizontal peak location was 0.51 mm nasal (SD: 0.72 mm), the mean vertical peak location 0.20 mm superior (SD: 0.64 mm). These values are on the same order as those obtained with the PAR. Both methods demonstrate a tendency for photoreceptors to be oriented toward the nasal side of the pupil.
Different authors [8,13,25,44] have compared the measurements of cone orientation with both the psychophysical method and a reflectometric technique in the same subjects. The two types of measurements gave similar estimates of the location in the pupil toward which the cones are aligned.

Photoreceptor directionality

Depending on method

The directionality factors depend on the angular tuning of photoreceptors inside the sample field. They are denoted ρ_x (and ρ_y), ζ (and ζ_x, ζ_c, ζ_y), ρ_s and ρ_m in methods SCE, ENEX, EX and EN, respectively.
Figure 6 shows the directionality factors ζ_x, ζ_y and ζ from a population of 20 normal subjects as a function of age.[23] The mean values and standard deviations of ζ_x, ζ_c, ζ_y, ζ are given in table 1. The factor ζ_x correlates with ζ_y ($r = 0.849$, $p < 0.0001$). The factor ζ does not vary significantly with age ($r = -0.136$, $p = 0.57$).

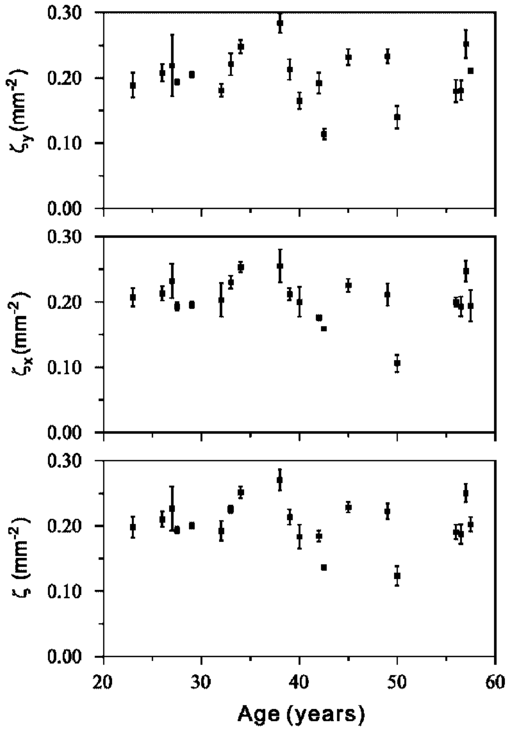

Fig. 6. Mean directionality factors ζ_x, ζ_y and ζ as a function of age (20 subjects). Each point is the average of three measurements. The bars represent ± the standard deviation of the mean.

Tab. 1. *Mean values and standard deviations of the directionality factors (20 subjects).*

	ζ_x (mm^{-2})	ζ_c (mm^{-2})	ζ_y (mm^{-2})	ζ (mm^{-2})
Mean	0.205	0.003	0.203	0.204
SD	0.034	0.023	0.039	0.035

Tab. 2. *Mean values and standard deviations of the directionality factors for the different methods.*

	Psycho-physics	Moving entry and exit pupils		Moving exit pupil		Moving entry pupil	
	Applegate[2]	Gorrand[23]	de Lint[13]	Blokland[44]	Marcos[29]	Marcos[29]	Roorda[34]
Eccentricity	Fovea	Fovea	Fovea	Fovea	Fovea	Fovea	1° nasal
Field (deg)	0.57	2	2 x 2	1.5	1	1	1 cone
Wavelength (nm)	670	543	514	568	543	543	550
Shape Factor	ρ_x	ζ_x	ζ_x	ρ_s	ρ_s	ρ_m	ρ_m
Mean (mm^{-2})	0.047	0.205	0.226	0.114	0.110	0.094	0.100
SD (mm^{-2})	0.013	0.034	0.049	0.011	0.027	0.015	0.013

The database of Applegate and Lakshminarayanan [2] also gives the directionality factors ρ_x and ρ_y. In the fovea the mean value of ρ_x was 0.047 mm^{-2} (SD: 0.013 mm^{-2}) and the mean value of ρ_y 0.053 mm^{-2} (SD: 0.012 mm^{-2}).

Table 2 allows us to compare the directionality factors obtained with the methods SCE, ENEX, EX and EN. For each of the three reflectometric methods, I have reported the measurements derived from two quite different designs. For example van Blokland [44] used a scanning exit pupil, whereas Marcos and Burns [29] took advantage of a cooled CCD camera conjugate with the subject's pupil. The sample field used by Marcos and Burns [29] (1 deg) was much greater than the field of Roorda and Williams [34] (1 cone!). Nevertheless the measured directionality factors are very close one to another in each category.

The mean value of ζ measured with moving entry and exit pupils is twice the values of ρ_s or ρ_m measured with only one moving pupil (exit or entry). This is not surprising since waveguide effects of photoreceptors intervene twice with method ENEX (in the direct and reverse paths). On the other hand waveguide effects have to be taken into account only in the direct path with method EN, and in the reverse path with method EX. Marcos and Burns [29] measured the factors ρ_s and ρ_m in the same subjects, and found that ρ_s was slightly greater than ρ_m in the fovea.

Finally the reflectometric shape factors ρ_s and ρ_m measured in the fovea are twice the psychophysical factor ρ_x, although waveguide effects seem to intervene in the same manner for each of these methods. This discrepancy will be considered in the section ''Discussion''.

Retinal eccentricity

Burns et al.[10] measured the directionality factor ρ_s across the central 6 deg of the retina. The sample field was 0.5 deg in the centre of the fovea, and 1 deg from 1 deg to 3 deg retinal eccentricity. The factor ρ_s increases rapidly from 0 deg to 1 deg retinal eccentricity (where it is equal to 0.152 mm^{-2}), which means that cones at 1 deg are much more narrowly tuned than the cones in the centre of the fovea. The factor ρ_s remains relatively constant from 1 deg to 3 deg. The same increase in directionality from the fovea to the parafovea was measured in psychophysics.[19]

Wavelength

Zagers et al.[48-49] developed an instrument for simultaneous measurement of foveal spectral reflectance and cone directionality. An imaging spectrograph (spectral range of 420-790 nm) was conjugate with the subject's pupil (the exit pupil being an horizontal bar of 0.8 × 12 mm). They measured the directionality factor ρ_s versus wavelength λ in a population of 21 subjects (for each 5-nm band in the range from 420 to 780 nm). Their experimental data were well fitted to the equation:

$$\rho_s(\lambda) = a + b\,\lambda^{-2}$$

This dependence of ρ_s on wavelength was predicted by the model of Marcos et al.[28]

Photoreceptor disarray

The directionality depends on the acceptance angles of individual photoreceptors and on the variability of their orientation within the tested photoreceptor population. Safir and Hyams[35] suggested that the acceptance angles of individual cones were narrow, and that the Stiles-Crawford effect was mainly due to the splaying of cones. But all following studies invalidated this model. MacLeod[27] developed a selective adaptation technique to study the variability of photoreceptor orientations and concluded from his experiments that the foveal cones were aligned with great precision (SD of pupil intercept position: 0.32 mm). Burns et al.[10] measured the peak location in the pupil as a function of the position of the entry pupil J (Fig. 4) and gave evidence that cone disarray for normal subjects is very small. Finally, Roorda and Williams [34] measured the orientations of individual cones and found the average disarray to be 0.17 mm in the subject's pupil. They pointed out that this disarray accounts for less than 1 % of the breath of the overall tuning function!

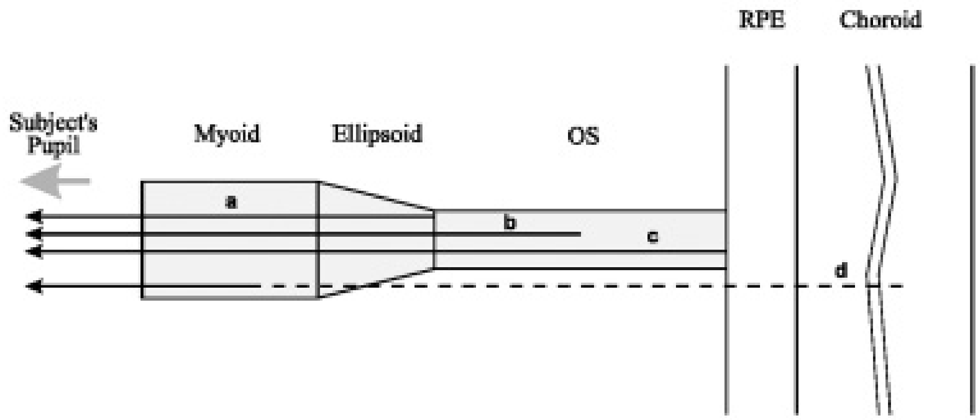

Fig. 7. Sources of light contributing to the directional component in the subject's pupil.

DISCUSSION

Origin of the directional component

The characteristics of the different fundus layers likely to reflect, scatter or absorb light were summarised by van Norren and Tiemeijer,[46] and Delori and Pflibsen.[14] The retinal pigment epithelium (RPE) and the choroid contain melanin granules, whose absorption spectrum decreases monotonically with increasing wavelength throughout the visible spectrum. Blood inside the choroid has an optical density which is high at 543 nm, but minimal in red: therefore the contribution of the choroidal stroma and the sclera to the reflection process remains small at 543 nm, but preponderant over 600 nm.

Hereafter we call photoreceptor those of its components which have indexes of refraction higher than the index of the interphotoreceptor matrix (Fig. 7), i.e. the myoid, the ellipsoid and the outer segment (OS). The myoid collects light from the pupil, and the outer segment is the photosensitive pigment-bearing zone. In 1946, O'Brien [31] formulated a theory in which he suggested that the ellipsoid of the cone acts to funnel the energy from the myoid into the OS. Thus the OS of the cone has higher energy density than the myoid for rays incident normally or near normally because they integrate over the area subtended by the myoid. But for larger angles of incidence on the photoreceptor, rays strike the tapered ellipsoid at angles less than the critical angle, and a part of the energy is then refracted out of the photoreceptor. In 1949, Toraldo [42] refined this model by considering the photoreceptor as a dielectric waveguide, and the ellipsoid as an impedance-matching device between the myoid and the OS.

The directional component of the distribution of light in the subject's pupil comes from light guided back and radiated from the myoid to the pupil. Figure 7 depicts the principal sources of this directional component. In green light, these sources are the ellipsoid (''a''), the lamellae [45] inside the OS (''b''), and the OS-RPE interface (''c''). The OS-RPE interface reflects some light since the RPE cytoplasm refractive index is lower than the OS index. Recently Pallikaris [32] et al. reinforced this source of reflection ''c'' by measuring the reflectance of individual cones every hour for 24 hours. The temporal change in reflectance is likely to be related to the process of disc shedding in the RPE.

For wavelengths greater than 600 nm, blood absorption is minimal, and thus light backscattered from the sclera or the choroidal stroma can follow the path ''d''. This light is unlikely to be captured by the OS tips, but can excite guided modes in the ellipsoids and the myoids. Doble et

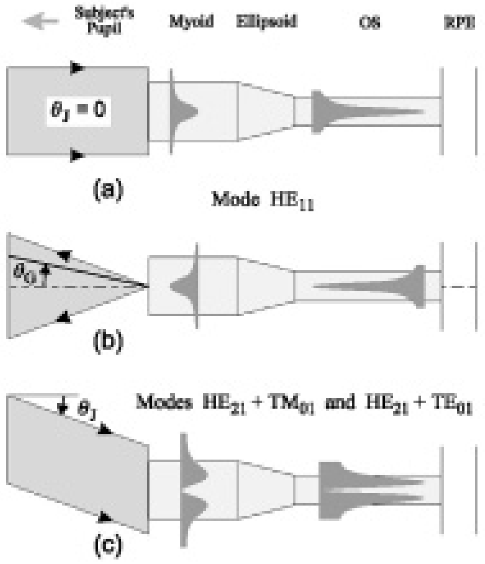

Fig. 8. (a) The wave coming from J excites the modes HE_{11} which are guided through the photoreceptor. (b) Light reflected by the OS-RPE interface launches the modes HE_{11} backwards. (c) The modes TE_{01}, TM_{01} and HE_{21} are also launched for small or medium angles of incidence.

al.[15] gave evidence to this source of light "d" by imaging the cone mosaic at 750 nm with the Rochester adaptive optics ophthalmoscope.

Discrepancy between directionality factors derived from different methods

The reflectometric shape factors ρ_s and ρ_m measured in the fovea are twice the psychophysical factor ρ_x. The aim of this section is to discuss this discrepancy. Enoch [17-18] demonstrated that the photoreceptors behave as waveguides by observing modal patterns inside outer segments. The number of modes that are guided by a waveguide depends on the waveguide parameter [38] V defined by:

$$V = \frac{\pi\, d}{\lambda}\sqrt{n_{co}^2 - n^2}$$

where λ is the wavelength in vacuum, d the waveguide diameter, n_{co} and n the respective refractive indices of the core and surrounding medium. When the test field is centred around the foveola, the retinal area is occupied much more by cones than by rods. Using values available in the literature [7,12] yields $V = 3.38$ and 2.58 for the myoid and outer segment from the foveolar cone. Only the modes HE_{11} (2 modes), TE_{01} (1 mode), TM_{01} (1 mode) and HE_{21} (2 modes) have lower cut-off values, and thus are capable of propagating through the myoid, the ellipsoid and the OS. These modes may be launched by the wave incident upon the myoid.[39] When the entry pupil J is aligned to the photoreceptor axis, only the modes HE_{11} can be excited (Fig. 8 A). As the incidence angle θ_J increases, the modes TE_{01}, TM_{01} and HE_{21} can also be excited (Fig. 8 C). Finally when J is far from cone axes, light incident upon the myoid cannot launch any guided mode. The total power carried by guided modes is maximal when $\theta_J = 0$, and decreases as θ_J increases.

He et al.[25] found that psychophysical measurements (method SCE) give broader estimates of cone directionality than do optical measurements (method EX) when measured in the same indi-

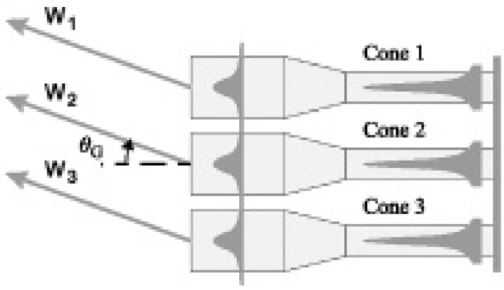

Fig. 9. Light radiated from adjacent cones may add coherently at the pupil plane.

viduals, under similar conditions. They also pointed out that a broad psychophysical tuning function from a given subject did not necessarily correspond to a broad optical tuning function in that subject. Figure 8 depicts the conditions at the retina with the reflectometric method EX. The wave coming from J (aligned to the myoid axis) excites the modes HE_{11}, which are guided through the myoid, the ellipsoid and the OS (Fig. 8 A). Light reflected by the OS-RPE interface may launch guided modes backwards, then be radiated toward the subject's pupil, contributing to the directional component (Fig. 8 B). Gorrand and Delori [24] presented a model where they defined coupling coefficients at the OS-RPE interface and gave theoretical and experimental arguments that coupling between the modes HE_{11} inwards and the modes TE_{01}, TM_{01} and HE_{21} backwards is very poor. Consequently power guided backwards is carried mainly by HE_{11} modes. The reciprocity theorem of optics predicts that the solid angle into which light is radiated from the myoid to the pupil is identical to the angle from which the myoid accepts light. Therefore light carried by modes HE_{11} backwards is radiated from the myoid to the pupil in a solid angle much smaller than the "effective" acceptance angle of the myoid (which takes also into account the modes TE_{01}, TM_{01} and HE_{21}). As a consequence the optical directionality factor ρ_s is higher than the psychophysical factor ρ_x. Another physical phenomenon likely to increase the factor ρ_s comes from the interferences between wavelets radiated from adjacent photoreceptors (Fig. 9); Marcos and Burns [28] developed a model where each cone acts as a small coherent light source, so that light with different phases will add coherently at the pupil plane.
Marcos and Burns [29] developed the reflectometric method EN, which was likely to give directionality factors ρ_m closer to the psychophysical factor ρ_x. Indeed the total amount of light guided as a function of entry pupil position represents a measure of the waveguide properties of the photoreceptors and should be more similar to psychophysical estimates of photoreceptor directionality than to the estimates from the method EX. But they found that factors ρ_m were twice the psychophysical factors ρ_x (Tab. 2). Figure 10 depicts their experimental conditions at the retina. For medium angles of incidence θ_J, only the modes TE_{01}, TM_{01} and HE_{21} are excited and guided through the photoreceptor (with leakage from the ellipsoid and OS). Gorrand and Delori [24] showed that coupling at the OS-RPE interface between the modes TE_{01}, TM_{01} and HE_{21} inwards and backwards is poor. Consequently the power carried by these modes backwards and radiated from the myoid to the subject's pupil is small, and the optical factor ρ_m is likely to be much greater than the psychophysical factor ρ_x.

Stiles-Crawford effect and optical aberrations

Every method demonstrates a tendency for photoreceptors to be oriented toward the nasal side of the pupil. Since the fovea is on the temporal side of the eye optical axis, it is commonly assumed that this nasal shift of the SC peak favours rays whose angles of incidence upon the cornea are low, i.e. rays with small aberrations (this nasal shift would be 0.42 mm if the angle α

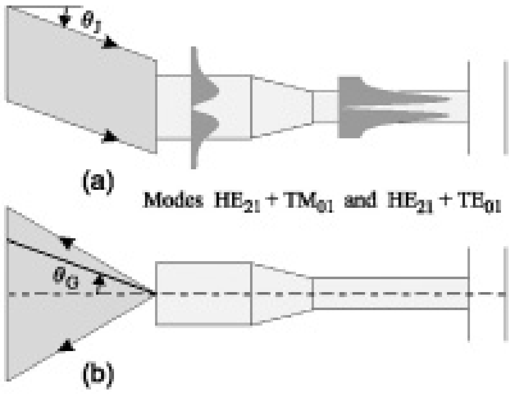

Fig. 10. Experimental conditions at the retina of the "Moving Entry Pupil" method.

between the optic and visual axes was 5°). Indeed cone directionality produces a pupil apodisation, limiting the effective pupil size, and potentially reducing the impact of aberrations in pupil areas away from the location of maximum luminous efficiency.

In order to answer the question whether the retina acts like an optimal instrument, Marcos and Burns [30] carried out a nice study by measuring the wavefront aberration and cone directionality functions in 24 eyes (right and left eyes of 12 subjects). Their conclusion was that cone directionality apodisation does not always occur at the optically best pupillary region and that in general the ocular optics and cone alignment do not develop toward an optimal optical design.

Stiles-Crawford effect and visual performances

The directional properties of cones minimize the capture of stray light and produce a pupil apodisation. Different authors studied the functional effect of this pupil apodisation on visual performance.

Atchison and Scott [3] measured contrast sensitivities with a 6 mm pupil diameter and three SCE conditions (normal, neutralised and doubled). The SCE could be neutralised or doubled by means of filters made of photographic film. They used 6 mm pupils because this represents a reasonable upper limit to pupil sizes under photopic conditions for which the SCE is likely to have its maximal effect. Atchison et al.[4] investigated the influence of the S-C peak location on visual acuity and contrast sensitivity. Apodising filters were used to move the peak far from the natural position. These two studies indicate that the SCE plays a minor role to improve visual performance when eyes are in focus.

Alignment process

Photoreceptor alignment is thought to be governed by a phototropic mechanism that actively orients their axis toward the entrance pupil of the eye.

Eckmiller [16] proposed that the alignment of photoreceptors is accomplished by a feedback-controlled bending of the cell at the myoid. Certain unspecified local changes occur within the myoid that are appropriate to activate molecular motors and induce local movements by cytoskeletal elements (microtubules and microfilaments). Bending can be accomplished by a differential change in the length of the myoid at different positions around the cell perimeter.

But we saw in figure 5 that for three of the subjects (S4, S10 and S13), foveal photoreceptors were oriented to pupil locations which were further than 2 mm from the pupil centre; at least in these eyes photoreceptor alignment does not seem driven by light.

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