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CONTRIBUTION TO THE THEORY OF PHOTOPIC VISION -- RETINAL PHENOMENA

H. Calvet

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16. Abstract

Principles of thermodynamics are applied to the study of the ultramicroscopic anatomy of the inner eye. Concepts introduced and discussed include: the retina as a three-dimensional sensor, light signals as coherent beams in relation to the dimensions of retinal pigments, pigment effects topographed by the conjugate antennas effect, visualizing lights, the autotrophic function of hemoglobin and some cytochromes, and reversible structural arrangements during photopic adaptation. A paleoecological diagram is presented which traces the evolution of scotopic vision (primitive system) to photopic vision (secondary system) through the emergence of structures sensitive to the intensity, temperature and wavelengths of the visible range.

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CONTRIBUTION TO THE THEORY OF PHOTOPIC VISION - RETINAL PHENOMENA

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Just as respiration manifests itself essentially by a chemical exchange between an inner and an outer medium, so vision may be considered the resultant of a physical linkage between the eye and ambient radiation.

We would like to show how, in the course of evolution, the eye has progressively adapted to its luminous environment. In passing from an anterior to a posterior medium it has encountered more and more complex radiation. Subjected to the action of such kinds of radiation it has been able to modify its structures and its functions.

Photopic or diurnal vision is based essentially on the preponderant functioning of the cones. It requires a somewhat high energy threshold. This type of vision makes focal perception possible and defines forms and colors.

The other type of vision deals with a lower energy level. It is known as scotopic or nocturnal vision and is conditioned by the activity of the rods. It makes possible peripheral vision, less cleancut and more general but more sensitive to movements and to minute differences in luminosity.

We will identify the seat of photopic vision with the macular area approximately 2mm in diameter. This area is centered in the fovea or foveola. It corresponds to the zone where the surface density of the cones is greater than at any other point of the retina (Figures 1 and 2).

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*Numbers in the margin indicate pagination in the foreign text.

[1] Dr. Henri Louis Calvet, Dissertation, Faculty of Medicine, Montpellier, 1946; Specialty, Ophthalmology, Paris, 1948; Asst. Ophthalmologist, 15-20 group, 1950; Consultant Ophthalmologist for group of factories of Radiotechnique et Usine Associees, 1951; Charter member, World Society of Ergophthalmologists, Amsterdam, 1968: Treasurer, French Ergophthalmological Society, Paris, 1971; Associate member, Stanford Research Institute, 1973; numerous international publications in particular on fundamental physiology of vision and especially on light/matter interaction at the endocular level

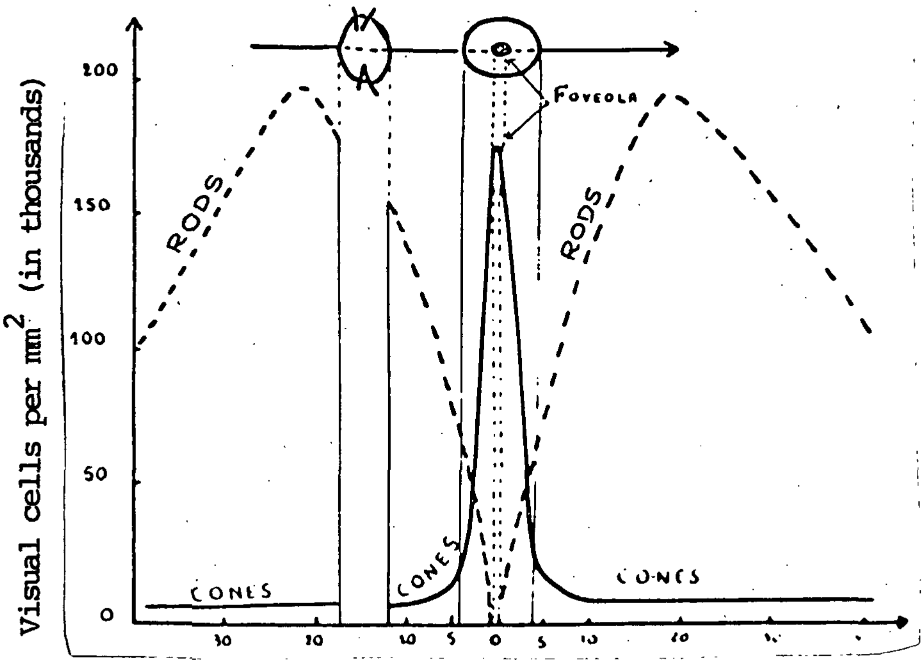


Fig. 1. Distribution of photoreceptors (Osterberg modified)

a - sclera
b - choroid vessels
c - Bruch's membrane pigment epithelium
d - rods and cones
e - outer limiting layer
f - outer granular layer
g - outer plexiform layer
h - inner granular layer
i - inner plexiform layer
j - ganglion cells
k - optic nerve fibers
l - inner limiting layer

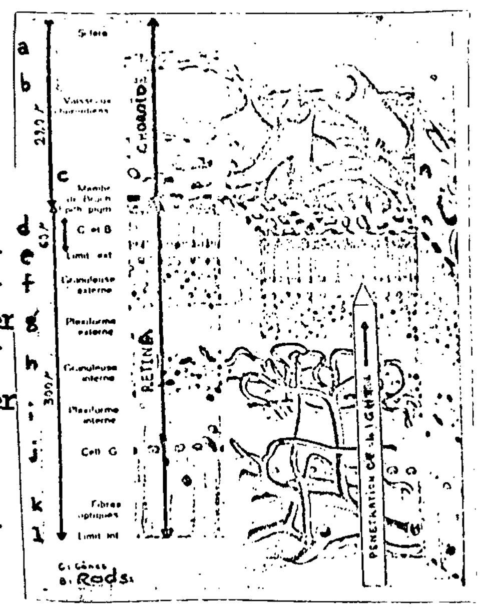


Fig. 2. Diagram of retinal vascularization (Podesta and Ulrich modified by Calvet)

It is admitted that the action of the photons on the retina is photochemical. This has given rise to a comparison between the retina and a photographic plate with the usual properties: rigidity, indeformability, immobility and a thickness so small as to be ordinarily negligible.

Such a comparison scarcely accounts for the phenomena which occur in the retina.

Our investigations have led us to propose a different concept that places great importance on microdeformations of the retina as well as on its thickness.

Moreover it takes /14
into account some elements and phenomena, whose role has been overlooked until now and which make useful contributions to the explanation of vision.

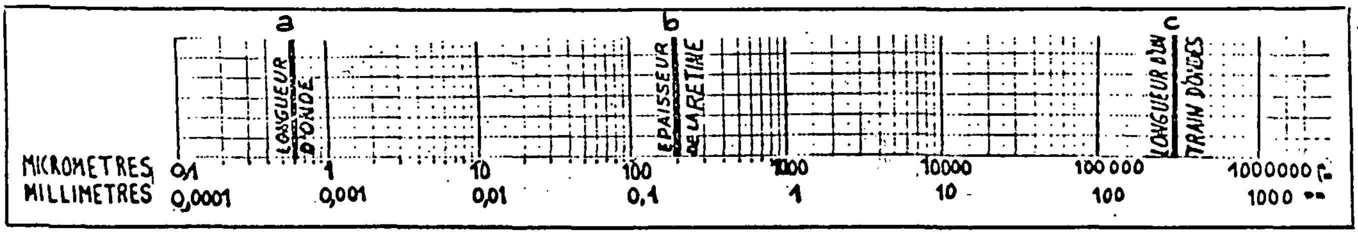


Fig. 3. Comparison of an anatomical dimension with two optical dimensions - logarithmic scale.

Key: a - wavelength
b - thickness of the retina
c - length of a wave train

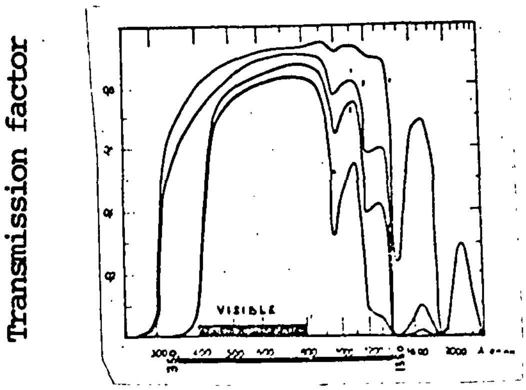


Fig. 4. On a wavelength logarithmic scale ranging from 250 to 2500 nm the figure shows the transmission factors: Curve 1 - cornea, Curve 2 - cornea and aqueous together, Curve 3 - cornea, aqueous and crystalline lens together, Curve 4 - totality of optic media of the human eye. (Redesigned after Boettner and Wolter, 1962, with a slight modification) (Crouzi) (Remodified by Calvet)

The principal ones refer to:

— analysis of light penetration at the level of the deep membranes of the eye,

— the presence of thermal intraocular gradients,

— the existence of types of "visualizing light" that broaden the specter of visible light,

— the activity of certain pigments, such as hemoglobin and some cytochromes, which have an autotrophic function and also play an auxiliary role in vision.

Of course, this model respects all known data in respect to the anatomy and physiology of the eye and the physics of light.

First of all it is interesting to compare retinal thickness, which constitutes a third dimension neglected until now, with two of the basic dimensions that characterize the structure of natural light. These are respectively:

— wavelength,

— average length of a wave train.

Two figures give an idea of these values. The first is anatomical (Fig. 2) and the second is a diagram on a logarithmic scale (Fig. 3). They show that the (average) thickness of the macular retina is about 200 microns (the length of a cone alone) occupies 80 microns). The wavelength of visible light is around 0.6 microns.

Natural light, considered incoherent when compared with lasers, is also made up of successive wave trains ordinarily 300,000 microns long. This is proved by the fact that it is possible to produce interference patterns with natural light.

If the thickness of the retina is taken as a unit, we may say that at a given moment the retina is engaged by several hundred wavelengths and that a thousand retinas would have to be stacked up to cover a wave train. Thus natural light acts as a temporarily coherent light in respect to retinal receptors.

A parallel analysis, which would compare the length of a wavelet of natural light with the distance separating the rods or cones from each other, would lead us to admit that natural light also acts as though it were spatially coherent.

Moreover, we may legitimately suppose that the propagation of reds is deeper than that of violets. Here "red" and "violet" refer not only to the colors of the visible spectrum (which is rather arbitrarily limited to wavelengths between 400 and 800 nm) but also to the bands which cover them toward the small and large wavelengths. For these "reds" and "violets", which are undoubtedly present in daylight, are not completely arrested by the anterior portions of the eye, as is shown by the curves of Boettner and Wolter (Fig. 4). Thus the energy that reaches the deep membranes embraces two lateral bands that frame the visible band. One lies toward the infrareds (800–1350 nm), the other toward the violets (350–400 nm).

The energy supplied by these two bands is as natural to the eye as "natural" food is to the digestive system, where problems would arise if the amount of food were limited strictly to portions that can be assimilated.

Even if the transparency of the anterior organs were low in regard to these wavelengths, their importance in perception may be noteworthy because of the high intensi- /15 ty produced by these bands due to sources and circumstances.

The phenomenon of stage penetration already referred to is comparable to that which controls the propagation of electromagnetic waves in conductors and in electronics is known as "skin thickness" for high frequencies. If we accept a similar law for the light arrested by the deep membranes, we may say that the infrared at 1350 nm would penetrate four times as far as the violets at 350 nm.

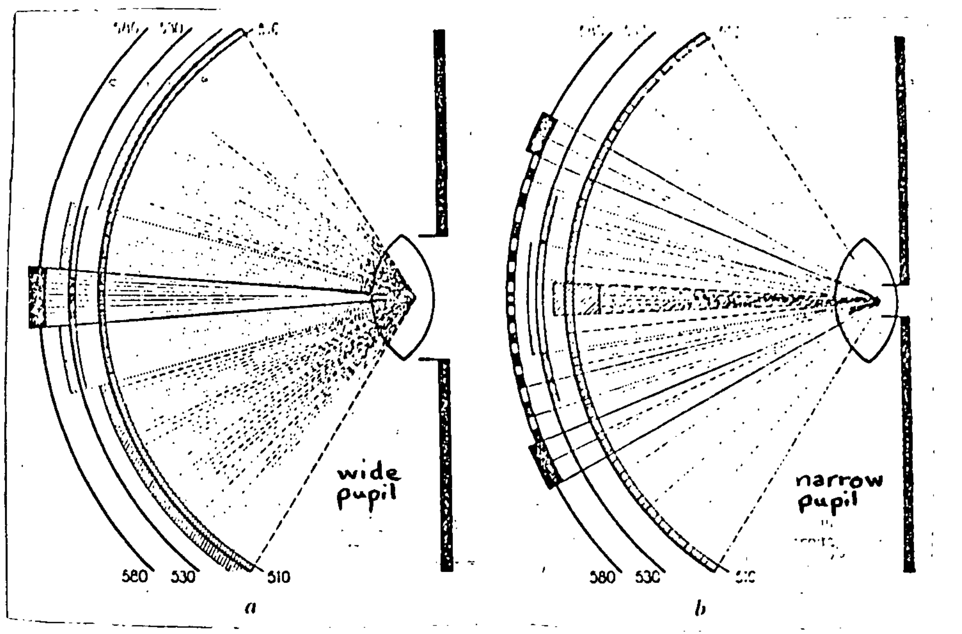


Fig. 5. Definition of retinal zones of penetration - distribution of energy as a function of dispersion and diffraction of the rim of the pupil and of depth of penetration as an "optic relay effect". a) mydriasis: scotopic vision, b) myosis: photopic vision. Between a and b phenomenon which tends to invert zone arrangement (Calvet diagram).

Thus, corresponding to incident energy the retinal zone exhibits physical levels of arrangement like that of onion skins. Precisely the anatomical structure of the eye corresponds strictly to this sort of energy stratification. This explains the close link between the eye and light. We should note in passing, that the distribution of energy, not deeply but superficially, is controlled by the simultaneous action of refraction and dispersion, which are a function of the indices of the ocular media,as well as of diffraction, which depends upon pupil diameter (that may vary from 1 to 4 according to the subject).

A very much simplified diagram, in which for teaching purposes the effects mentioned above have been grossly exaggerated, encapsulates these phenomena (Fig. 5).

Let us now return to the cone layer. It corresponds to the depth of penetration of the visible band. Just before reaching this layer the light traverses a zone which is the inner part of the outer segment (Fig. 6). It corresponds to a cell territory occupied by the myoid as well as by numerous mitochondria which abound in the cones although they are much less plentiful in the rods.

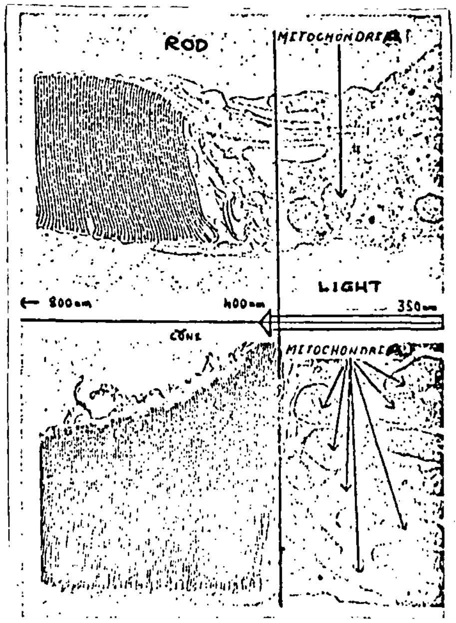


Fig. 6. Photograph (44,000 diameters) of cones (below) and rods (above) by Kuwabara. Phenomenon of mitochondrial concentration in the cone (after Calvet).

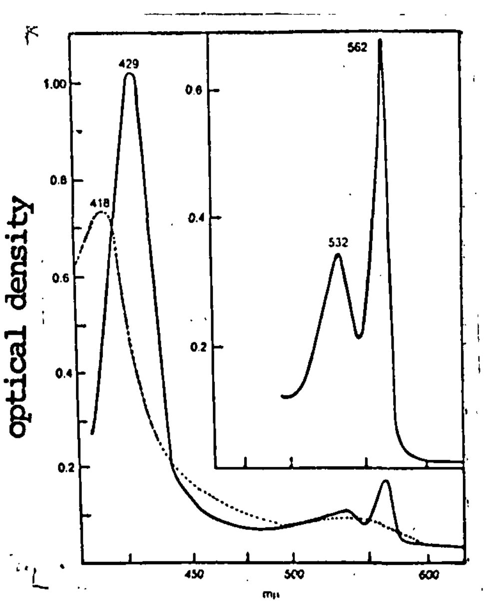


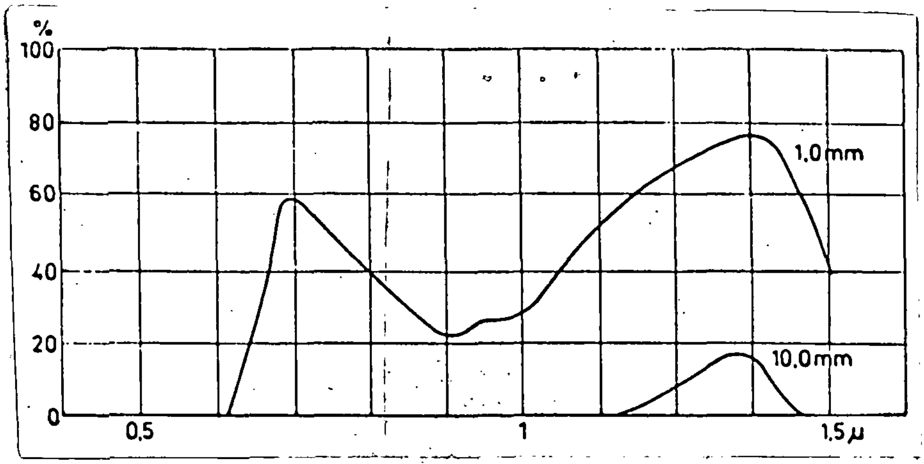
Fig. 7. Cytochrome absorption spectrum (cytochrome b). Solid line: reduced form ($Na_2S_2O_4$); broken line: oxidized form (after Bromstein et al.)

Now, in the interior of their membranes the mitochondria contain cytochromes, which are photosensitive pigments, whose absorption maximum is in come cases around 400 nm (Fig. 7). The cytochromes themselves are made up of chromoproteins with a prosthetic radical consisting of a tetrapyrolithic nucleus containing a metal atom (of the iron type). In our opinion, this typical molecular architecture justifies attribution of the autotrophic function. /16

Let us go over now to the other side of the cone layer, i.e. toward the rear, following the path of the light. Here we find the pigment epithelium, whose absorption layer shows a maximum in the 900 nm band (Fig. 4) and the energy absorbed at this level determines at that point a true thermal gradient.

Still farther back is the choroid, which is reached by the proximate infrared (up to 1350 nm). Now this section is characterized by a great deal of melanin and hemoglobin, which are true absorptive and photosensitive pigments.

Hemoglobin, the basic component of the blood, in the infrared shows a strange absorption curve with a maximum squarely in the 900-1350 nm band (Fig. 8). Now the chemical relationship between hemoglobin and cytochrome is very close. The latter also has a prosthetic radical with a tetrapyrolithic nucleus containing a metal atom (iron) and making hemoglobin likewise autotrophic. For there is a close analogy with chlorophyll, which is responsible for photosynthesis. The chemical structures of its prosthetic radic-



al are identical, except for the metal atom, where magnesium replaces iron.

This latter level of choroid absorption is matched by a second thermal grädient.

Fig. 8. Transmission curve for oxyhemoglobin

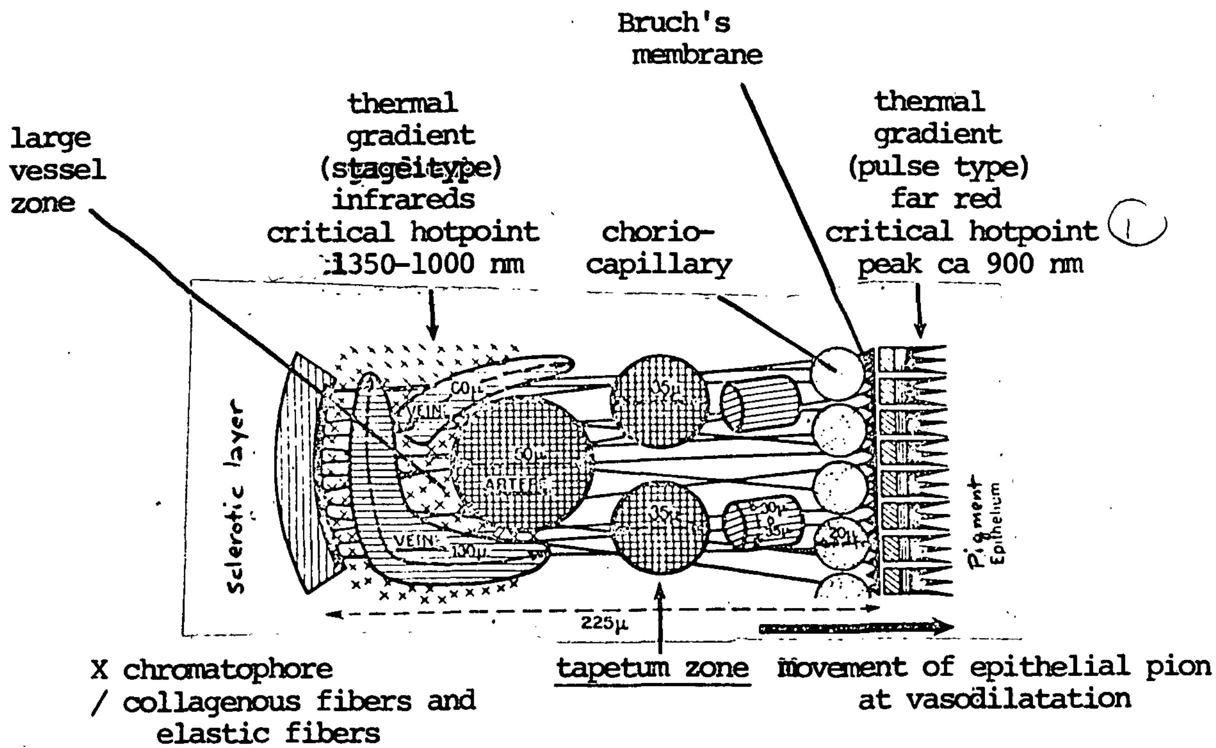


Fig. 9. Calvet diagram of functional unit: sclero-choroid-retinal complex, figuration of choroid thermal gradients (stage type), retinal thermal gradients (pulse type)

All the facts just presented suggest a new terminology for the basic mechanisms of retinal vision and facilitate the analysis of the phenomenon of photopic adaptation.

Actually in the case of daylight, on the one hand the post-retinal thermal gradients set up by the infrareds induce a turgescence which results in a forward surge,

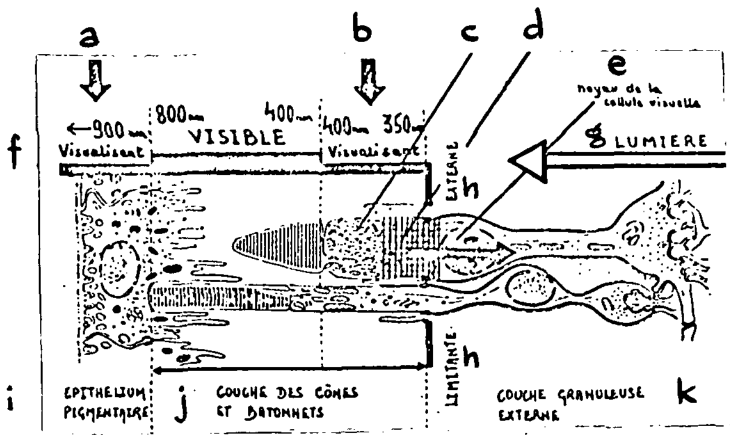


Fig. 10. Diagram of first neuron of human retina (a cone above and a rod below, after Missoten). Energy penetration by stages, according to λ, in deep ocular media. Action of myoid muscle (after Calvet).

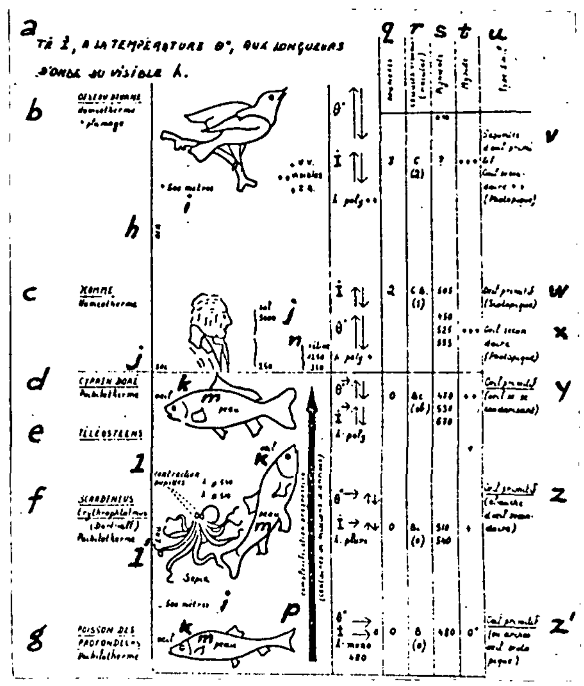
Key: a - thermal gradient of retina
b - mitochondria (cytochromes)
c - mitochondria
d - myoid muscle
e - nucleus of visual cell
f - visualizing
g - light
h - outer limiting membrane
i - pigment epithelium
j - layer of rods and cones
k - outer granular layer

while on the other hand the mitochondria that capture the proximate ultraviolet, being located ahead of the cone layer, create traction through contraction of the myoid muscle under the influence of glycogenic modifications induced by the captured energy and this action combines with the surge referred to above.

Thus everything takes place as if, by means of micrometric displacements, some elements of the retina had just taken up an optimal position in respect to the light.

This will be borne out by the following two diagrams. The first (Fig. 9) represents the sclero-choroid-retina complex, which constitutes a "functional unit". It is characterized by the intimate connection between the sclerotic layer and the superimposed lamellae of the lamina fusca, whose prolongations in the form of collagenous and elastic fibers travel thru the stroma. These fibers reach the outer and middle zones of the Bruch membrane, where they form veritable mooring boundaries and a root system layer. The pigment epithelium is integral to them. The left side of the figure shows the zone of the large vessels gorged with hemoglobin. There is also a representation here of the heavy concentration of melanocytes and this is the level where we find the choroid thermal gradient.

At the right we see first of all the capillary layer, then Bruch's membrane with its mooring masses and finally the pigment epithelium seat of the retinal thermal gradient.



EVOLUTION OF VISION
Emergence of functions sensitive to intensity I, to temperature θ° and to wavelengths of visible light λ

Fig. 11. Evolutionary biological transformations controlled by radiations from the ecological environment. B: rods, C: cones (Calvet diagram)

Key:
- a - sensitivity to intensity I°, to temperature θ° and to wave-length of visible light λ
- b - diurnal bird, homeotherm, plumage
- c - man, homeotherm
- d - goldfish, poikilotherm
- e - teleosts
- f - Scardinius erythrophthalmus (Dartnall), poikilotherm
- g - deep sea fish, poikilotherm
- h - air
- i - 500 meters
- j - ground
- k - eye
- l - pupillar contraction
- l'- water
- m - skin
- n - retina
- o - [not used]
- p - progressive complexity over thousands of years
- q - eyelids
- r - visual cells, maculae
- s - pigments
- t - myoid
- u - type of eye
- v - sequels to primitive eye, secondary eye (photopic)
- w - primitive eye (scotopic)
- x - secondary eye (photopic)
- y - primitive eye (moving toward secondary)
- z - primitive eye (outline of secondary eye)
- z'- primitive eye (or archeo-scotopic eye)

In the second diagram (Fig. 10) we see the cone layer on a large scale. (A rod issintroduced by convention). We notice that the light goes from right to left. The diagram also represents the stage arrangement of the phenomena and organs. We find successively from left to right:

— the pigment epithelium where absorption of the peak in the 900 nm range occurs,

— the cone layer where visible light is absorbed,

— the sublayer of mitochondrial concentration and of the myoid, which also has further ramifications,

— the membrane referred to as the outer limiting layer,

— the outer granular layer, which contains the nuclei of the visual cells and the ramifications of the myoid, whose contractile action is shown by an arrow.

Thus, in conclusion, from the time of adaptation to photopic vision reversible structural arrangements take place in the retina.

In our time the differentiation in human visual organs between photopic and scotopic vision is very marked. Using as our guide the action of light as a function of media and over a period of time we may propose an evolutionary model, which explains this differentiation and takes us back to the primitive unicity (Fig. 11).

Let us consider first of all the deep sea fish, then go to surface fish, then to the ground level populated by mammifers like man and finally up into space with the bird.

The determining element is the nature of the luminous spectrum, which conditions life at the respective ecological levels.

By emergence of functions we would like to express the way in which structures appeared that are sensitive to intensity of "I", to temperature of "$\theta°$" and to wavelength of visible light or "λ",

In the sea 500 meters down, where the medium is definitely isothermal, filtered daylight has its spectrum reduced to a ray of 480 nm. At this level the eye of the fish is taken as the reference or "primary" eye. It has only rods with filiform myoid and the only visual pigment shows a selective absorption between 470 and 490 nm.

The fish living closer to the surface where the spectrum is broader typically exhibits the characteristics of the Dartnall fish: it has two visual pigments with absorption peaks around 510 and 540 nm. But this fish presents us with an enigma: the proportion of the two pigments depends either upon water temperature or upon illumination. This accounts for the role played by water temperature in respect to the fish's skin. This fundamental role will persist in the homeotherm, who has merely enclosed "in his bag of skin some of the medium in which the fish swims". At this level we find the outline of a more complex eye, which we will call "secondary", superimposed on the primary eye for functional adaptation to light and heat variations.

This complication of factors corresponds to the light sense, to the awakening of the color sense and to the "thermal component" of vision and it will be accentuated in the surface fish and later more particularly in man, where scotopic vision is a survival of deep sea vision. Photopic vision is a later acquistion. Due to paleo-ecological adaptation to light, which occurs at ground level and has a spectrum ranging approximately from 260 to 3000 nm, the membranes of the eye receive a band extending from 350 to 1350 nm. Classically the retina uses only the section from 400 to 800 nm, yet lateral bands from 350 to 400 nm and from 800 to 1350 nm cooperate in the visual act as sources of visualizing energy that control the phenomenon of photopic adaptation while adhering to thermodynamic principles.

The bird, endowed with a richer spectrum, shows the most advanced differentiation: each of its eyes manages to have two retinal territories of macular vision.