# THE NEW PHYSIOLOGY OF VISION

## Chapter X. The Major Visual Pigments

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THE two preceding chapters of this treatise dealt with the part of the spectrum in the wavelength range between 400 m$\mu$ and 500 m$\mu$ and elucidated the nature of the visual process by which the colours ranging from blue to violet in that region are perceived. We next proceed to explore the rest of the spectrum in the wavelength range between 500 m$\mu$ and 700 m$\mu$ with a view to discover what the characters of the spectrum in this region can reveal to us regarding its origin.

Visual inspection enables the spectrum between 500 m$\mu$ and 700 m$\mu$ to be divided roughly into three parts. The first part between 500 m$\mu$ and 550 m$\mu$ may be described as the green sector of the spectrum. In the second part which ranges between 550 m$\mu$ and 600 m$\mu$ we observe a rapid progression of colour, from green to a greenish-yellow and then to a pure yellow and beyond this again to an orange-yellow hue and then orange. The third part of the spectrum between 600 m$\mu$ and 700 m$\mu$ exhibits colours ranging from orange to crimson red through various intermediate hues. The colour sequence thus summed up has in the past been sought to be explained as the result of the superposition of the "fundamental" sensations of green and red respectively, their relative importance varying over the range, green being dominant at one end and red at the other. That this view is erroneous and needs to be rejected becomes clear when the actual facts of the case are set out and we consider their theoretical significance.

The most striking feature of the spectral range between 550 m$\mu$ and 600 m$\mu$ is the appearance within that range of a strip exhibiting a pure yellow hue. This colour presents no similarity either to the green or to the red of the spectrum, while the colours observed on either side of the strip may be described as a superposition upon a pure yellow sensation of weaker green and red sensations respectively, their proportion to the yellow increasing as we move away from the wavelength at which the sensation perceived is pure yellow. It may be remarked also that the pure yellow appears in the spectrum in a region where the luminous efficiency is very high and indeed not much less than the maximum.

The facts stated above justify us in recognising the wavelength range between 550 m$\mu$ and 600 m$\mu$ as that in which yellow is the dominant sensation. We may also justifiably infer that the yellow sensation results from the presence in the retina of a pigment which has an absorption peak at the point where the pure yellow sensation manifests itself in the spectrum. Thus, instead of relegating the yellow of the spectrum to the position of a minor or secondary sensation, we accord to it its rightful place as the principal or major visual sensation, while blue, green and red which appear in the parts of the spectrum where the luminous efficiency is smaller and which are indeed the most colourful parts of the spectrum should nevertheless be considered as playing only a minor role in vision. The identification of the visual pigment which functions as the receptor of the yellow in the spectrum accordingly assumes very special importance.

The statement that yellow is the major visual sensation is no more than an explicit recognition of the factual situation. Inevitably, therefore, such recognition is essential for a satisfactory or successful elucidation of the entire body of visual experiences in the field of colour. In particular, when we examine the hues exhibited by various objects in daylight and seek to correlate them with the spectral character of the light diffused or scattered by the object and reaching the eyes of the observer, we find that the presence or absence of the yellow in that spectrum plays the determining role. We shall not here enter more deeply into this subject, as it will be dealt with very fully in later chapters under the heading of the visual synthesis of colour. In the present chapter, we shall concern ourself principally with the identification of the visual pigment in the retina which enables us to perceive the yellow sensation. For this purpose, we shall consider the characteristics of the spectrum in greater detail.

*Hue Discrimination in the Spectrum.*—As has already been remarked, a rapid progression of colour is noticeable in the spectral range between 550 m$\mu$ and 600 m$\mu$. Many authors have determined the minimum change of wavelength necessary at various points in the spectrum to produce an observable change of hue. There is general agreement that the shift of wavelength needed is everywhere rather small except near the very ends of the spectrum. It is exceptionally small at two particular points in the spectrum; one of them is at 490 mμ where the blue of the spectrum changes over rapidly to green. The other point is at 579 mμ where the spectrum exhibits a pure yellow hue, the observed colour changing rapidly to a greenish-yellow and to an orange-yellow respectively on the two sides of it.

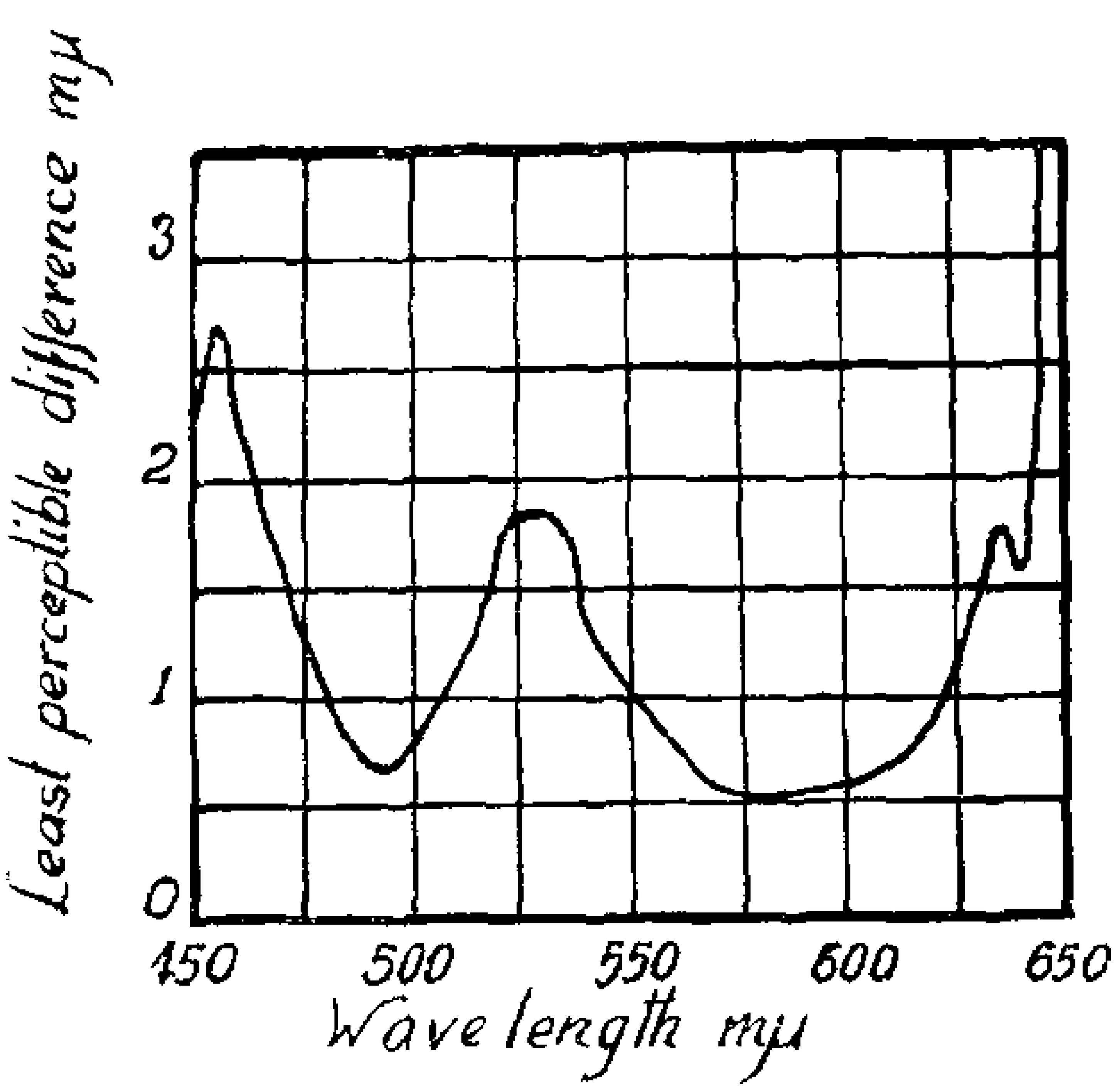


FIG. 1. Curve of Hue Discrimination.

Figure 1 reproduces the results of an extremely thorough and accurate study of hue discrimination made at the Bureau of Standards in Washington by E. P. T. Tyndall, and presented as a graph in a paper by that author (*Jour. Opt. Soc. Am.*, Vol. 23, 1933, page 15). It will be noticed from the graph that the least perceptible difference in wavelength reaches its minimum value of 0·5 mμ at 579 mμ. That this is exactly where the spectrum exhibits the pure yellow colour is readily verified by observation. Visual comparison in a wavelength spectrometer of the two lines of the mercury arc spectrum appearing at 5770 Å and 5790 Å reveals that the two lines differ noticeably in colour, the former appearing distinctly greenish in hue, while the latter appears as a perfect yellow. Placing a marker in a continuous spectrum at the point separating the greenish-yellow from the orange-yellow regions and taking the average of a series of readings, the mean comes out as 579·5 mμ ± 0·5 mμ. This agrees very closely with the point in Tyndall's graph at which the power of hue discrimination is at its highest.

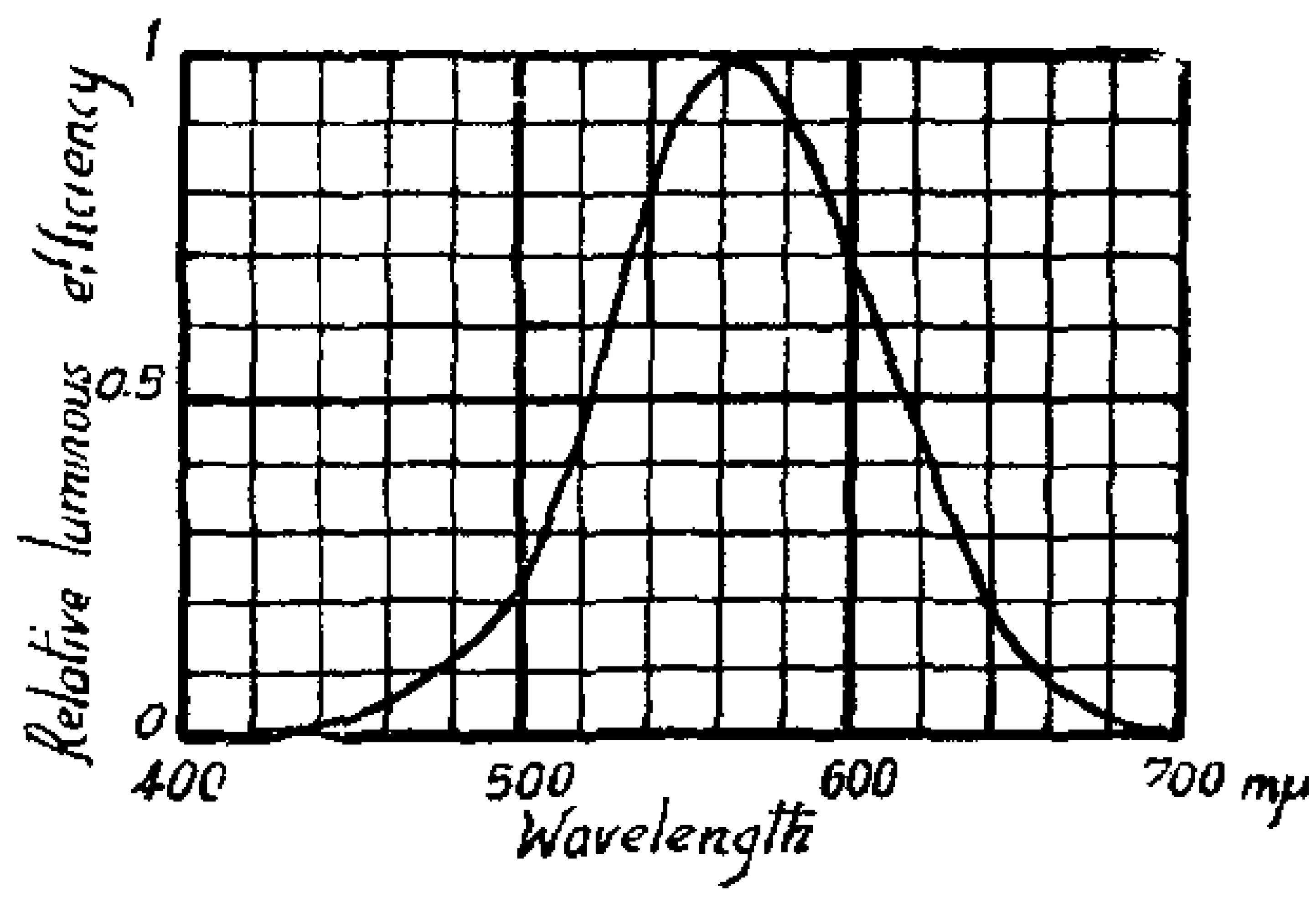


FIG. 2. Luminous Efficiency in the Spectrum.

It is evident from what has been stated above that the curve of hue discrimination is of great importance in its bearing on the visual processes which result in the perception of colour. It is necessary, however, to consider its indications along with those furnished by the curve exhibiting the variations of luminous efficiency over the visible spectrum. Figure 2 exhibits the form of that curve for foveal vision as actually determined. It will be seen that the luminous efficiency reaches its maximum value at 565 mμ. But as the efficiency falls off from the maximum more slowly towards greater wavelengths, the efficiency in the yellow at 580 mμ is not markedly smaller than the maximum. On the other hand, it will be seen from the figure that the luminous efficiency falls to much smaller values at 530 mμ and 630 mμ which are the wavelengths at which the colours in the spectrum are respectively pure green and pure red.

The remarkably high power of colour discrimination exhibited at 579 mμ, also to a lesser extent on either side of 579 mμ is a clear indication that these features have their origin in a powerful absorption by a visual pigment having a well-defined peak of absorption at 579 mμ. But the maximum of luminous efficiency appears at 565 mμ and not at 579 mμ. Likewise, the hue discrimination curve exhibits a markedly asymmetrical course, running steeply between 550 mμ and 579 mμ and much less steeply between 579 mμ and 600 mμ. These features indicate that other visual pigments also play a not unimportant role in these spectral regions.

*Identification of the Principal Visual Pigment.*—The blood-pigment heme in its various forms is known to exhibit an extremely powerful absorption of light in the spectral range with which we are now concerned. Since the presence of heme in one form or another within the substance of the retina can be safely assumed, we may proceed to examine whether its known spectroscopic behaviour can furnish a clue to the explanation of the facts of colour perception in human vision.

Heme is present in human blood principally as the compound known as oxyhemoglobin which gives it a red colour. The addition of a drop or two of blood to water contained in a cuvette results in the exhibition of a powerful absorption of light. Examination through a spectroscope reveals a sharply-defined dark band at 579 mμ and a much broader and weaker absorption band around 546 mμ. Reduction of the pigment to the form of hemoglobin by the addition of a little sodium dithionate results in a remarkable change in the characters of the absorption. It then manifests itself as a diffuse band of which the maximum may be located around 555 mμ. These facts are clearly brought out in Fig. 3 in which the absorption curves of oxyhemoglobin and hemoglobin determined spectrophotometrically have been exhibited.

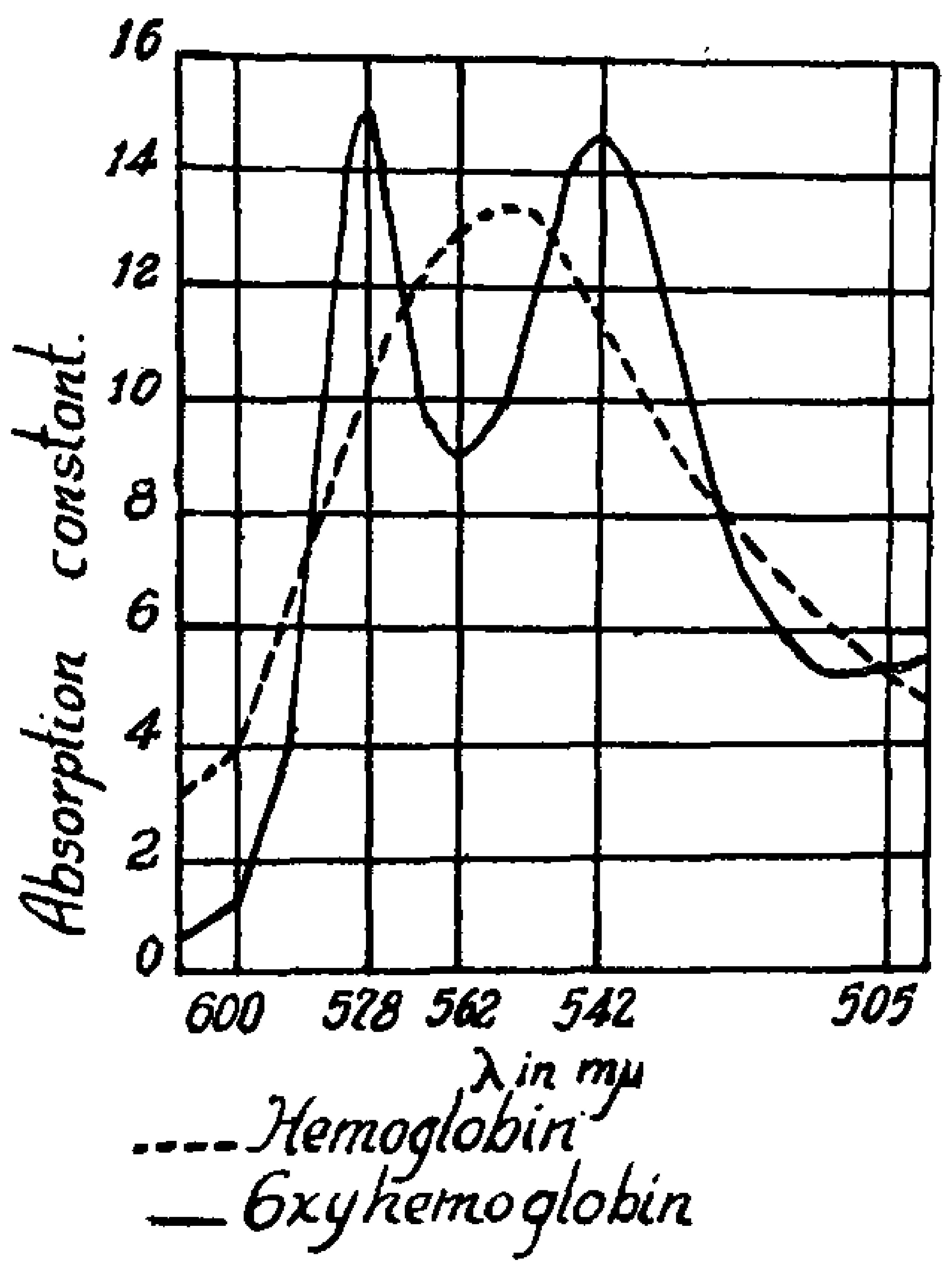


FIG. 3. Absorption Cuives of the Blood Pigment.

The curves have been copied from a paper by David L. Drabkin appearing in the *Barcroft Memorial Volume on Hemoglobin* (Butterworth's, London, 1949). In another paper appearing in the same publication, Felix Haurowitz has reproduced spectrum photographs exhibiting similar features; the positions of the absorption bands of oxyhemoglobin have been marked therein as 579 mμ and 546 mμ respectively.

The exact coincidence of the absorption at 579 mμ exhibited by oxygenated blood with the position in a continuous spectrum of the strip exhibiting a pure yellow colour can be readily verified by holding a cuvette containing water to which a few drops of blood have been added behind the eye-piece of a wavelength spectrometer and viewing a continuous spectrum through it. The absorption band just covers the yellow strip in the spectrum, while measurements with the wavelength drum give the position of its centre as 579 mμ. The inference appears fully justified that the heme pigment in the fully oxygenated form is present in the human retina and that it is indeed the principal visual pigment which enables us to perceive the most highly luminous part of the spectrum. This inference is further confirmed and reinforced when it is remarked that the sharpness of the absorption band at 579 mμ and its great intensity are matched by the narrowness of the strip in the spectrum exhibiting the pure yellow colour and the very high luminous efficiency of the part of the spectrum in which it appears.

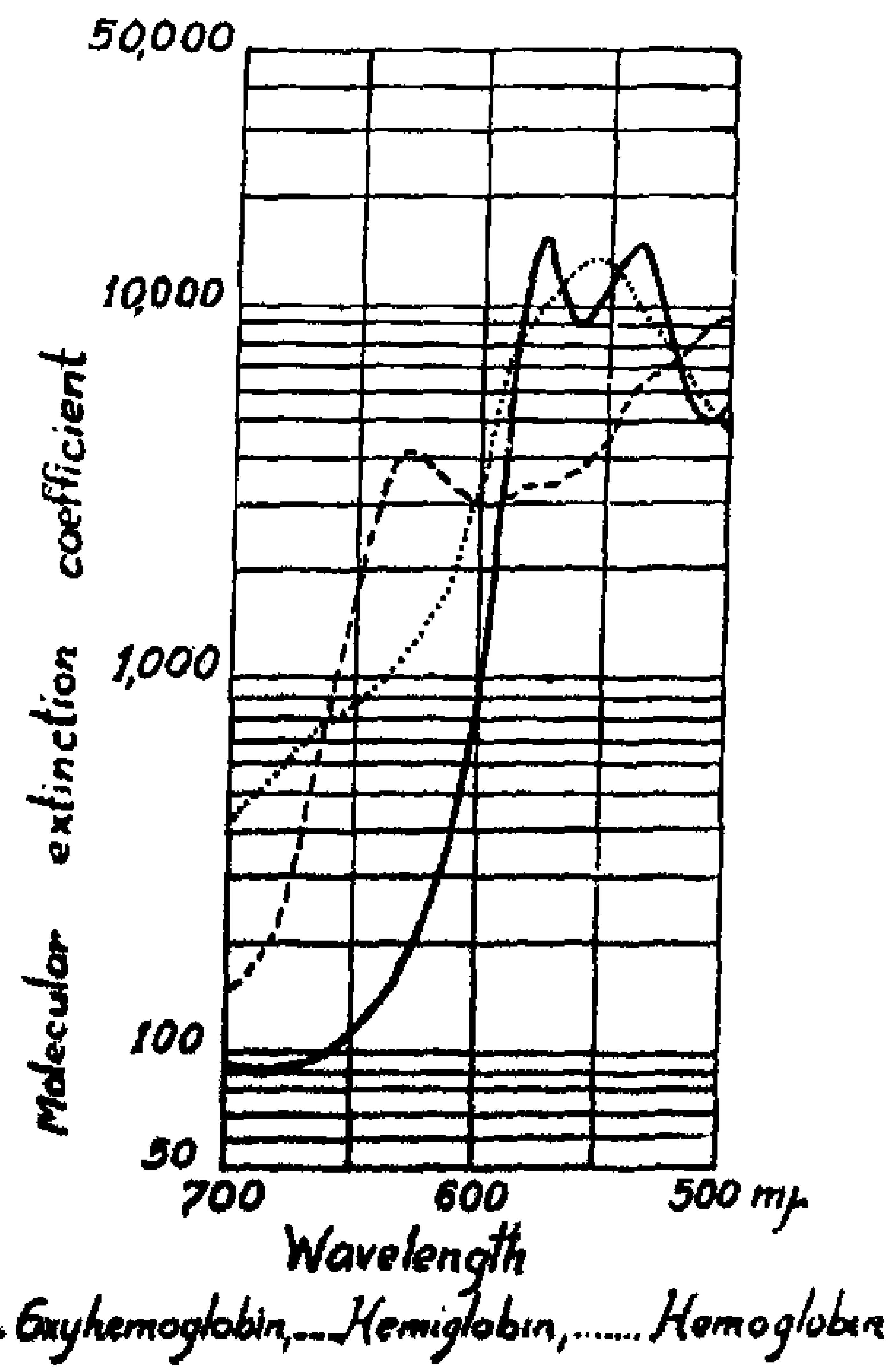


FIG. 4. Molecular Extinction Coefficients of Heme Pigments.

*The other Visual Pigments.*—As has already been remarked, the heme pigment in its oxidised form would not suffice by itself fully to explain the observed characteristics of the spectrum even within the restricted range of wavelengths between 550 mμ and 600 mμ in which yellow is the dominant sensation. To obtain a complete picture of the situation, we have to consider also the wavelength range between 500 mμ and 550 mμ and the range between 600 mμ and 700 mμ. In these two ranges, the predominant colour sensations are those of green and red respectively. It may reasonably be inferred that we are also concerned with two other visual pigments whose contributions to the luminous efficiency are important respectively in these two regions.

It is well known that there are two other pigments chemically related to oxyhemoglobin which are known respectively as hemoglobin and hemiglobin. The first of these results from the action of reducing agents on oxyhemoglobin and the second by its auto-oxidation. It may therefore reasonably be assumed that the human retina contains three pigments based on heme whose spectroscopic behaviours are respectively similar to oxyhemoglobin, hemoglobin and hemiglobin.

Figure 4 exhibits the molecular extinction coefficients of these three pigments over the wavelength range between 500 mμ and 700 mμ, reproduced in part from the plate at the end of the book by Lemberg and Legge on *Hematin Compounds* (Interscience, New York and London, 1949). The proportions in which the three pigments are present in the retina would determine their contributions to the perception of luminosity and colour in the spectrum. In a general way, it can be seen that the superposed effects of the three pigments would explain the observed characteristics of the spectrum in respect of colour and luminosity over the range of wavelengths between 500 mμ and 700 mμ. Particularly noteworthy is the fact that a steep drop in the molecular extinction coefficient of hemiglobin appears at about 630 mμ (*see* Fig. 4), while there appears in Fig. 1 a sharp dip in the hue-discrimination curve at about the same wavelength. A steep drop in the molecular absorption coefficient of one of the visual pigments operating in this region would necessarily result in a marked improvement in hue discrimination at the same wavelength.

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## CRYSTAL SYMMETRY AND MAGNETIC PROPERTIES

S. BHAGAVANTAM

A CRYSTAL is built by an infinite periodic repetition in space of identical structural units. Conventionally, by the symmetry of a crystal is meant the symmetry of its spatial structure. The set of all spatial transformations which transform every point of such a structure into another point equivalent to it and also every direction into an equivalent one, forms a group which is called the space group of the crystal. There are 230 space groups and it is well known that these space groups constitute the basis for all the distinct patterns that can be identified in crystals. If we consider only the symmetry of directions at a point in a crystal, the set of all rotations and rotation-inversions which transform every direction of the structure into an equivalent direction form a group which is called the point group of the crystal. There are 32 distinct point groups of spatial transformations and these are called the 32 classes in crystallography.

The macroscopic properties of a crystal depend only on its symmetry of directions which is its point group symmetry. This dependence of the macroscopic properties of a crystal on its point group symmetry is given by Neumann's principle, which states that "every physical property of a crystal must possess at least the symmetry of the point group of the crystal". This principle, put forward by Neumann, is of fundamental significance and needs to be examined with great care in regard to the nature of physical properties one wants to deal with as well as the concept of symmetry one has in mind when one is referring to a crystal.

Since the discovery of X-rays and of even more powerful tools for investigating the internal structure of crystals, our knowledge of the crystal structure has deepened. We know that the theoretically expected spatial structure of a crystal agrees with the spatial disposition