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Visible electromagnetic radiation in the eye

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Dedicated to Prof Jay M Enoch

This contribution, dedicated to honor Jay M Enoch, will give a short and rather limited overview of some of his very important research achievements in vision, trying to pay due appreciation to them and, in so doing, to be informative and pedagogical. Visible electromagnetic radiation processed by eye optical-neural system provides the basis for visual transduction into physiological activity. Enoch is responsible for important contributions, in collaboration with other researchers, to the Stiles-Crawford effect, namely, the directional sensitivity of photoreceptors to light entering into the eye. Moreover, it is due to Enoch that we owe the first experimental demonstration of the wave propagation of light, in the form of states known as propagation modes, in vertebrate visual photoreceptors. Such states of light contain, in ordinary conditions, a very large number of photons and have a dual character: after having propagated along photoreceptors, according to classical electromagnetic optics, their detection in the retina proceeds due to the absorption of their photon contents.

Keywords: Electromagnetic radiation, Propagation, Photons, Eye vision mechanism.

1 Introduction

Phenomena related to electromagnetic radiations and their propagation are ubiquitous. More specifically, electromagnetic radiations, and their photon fluxes and interactions with retinal receptors have a fundamental character. The paper will treat the propagation and phenomena of light in vertebrate visual receptors (to which Prof Enoch made very important contributions) and, later, it will proceed to overview the photon contents of radiations and their properties and consequences. This work is planned as follows. Section 2 summarizes the propagation and phenomena of visible light in vertebrate visual receptors and the important contributions made by Enoch and other researchers; see [1] for an overview. Section 3 discusses the photonic contents of visible radiation and how it gives rise to transduction briefly. Section 4 contains conclusions and comments.

2 Classical propagation phenomena

2.1. A short description of human eye retina

About 70 per cent of the information received by the human brain proceeds through visual perception in the eyes from our surroundings. Human eye (and the eyes of a full variety of living creatures) start to process that information by absorbing the electromagnetic radiation in their Human Visual System (VHS). For HVS the visible wavelengths range is 400 to 700 nm. Ultraviolet radiation is absorbed by other tissues

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(for example, the cornea and the intraocular lens) in the eye, while infrared (IR) one is not perceived although it is received as well from Sun radiation and other IR sources.

The retina is a highly complex biological tissue formed by ten layers [1]. To consider a simplified model, it will suffice to describe the retina as formed by: i) an external layer (pigment layer, or pigmented epithelium), in which incoming light from outside the eye gives rise to an optical image, ii) a second layer, behind i), formed by the photoreceptors (also named receptors), iii) the remaining layers, behind ii), contain: outer synaptic layers, horizontal cell, bipolar cells, amacrine cells, inner synaptic layer, ganglion cells, nerve fiber layer and the inner limiting membrane. The set of layers iii) transmit information from the retina to the optic nerve.

Individual retinal vertebrate photoreceptors play crucial and successively complementary roles. They are optical waveguides for the electromagnetic radiation, as it was experimentally demonstrated by Jay M Enoch earlier in 1961 [2]. Subsequently, the radiation is absorbed by these biological waveguides to be processed. Photoreceptors morphology is nowadays studied extensively [3] for a state-of-the-art analysis by 2009. We can distinguish two differentiated types, depending on their role in the visual perception mechanism: rods and cones. Rods are long and narrow and responsible for the scotopic vision. Cones are short and thick and responsible for the photopic vision. Rods are sensible to radiations of low intensity, while cones are sensible for colors vision. Vertebrate rods and cones are elongated and polarized, with closely similar structures. The transverse size of one single photoreceptor is, on average, a few microns. They indeed behave as inhomogeneous absorbing optical waveguides [4].

A photoreceptor (rod and cone) is divided into the so called inner and outer segments. The inner segment is formed by mitochondria, nucleus and endoplasmic reticulum (connecting to synaptic terminals): besides providing energy and performing protein synthesis, the inner segment behaves as a microwaveguide for light confinement. The outer segment contains the machinery required for transduction. The inner segment is closer to the pigmented epithelium than the outer one. So, the inner segment traps the incoming light entering into the eye and guides it to the outer segment where the photon is captured and transduction occurs. More specifically, the outer segment contains, besides other biological tissues, a stack or column of parallel disks (spaced more or uniformly at intervals of about 28 nm). The disks contain photoreceptor molecular devices, responsible for the absorption of light.

In the following section, the incoming light, its propagation and effects on receptors are described using classical optics.

2.2. On the contributions by Enoch

In their pioneering work in 1933 [5], Stiles and Crawford determined that light entering the periphery of a dilated pupil of an eye was a less effective stimulus for vision than entirely similar light, with the same physical characteristics (intensity, spectrum of wavelenths, etc.) entering the center of the pupil. This established experimentally the sensitivity of photoreceptors to the angle of incidence of light on a retina as an important factor in human vision. More specifically, cones exhibit high directional sensitivity, that is, they respond preferentially to light incident through the center of the pupil. This became known as the Stiles-Crawford effect. It gave rise to a very active research, as described below.

During about three decades, Enoch and other researchers [6] extended the investigations on the Stiles-Crawford effect and obtained important results on all questions of receptor optics, in particular directional sensitivity and receptor alignment (for normal eyes in vertebrates and for eyes pathologically altered), in retinal receptors.

Regarding orientation and consequences in vision mechanism, in particular, directionality is shown to hold for both rods and cones. A panoramic view of those works is presented in [6]. A generalization was studied later by Enoch *et al* for the modelling of birefringent optical waveguides, with influence on the light stimulus distribution in optical nerve fiber of the retina [7].

In the first direct experimental demonstration done by Enoch, establishing that the receptors of vertebrates were optical waveguides, he observed the characteristic patterns of propagation modes in waveguides [8]. This gave rise to further investigations by him and other researchers. All that is also presented in [6]. These waveguiding properties of receptors are also treated classically. A summary of those works and results is the following:

1) Although ideally one would like to study waveguiding properties of the retina in living eye and in spite of a variety of additional experimental information, it was adequate and necessary to work with excised retinas, in undamaged samples adequately preserved long enough to make measurements.
2) A few species of vertebrate animals were selected for the experiments with their retinas: albino rats, frogs, goldfish, salamanders, squirrels, monkeys, to give some examples.
3) In particular, an instrument based upon microspectrometry was designed by Enoch enabling to study waveguide properties of a single receptor (see references in chapter 5 in [6]).
4) An approximate (ideal) model for describing waveguiding properties of one single receptor consists in assimilating it to a cylindrical dielectric waveguide of circular symmetry and radius R. The waveguide has two different indices of refraction (each of them being a constant): one inside (n_1) and another one outside (n_2) it, with $n_1 > n_2$. (See Fig 1).

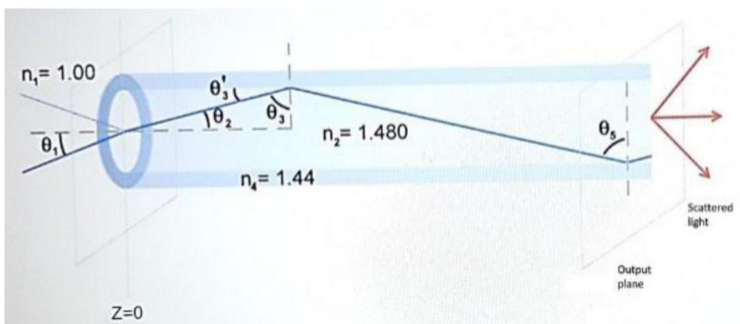

Fig 1. A schematic description of the geometry and ray confinement by total internal reflection, in a cylinder optical waveguide. The values indicated for refractive indices are typical ones, for the case of a standard optical waveguides made by glass.

Notice that, for a general treatment, the absorption properties of the optical photoreceptors have to be taken into account. Then, this implies the introduction of a complex refractive index: $\tilde{n} = Re\tilde{n} + iIm\tilde{n}$, where $Re\tilde{n}$ stands for the real part accounting for the transmission properties, and $Im\tilde{n}$ stands for the imaginary part, accounting for the absorption properties of the optical photoreceptors [9].

As rough (averaged) estimates for a single photoreceptor, one could take: R between 1.1 to 1.4 microns, $n_0 \approx 1.3$, $n_1 - n_0 \approx 0.06$, see the discussion in chapter 5 in [6]. Consequently, one can use such a model and standard conventions to refer to its propagation modes (see chapters 6 in [6] and [10]).

In short, for a given waveguide and electromagnetic radiation with fixed wavelength λ (in vacuum), there exist a discrete set of waves propagating confined indefinitely along the waveguide. These waves are named as the propagation modes. The electromagnetic fields, characterizing each propagation mode, decrease rapidly in the transverse directions to the axis of the waveguide and determine a characteristic three-dimensional distribution of electromagnetic energy density propagating indefinitely along the waveguide. There is one mode, the so-called fundamental one, such that it exists for any wavelength. In qualitative terms, even if it describes confined propagation, it amounts to the smallest concentration of energy inside the waveguide. For all other propagation modes, there are restrictions on their wavelengths and they can be classified so that the higher their order is, the more concentrated is the energy in the waveguide.

The modal patterns commonly observed in vertebrate receptors correspond approximately to the following propagation modes or linear combinations thereof, for the approximate (ideal) model discussed above in the present item 4. In increasing order, these propagation modes are: HE_{11} (the fundamental one); TE_{01}, TM_{01}, HE_{21}; (TE_{01} or TM_{01}) + HE_{21}; HE_{12}; EH_{11}; HE_{31}; HE_{12} + (HE_{31} +/or EH_{11}); HE_{31}+ EH_{11}; EH_{21} or HE_{41}; TE_{02}, TM_{02}, HE_{22}; (TE_{02} or TM_{02}) + HE_{22} (see Fig 2). See chapter 5 in [6].

5) By observing directly waveguide modal patterns in individual photoreceptors, it is concluded that the set of receptors in the retina of a vertebrate can be regarded as a bundle of optical fibers.

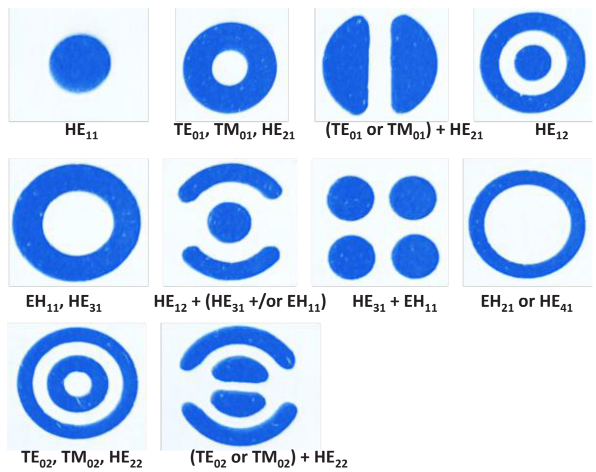

Fig 2. Graphical representation of low-order electromagnetic modes as formed in an optical waveguide for light confinement. Optical photoreceptors support these types of propagation modes as light enters and propagates confined along the former, under conditions of total internal reflection.

3 Photon contents and their action in vision processes

Electromagnetic radiation is formed by quanta (photons): one photon contained in a radiation with wavelength λ has energy hc/λ, where c is the velocity of light in vacuum and h is Planck constant. Experiments aimed at detecting one single photon in vision (and achieving it with increasing efficiency) have a rather long story along the 20th century. G I Taylor in 1909, carried out a pioneering experiment [11] employing visible light emitted by a dim light source and requiring exposition times up to three months!. This pioneering experiment showed that only one photon, passing through a double slit at a time, suffices to produce interference. This experiment was followed by others which confirmed and sharpened the results in [11]. For further experiments in which only one photon was detected and, so, establishing the interference of a single photon with itself, see [12,13]. At this stage, it is illustrative to quote [14] the following mean photon-flux densities (given in photons/s-cm^2) in electromagnetic radiations emitted by various sources: starlight: 10^6; moonlight: 10^8; twilight: 10^{10}; indoor light: 10^{12}; sunlight 10^{14}; laser light (a 10 mW He-Ne laser beam with wavelength 633 nm): 10^{22}.

We shall consider various standard heated bodies, as sources emitting electromagnetic radiations. Let us consider an ordinary light bulb (in a household lamp): usually, the bulb contains a coil of Tungsten wire suspended inside the glass envelope, which also encloses an inert gas. A voltage is applied to the ends of the filament outside the glass envelope, so that an electric current flows through the coil. When the filament becomes incandescent (say, at absolute temperature 2750 K), it glows and radiates light, with a continuous spectrum of wavelegths. Such a continuous spectrum includes the interval of visible light. Photons emitted by the filament have all wavelengths contained in that continuous spectrum. Other important examples are the Sun, blackbody radiation and thermal ones as standard examples. Thermal radiations are those obtained when blackbody radiation is passed through some linear filter (apertures, gratings, mirrors, lenses, polarizers, spectral filters). Those are typical sources of light giving rise to visual perception by the eye.

The sensitivity of the eye to detect photons is very high. In a human eye, fully adapted (after an adequately long time) to darkness, Hecht, Schlaer and Pirenne in 1942 [15] conducted an experiment, in which the immediate goal was to find the least possible intensity of light that permitted a subject to see flashes of controlled color, size, location and duration, for variable intensity. The result of the experiment was that the absorption of one single photon of light with wavelength 510 nm by a tiny area of a rod (during a millisecond flash) in an eye suffices to generate one nerve impulse. See [1] for detailed explanations. Further experiments confirmed the very important finding in [15]. In a pioneering work carried out by S I Vavilov and coworkers, in 1933 [16], regarding the perception of light by the eye, they conducted detailed visual investigations of quantum fluctuations. The eye adapt so well that a flux of a few tens of photons per second through the pupil initiates vision: fluctuations phenomena also occur.

By taking into account that 1 $cm^2 = 10^8$ $micrometers^2$, one can infer directly from the above data the average number of photons which go across the transverse section of one single photoreceptor per second. That enables to understand the results of the experiment in [15]. Conversely, as a simple practical recipe, the propagation of electromagnetic radiations with wavelengths below the ultraviolet threshold and containing large mean photon-flux densities can be treated classically (disregarding its photon contents) and even through classical Optics, with sufficient accuracy. This holds, in particular, for visible radiations. This justifies a posteriori that visible light, as it propagates in photoreceptors can be regarded as a classical radiation [2].

Photons and their quantum nature play a key role in the absorption of light in photoreceptors. At the molecular level, absorption of light in the disks of the outer segment of a rod starts by the capture of one photon by an organic molecule named rhodopsin. The probability that a photon with wavelength 500 nm propagating down a rod outer segment of length 60 microns be captured by one rhodopsin molecule has been estimated to be about 89 percent. One single photon can produce a rearrangement of only one rhodopsin molecule out of 109 molecules contained in the rod. Rhodopsin, like all visual pigments, is a member of a family of receptors named GPCR (meaning G-protein coupled receptor), a large helical protein: the family comprises a large number of receptors (including hormones, neurotransmitters, peptides and even small ions). The importance of the G-protein stems from the fact that in vertebrate and invertebrate photoreceptors investigated (including retinal rods and cones), transduction is affected by a sequence of reactions initiated by a GPCR protein. We shall not extend further on this. See [3,17].

4 Conclusions

We have presented a brief description of the history of optical photoreceptors, both for theory and experimental studies. This subject concerns the earlier and pioneering work of Jay M Enoch, who in particular, first evidenced that vertebrates optical photoreceptors behave as optical waveguides. His studies gave rise to this key branch of visual optics, which has been extended to more specific studies, connecting applications and techniques to characterize visual mechanism and, in some cases, with a link to clinical applications. For obvious reasons, we have not entered into this last matter.

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