Receptive systems : mediating certain light reactions of the pupil of the human eye

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MEDIATING CERTAIN LIGHT REACTIONS
OF THE PUPIL OF THE HUMAN EYE

H. BOUMA

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in dank opgedragen aan mijn ouders

en aan mijn echtgenote

CONTENTS

1. INTRODUCTION

In the retina, the neural network at the back of the eye, incident light quanta are absorbed by receptor cells. These signal the absorptions to other parts of the network where the signals are transformed in several ways by the neuron circuitry involved. The resulting signals (impulses) are led to the brain by the optic nerve. In the brain they give rise to processes that correspond to a sensation called vision or visual perception.

Apart from conscious vision, several other processes are initiated by absorption of quanta in the retinal receptors and by subsequent transformation of signals in the retinal network. The resulting signals are also passed on to the brain by the optic nerve. These processes include reflexlike activities in several muscles causing balancing reactions of the body, eye movements, lens accommodation, and also changes in pupil size.

Retinal receptors may be divided into two categories: rods and cones. This may be done on anatomical, photochemical, electrophysiological and psychophysical grounds. Anatomically, the differences between rods and cones that become apparent under the microscope are considerable. Photochemically, their absorbing pigments show different absorption and bleaching spectra and different rates of regeneration. Differences between rods and cones can also be traced in the various potentials that can be picked up from the eye and they manifest themselves also in vision.

With respect to vision, rods are especially involved in conditions of low intensities, large and peripheral fields of view, and slow changes of illumination. Under these rod-prevailing conditions, vision is called *scotopic*. High illumination, central and detailed vision, and rapid changes of illumination are conditions for *photopic* vision, initiated by cones. In conditions intermediate between purely scotopic and purely photopic, vision is called *mesopic*. Since this distinction finds its origin not only in the receptors but also in functional properties of the neural network, the concepts scotopic and photopic vision are more appropriate than the terms rod and cone vision. This, in fact, is the present basis of the duplicity theory of vision that was proposed some 70 years ago by Parinaud and by Von Kries [66]).

Generally, it is not known to what extent the unconscious reflexlike reactions to light and conscious vision are mediated by functionally the same neural circuitry in the retina. Accordingly, there are no *a priori* reasons for classifying the unconscious reactions in scotopic and photopic muscle activities. It must be admitted that, in the general sense, it is an attractive hypothesis to assume that optic nerve signals might be labelled either scotopic or photopic.

Pupillary reactions belong to muscle activities that can be initiated by light

absorption. Apart from this, pupil size is influenced by a large number of other stimuli, most of which are connected with psychological conditions. The structure of all components by which pupil size can be influenced may be defined as the *pupillary system*. The components have in common that they can exert influence upon the effector of the pupillary system, which is the iris membrane in the front part of the eye. Usually, the components or subsystems are themselves complicated and may be called systems as well.

With regard to the light reactions, it is convenient to distinguish between a *receptive system* and a *motor system*, which are subsystems of the pupillary system. The receptive system comprises all activities by which light absorption in the receptors leads to stimulation of the pupillary motor centres. It will constitute the main object of the investigation. The motor system includes the transformations from stimulation of the motor centres to movements of the pupil.

The question that gave rise to the present investigation concerned the pupillary reaction to illumination from sodium and mercury lamps. Any difference in pupillary reaction may add information to the solution of the problem why most people prefer sodium illumination on roads. We started by measuring pupil size as a function of wavelength and intensity of a steady retinal field, since these are the two variables involved. When we compared the influence on pupil size with the influence on visual brightness, we found great differences, the pupil reacting relatively stronger to the shorter wavelengths. These effects must originate from differences between the absorbing pigments in the receptors involved. Further experiments revealed that not only the absorbing pigments but also the receptors themselves are different: pupil size is mediated by rods whereas, simultaneously, brightness impression is mediated by cones. This finding cannot be fitted into the scotopic-photopic scheme of the duplicity theory.

The difference between pupil size and brightness was at first described as a discrepancy, which term holds only if a direct correspondence between pupillary behaviour and vision is assumed. This correspondence need not always be denied but may adversely affect the fruitfulness of the investigation if stated at the outset. Thus, parallels between visual and pupillary data have not been allowed to play more than an operational part. As a consequence we have to distinguish between *visual receptors* and *pupillary receptors* and to assume no *a priori* identity either with regard to functional behaviour or to retinal distribution.

Since pupillary contraction is an overall response, it is quite possible that the light scattered in the eye contributes to it, as has long been recognised. Evidence collected by Campbell and Alpern [24] suggested that this scattered light even constituted the main source of pupillary contractions in response to steady

illumination. This raised the interesting question as to how pupillary receptors are distributed over the retina and to what extent retinal illumination by entoptical scatter plays a part.

The manner of convergence of the signals from the many pupillary receptors to one motor signal may appropriately be called the *organisation of the pupillary receptive field*. According to Adrian [3]) a *receptive field* is the surface innervated by a single afferent fibre. We shall use it in a slightly extended meaning as the area from which signals may pass to a particular unit. Though the problem of the organisation of this receptive field has been attacked in the past, no consistent interpretation of the experimental data has been reported. Generalisation from pupillary results obtained with very large fields of view where stray light plays no part, led us to a possible answer to this question.

Since the reactions to steady illumination constitute only one of the several reactions of the pupil to light and in principle even the simplest one, it was felt that a dynamic type of reaction, in this case the reaction to a light flash, should also be studied. These dynamic reactions differed from the steady-state reactions and showed complications in all the aspects investigated. For these reactions, a classification into scotopic and photopic responses turned out to be possible.

In the following chapters we shall first give a description of the pupillary system in general (chapter 2) and of the light reactions in particular (chapter 3). This survey of the literature will enable us to focus the problems to be investigated somewhat more sharply. Turning to our own experiments, we shall start with a brief discussion of the various methods by which pupil size can be measured. The subjective entoptical method that we made use of will receive some extra attention. Next, the optical arrangements will be described (chapter 4). Experimental procedures (chapter 5) have been designed to minimise the influence of pupillary movements affecting the results.

For the reactions of the pupil to steady illumination, some properties of the receptors involved (chapter 6) as well as the organisation of the pupillary receptive field (chapter 7) will be discussed. Next, reactions of the pupil to flashes will receive attention, again with regard to the properties of the pupillary receptors (chapter 8) and to the organisation of the scotopic and photopic receptive fields (chapter 9). It is hoped that the main findings summarised in chapter 10 indicate some of the avenues open to further research.

2. GENERAL ASPECTS OF THE PUPILLARY SYSTEM

In the first chapter we defined the pupillary system as the structure of all components that may influence pupil size. The present chapter contains a survey of this pupillary system. We start with a description of the anatomical basis and the physiological processes involved (sec. 2.1). As appears from the wide range of stimuli that cause pupillary reactions, the system is rather complicated. Does the pupil serve a purpose in vision as various authors have tried to establish? We shall consider the meaning of the concept "function" before outlining the consequences of pupil size on perceptual faculties (sec. 2.2).

Since the iris (rather than the pupil) occupies the central position in the pupillary system, we shall examine two aspects of the iris in greater detail. First, les us consider to what extent passive mechanical properties of iris tissue exert a critical influence on pupillary movements (sec. 2.3). Next, we shall deal with the muscles in which the double, antagonistic innervation exerts influence (sec. 2.4).

Much information in this and in the next chapter has been taken from the handbooks of Davson [34] (Lowenstein and Loewenfeld [78] on the pupil), Gellhorn [46], Kuntz [67], and Maximow and Bloom [84].

2.1. Anatomical and physiological data

The pupil of the human eye is a circular hole in the iris membrane. This membrane is located just in front of the lens and is attached laterally to the ciliary body (fig. 2.1). The iris membrane divides the space in front of the lens
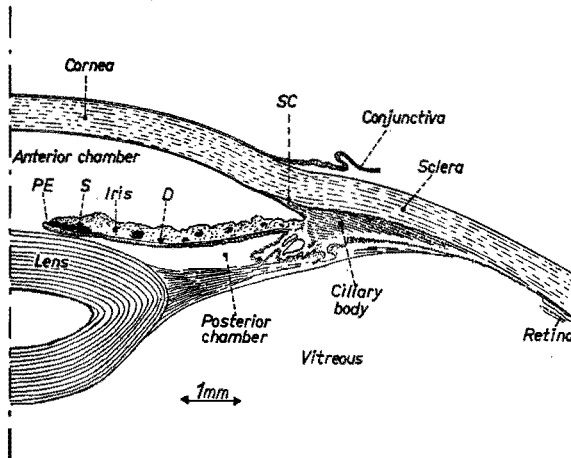

Fig. 2.1. Part of a meridional section of a human eyeball.
PE — pupil edge, S — sphincter pupillae, D — dilatator pupillae, SC — canal of Schlemm by which the chamber water is drained off; after Schaffer, in Maximow and Bloom [84].

and the vitreous body into the anterior and posterior eye chambers which are filled with 99 % water. The iris membrane itself consists of two muscle-like structures and of very loose connective tissue containing blood vessels and nerves. One of the muscles, the sphincter pupillae, consists of normal smooth muscle tissue and is located just around the slightly dentated pupil edge. Its fibres run in a tangential direction, causing reduction of pupil size when contracting. The dilatator pupillae is an elastic, and possibly also muscular, thin membrane (some 10 μ) located on the posterior side of the iris. Its fibres show a radial direction and must be held responsible for enlargements of the pupil. The epithelial cell layer just behind the dilatator contains the main mass of pigment so that the iris membrane is an iris diaphragm.

In physiological conditions the pupillary diameter can vary between 7·5 and 1·5 mm on the average at the age of 20, the range gradually shrinking with age to 3 to 1 mm at the age of 80 (Trendelenburg [122]). However, the differences between individuals are great. Normally both pupils are of the same size in steady state as well as during movements. Also, pupillary fluctuations are equal for the right and the left pupils (Lowenstein and Loewenfeld [77], Stark, Campbell, and Atwood [113]). This behaviour is based on the coupling of the controlling centres. Deviations between left and right pupils up to 0·5 mm are considered to be within the physiological range.

The innervation of pupillary muscle is effected by parts of the autonomic nervous system, governing all kinds of autonomic functions in the body. It may be divided into a parasympathetic (ps) and a sympathetic (s) part on anatomical and, to a large extent, also on functional grounds.

The parasympathetic system is active particularly when the body is relaxed. Its fibres run from the brain stem directly to the various parts of the body. The pupillary parasympathetic fibres (fig. 2.2) arise from pupillomotor centres in the brain stem and reach the iris membrane by way of the oculomotor nerve and the ciliary ganglion, located at the back of the eye cavity. Parasympathetic activity causes pupillary constriction by activation of the sphincter muscle.

The sympathetic system is active especially during the working phase of the body. Its fibres originate in nerve centres in the spinal cord (spinal ganglia) which in turn may be influenced by higher centres in the hypothalamus. The various parts of the body are reached by way of the sympathetic tracts in front of the spinal column. The pupillary sympathetic fibres (fig. 2.2) come from centres in the cervical part of the spinal cord. They run to the upper cervical ganglion, which is part of the sympathetic tracts. From here they accompany the blood vessels to the eye. Sympathetic activity causes pupillary dilation. As yet, it is not quite certain which iris muscle is innervated by sympathetic fibres, but probably the sympathetic fibres act on the sphincter as well, causing a relaxation. This will be discussed in sec. 2.4. According to this view the sphincter muscle would be controlled by a double, antagonistic innervation.
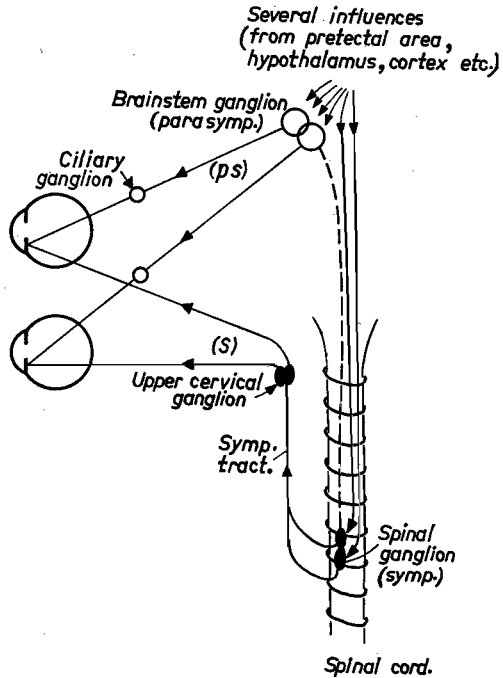
Fig. 2.2. Diagram of parasympathetic (ps) and sympathetic (s) neural pathways, along which the motor innervation of iris muscle is effected.

2.2. Pupillary reactions and their consequences

There are a great many causes for pupillary movements. The majority give rise to a dilation. This is the case with pain, noise, arousal, attention, fright, anoxia, etc. Stimuli that cause pupillary constriction are sleep, increased blood pressure *), accommodation and/or convergence, and light. In fact, accommodation and convergence do not cause pupillary reactions. They are only accompanied by pupillary movements (synergic movements or synkinesis). Except for the reactions to illumination, all these reactions are part of more general changes of the activity of the autonomic nervous system. Thus, the pupil is to some extent an indicator of this activity.

The stimuli exert influence on the pupil because their pathways converge on to the pupillary motor system. This occurs mainly in two centres: the parasympathetic pupillomotor centre in the brain stem and the sympathetic pupillomotor centre in the spinal cord. In man, most influence is exerted by either activation or inhibition of the parasympathetic centre.

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*) The reaction to increased blood pressure is caused by a nervous component rather than by the purely mechanical component arising from the greater filling of the iridical vessels [46].

The thorough connections with the autonomic nervous system make it plausible that conditioning of pupillary reflexes is possible. Though this has sometimes been reported in the literature, it has never been proved satisfactorily (Young [136]). Some voluntary influence on pupil size is possible by way of reflexes such as emotion, pain, accommodation, and frowning. None of the authors who have worked on the subject have found evidence that the light reflex was subject to conditioning. In fact, light exerts a very direct influence on the pupil. In view of this it may readily be accepted that the phylogenetic origin of the light reflex is a direct sensitivity of the iris membrane itself to light, something which is still found in many lower vertebrates (Weale [133], Von Campenhausen [25]).

Since vision also exerts some general influence on the autonomic system as a whole, it seems logical to suppose that, apart from the direct light reaction mentioned above, there is also some indirect light reaction. This may be taken to resemble closely the reaction to noise. Its occurrence is possibly masked by the direct light reaction.

Influences of pupil size on perceptual faculties

Pupillary movements affect various perceptual phenomena. These influences are usually summarised under the heading "pupillary functions". If the concept "function" is used as activity proper to something, we can agree with it. Often, however, it is used in the less neutral sense as "being of positive value". In the teleological view it is thought improbable that 'Nature' might perform activities which had better be left undone, as judged from a designer's point of view.

It must be admitted that many properties of biological objects fit into the teleological framework. Thus, the position of the iris diaphragm is precisely at the most favourable position for image quality. Moreover, the eye can operate under a wider range of illuminations than would be possible with fixed pupil size. One can also be grateful that the pupillary light reflex is of considerable help as an indicator of the degree of narcosis.

Several properties, however, are neutral or ambiguous, or even negative, with respect to their influences. Thus, it is not clear whether pupillary fluctuations or the slow dilations are very helpful to vision. To this category also belong the many pupillary reactions of psychical origin, by which other people can obtain some impression as to one's psychical state. The optimal pupil size for visual acuity or retinal illumination is lost by these psychical reactions, which may be considered to be of negative value. The decrease in the range of adjustment with age is certainly of negative value and if desired, the various iris diseases that menace vision can also be placed in the negative category.

This list seems somewhat too heterogeneous to support a scientific hypothesis that the pupil is designed to make the best of the possibilities open to it. Since the teleological framework unilaterally stresses properties whose positive

influence can be understood, it may be a misleading concept. Also, it may blur the fact that we do not yet understand the phylogenetic and embryologic origins of the various pupillary reactions. It is for these reasons that we prefer the neutral meaning of the word "function" and in order to avoid confusion, we shall substitute a description in general terms.

The main influences of pupil size concern:
(a) retinal illumination,
(b) visual acuity,
(c) prevention of fading,
(d) discomfort glare,
(e) human communication,
(f) flow of aqueous humour.

(a) Retinal illumination

Taking the maximum diameter as 7·5 mm and the minimum diameter as 1·5 mm, the pupil can adjust the retinal illumination by a factor 25 at best. The total range of light intensities under which the eye can operate exceeds twelve log units, the limits being set on the low side by a few quanta falling within the integration interval on the retinal integration area, and on the high side by the injury level (Weale [134]). Thus, the influence of the pupil governing 1·4 log units at most seems not very impressive. In actual fact, however, the pupil enlarges the number of log units the eye can handle by these 1·4 log units since this is effective especially at the extremes of the intensity scale. Thus, on the one hand, the pupil may prevent retinal burning lesions due to occasional blinks at the sun while, on the other hand, it makes vision in dim light essentially better, compared with a pupil of fixed average size.

In general a large pupil affects the rods more than the cones, since the latter show a strong directional sensitivity (Stiles-Crawford effect). Consequently, the maximum influence of the pupil on the amount of light absorbed by cones is reduced to a factor of 12. Since at high intensities, the visual scotopic system mediated by rods is saturated, the effect of a small pupil size with respect to adaptation is greatest for the cones (diameters 1·5 to 5 mm) whereas at low intensities rod vision is affected selectively. Transient light reactions of the pupil seem to be of restricted impact on perceived brightness.

(b) Visual acuity

As the refractive media of the eye show spherical and chromatic aberration, the sharpness of the retinal image gains with pupillary constriction. This is one of the reasons why visual acuity improves at higher illuminations. Since the percentage of the amount of light entering the eye and diffracted at the pupil edge increases with decreasing pupil size, too large a contraction of the pupil

deteriorates the quality of the retinal image (Leibowitz [69]). There is some evidence that steady-state pupil size corresponds to the flat optimum of visual acuity (Campbell and Gregory [23]). As yet, the mechanism by which such feedback would be achieved is unknown.

Due to the accommodation-convergence synergic movements, the focal depth increases automatically when looking at near objects.

Though the importance of pupillary movements for visual acuity is generally understood, there is a lack of quantitative data on this subject.

(c) Prevention of fading

It is known that a fully stabilised retinal image causes visual impressions to disappear rapidly. Since pupillary movements influence retinal illumination, small pupillary fluctuations might contribute to the prevention of this fading. As, however, intensity fluctuations due to pupillary unrest do not exceed 20%, this influence is much smaller than the influence of involuntary eye movements and can, in fact, hardly be detected at all (Stark et al. [113,114]).

(d) Discomfort glare

There are indications that tensions in the intra-ocular muscles, including the iris, are among the constituent factors of discomfort glare (Fugate and Fry [44]).

(e) Human communication

Since pupil size and pupillary movements constitute a factor in facial expression, they play some part in human communication. Physiologically, the momentary state of activity of the autonomic nervous system is somehow indicated. From a psychological point of view, it has to be described in terms of arousal, attention, etc. Such indications, which occur unwittingly, are used in psychotherapy and misused in testing consumers' unconscious reactions to new industrial products.

(f) Flow of aqueous humour

The aqueous humour in the eye chambers is produced by the ciliary body and next passes from the posterior chamber via the narrow slit between the eye lens and the iris to the anterior chamber, from where it is drained off by the canal of Schlemm located in the cornea-scleral junction (fig. 2.1). This stream of fluid results in a renewal of aqueous humour in the anterior eye chamber every $1\frac{1}{2}$ hours.

Schouten [105] pointed out that it is quite conceivable that the iris influences this stream by acting as a hydrodynamic valve.

2.3. Passive mechanical properties of iris tissue

The iris muscles evince a simple counteracting behaviour: the contractive action of the sphincter is counteracted by the dilative forces of the dilatator. If the two forces balance each other for some time, the pupil is in a steady state.

The total inward-directed radial force F_i can be expressed as: $F_i = \int_0^{2\pi} F_s \, d\zeta =$ $= 2\pi F_s$, in which F_s is the sphincter force in the direction of the muscle fibres and $d\zeta$ is the angle subtended by the sphincter part as viewed from the centre of the pupil (fig. 2.3). In the equilibrium state the total inward-directed force F_i equals the total dilatator force F_d. Thus the equation $F_d = 2\pi F_s$ holds.

The time functions of pupillary movements will depend on the time functions of the forces F_s and F_d and on the passive mechanical properties of the iris tissue on which these forces act. The forces depend in their turn on the characteristics of the innervation, the neuro-muscular transmitters and the muscular contraction process. The main passive properties are mass, friction, and stiffness (elasticity).

In actual fact, the relationships are more complicated, since the system cannot be considered to be a passive one set in motion by a force from outside. Stiffness and friction parameters change under the influence of nervous stimulation and the changes of stiffness may even constitute the main cause of the contraction (parametric driving).
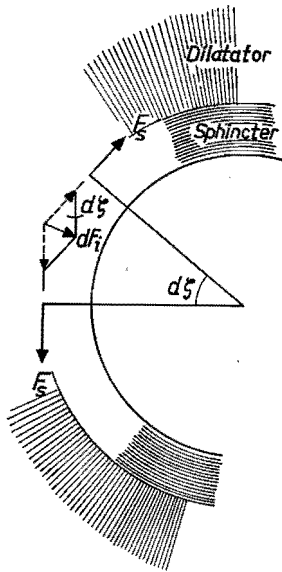
Fig. 2.3. Relationship between the sphincter force F_s in the direction of the muscle fibres and the inner-directed force $F_i = \int dF_i = \int_0^{2\pi} F_s d\zeta = 2\pi F_s$.

We shall confine this discussion to the passive movements that are to be expected if no active muscular forces are present. The problem to be discussed is whether observed pupillary movements can be identified with these passive mechanical movements or not. Where the observed movements cannot be explained on the basis of passive movements only, it must be supposed that active muscular forces are continuously present. In this case pupillary movements are governed at least partly by the characteristics of the innervation process.

Normally a light flash gives rise to a pupillary reaction with a time function as shown in fig. 2.4. We note a latent period (≈ 0.2 s), a contraction (≈ 0.5 s)
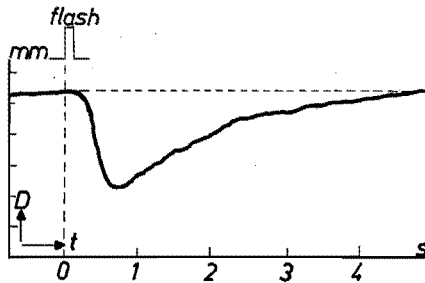
Fig. 2.4. Time function of a pupillary contraction in response to a flash of light.

and a slower dilation (≈ 3 s) *). According to Drischel [38]), the total reflex curve may be readily compared with the aperiodic oscillation known from mechanics. This suggests that the movement may be described in terms of a linear differential equation of the second order, in which the mass m, the friction r and the dilatator stiffness s of the iris membrane are the parameters:

$$F = m\ddot{x} + r\dot{x} + sx, \qquad (2.1)$$

where F represents the active radial force working on the system, x the amplitude of displacement, $\dot{x}$ the velocity and $\ddot{x}$ the acceleration of the pupil edge.

The solutions of this equation are well known. Without any active force present ($F = 0$), the movement will show:

if $r^2/4sm < 1$, damped oscillations with a frequency $f = (1/2\pi)\sqrt{s/m}$;

if $r^2/4sm = 1$, critically damped, aperiodic movements with a time constant $r/2s$;

if $r^2/4sm > 1$, overdamped movements with a time constant approaching r/s for large values of $r^2/4sm$.

An example of each of these situations, when F is a step function, is shown diagrammatically in fig. 2.5.

Let us now try to calculate the values of m, r and s (in c.g.s. units).

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*) The exact values show considerable individual differences (Drischel [38], Petersen [87]).
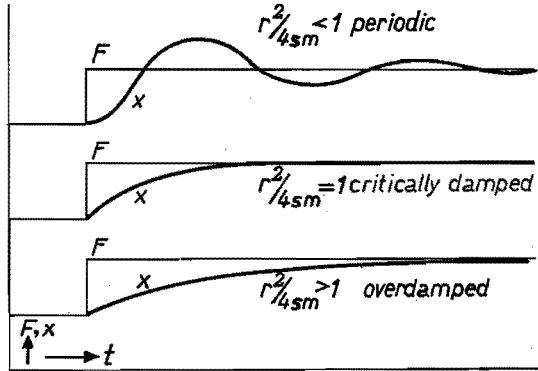
Fig. 2.5. Responses to a step function in an external force F of a passive system obeying a linear differential equation of the second order.

The mass m can be found from the volume and density of the moving part of the iris membrane. The approximate dimensions are sketched in fig. 2.6, from which results $m = \pi h \, (c^2 - b^2) \approx 2.10^{-2}$ g. Since on the average all parts of the iris move about half as much as the pupil edge, the equivalent mass is about 10^{-2} g.

The stiffness s depends on the effective cross-section and on the specific stiffness of the dilatator membrane, assuming that a constant specific stiffness exists. Unfortunately, I have not been able to find any data for the stiffness of the dilatator. However, for different elastic tissues as the aorta wall and normal rubber, the elasticity modulus E is of the order of 10^7 dyne cm^{-2}. From measurements of sound velocity in the biceps muscle a value $E = 2.10^6$ dyne cm^{-2} results (Schouten, Vredenbregt, and Westhoff [106]). Taking $E = 5.10^6$ we find for a membrane thickness of 0.01 mm: $s = 2\pi b \, h' \, E/a \approx 3.10^4$ dyne cm^{-1}.

From these values of m and s it follows that the resonance frequency f would be $(1/2\pi) \sqrt{s/m} \approx 300$ Hz. Another way to find the order of magnitude of the resonance frequency is to use the velocity of sound waves, which is $v = \sqrt{E/\rho}$,
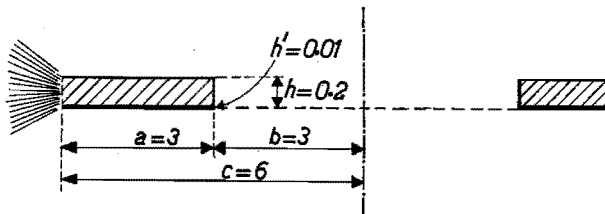
Fig. 2.6. Schematic cross-section of the iris membrane. Values indicate the approximate dimensions (in mm) of some iris components.

when ρ is the density of the material. The elasticity modulus of the iris membrane will be mainly accounted for by the elasticity of the dilatator membrane. The density of the material is unity, but since the iris membrane is about 20 times as thick as the dilatator membrane, the effective density of the latter is 20 times as high. As a result $v = \sqrt{5.10^6/20} = 500$ cm/s. Combined with a wavelength $\lambda = 4a = 1\cdot2$ cm (fig. 2.6) we find a resonance frequency $f = v/\lambda \approx 400$ Hz. The pupillary oscillations that have actually been observed are all below 10 Hz. The fact that oscillations with frequencies around the resonance frequency do not occur, must be attributed to frictional damping.

The friction r is composed of two components: an internal friction r_i within the iris membrane, which is to be localised mainly in the muscles, and an external friction r_e between the moving pupil and its water environment. Accordingly, $r = r_i + r_e$. Probably, the internal friction will make the larger contribution to total friction. Unfortunately, no reliable data are available about the internal friction in muscle tissue. For the biceps muscle, there is some evidence that the quotient r/s is of the order of 50 ms (Schouten, Vredenbregt, and Westhoff [106]). If we suppose that this relation may also be applied to the dilatator membrane (which is, in fact, quite uncertain), we calculate for the dilatator $r_i \approx 2.10^3$ dyne.s.cm^{-1} and supposing a similar value for the sphincter, we arrive at $r_i \approx 4.10^3$ dyne.s.cm^{-1}. For the external friction Stokes' law may be applied, which gives the result $r_e = 4.10^{-2}$ dyne.s.cm^{-1}. The external friction is clearly negligible.

The values $m = 10^{-2}$ g, $s = 3.10^4$ dyne cm^{-1} and $r = 4.10^3$ dyne.s.cm^{-1} give $r^2/4sm \approx 10^4$. If this value is approximately correct, the iris membrane must show overdamped behaviour. The time constant then amounts to $r/s = 0\cdot1$ s. The mass is too small to exert any influence on the movements. The value of 100 ms has to be compared with the observed time constants of pupillary movements, which amount to about $0\cdot3$ s (contraction) and $1\cdot0$ s (dilation). The difference is too small to permit a definite conclusion, since the estimation notably of the internal friction has been very rough. If we have underestimated the quotient between friction and stiffness, the pupillary movements may be critically limited by these passive mechanical properties. If the quotient is either correct or overestimated, pupillary movements are governed by the rate of rise and descent of muscle tensions. In this case it is almost certain that the sphincter plays the main part during contraction as well as during dilation, since muscle activity of the dilatator, unlike passive behaviour, is presumably incapable of slowing down the dilation.

According to this view, the sphincter muscle can relax only towards a certain diameter which is a function of momentary transmitter concentration. The dilatator, whether innervated or not, pulls the sphincter to this diameter and the high stiffness of the innervated sphincter then permits only negligible further dilation. Hence, the time function of actual pupillary dilation reflects the time

function of transmitter concentration. During dilations, superimposed fluctuations in pupil size show that muscle activity is still present.

The most likely conclusion is that passive mechanical properties of the iris tissues do not critically influence the time function of pupillary movements. This conclusion is in no way new. Several investigators never doubted that pupillary movements are due to innervation functions only (Poos [89,90], Lowenstein and Loewenfeld [72,74], Drischel [38]). In fact, some known phenomena do not fit the description of pupillary movements as aperiodic movements. First, several pathological conditions in the innervation pathways influence the time functions of pupillary movements, some of them in the direction of higher contraction speed (Lowenstein and Loewenfeld [74]). Secondly, some investigators observed that the pupil was stationary for some 0·1 s in its most contracted state when reacting to a flash of light (Haltezeit, see Petersen [87]). These phenomena cannot be explained on the basis of passive mechanical properties alone. Van der Tweel [124]) stated explicitly that dilatator properties are not of critical importance during the contraction phase of pupillary movements. He held the opinion that the dilation phase, on the contrary, is governed by the passive properties of the mechanical system. According to the arguments presented, it seems more likely that the rate of relaxation of the sphincter is reflected in pupillary dilation. Further evidence on the values of stiffness and friction parameters is needed before the role of the passive mechanical properties of the iris tissues can be settled.

2.4. Innervation of iris muscle

It has been mentioned that the innervation of iris muscle is performed by both parts of the autonomic nervous system. A simple hypothesis would be that the sphincter muscle is innervated by the parasympathetic system whereas sympathetic activity stirs the dilatator. However, the available evidence does not correspond to this hypothesis. There is ample evidence that parasympathetic activity acts on the sphincter but sympathetic influence is probably not operative in an excitatory sense on the dilatator, but rather in an inhibitory (relaxing) sense on the sphincter. This view is favoured by the uncertainty as to the muscle properties of the dilatator *). Further, a double, antagonistic innervation of smooth muscle has been shown to exist. If the sphincter has a double, antagonistic innervation, the actual dilation must still be brought about by (elastic or muscular) properties of the dilatator.

When viewed under the microscope, the human dilatator membrane has no muscle appearance [84]). The fibrillated parts of the cells are arranged as a

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*) Loewenfeld [72]), in a survey of the extensive literature on this point, arrives at the conclusion that the dilatator has muscular properties.

separate membrane at the border of the cell bodies. Apter [9]), in experiments on cats, reported no radial forces in the dilatator after sympathetic stimulation. These data indicate that sympathetic stimulation probably does not act on the dilatator. Then, dilation must be caused by way of active relaxation of the sphincter, as suggested long ago by Poos [89]). Apart from a number of pharmacological arguments he thought the sphincter so much more powerful than the dilatator, that it needed a double, antagonistic innervation to keep its force within dilatator limits. Direct physiological evidence was presented by Hess, Koella and Szabo [58,59]). They showed that the contracted sphincter relaxes under the influence of the sympathetic agent adrenalin. Bülbring [21]) carried out an electrophysiological study on this effect.

In addition to innervated muscle properties, a purely mechanical stimulation can also cause a contraction in the rather undifferentiated smooth muscle cells (Hess and Koella [59]).

2.5. Conclusions

A general survey of the pupillary system shows that the pupil is sensitive to a great many stimuli, which may roughly be divided into light stimuli and psychical stimuli. When studying one of the reactions of the pupil, the disturbing influence of the other reactions must be kept in view. The existence of these many reactions may be understood from the fact that the controlling centres of the pupil belong to the autonomic nervous system. Contrary to many autonomic reflexes, pupillary reflexes seem not to be subject to conditioning. To some extent, changes in pupil size can be induced voluntarily. Due to the close connections between the pupillary nervous centres, the pupils of both eyes show equal size and equal movements.

Pupil size is of influence on various perceptual phenomena. Both the reaction to light and the synergic movements with accommodation and convergence are generally of positive value in vision in a sense that more details or contrasts can be perceived. Several other reactions of the pupil cannot profitably be fitted into a teleological framework, which is believed to be unsuitable for a general analysis of biological phenomena.

Concerning passive mechanical properties of iris tissue it has been established that its mass is too small to exert any influence on pupillary movements. Of friction, only the internal component need be considered. It is so large that the passive pupillary movements are definitely of the aperiodic overdamped type, the time constant being given by the quotient of friction and stiffness. This time constant is estimated to be some 100 ms, but the accuracy of this value is too low to permit a definitive conclusion that the passive properties are of no influence on pupillary movements, which show time constants 3-10 times as high.

It seems likely that contractions and dilations of the pupil are caused by

contraction and relaxation of the sphincter muscle only, the dilatator keeping it under tension when it relaxes. Hence, the sphincter is controlled by a double, antagonistic innervation: it contracts by parasympathetic stimulation and it relaxes by sympathetic stimulation. According to this view, there is no need to suppose the dilatator membrane to be muscular.

3. LIGHT REACTIONS OF THE PUPIL

3.1. Introduction

In the previous chapter we mentioned a large number of pupillary reactions. In this chapter we shall confine our attention to the light reactions. The neural pathways along which the signals for these light reactions are conducted may be divided into receptive and motor parts. The receptive part (fig. 3.1) begins at the retinal light receptors. The nerve signals triggered by light absorption then pass the complicated nervous circuit of the retina. This results in pulses (spikes) conducted by the optic nerve. Half of the fibres of the optic nerve decussate in the chiasma opticum. Just before the lateral geniculate nuclei (LGN) are reached, the pupillary fibres branch off to a neighbouring ganglion (pregeniculate nucleus PGN) in the pretectal area. From each side, the signals are then conducted to both parasympathetic pupillomotor centres in the brain stem, where begins the common motor part of the loop described in sec. 2.1.

The light reactions of both pupils turn out equal, irrespective of the distribution of illumination among the two eyes. This can be gathered from the two decussations between the left and the right parts of the loop. The sympathetic pupillomotor centres are also influenced by the optic nerve signals, though less directly.

In this chapter attention will be directed mainly to the literature on the receptive part of the pupillary system, since this is the subject of the present study. We are especially interested in the properties of the receptors and in the
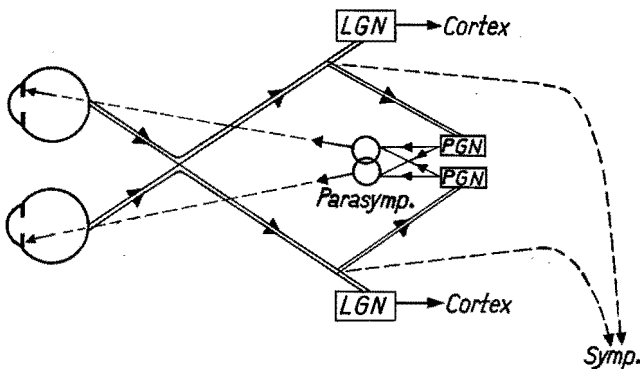

Fig. 3.1. Light reactions of the pupil. Diagram showing neural pathways of the receptive system.
PGN — pregeniculate nucleus (pupillary receptive centre);
LGN — lateral geniculate nucleus (in the visual pathways).

organisation of the receptive field as established in the retina and in the receptive centres of the brain stem.

All data collected from the pupil in principle provide information about the total pupillary system or, in so far as the light reaction is independent, about the pathways serving the light reactions. The overall aspect of pupillary behaviour can be studied by a servo-analytical approach, in which the relations between the time functions of light input and pupillary output are studied systematically.

In trying to collect information about a particular component part, certain precautions in the experimental techniques and the evaluation of the results are necessary to isolate the properties of the component under consideration as far as possible from the interfering influences of other components. Since the magnitude of these influences is usually unknown, one can hope to control them only by keeping them constant. For example, when it is desired to isolate the absorption spectrum of the retinal receptors, pupillary responses to mono-chromatic illuminations of equal energy should not be measured, since the pupillary responses may be different and the linearities and alinearities of the motor components come into play. One had better measure the energy of such stimuli as produce equal pupillary responses. The influence of several component parts is ruled out once the pupil is used as a zero-indicator only. From measurements of this type, using a constant-response criterion, one can never be sure at what stage in the loop the various input effects that cause equal outputs are themselves equal. In the example mentioned above, the simplest interpretation is one in terms of the absorption spectrum of one type of receptors. The possibility cannot be ruled out, however, that several kinds of receptor act together to produce a result that cannot be distinguished from the activity of one kind of receptor when viewed from outside.

The advantages of using equal-response criteria when investigating biological systems are well known. For this purpose the physical stimuli have to be adapted to the demands of the system under consideration.

In the next section of this chapter we shall give a short description of the servo-analysis of the total loop (sec. 3.2). We shall then direct attention to the various light reactions of the pupil. Three categories will be distinguished:
– steady-state or static reactions; sec. 3.3;
– transient or dynamic reactions; sec. 3.4;
– less direct reactions, such as fluctuations and after-effects; sec. 3.5.

In the past, the value of distinguishing static from dynamic reactions has often not been recognised. It must be admitted that no *a priori* evidence is available that this distinction is of wider importance than that of distinguishing experimental criteria. As will be discussed in the final chapter, the differences in experimental results gained with both kinds of criteria justify the conclusion that this distinction is reflected in the organisation of the system.

3.2. The feedback character of the light reflex

In recent years much attention has been paid to an analysis of the pupillary system from the general viewpoint of servomechanisms (Stark and Sherman [112], Stegemann [118], Wagner and Bleichert [131]). The feedback character of the pupillary light reflex has long been known (Heddaeus [56] wrote in 1904: "The pupil moves because it moves") but exact analysis along these lines has only recently been undertaken. This approach may offer a prediction of the time function of pupillary diameter in response to any time function of illumination. The importance of such an overall description of a feedback system has for long been acknowledged in electronic and mechanical engineering.

Usually, the analysis is based upon amplitude and phase relations between light input and pupillary output for different frequencies of sinusoidal light stimuli in open-loop conditions, in which pupillary movements have no influence on retinal illumination. These data may profitably be visualised in Bode (fig. 3.2) or Nyquist (fig. 3.3) diagrams, the shapes of which depend on the experimental conditions (subject, intensity, adaptation, etc.). It turns out that the pupil cannot follow changes in retinal illumination with frequencies above 4 c/s. If the system is linear, pupillary behaviour in response to a light stimulus of any time function can be predicted from the diagrams. However, the system is in a high degree non-linear. Still, this linear approach offers a satisfactory description of the conditions under which instabilities occur (Stark [114-116] and Baker [115]).

A small increase ΔE in pupillary illumination E increases the light flux Φ entering the eye by an amount of $\Delta_1\Phi = A.\Delta E$ (A stands for pupillary area). The feedback loop causes a decrease ΔA in pupillary area, by which action the light flux decreases again by an amount of $\Delta_2\Phi = E.\Delta A$. The gain $G = \Delta_2\Phi/\Delta_1\Phi = E.\Delta A/A.\Delta E$ represents the fraction of the increase of light flux that is fed back by the characteristics of the loop.

A feedback system is stable if the absolute value of the gain is less than unity at a phase difference between input and output of 180°. The pupillary loop amply fulfils this condition ($G_{180°} = 0.18$), as is best shown in the Nyquist diagram, and is therefore a very stable one. By increasing the gain artificially by illuminating the retina with a narrow pencil of light just inside the pupillary edge Stark [114]) was able to induce instability. The resulting oscillations showed the predicted frequency of about 1.5 c/s.

In translating the outcome of an analysis of the pupillary loop in terms of electronic circuits (introducing filters, delay lines, logarithmic elements, etc.) one hopes to find that these elements can be fitted into anatomical and physiological data. In this way, the operation of some of the components might be elucidated. The first attempt to draw conclusions in this direction was made by Van der Tweel [124]). He found that l.f. cut-off in the visual and the pupillary systems coincided, while h.f. cut-off differed considerably, the visual system showing the highest fusion frequency. On this basis it is likely that pupillary h.f. cut-off is not localised in the retina. Since neuro-muscular transmission in smooth muscle is known to be slow, it seems quite possible that pupillary h.f. cut-off takes place here.

In trying to find a mathematical description of the relation between light input and pupillary output one has to take into account several non-linear terms, representing the process of logarithmisation of the light signal, the asymmetry between contraction and dilation, etc. Stark's formulae describing this relation are therefore of a complicated nature and it has not been quite possible as yet to simulate pupillary behaviour quite satisfactorily, though a good approximation has been achieved (Sandberg, Sobel, and Stark [102,109,110], Hornung and Stegemann [61]).
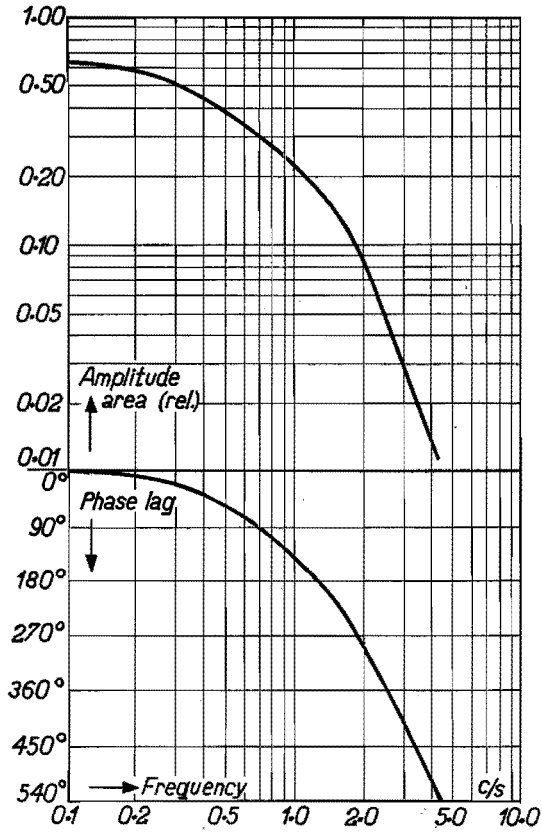
Fig. 3.2. Bode diagram showing relative amplitude (upper curve) and phase lag (lower curve) of the pupillary response as a function of the frequency of the light stimulus. Open loop. (Stark and Baker [115]).
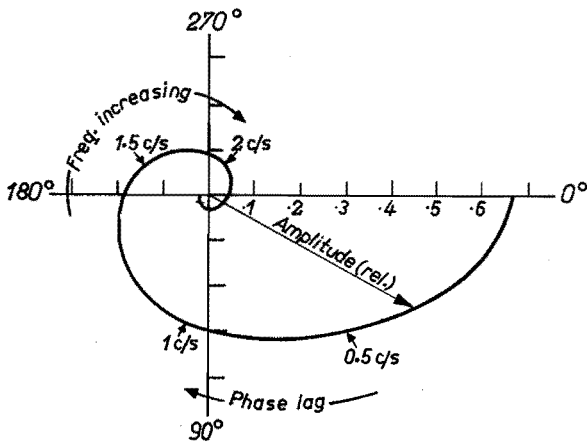
Fig. 3.3. Nyquist diagram showing the data of fig. 3.2 in one polar diagram (Stark and Baker [115]).

The overall gain of the system provides the main information necessary for calculating the influence of the pupil on retinal illumination and visual functions. Measurements of the gain under steady-state conditions have been carried out long before the servo-analytical approach came into use.

Though information about the role of the component parts is restricted so far, the servo-analytical approach has improved insight into general aspects of the loop. It would also be useful to analyse the influence of pupil size on visual acuity in terms of a feedback coupling. Connections between the light reflex and the accommodation and convergence synergic movements might then be revealed. This approach seems not to have been undertaken so far, which is probably due to the difficulties met with when trying to measure rapid changes of visual acuity.

3.3. Steady-state reactions

The equilibrium state of the pupil that is reached after some time as a reaction to constant retinal illumination may be defined as the steady-state or static reaction. The static diameter decreases when light intensity increases. Curves showing the overall relation between pupillary diameter and luminance of a large field were first given by Weiler [135] in 1910. The results obtained by eight different authors concerning 34 subjects in all have been summarised by De Groot and Gebhard [35]. Figure 3.4 shows average diameters as well as maxi-
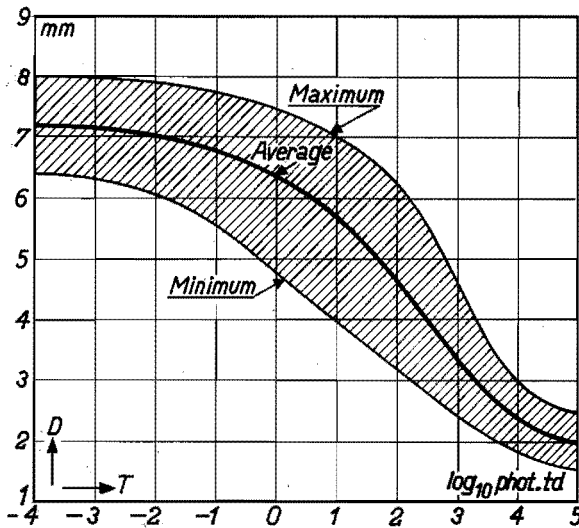
Fig. 3.4. Pupillary diameter D in response to a steady retinal illumination T.
Data provided by young observers, taken from the literature (DeGroot and Gebhard [35], Spring and Stiles [111]). White light. The hatched region indicates the area in which the average values obtained by the various authors are located.

mum and minimum diameters summarised by them, to which have been added data supplied by Spring and Stiles [111]). The steep parts of the curves show a gradient of 0·8-1·9 mm per log unit of retinal illumination, corresponding to about 0·7-1·2 mm per log unit of luminance of the outer field. De Groot and Gebhard also present a precise mathematical description of the results. Owing to the great individual differences and the dependence of the results on various unanalysed factors such as age and field configuration, this description is of limited value.

Pupillary receptors

Regarding the receptors mediating steady-state reactions of the pupil it is generally assumed that both rods and cones are involved as is the case in visual processes. Evidence in favour of this view was presented by Laurens [68]). In measuring pupillary diameters 20 seconds after the onset of illumination he found a spectrum of the pupillary sensitivity somewhere between the well-known absorption spectrum of rods (max. 510 nm) and that of cones (max. 555 nm). At decreasing intensities this pupillary spectrum shifted to shorter wavelengths, thus imitating the Purkinje-shift of visual brightness, which is due to the relative prominence of rods in dim illumination and that of cones at high illumination levels. However, his work leaves much to be desired, since for reasons of speed he measured equal-energy spectra instead of equal-response spectra. Furthermore, he used a very small field of view: the subject looked at a slit the length of which subtended only one degree. Such a small field may easily introduce interaction with transient reactions due to involuntary eye movements. And, as he explicitly mentions, he did not wait until a steady-state was reached.

The first evidence against the view that pupillary and visual processes depend on the same receptors comes in 1934 from Luckiesh and Moss [79]). They found pupil size greater in sodium than in tungsten light, the difference being of the order of 0·5 mm at a luminance level of 500 cd/m². On this basis Van Liempt [70]) advocated the use of sodium light in portrait photography because large pupils add to a person's attractiveness. In 1940, Van Liempt and De Vriend [71]) published data on the subject from which they drew the conclusion that pupillary efficiency is different from brightness efficiency, the pupil reacting relatively better to shorter wavelengths.

After it had been discovered that some properties of the steady-state reaction of the pupil (illumination level and time function of dark adaptation) resemble those of photopic vision mediated by cones, Wagman and Gullberg [129]) undertook experiments to demonstrate the influence of rods. For a criterion of 0·5-mm contraction they found good correspondence between the pupillary spectrum and the scotopic-visibility spectrum, from which they concluded that at low illuminations rods mediate the static reflex of the pupil. Concerning the spectrum at higher intensities they make the casual remark: "there is no indication that the

pupillary visibility curve as determined here for a dark-adapted eye ever shows a cone response with a maximum visibility at about 580 mμ". We confirmed this finding when we found the pupillary spectrum at high intensities showing a maximum at 490 nm close to the maximum of the scotopic-visibility spectrum (510 nm) [14a]). Recently, Alpern and Campbell [6]) reported spectra of the static pupil in which both a rod and a cone component were present (8° field).

In 1948, Spring and Stiles [111]) found a small directional sensitivity for the static pupillary light receptors (52° field, 1000 td). Since cones show a large directional sensitivity and rods do not, this leads to the conclusion that in static contraction cones play a restricted role only. However, for a 1° foveal field, Alpern and Benson [5]) reported a directional sensitivity of the same magnitude as that of cones. The conclusion is that rods play an important part in steady-state contraction whereas the amount of influence by cones is uncertain.

The question now arises at what level of illumination these effects were found. For white light or for monochromatic light of intermediate wavelengths the retinal illuminations necessary for 0·5 mm contraction are reported between 0·01 and 100 td. For static contractions of 3·5 mm the illumination must be of the order of 500 td (fig. 3.4). We conclude that at scotopic intensities no substantial pupillary contraction has been found. The illuminations at which the static pupil reacts to light are either in the mesopic or in the purely photopic range.

Until recently no attention was paid to the effect that rods would mediate steady-state reactions of the pupil at intensities at which they play only a restricted part in vision. We shall turn to this problem in chapter 6.

The organisation of the steady-state receptive field

According to chapter 1, the organisation of the steady-state receptive field concerns the manner of convergence of the signals from the many receptors in the retina towards one motor signal for the steady-state pupil. Two aspects may be distinguished. First, one can ask what the contributions of small retinal areas are if they alone are illuminated. Secondly, the manner of convergence of the signals from various simultaneously illuminated areas is of importance.

Concerning the first question, Crawford [29]) measured static pupil size in reaction to illumination from a glare source projected on various parts of the retina. The efficiency of the illumination with respect to the pupil turned out highest in the fovea, while decreasing rather sharply towards the periphery. Ring-shaped fields gave essentially the same results. These results corresponded well with earlier experiments of Hess [57]), which were of a dynamic nature.

When foveally centred fields of various sizes are used the results turn out different. In 1896, Vervoort [126]) compared squares of 4° and 8° and found that pupillary constriction did not change if the product of area and illumination

was kept constant. Over a greater range of field diameters up to 65° Crawford [29]) found the same integration: pupillary contraction is governed by the total light flux that enters the eye irrespective of the size of the illuminated area. For fields smaller than 6° a small deviation from this rule was found in the sense that the efficiencies were slightly lower. The handy integration law, which has become well known, was found by Crawford to apply also to fields of irregular shape. Considered on its own merits, these experiments point to a linear integration of the incoming light, or in retinal terms, to an almost homogeneous population of receptors reacting in proportion to illumination. This view is in contradiction with the former conclusion that sensitivity shows a sharp decrease from the fovea towards the periphery.

The lack in agreement between the two kinds of experiment has long been recognised. Hess [57]) chose an easy way out by rejecting Vervoort's results without repeating his experiment. Crawford [29]) concludes that "the pupillomotor efficiency is a function of pattern quite as much as it is a function of intensity. The underlying mechanism may be localized in the retina or it may be of a psychological nature". Van der Tweel [124]) considers Crawford's data not entirely free from contradictions.

The problems touched upon here will be considered further in chapter 7.

3.4. Transient reactions

General information

The pupil reacts to variations of light intensity with dynamic or transient reactions. In general, contractions occur rapidly with rather short latency times whilst dilations are much slower. The introduction of the time parameter offers extra possibilities for obtaining information on the component parts of the loop. On the other hand, the experiments are relatively difficult to perform, not only because measurements of movements are more elaborate than static measurements, but essentially because it is more difficult to get equal responses which are of help in deciding which components the observed phenomena originate from.

The reaction to a flash of light, after a short latency interval of about 0·2 s, is a contraction ($\approx$ 0·5 s) followed by a slower dilation (some seconds). A positive step function in light intensity gives rise to a similar movement, the pupil often showing a large overshoot. This indicates a higher sensitivity of the dynamic system as compared to the static one. In fact, this difference may amount to more than 6 log units of light intensity.

A negative step function causes only a slow dilation (latency time $\approx$ 0·4 s) while a negative light pulse ("dark flash") gives a contraction followed by a dilation. This paradoxical effect is due to a reaction to the increase of illumina-

tion at the end of the negative pulse, the negative step itself having no influence, as Redhead, Stark and Payne [91] have pointed out.

Figure 3.5 shows schematically the above-mentioned reactions.

With a limited number of subjects, Van der Tweel [124] confirmed the simple exponential time course of contraction and dilation first described by Reeves [92],
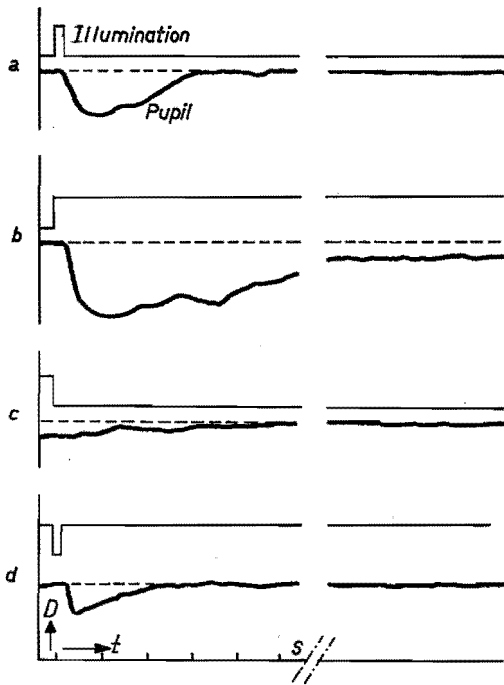
Fig. 3.5. Pupillary reactions to:
(a) a flash of light,
(b) a sudden increase in illumination (positive step),
(c) a sudden decrease in illumination (negative step),
(d) a short interruption of the illumination (dark flash).
   A notable asymmetry occurs between the responses to an increase and to a decrease in illumination.

the time constants being about 0·3 and 1·5 s, respectively. This relation also holds for most of the curves published by Petersen [87]. Van der Tweel interpreted the exponential time function in terms of transmitter concentrations.

Concerning the influence of light intensity of a flash on the resulting contraction, the results of Lowenstein and Loewenfeld [76], Fugate [43] and Baker [12] indicate an overall gradient between 0·2 and 0·6 mm increase of contraction for each log unit increase of light intensity. This value is about four times lower than reported for steady-state contractions.

When illumination ceases, the pupil gradually dilates until it reaches its final value.

> The actual amplitude and time function of these pupillary movements again show strong individual differences, on which topic Petersen [87]) and Drischel [38]) have given quantitative information. In line with Lowenstein and Loewenfeld [74],) Drischel concludes from his findings that different types of reaction may be distinguished: the "hyperkinetic type" shows short latency times, slow contractions and relatively rapid dilations, whereas the "hypokinetic type" combines long latency times, rapid contractions and slow dilations. As these results concern only one type of illumination it is difficult to compare the results of different authors or to condense the results in a small number of basic parameters.
>
> The speed of the dilation seems to depend not only on pupillary diameter but also on the recent history of pupillary contraction and of illumination. Thus, Reeves [92]) found a time constant of about 7 s after full adaptation to bright light which is much higher than he found with dilation after a flash of light (1·2 s). Contrary to this, Wagman [130]), in a short note, reports the time function of pupillary dilation after illumination within a restricted intensity range to be dependent solely on initial pupillary diameter.
> Alpern and Campbell [7]), after extinguishing a very bright illumination, found pupillary dilation to occur in three distinct phases. During the first 10 s there is a dilation, immediately followed by 20 s of contraction. Then, the final dilation begins showing a time constant of about 5 min. The actual time course of dilation seems therefore to depend very much on the illumination prior to dilation, especially when this illumination is high. Our own experiments, as far as they go, are in agreement with this conclusion. The problem would seem to need more thorough investigation.
> According to Brown and Page [20]), the dark-adapting cones would exert a direct influence on the dilating pupil. Van der Tweel [124]) pointed out that their experiments do not permit such far-reaching conclusions. Still, the hypothesis as such has received support from a recent finding by Alpern and Campbell [7]). Pressure on the eyeball during adaptation, which interrupts the blood supply and thereby neural activity, increases the speed of the dilating pupil. Pressure exerted in the same circumstances on the other eye, which has not been illuminated, causes no such dilation, thus eliminating possible direct influence of pressure itself.
> In comparing pupillary dilation with retinal processes we must bear in mind that pupillary contractions of say 3 mm require high light intensities. It seems likely that adaptive changes below the level of steady-state reactions do not exert influence on pupil size. Even if adaptive state and pupillary diameter were coupled directly, it is nevertheless unlikely that their time constants would show equal values. We may expect that closer examination of dilative speed of the pupil after various durations and intensities of the stimulating light will throw more light upon a possible coupling between retinal adaptation and pupillary behaviour during dark adaptation.

Pupillary receptors

The expectation, based upon a supposed analogy between the visual and the pupillary receptive systems, that dynamic pupillary reactions at low intensities are mediated by rods whereas cones prevail at higher intensities is supported by the spectral data available. As early as 1892 Sachs [101]) found that replacement of an illuminated piece of paper by another one of different colour caused no pupillary reaction provided the subjective brightness of the two objects was equal. This also applied for the intensity range where the visual Purkinje shift occurs. Abelsdorff [1]) repeated the experiments more quantitatively with essentially equal results. Thus, brightness impression and pupillary functions depend upon the same receptors. The spectrum of pupillary thresholds in dark-adapted

conditions was shown by Schweitzer [107]) to be identical with that of the scotopic system. Under photopic circumstances the spectrum of the cones was found by Alpern and Campbell [6]) to be fully reflected in dynamic pupillary behaviour. Our own experiments, which will be described in chapter 8 agree with data from the literature in that they also point to a close connection between dynamic pupillary reactions and brightness impressions.

The organisation of the receptive field for transient reactions

How does dynamic pupillomotor sensitivity vary over the retina? The answer resembles that given for static sensitivity: the efficiency is high in the central area and diminishes towards the periphery (Abelsdorff and Feilchenfeld [2], Hess [57], Hesse [60]). Hess derived the conclusion that only a slightly eccentric area (diameter about 30°) around the fovea contributed substantially to pupillary contraction. For larger eccentricities the contraction was not absent but, in line with earlier ideas of Heddaeus [54,55]), Hess attributed these activities mainly to stray light reaching the central area. Most authors who have worked on the subject since are of the opinion that the intra-ocular stray light contributes substantially to pupillary contraction. More recently the above results have been checked by Harms [53]), who arrived at a roughly similar conclusion. In addition, he found that visual and pupillomotor thresholds varied in the same way when he moved the stimulating field over the retina, with one exception: the foveal dip of visual thresholds in the dark-adapted state was not reflected in the pupillomotor threshold. Repeating his experiments, Schweitzer [107]) found the dip expressed both in visual and pupillary thresholds. A possible explanation of this discrepancy will be put forward in chapter 9.

With respect to the cooperation of signals from various retinal areas for the pupillary threshold Schweitzer [107]) found neither integration (as was the case for the static pupil) nor an agreement with visual measurements. In some subjects he even found a well-expressed over-integration, the total light flux necessary for a pupillary treshold reaction decreasing with increasing field size. According to Schweitzer the origin of this as yet unexplained over-integration must probably be located in the receptive centres of the brain stem.

Cones as well as rods are involved in dynamic pupillary reactions and the organisation of the receptive field for cone-mediated reactions may be expected to be different from that for rods. Both will be considered in chapter 9.

Apart from the organisation of the receptive field for reactions mediated by either rods or cones, one may inquire into the cooperation between rod and cone signals in circumstances in which both may be supposed to be active. Experiments on this problem have been performed by Alpern and Campbell [6]). Using sinusoidal variations of light intensity and a threshold criterion for the pupil, they concluded that a summation of the logarithms of rod and cone signals

occurred. Our own experiments, performed with flashes, gave different results (chapter 8).

3.5. Fluctuations and after-effects

Fluctuations

Under normal circumstances the pupil always shows fluctuations, the phenomenon being known as the pupil's unrest. These fluctuations are superimposed on other reactions. If the pupil is near one of its extreme values, the amplitude of the fluctuations is generally less than 0·10 mm. At intermediate diameters and light intensities amplitudes of about 0·5 mm may be reached. This effect is only partly due to the feedback characteristics as initiated by transient reactions due to movements of the eyes and of the eyelids. The effect occurs also with a very large retinal field, when lid closures are suppressed, and is therefore brought about by other causes too. Obviously, pupillary fluctuations that are too small to cause a change of retinal signals escape from retinal control (Stark [114]). Pupillary fluctuations generally increase with the state of fatigue.

> Since the fluctuations of both pupils are coupled (Lowenstein and Loewenfeld [77], Stark, Campbell, and Atwood [113]), their origin must be found in the nervous control centres. According to Stark et al., the effect is due to inherent variations of the number of steering impulses. It is assumed that fatigue deteriorates the steering capacities of the centres, possibly due to a state of instability of the autonomic nervous system as a whole. However, the influence of other causes such as blood pressure can certainly not be ruled out.

In certain experiments on static pupil size we noted that the pupil suddenly started to oscillate (amplitude $\approx$ 0·5 mm, frequency $\approx$ 0·3 c/s), the maximum diameter during the oscillations being less than the diameter before the oscillations started, see fig. 5.2. The decrease in the average diameter can be readily explained by assuming that the phenomenon is caused by rhythmic contractions due to pulse trains, the interval between the trains leaving no time for full dilation. Usually, the phenomenon disappears after some minutes. The frequency of occurrence depends on the state of fatigue. The literature mentions this phenomenon as "hippus", a common symptom of certain diseases of the nervous system.

The influence of fluctuations on pupillary measurements will be considered in chapter 5.

After-effects

The rather slow dilation after prolonged illumination belongs to the transient reactions. During this dilation a peculiar phenomenon may sometimes be noticed, which, at best, is only indirectly related to the preceding illumination. The phenomenon consists of an interruption of the slow dilation by a contraction of some minutes' duration, whose start may vary between two and ten

minutes after the light has been switched off (Crawford [29]). Normally, pupil size diminishes with about 0·5 mm. Sometimes, especially when this contraction is rather large, oscillations of the hippus type occur (fig. 3.6). They are usually accompanied by the occurrence of increased amounts of "eigengrau" which
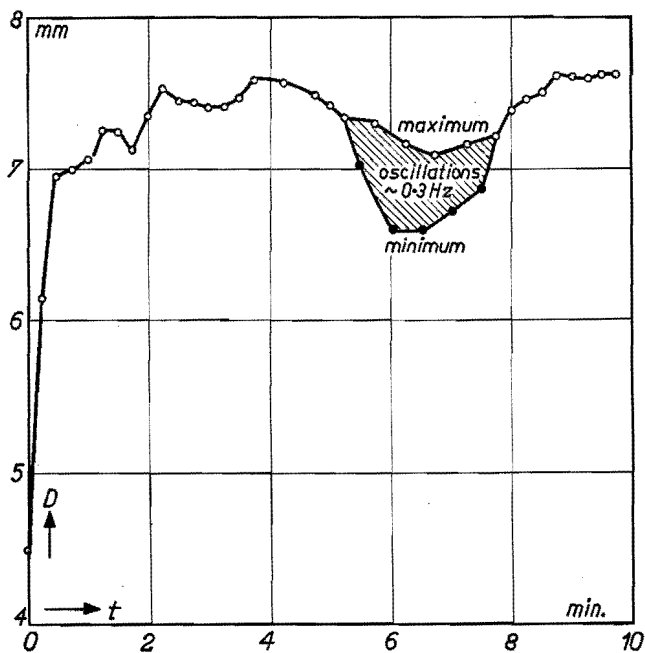
Fig. 3.6. Measurement of pupillary diameter D after extinguishing a bright illumination. The irregular dilation is interrupted by a period of oscillations. Observer H.B.

manifest themselves as vague dim clouds, drifting slowly in the visual field.

3.6. Conclusions

Reactions of the pupil in response to retinal illumination may be divided into three categories: steady-state reactions, transient reactions, and fluctuations. A servo-analytical approach yields overall time relationships between illumination and pupil size. If properties of component parts of the pupillary system are investigated, more classic methods are convenient. In this respect one can avoid the influence of non-linearities in the motor system by using the pupil as a zero-indicator only.

Although the literature on retinal receptors that mediate steady-state reactions shows that rods play an important part, there are nevertheless indications that cones too are involved. The intensity range in which the pupil has been found to react to steady illumination is not scotopic, but either mesopic or photopic. As

regards the organisation of the receptive field for steady-state reactions the data seem contradictory: some experiments point to a homogeneous sensitivity over the retina whereas others indicate a well-expressed foveal maximum.

The literature on transient reactions of the pupil shows that they are mediated by the same receptors as those involved in vision. Thus, rods prevail when vision is scotopic, whereas cones have been shown to play a part under photopic circumstances. The few investigations into the organisation of the receptive field reveal some differences between the pupillary and the visual systems. Here, the overall character of pupillary reactions seems to be of decisive importance.

Pupillary fluctuations increase with illumination. However, the influence of illumination is not always as straightforward as one would wish with respect to the reproducibility of the measurements. In fact, the fluctuations also depend on parameters other than illumination. The oscillations known as hippus seem to be only indirectly related to illumination.

4. APPARATUS

In this chapter we shall first give a short description of the various methods by which pupil size can be measured, followed by a more detailed discussion on the entoptical method used in this study (sec. 4.1). We shall then consider the optical arrangements by means of which we obtained the various light stimuli (sec. 4.2). Efficiency in collecting the required data was increased by the use of an autonomic registering device which will be described in sec. 4.3.

4.1. Pupillometry

Several methods have been used during the last century to obtain reliable measurements of pupil size. Since interest in pupillary reactions was never lacking, the various methods have followed close on the heels of technological advances. Thus the accuracy as well as the speed of the measurements have increased, while the originally good accessibility of the results, after a temporary deterioration due to the use of film techniques, has been re-established. In addition, the illumination which may interfere with the measurements can now be avoided by the use of infrared radiation. A negative aspect of these developments is that the complexity of the apparatus has gradually increased.

The available methods may be classified into four groups:

(1) A *direct comparison* with some sort of scale. In order to avoid parallax the scale may be imaged in the plane of the pupil. The method is simple and rapid, the accuracy is about 0·2 mm. These properties meet normal clinical demands.

(2) *Photographic methods.* Two different ways are known for measuring pupil size photographically. The first method was used as far back as 1885 when Bellarminov [14]) moved a film closely behind a slit. The slit was placed immediately before the centre of the pupil so that the pupillary movements were recorded (fig. 4.1). The method has recently been used in a modernised form by Fugate [43]), by Van der Tweel [124]), and by Baker [12]), who combined it with photo-electric registration. The imaging of the pupillary diameter on the slit, which is of critical influence and the possible inconstancy of the velocity of the film are
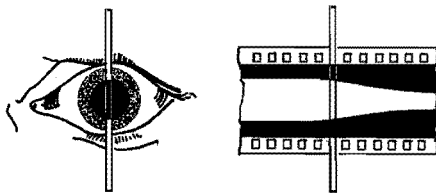

Fig. 4.1. Photographic registration according to Bellarminov [14]). The diameter of the pupil is imaged on a slit with a moving film behind.
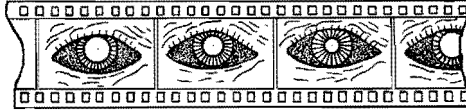
Fig. 4.2. Cinematographic registration of pupil size.

some of the inaccuracies. The other way is to use cinematographic techniques (fig. 4.2). Lowenstein [73]) has long been a pioneer in this field, at first using ultra-violet radiation so as not to interfere with the stimulating light. Since u.v. radiation is not harmless to the eye, the development of infrared-sensitive emulsions caused a rapid change in favour of the use of infrared radiation for registering pupil size.

The main advantage of the photographic method is that an accurate registration of all sorts of pupillary movements is achieved. It is a disadvantage that the results are not available until some hours after the actual experiments. In addition, time-consuming measurements of the films are necessary. Nevertheless, in 1956 Petersen [87]) arrived at the conclusion that the photographic method was still superior to any other method. The scanning techniques (see below) since developed have proved to be better still.

(3) *Photo-electric methods*. When illuminating the iris membrane the total amount of reflected light depends on pupil size. This amount of light can be measured photo-electrically by means of a photocell or photomultiplier, the signals of which then contain information about pupil size. These signals can be measured and registered directly. In 1941 Matthes [83]) first used this method which was later further developed by Cüppers [31]), who used infrared radiation.

The relationship between the portion of reflected light and pupil size is dependent on the reflectance characteristics of those parts of the eye that are illuminated, of which mainly the reflectance of the iris membrane shows considerable individual differences. Since the reflected amount of light turns out to be approximately proportional to the illuminated area of the iris membrane, relative changes of pupillary area can be measured by using this method. It must be considered a disadvantage that no absolute measurement of pupil size can be obtained, unless some separate calibration is made for each eye.

In modern scanning techniques this difficulty is avoided. The eye is scanned with a narrow pencil of infrared radiation. The duration τ_i of the diminution of the reflected intensity as caused by the lesser reflectance of the pupil contains the information on absolute pupillary diameter or area (fig. 4.3). Three techniques are available to date:

(a) The time interval τ_{max} that the scanning pencil needs to pass pupillary diameter is proportional to this diameter. The scanning can be restricted
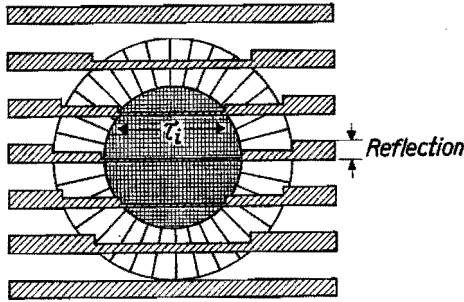
Fig. 4.3. Measurement of pupil size by way of scanning. The time τ_i during which the pupil is scanned, is characterised by the occurrence of less reflection. The horizontal diameter of the pupil is proportional to τ_{max}, the vertical diameter is represented by the number N ($\tau > 0$) of lines by which the pupil is scanned. Pupillary area is proportional to $\Sigma \tau_i$.

to a narrow zone passing over the pupillary centre. The position of the pupil relative to this zone is of direct importance.

(b) Schouten [105]) suggested a method in which the number of lines N that passes over the pupil when the total pupil is scanned is used as a direct digital indication of pupillary diameter.

(c) The total time $\Sigma \tau_i$ during which the pupil is scanned is proportional to pupillary area.

The scanning method was first described by Lowenstein and Loewenfeld [75]) in 1958. Recently, Asano et al. [11]) described a pupillometer based on the electronic scanning techniques as used in television. Since television techniques have been fully evolved this method seems preferable. The general applicability, the immediate accessibility of the results, and the high accuracy which can be obtained with the scanning method make it almost ideal for pupillary measurements. The complexity of the apparatus must be mentioned as a still serious disadvantage.

(4) *Entoptical method.* The entoptical method is based on the principle that one is able to observe one's own pupil very much enlarged. This is achieved by projecting the pupil edge on one's retina from a point source located just in front of the eye (fig. 4.4). Then one observes an illuminated disc, the edge of which corresponds to the pupil edge. All movements of the pupil are accompanied by variations in the size of the disc. Starting from this observation, a method was developed for accurately measuring the pupillary diameter, which method has been superseded in the last 25 years by objective methods. It will be argued that in a restricted range of application this subjective method, which we used in our investigation, has some definite advantages over other methods.

If one projects the pupil on the retina twice by using two point sources, the observer sees two light discs. By adjusting the distance between the points the observer makes the two projection discs touch one another. In case of an
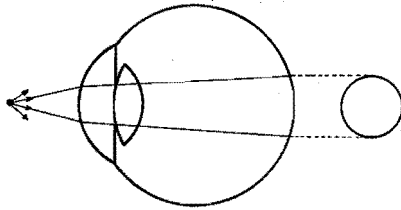
Fig. 4.4. Entoptical observation of pupillary movements. The pupil edge is projected onto the retina from a point source just in front of the eye.
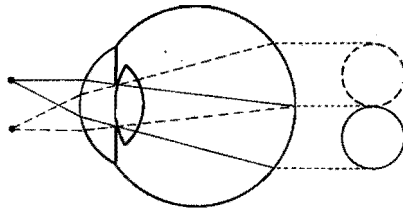

Fig. 4.5. Entoptical measurement of pupillary diameter. When the two projection discs touch one another, the distance between the point sources equals the effective pupillary diameter.

emmetrope, non-accommodated eye, the distance between the point sources then equals the effective diameter *) of the pupil (fig. 4.5). The value obtained is independent of the distance of the points to the eye. According to Broca [19] the principle of this method is attributed to Fick, but I have tried in vain to find Fick's original paper. In 1864 Fick [42] only mentions the entoptical projection with one point source.

The main advantages of this method arise from the high level of accuracy that may be attained (about 0·05 mm), the simplicity of the apparatus, and the rapid completion of the results. Besides, the observer is able to perceive all movements himself, including any deviating ones.

The possible influence on the pupil of the illumination necessary for seeing the projection discs must be considered a disadvantage. In addition, the observer must learn to avoid accommodation. A fundamental restriction is that quantitative measurements are possible only when pupillary velocity is low. Observation of rapid movements is, however, quite possible. For certain applications the subjective character of the measurements may be considered disadvantageous, e.g. when accurate data are needed from untrained observers. Crawford [29] even rejected the method because the observer had to concentrate on the disc positions. According to our experience, this extra attention does not disturb the measurements.

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*) Due to refraction by the cornea, the effective diameter of the pupil exceeds the anatomical diameter by some 10%. In the available methods this effective diameter is measured.

Interesting applications arise from the fact that under any circumstances a rapid, accurate indication of pupillary behaviour is possible. Thus, it is used in clinical practice to obtain an optimal dosage of drugs acting on the pupil, without necessitating frequent clinical inspection, or to measure the influence of road illumination on pupil size. In situations of this kind a pocket-size pupillometer (fig. 4.6) is very handy.

The entoptical method has been used, among others, by Sachs [101], Hess [57], Luckiesh, and Moss [80], and Van Liempt and De Vriend [71]. Pupillometers of the entoptical type have been constructed by Houdin [62] (1870), Broca [19] (1924), and Moss [85] (1932). The point sources were usually obtained by illuminating a small hole, which was sometimes realised by using two perpendicular slits. Moss constructed a very stylish pupillometer of such small dimensions that it could be mounted on a pair of spectacles.
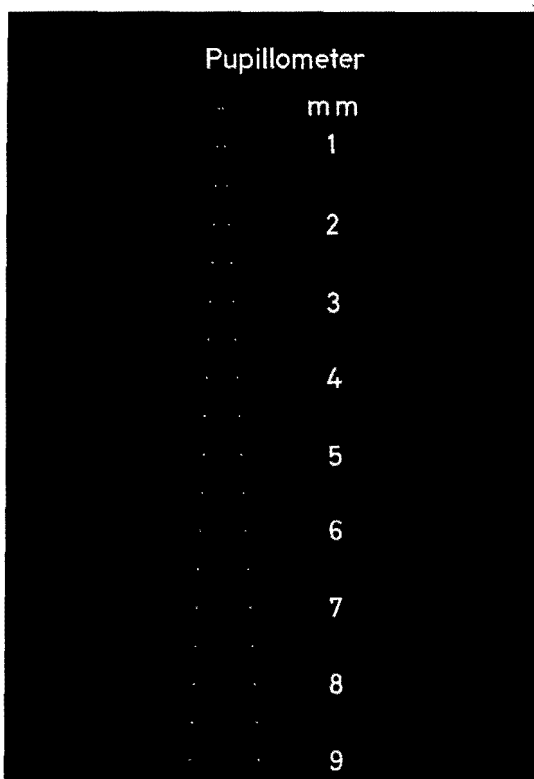
Fig. 4.6. Photographic negative, used as an entoptical pupillometer.

The accuracy obtained with this method is at most of the order of the dimensions of the point sources, generally about 0·1 mm. In 1937 Schouten [103,104] obtained very small point sources by reflecting a small filament on the surface of two tiny silver grains. As may be deduced from fig. 4.7, the diameter q of the virtual image is of the order of $Qr/2l$, where r stands for the
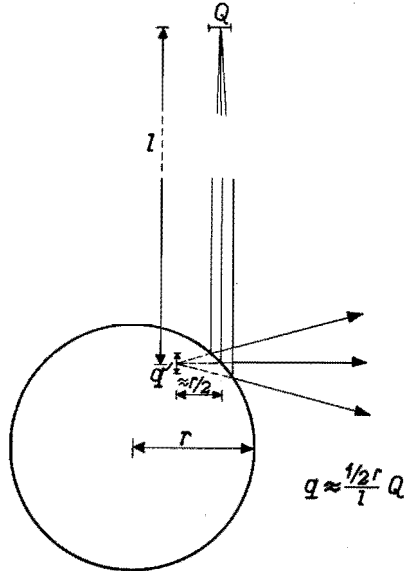
Fig. 4.7. A filament (size Q) is imaged by the surface of a small grain (radius r) located at a distance l. The size q of the virtual image is approximately $rQ/2l$.

radius of the grains and Q for the diameter of the filament, located at a distance l from the grains. Taking $r = 1$ mm, $l = 30$ mm and $Q = 2$ mm, it follows that $q \approx 0.03$ mm. Thus a very high degree of accuracy can be reached. Schouten attached the grains to a pair of compasses in order to facilitate the reading.

In the first part of our experiments this type of pupillometer was used along with a potentiometer to get automatic readings (fig. 4.8). Later on a modified version was used in which we employed a micrometer construction, and a helical potentiometer of exactly ten turns (fig. 4.9) *). This provided the opportunity of a direct digital reading and registration in 0·01 mm units, without a calibration table being necessary. In this type, the point sources move symmetrically. With a value of $r = 0.4$ mm, Q and l being unchanged, the accuracy is about 0·01 mm. Normally the fluctuations of the pupil are much greater than 0·01 mm. However, in the dark the pupil is sometimes very stable which enabled us occasionally to measure pupillary changes down to 0·02 mm. The reflecting surface of the grains is projected on the retina several hundred times enlarged; for this reason it is desirable to have them polished optically smooth.

In case the eye is not emmetrope or in some state of accommodation, the distance a from the point sources to the eye is of some consequence. The implications can readily be seen from simple geometrical drawings. An example is shown in fig. 4.10, in which the eye receives a sharp image from a point, b cm in front of the eye (100/b diopters

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*) Both types of pupillometer were constructed by Mr H. S. Fuchs and Mr H. E. M. Mélotte of the Institute for Perception Research.
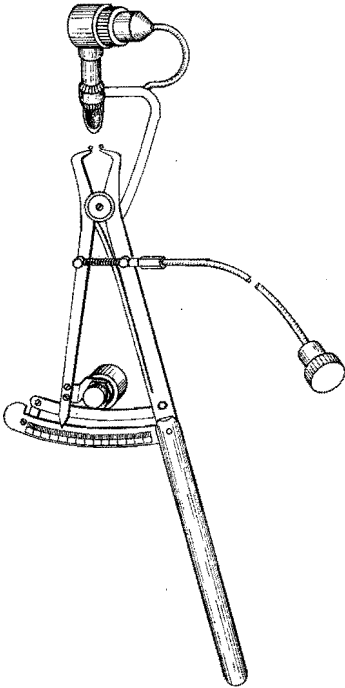
Fig. 4.8. Entoptical pupillometer on which, according to Schouten [103,104], two grains are mounted on a pair of compasses. A potentiometer permits automatic reading and registration.
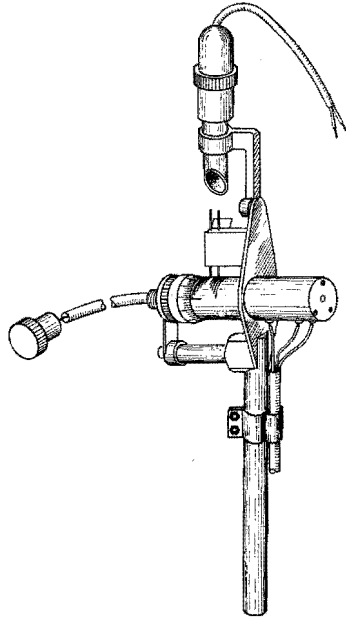
Fig. 4.9. Entoptical pupillometer, based on a micrometer construction. It is provided with a helical potentiometer.

accommodation or myopic). As in the case of the emmetrope eye we construct those rays that come together in the fovea. Thus we get:

$$D_{\text{pupil}}/D_{\text{grains}} = b/(b-a) \approx 1 + a/b.$$

Taking $a = 2$ cm and $b = 50$ cm we get a correction factor of some 4%. For the general case in which the dioptric situation of the eye deviates d diopters from the normal situation, the correction factor is ad per cent. This also applies to the spherical aberration of the refractive surfaces of the eye, which also cause such a deviation. The spherical aberration, however, is only of the order of one diopter (Iwanoff [63]), so that the resulting deviation may be neglected.

Since the correction factors do not affect the results in any essential way, we have neglected them.
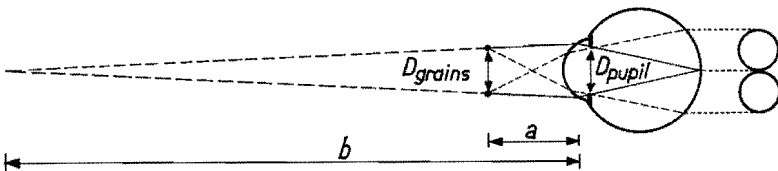
Fig. 4.10. The geometry of the light rays when an eye is focused at a distance b; $D_{\text{pupil}}/D_{\text{grains}} = b/(b-a) \approx 1 + a/b$, by which the correction factor for the measured pupillary diameter amounts to $100.a/b$ per cent.

4.2. Optical arrangements

The aim of the optical arrangement as it has normally been used is to offer the subject monocularly a test field and a conditioning field that can be varied independently in intensity, wavelength, time of onset, duration, field configuration, and place of incidence within the pupil.

In order to prevent actual pupil size from influencing the amount of light entering the eye (open loop) it is desirable to concentrate the light on a small spot within the pupil. Moreover, this method of Maxwellian view enables one to combine high light intensities with a rather large field. In this respect other ways of escaping from the influence of the pupil, such as paralysing its muscles or using a diaphragm as an artificial pupil are far less promising.

The basic arrangement of the apparatus that meets the requirements is shown in fig. 4.11. The small diaphragm O_1, illuminated by a projection lamp, is imaged twice, viz. in O_2, where a pair of shutters SS controls the timings, and in O_3 where the centre of the subject's pupil must be located. For this purpose a head rest, a biting board, and a nose rest were used. The second light path has been arranged similarly. Its characteristic points are indicated by corresponding symbols with primes. Both pathways are combined by a beam splitter $M\frac{1}{2}$.
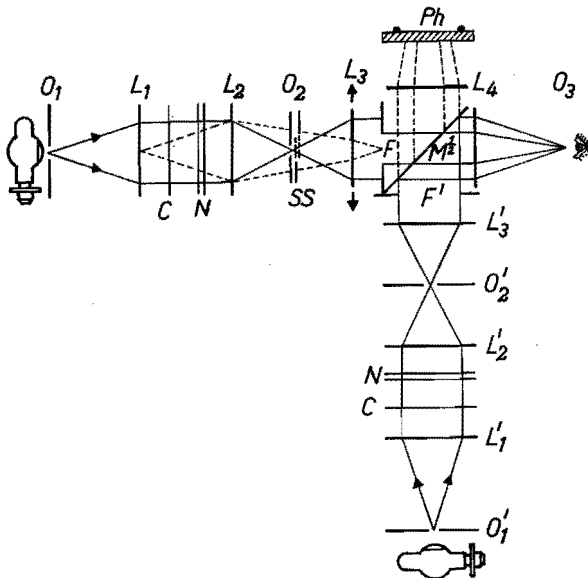

Fig. 4.11. Optical arrangement. Two independent pathways are combined by a beam splitter. The illuminated fields are seen in Maxwellian view.
O — diaphragms, L — lenses, C — colour filters, N — neutral filters, SS — pairs of shutters, $M\frac{1}{2}$ — beam splitter, Ph — photocell, F and F' indicate the focal planes from which the retina receives a sharp image.

The photocell Ph receives light from both pathways and is used for calibrating light intensities. Intensity and wavelength can be chosen by means of neutral filters N and colour filters C, respectively, located in the parallel beams. Several filters are fitted in one disc, which can be rotated so as to facilitate changes. The non-accommodated eye of the observer receives a sharp image of the focal planes F and F'. Dimensions, form, and location of the field can be chosen by putting suitable diaphragms in these planes. By shifting the lens L_3 perpendicular to the optical axis of the arrangement the position of the point of incidence on the pupil can be changed without size and position of the field of view being affected. This method has been used in order to perform measurements on the directional sensitivity of the retinal receptors (Stiles-Crawford effect).

Peripheral fields were realised by using an optical arrangement which could be rotated around a vertical axis. As the pupil of the observer (fig. 4.11, O_3) could be positioned into the prolongation of this axis, the light amount striking the retina was independent of the perimetric position of the light stimulus. The centre of the retinal field could be varied from 70° at the nasal side to 40° at the temporal side.

Very large homogeneous fields have been realised by means of an Ulbricht [125]) sphere. Spheres of two different sizes were used, 230 and 110 mm in diameter, respectively, of which the latter turned out to be the most convenient. Two openings in the sphere with diameters of 10 mm and 23 mm were used for illumination and for looking inside, respectively. The illumination was realised from outside the sphere, by illuminating a spot just beside the opening for the eye. By diffuse reflection from there the sphere was illuminated homogeneously (fig. 4.12). In this way a homogeneous illumination of the full visual field is obtained. This situation will be referred to as "180°" field. The marks are used to indicate that the retinal receptors cover only some 120° of this field.

In most experiments with the Ulbricht sphere the natural pupil was used. In some experiments the pupil of the illuminated right eye was widened artificially by means of homatropin. The quantum flux incident upon the eye was calculated from the illumination on the surface of the sphere and the diameter of the pupil.
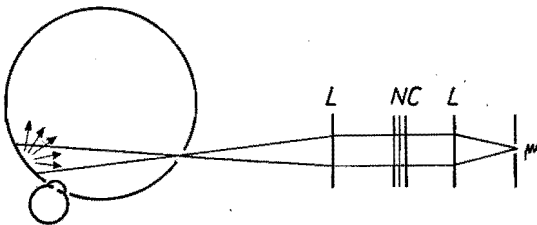

Fig. 4.12. Homogeneous illumination of the full visual field by means of an integrating Ulbricht sphere.

Details of the arrangement

The *light source* consisted of a projection lamp with internal mirror, giving a high light output in a restricted solid angle (Philips No. 13113C/04 8V, 50 W, colour temperature 2700 °K). It was fed by a stabilised current *). In combination with a fan a very constant light output was reached, short-term fluctuations being less than 1 % and the total decrease of intensity less than 30 % in a hundred hours.

In general, uncorrected spectacle *lenses* were used, which turned out to be satisfactory. The light beams in particular have been found to be sufficiently parallel for the interference filters. Spherical aberrations cause non-uniform illuminations, which were avoided in the field of view by way of imaging the homogeneously illuminated lens L_1 in the focal plane F, which in turn is imaged on the retina. For the measurements in which the point of entry in the plane of the pupil was varied, we used an anastigmatic lens.

Metal-coated glass sheets were used as *neutral filters**)*. Especially those of higher densities showed some wavelength dependence, which was accounted for in the intensity calculations. The light successively passed three discs containing 6, 6 and 3 filters, respectively. The differences in optical density between two adjacent filters in the discs amounted to 2, 0·4, and 0·15 log units, respectively. In this way a range of 12 log units was covered in steps of 0·15 log units.
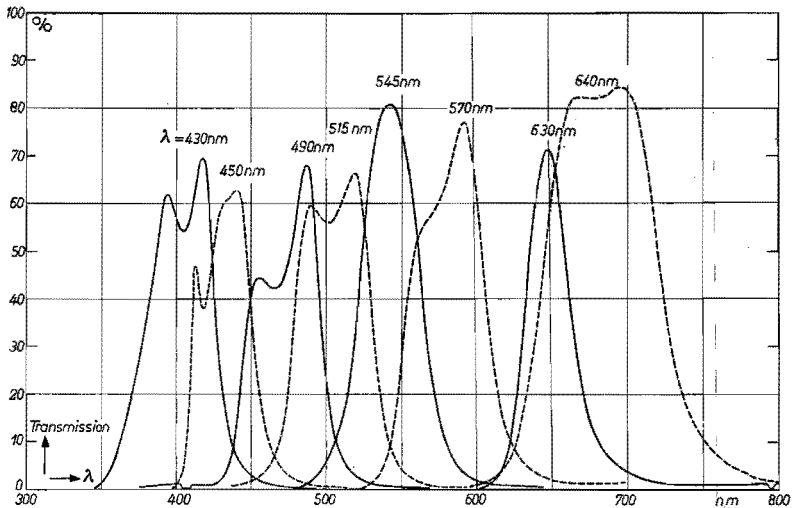
Fig. 4.13. Transmission characteristics of the eight interference filters used. The numbers indicate the average wavelengths of stimulation of the visual brightness functions, which deviate from the wavelengths of maximum transmission for extreme wavelengths in particular.

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*) The current stabiliser was developed by Mr D. J. H. Admiraal of the Institute for Perception Research.
**) These neutral filters were made by Mr J. van der Wal of Philips Research Laboratories.

Eight Balzer interference filters were used as *colour filters*. The half-width of their transmissions was of the order of 50 nm. The transmission characteristics [*]) are shown in fig. 4.13. In the wavelength range from 500-600 nm, the calibrations were performed with an absolute accuracy of 0·1 per cent transmission. Due to the high absorption by the visual pigments that occurs for these wavelengths, a low transmission in this range may nevertheless lead to a substantial contribution to total stimulation. During each session, the amount of light was measured in photopic lumens. The colour temperature of the lamp and the transmission characteristics of the colour filters must be known to enable the equivalent quantum flux to be calculated at the wavelength of maximum stimulation of the photopic system.

A check on the accuracy of these evaluated transmissions can be obtained by measuring scotopic and photopic brightness spectra for some observers, which must be expected to approximate the spectra of the CIE standard observer. In doing so, the deviations were of the order of 0·1 log unit, except for the extreme wavelengths. In particular the filters 630 and 640 nm gave a systematic deviation of 0·4 log units from the scotopic standard observer (see fig. 6.3). Probably, this deviation must be attributed to the fact that the scotopic spectrum shows a sharp cut-off towards longer wavelengths in this region, which may easily lead to inaccuracies with these filters of 50 nm width. We have not corrected for these systematic deviations.

A *Weston photocell*, connected to a current-compensating circuit, has been used for calibrating light intensities. It was adapted for the photopic sensitivity curve. The measurements were made with white light, the outcome being expressed in photopic lumens. This outcome was evaluated in terms of quantum-flux by taking into account the colour temperature of the lamp and the transmission characteristics of the filters used. The sensitivity of the photocell was dependent on the angle of incidence in case this angle differed more than 40° from perpendicular incidence. If necessary, this directional sensitivity was accounted for. In combining all kinds of error sources in calibration, the accuracy of light intensities was within 10%, corresponding to 0·04 log units, which is smaller than the systematic deviations introduced by the colour filters.

Each element of the pair of *shutters* consisted of an interceptor of the light beam, mounted on the armature of a relay. Two shutters were used together in order to utilise only the release of the relays, as its duration (2 ms) and reproducibility are far better than of the attraction. The controlling signal was obtained from a condenser-resistance circuit (flash duration variable between 20 and 500 ms, accuracy better than 5%). Later on this circuit was replaced

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[*]) Dr A. Bril of Philips Research Laboratories was so kind as to perform these calibrations.

by an electronic cascade counter *), which gave a far greater range and better reproducibility (duration $\geqslant 3$ ms, accuracy ≈ 1 ms).

An adjustable *head rest* supported the observer's head. It consisted essentially of a chin rest, two temple steadiers and a forehead support. When a properly chosen fixation object was used, the observer could maintain his eye position with an accuracy of about 1 mm, as was found from an external check. In cases where the position of the eye was of decisive importance (as in the case of measurements of the Stiles-Crawford effect), an extra nose rest was used, which fixed the bony part of the nose to the optical arrangement. In a later stage of the experiments we used a biting board, which ensures a better stability of the eye position at the cost of some extra inconvenience to the observer.

A *fixation mark* could be provided for either by putting a suitable filter and diaphragm in the second light path, or by putting the point of a glass rod, drawn out to a glass fibre, in the focal plane F or F^1. The glass rod was illuminated by a small lamp with a red filter. The glass fibre serves as a light conductor and gives a very small light spot of adjustable intensity.

4.3. Automatic registration

In order to save the experimenter many hours of dull work, the filters were fitted to discs which the observer could handle himself, whereas registration was automatic. For this purpose, electrical contacts were mounted around the spindle of each disc which permitted automatic registration of their position. The settings of continuous variables such as pupillometer, neutral wedges, etc., could also be registered. By merely pressing one button, the observer could register all variables automatically.

The use of this equipment enables the observer to perform the experiments all by himself. Since he is not aware of the actual outcome of his measurements, he is not tempted to influence his settings by what he expects to find. With the help of this registering device, a trained observer achieves an average of 25 measurements of static pupil size or of contraction amplitudes to light flashes, during an experimental session of $1\frac{1}{2}$ hours (2-4 settings for each measurement). Consolidation of the results in the form of tables and graphs takes about one extra hour.

Details

Automatic registration of the continuous variables has been realised by coupling a potentiometer to the revolving spindle controlling the variables. The resulting potentiometer setting was measured and digitalised by an analogue-digital converter (Philips No. P.R. 7800). At its output the signal is coded as a series of contacts, which could be handled by an electrically operated adding

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*) The cascade counter was developed by Mr G. J. Moonen of the Institute for Perception Research.
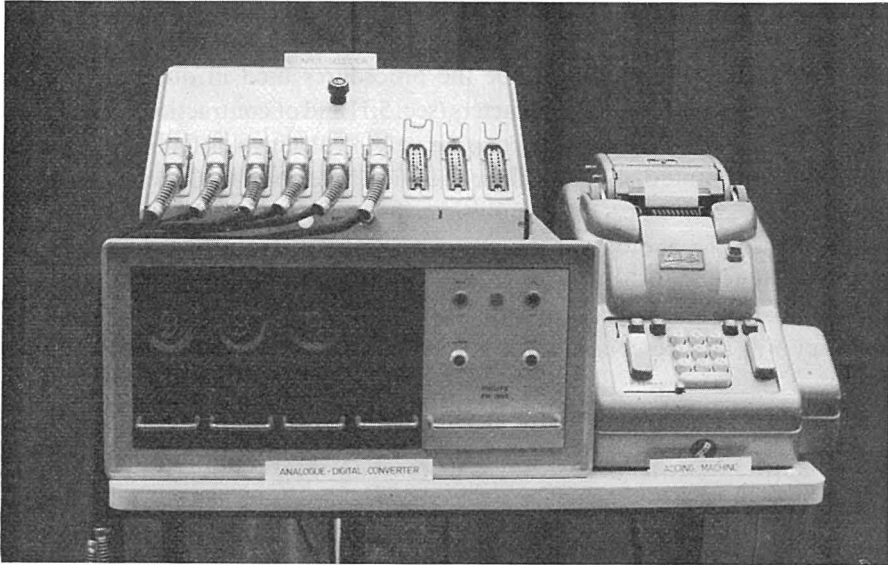
Fig. 4.14. Automatic registration equipment: input selector, analogue-digital converter and adding machine.

machine (Addo-X). Discontinuous variables such as the position of the filter discs and the shiftable lens were made manifest by an internal contact and fed directly into the adding machine. An input selector *) governed the sequence in which the various settings were offered to the adding machine and provided for the reset. An additional input socket offered the observer the possibility of having extra numbers registered. This was of importance when reporting numbers of perceived flashes and under certain circumstances also for the identification of the resulting set of numbers.

Figure 4.14 shows a photograph of the equipment.

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*) The input selector was developed by Mr G. J. Moonen of the Institute for Perception Research.

5. EXPERIMENTAL PROCEDURES

In this chapter we shall describe the procedures used in our experiments. Measurements of steady-state diameters (sec. 5.1) and of contractions in response to flashes (sec. 5.2) will be discussed separately. Problems arising from measurements of steady-state diameters will be specified. The entoptical method permits a somewhat better inspection of the steady-state character of the pupillary response than the photographic method which has often been used by others. It will be shown that the divergencies in the results obtained by various investigators may have been due to different measuring procedures. Measurement accuracy will also be considered.

5.1. Measurement of steady-state diameters

In chapter 3 we defined the steady-state reaction of the pupil as the equilibrium diameter reached after some time in reaction to continuous illumination. In fact, the pupil is always fluctuating. If small fluctuations occur around an average diameter, only the accuracy will be affected. Large fluctuations, however, depress the average diameter because fluctuations are asymmetrical in the sense that they tend to start with a contraction. Therefore it is essential to avoid fluctuations as much as possible. We aimed at this by using the following procedure.

Experimental procedure

After the observer had been adapted to darkness for at least 15 minutes, a steady light stimulus was presented to his right eye. Since the effect of this light on the pupil of the left eye was to be examined, the pupillometer was placed in front of this eye at a distance of about two cm. The illumination from the pupillometer was adjusted so as to reach the minimum intensity at which visual acuity still sufficed to make accurate adjustments; this corresponded to about one photopic troland.

The observer waited until the projection discs had reached constant size, which took about one minute, but sometimes much longer periods were required. Then he made the discs touch by adjusting the distance between the two point sources, after which he pressed a button in order to register the setting of the pupillometer. At each light intensity three to five adjustments of the pupillometer were made, the average of which was taken for further use. The same procedure was then applied for other illuminations which were presented in increasing order. Before each successive series began, the eye was again adapted to darkness.

No measurements were made during periods in which large fluctuations occurred. In general a period of some minutes' rest sufficed to stabilise the pupil again. Since we had the impression that these large fluctuations are correlated

with the state of fatigue, we tried to avoid them by carrying out most experiments during morning sessions.

The adaptation time of 15 minutes is not long enough to reach the fully dark-adapted state. In the first series of measurement adaptation times of 30 minutes were used. Since, however, the intensities at which the pupil reacts to continuous light are rather high (several log units above the visual threshold), an adaptation time of only 15 minutes was chosen and turned out not to affect the results. The two observers who carried out most experiments were slightly myopic (some two diopters); in other respects their vision was normal.

Fluctuations during continuous illumination

What kind of unwanted pupillary fluctuations or irregular movements can be observed during steady illumination? Small oscillations can always be observed, except under very low illuminations. Eye movements and blinks give rise to well-expressed transient reactions, which will have disappeared after some five seconds. Transients at the onset of illumination are sometimes rather persistent, the dilation after the initial contraction requiring time intervals from several seconds to several minutes. These dilations are not smooth but occur in steps interrupted by contractions. During these transients the fluctuations are markedly increased and the first indication that a steady diameter is being reached is a diminishment of the amplitude of the fluctuations, the pupil then dilating smoothly (10-30 s) to a constant value.

The occurrence of these prolonged transients is rather irregular: sometimes they are absent and sometimes they are of such persistence that the session has
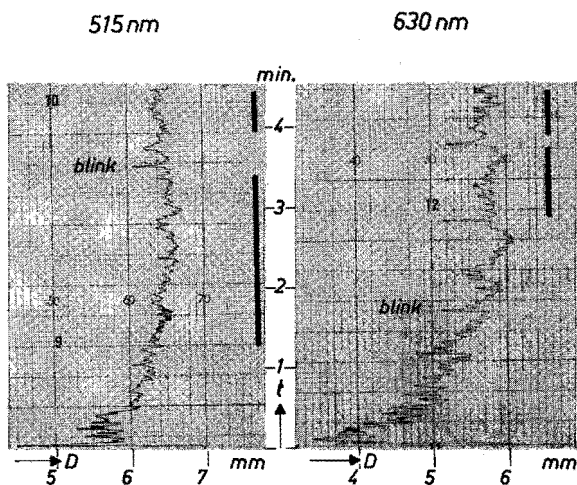
Fig. 5.1. Registration of pupillary diameter D in reaction to steady illumination. When $t = 0$, the steady illumination was increased by a factor of 10. The black lines mark the periods during which the observer judged the pupil to be sufficiently stable for measurements to be carried out. Field 20°, two wavelengths, observer H.B. The pupils are quiet.
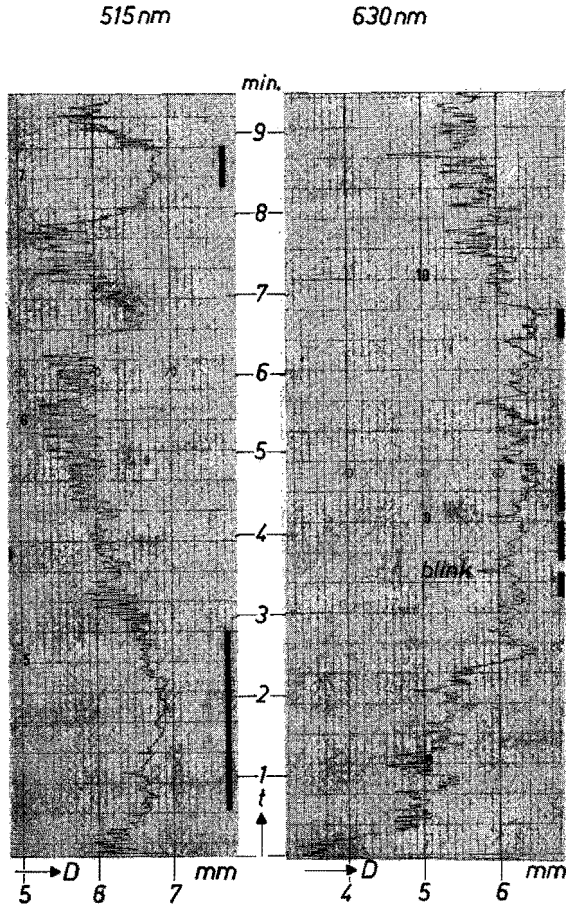
Fig. 5.2. Similar to fig. 5.1. This measurement was characterised by persistent oscillations. Enlarged pupillary fluctuations are asymmetrical in a sense that they depress the average diameter.

to be stopped. According to our experience they increase with the brightness of the field, especially when the final steady-state diameter is high. Next, they are more marked at foveal than at peripheral fields. Finally, as these transients have been found to increase with the state of fatigue, the probability of their occurrence will be greater as the day proceeds. Apparently we have to do with a state of instability in the neural control centres which is encouraged by illumination and by the general state of fatigue of the autonomic nervous system.

Figures 5.1 and 5.2 give illustrations of the phenomena described. The recorded parameter is the voltage of the potentiometer that is controlled by movements of the pupillometer (see fig. 4.9). The observer followed the pupillary movements by trying to keep the projection discs just touching one another. For rapid movements this is not possible. Figure 5.1 shows registrations for two

wavelengths taken from a session during which the pupils were rather quiet. The eye was illuminated by a 20° field, which was presented immediately after steady adaptation to an illumination of 1 log unit lower in intensity. Thus, what is being recorded is the transient reaction due to a tenfold increase of the illumination. Figure 5.2 shows a similar registration now taken during a session that had to be stopped due to persistent oscillations. The black lines indicate the few periods in which the observer considered the pupil as sufficiently stable to take readings. It will be seen that the enlarged fluctuations cause a considerable decrease in the average diameter, which is in accordance with our general experience. The persistent oscillations have been recorded in detail by Lowenstein and Loewenfeld [77].

Comparison with other procedures

When measuring steady-state diameters, one has to wait until the transient reactions have disappeared. In the literature this has usually been achieved by waiting for fixed time intervals after the onset of illumination [5,29,129]. These intervals ranged from ten seconds to three minutes, the constancy of the diameter after that time being judged either by its reproducibility or by separate experiments in which the influence of this time interval was explored. In order to avoid other transients, the observers were instructed to fixate as steadily as possible and to avoid blinks. This procedure is especially suitable when photographic techniques are used.

When applying the entoptical method, no fixed time intervals need be chosen since the observer sees the movements of his pupil and waits until the diameter has become constant before making adjustments. Blinks, etc., cannot be suppressed for long, but they can be avoided in the last few seconds before an adjustment is made. Nevertheless, if they do occur, the effect on pupillary diameter is clearly visible, so that the setting can be delayed. Thus, the main difference with the photographic technique is that the conditions required for steady-state measurements, viz. the absence of illumination transients and the absence of large fluctuations are under continuous inspection. This inspection can be achieved by other techniques as well.

The measurements reported in the literature show, in general, smaller diameters than were obtained by us (fig. 5.3). This might be attributed to individual differences, which are known to be considerable. However, since these differences were found at all of our seven observers, it is more likely that the experimental procedure exerts some influence. For this reason we have imitated some of the procedures reported in the literature. We compared the following procedures.
(a) Closed-loop with open-loop situations. It may be that oscillations that tend to depress the pupillary diameter differ in the two conditions.
(b) Adjustments after fixed time intervals with adjustments according to the inspection procedure.
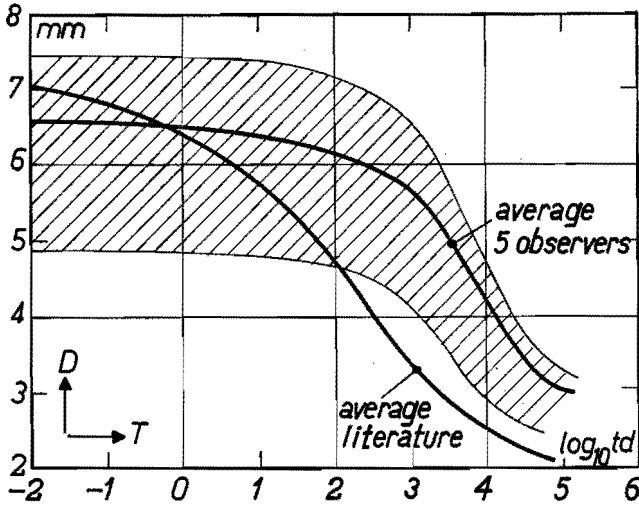
Fig. 5.3. Comparison of entoptical measurements (five observers) with the average of the data reported in the literature. The dissimilarities seem too large to be accidental and are probably influenced by methodological differences.

(a) In fig. 5.4 steady-state diameters, measured according to the inspection procedure described, at illumination through the natural pupil *) (closed loop) are compared with those at illumination through the pupil centre only (open loop). It is clear that the results are very similar, the conclusion being that this difference in illumination conditions has no important influence on the results.
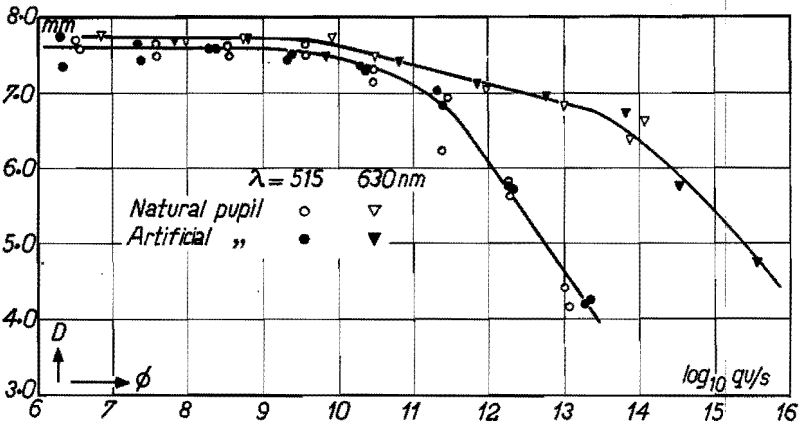
Fig. 5.4. Comparison between closed-loop situation (natural pupil) and open-loop situation (artificial pupil) with regard to their influence on steady-state diameter D. No significant differences occur. Field 18°, two wavelengths, observer H.B.

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*) This has been achieved by putting frosted glass in the focal plane F of fig. 4.11. In the calculations of light intensities in the case of a natural pupil we made use of the fact that both pupil are of equal size.

(b) Investigating the influence of the time interval, we subjected the observer to a steady illumination, which was increased by one log unit at time $t = 0$. The observer followed the movements of his left pupil with the pupillometer as closely as possible. At times $t = 10n$ seconds ($1 \leqslant n \leqslant 9$) he heard a weak click as a sign to press the registration button. Figure 5.5 shows the results obtained for two wavelengths in various intensities, which may be compared with the diameter according to the inspection method. Similar results in which those for $n = 1$-3 and 7-9 have been averaged for comparison with the diameters according to the inspection method are shown in fig. 5.6 as a function
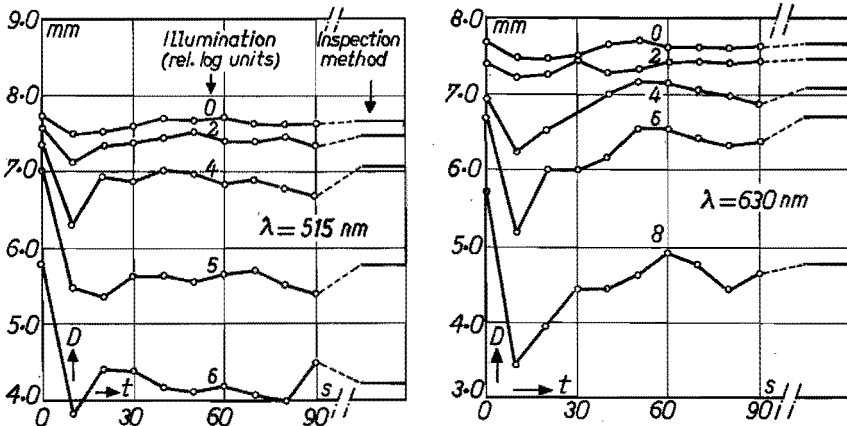
Fig. 5.5. Pupillary diameter D, measured at fixed time intervals ($t = 10\, n$ seconds; $0 \leqslant n \leqslant 9$) after a sudden tenfold increase in illumination, for several values of the initial illumination. The lines serve only as connections between the points. The black horizontal lines at the right show the diameters that were judged to be steady by the observer (inspection procedure); they are generally somewhat larger than the diameters measured at fixed moments. Transients for a short wavelength (515 nm, left curves) require shorter time intervals than are needed for a long wavelength (630 nm, right curves). Field 18°, observer H.B.

of intensity. It must be emphasised that during none of these measurements did abnormal fluctuations of the described type occur, whereas movements of the eyes and of the eyelids were restricted to the moments immediately after the clicks.

At a wavelength of 515 nm, the diameters in the fixed-time procedure are 0·0 - 0·2 mm smaller than in the inspection procedure. At a wavelength of 630 nm, however, the differences are more pronounced, especially at illumination values at which high brightnesses are accompanied by a large pupillary diameter. The differences of 0·0 - 0·5 mm diameter correspond to differences in illumination of 0·0-1·0 log units, which is considerable. For very low as well as for very high contractions the differences vanish.

We conclude that the inspection method produces larger diameters than the fixed-time-interval method. The amount of difference depends on the intensity increase, the stability of the observer's pupil, and also on the movements of the
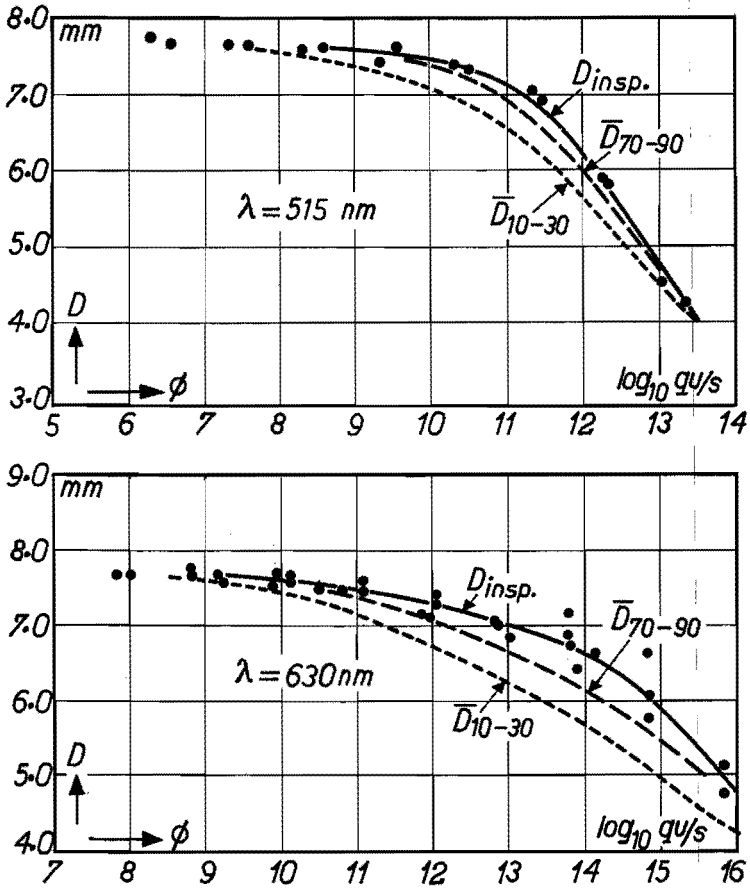
Fig. 5.6. Average results obtained in a way similarly to those in fig. 5.5. Full curves show steady-state diameters measured, using the inspection procedure. Broken curves show average diameters $\bar{D}_{10-30}$ ($n = 1, 2, 3$) and $\bar{D}_{70-90}$ ($n = 7, 8, 9$). The inspection procedure yields higher diameters than the fixed-time-interval method. Even after an adaptation interval of more than one minute, differences are clearly expressed. They are smaller for a short wavelength (515 nm, upper curves: $\Delta D \approx 0.2$ mm, $\Delta \log \Phi \approx 0.2$ log units) than for a long wavelength (630 nm, lower curves: $\Delta D \approx 0.4$ mm, $\Delta \log \Phi \approx 0.7$ log units). For very small and very large contractions, the differences tend to vanish.

eyes and of the eyelids. Due to these movements, untrained observers or observers who do not know beforehand at what moment a measurement will be made, will on an average show still smaller diameters. Accordingly, the outcome of these experiments is only qualitatively applicable to the results gathered from the literature. It is remarkable that the differences should depend on illumination parameters (intensity, wavelength). Since usually it is illuminations necessary for a constant response that are compared, the results will be affected by the procedure selected. Clearly, the transients and the occurrence of fluctuations are governed by other illumination parameters than is the final stable diameter which we defined as steady-state response.

Thus, at normal continuous illumination, the pupillary diameter is governed by a combination of separate pupillary reactions: a reaction causing a stable diameter, a set of transient reactions, and an instability reaction. We have tried with our inspection method to isolate the stable diameter defined in chapter 3 as steady-state diameter.

Reproducibility of steady-state results

In order to obtain information about the reproducibility of the steady-state measurements we performed some experiments in which we took 7-9 successive independent settings for each intensity. The standard deviation ΔD (per setting) ranged from 0·04 to 0·22 mm with an average of 0·12 mm. There was an obvious systematic trend in the successive settings for all ΔD-values larger than average, which showed the changes in pupillary diameter during the one minute or so during which the settings were taken. The measurements were repeated on 3 days. The spread of the average diameters of each day was of the order of 0·2 mm, but in other sessions larger values (up to 1 mm difference between minimum and maximum) occurred. The diameter D_0 in the dark showed fluctuations which were of the same order of magnitude. This diameter usually decreased somewhat during the day and also during a session, which effect is possibly connected with fatigue.

A low diameter in the dark, however, does not necessarily imply that the diameters in response to illumination will also be low during that session. Figure 5.7 shows an example of this phenomenon. It may be concluded that the daily variations of pupil size in the dark are not directly correlated with the daily variations in the presence of illumination. Due to this effect, it is of no advantage in steady-state contractions to use the contraction $C = D_0 - D$ instead of D as a measure for the influence of the illumination.
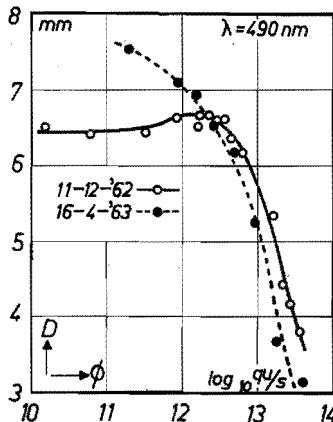

Fig. 5.7. Measurements carried out on two days. A low diameter in the dark does not necessarily imply a low static diameter in response to steady illumination. "180°" field, observer H.B.

However, if the pupillary diameter in reaction to illumination shows a certain deviation from the average, this trend usually persists during the session. Pupillary diameters in reaction to illumination (two wavelengths) are compared in fig. 5.8, in illustration of two sessions. Though the diameters in the two sessions show considerable deviations, the differences between the two wavelengths are almost equal. This means that if different illuminations are to be compared, it is advisable to offer them in one session, as was generally done in our experiments. This should be kept in mind when in subsequent chapters it is desired to compare results represented in different graphs, since they have usually been
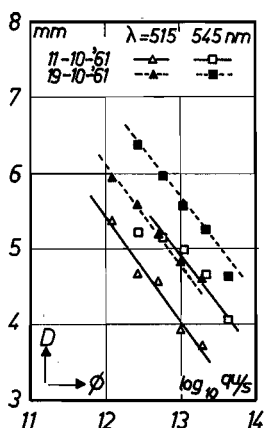
Fig. 5.8. Measurements for two wavelengths, carried out on two days. A low diameter in response to illumination persists during a session. Field 18°, observer H.B.

collected in different sessions. We shall present the experimental data in such a way that the graphs of the actual experiments show direct measurements (averages of 3-5 adjustments). For further interpretation, data of each separate session were compared before averaging.

5.2. Measurement of contractions in response to flashes

As has been mentioned in chapter 2 the pupil responds to a light flash with a contraction, followed by a slower dilation to its original diameter (fig. 5.9). The outline of experiments concerning this flash reaction would be greatly facilitated if such contraction could be characterised by a very small number of parameters only. Within certain limits it is possible to use a single parameter for which the initial velocity or the amplitude of the contraction may be taken (Van der Tweel [124]). When high-intensity flashes are used, this simple description breaks down (Stark, Van der Tweel, and Redhead [117]). Since the initial
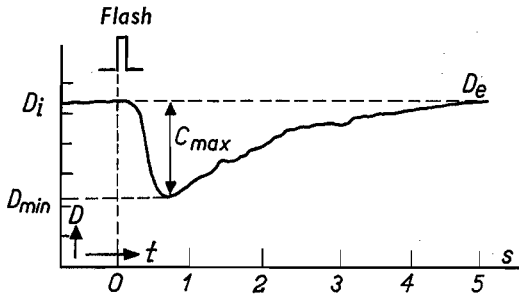
Fig. 5.9. Pupillary reaction to a flash of light. The initial diameter D_i and the final diameter D_e are equal. The amplitude of contraction C_{max} is defined as the difference between initial diameter D_i and minimum diameter D_{min}.

diameter D_i of the pupil in the dark may vary a good deal from day to day as well as during experimental sessions, it is of importance to know how these variations affect the reactions to a light flash. We have compared their influence on the minimum diameter D_{min} and on the amplitude of the contraction C_{max}, measured according to the procedure which will be described below.

Figure 5.10 shows D_i and D_{min} as well as C_{max} for the same series of measurements carried out on three different days, on which very different values for the initial diameters were found. This initial diameter turned out to decrease during the sessions. The reproducibility of C_{max} turns out six times better than that of D_{min}, indicating that the former is much more independent of the variations. Usually the differences in reproducibility were somewhat less spectacular, the standard deviation of C_{max} ($\approx 0 \cdot 10$ mm) being about half as large as that of D_{min}. One might ask whether some sort of relative contraction such as C_{max}/D_i might not show still less spread than C_{max} itself, thus providing an even better characteristic of the pupillary reaction. This turned out not to be the case.

We therefore chose C_{max} as characteristic of the pupillary response to a light flash, as is usually done in the literature. This choice presupposes a one-to-one relationship between amplitude and time function of the pupillary reaction, which condition will almost certainly not always be fulfilled. As long as responses of the same receptors are studied, this factor is of little influence. However, the interpretation of the data originating from different components of the pupillary system must necessarily be made with a great deal of reserve.

Experimental procedure

The consensual light reflex was studied as in steady-state experiments. The flashes were presented to the observer's right eye while the entoptical pupillometer was placed in front of his left eye. As a fixation mark a dim red cross or annulus was continuously present. At some moment when the observer focused on the fixation pattern he released a button, by which action his eye received
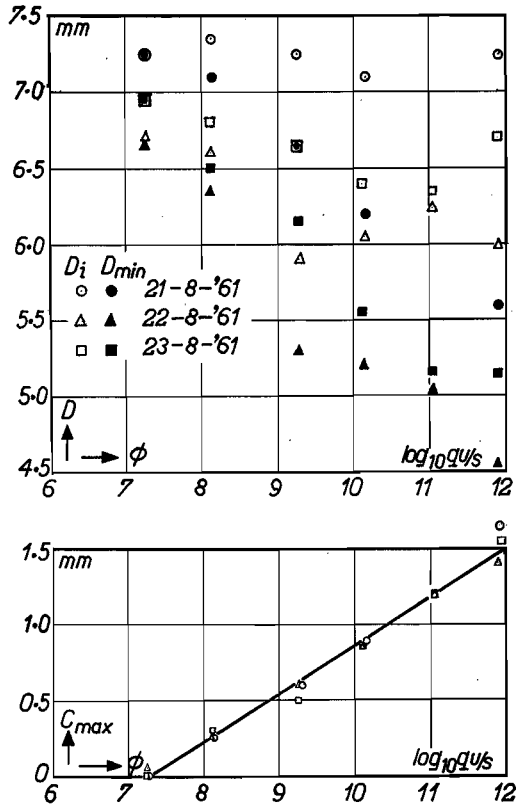
Fig. 5.10. Measurements of D_i, D_{min} and C_{max} carried out on three successive days. The reproducibilities of D_i and D_{min} (upper graph) are inferior to those of C_{max} (lower graph). Field 18°, 515 nm, flashes 100 ms, dark-adapted eye. Observer H.J.v.B.

a flash. In answer to this flash both his pupils reacted in the same way by showing a contraction. The moment he saw the pupillometer discs at minimum size he took notice of the distance between the edges. If the discs still overlapped he increased the distance of the point sources; if they became detached he decreased their distance. Then he delivered a second flash and repeated the process. Thus, by trial and error he found the distance between the point sources at which the discs just touched at their minimum size. An experienced observer needs some four flashes to reach a satisfactory setting. He then pressed a button to get an automatic registration of the pupillometer setting and the flash parameters.

The flashes usually cause the perception of the pupillometer discs to disappear for a short moment. This may sometimes have caused small contractions (smaller than 0·1 mm) to pass unnoticed.

In order to retain the original adaptational state of the retina and of the pupil, successive flashes were separated by an interval of 5-40 s, dependent on flash

intensity. This time interval is long enough to prevent pupillary flash reactions from being influenced by earlier flashes. In order to obtain experimental corroboration we measured pupillary contractions in response to weak flashes, first after full dark adaptation and then after a "conditioning flash" of higher intensity (3 log units). In both situations equal contractions were produced. Using the trial-and-error procedure, it is difficult to measure the initial pupil size D_i before the flash is produced that afterwards turns out to give a minimum diameter exactly in accordance with the pupillometer presetting. Instead we therefore measured pupil size D_e after recovery from the flash. Verification experiments proved that D_i and D_e did not show any significant difference.

Direct registration methods are in principle more suitable for measuring dynamic reactions than the entoptical method. Still, the simplicity of the apparatus, the high degree of accuracy, and the reasonable speed of the measurements seemed to justify the application of the latter method.

In order to provide a direct comparison between the influences of the various parameters on pupillary contractions and visual thresholds we measured visual thresholds with the same apparatus and usually during the same session. This was achieved by presenting to the observer several series of 5-20 flashes, the intensity of the flashes of successive series being decreased for about 0·1 log unit. The observer counted the number of flashes perceived and set this number down in the registering apparatus. From the psychometric function (frequency-of-seeing curve), which may be found from the observations, we derived the intensity at which 50 % of the flashes were perceived. The procedure followed here may only be applied when the threshold criterion used by the observer is fairly well established and somewhat independent of psychological factors. This turns out to be the case for the visual threshold.

5.3. Conclusions

In the pupillary reactions to steady illuminations three processes may be distinguished. First, the pupil contracts to a stable diameter around which small oscillations occur. This may be considered to be the steady-state reaction proper. Secondly, transient reactions occur in response to changes in retinal illumination (due to eye movements and movements of the eyelids). The transient reaction at the onset of steady illumination which may last for some minutes, may also be fitted into this category. Finally, fluctuations of an oscillatory type occur, which may be connected to a promoting influence of illumination to instabilities of the autonomic nervous centres of the pupil. The disturbing reactions cause a decrease in pupillary diameter and an increase in amplitude of the fluctuations.

The degree to which disturbing reactions are avoided has a direct impact on the experimental steady-state results. Since the three types of reaction are influenced differently by the illumination parameters, not only the absolute level

but also the ratio of illuminations that produce an equal response are affected. It is also likely that some of the individual differences reported in the literature are due to differences in the amount of disturbing reactions rather than to differences in the steady-state reactions proper. For these reasons a continuous inspection of pupil size is of importance in steady-state measurements. In this respect the photographic method is less suited for measuring steady-state diameters. Fatigue on the part of the observers should be avoided. Whether the retina is illuminated through the natural pupil (closed loop) or in Maxwellian view through an artificial pupil (open loop) has no significant influence on steady-state diameters.

The accuracy of the settings in our steady-state measurements is between 0·05 and 0·10 mm but, dependent on pupillary stability, the short-term reproducibility of the results is about twice this value. Day-to-day diameters may vary up to one millimeter, the variations of the diameter in the dark and of the diameter in reaction to illumination being of different origin.

Concerning the pupillary contraction in response to light flashes, the amplitude of the contraction C_{max} is a much better criterion than the minimum diameter D_{min}. For the accuracy as well as for the reproducibility of the reactions a value of about 0·10 mm has been obtained. The day-to-day variations are of the same order of magnitude. The amplitude of the contraction cannot always be regarded as an unambiguous criterion of the pupillary reaction to flashes of light

6. PROPERTIES OF PUPILLARY RECEPTORS FOR STEADY-STATE REACTIONS

In order to collect evidence on the properties of the pupillary receptors that mediate steady-state reactions, we have carried out measurements of pupil size when varying several parameters of the retinal illumination. As the influence of these parameters will be considered mainly for some constant effect on static pupil size, the activity in the motor system may be expected to be constant. If this expectation holds, the experiments will provide information on the receptive part of the loop that serves the static reaction of the pupil to light.

When varying the wavelength of the incident light (sec. 6.1) one obtains knowledge of the absorption spectrum of the absorbing pigment involved. Measurements in which the direction of incidence on the receptors is varied (sec. 6.2) discriminate between rod and cone receptors. The intensity levels at which these reactions occur (sec. 6.3) provide interesting data for a comparison between visual and pupillary receptors. For each of the parameters mentioned merely the influence on the pupil will be considered to begin with. Next, we will examine the extent to which pupillary results are in agreement or disagreement with scotopic and photopic brightness functions. In this way we shall build up an overall picture of the pupillary receptors for steady-state reactions.

In all experiments described in this chapter, the consensual reaction of the observer's left pupil has been examined as a function of the illumination of his right eye. Usually, retinal illuminations will be expressed as logarithmic units; 10^{α} scotopic trolands will be abbreviated to α log scot.td, 10^{β} photopic trolands to β log phot.td. In this chapter and in the next one the adjective "static" will often be omitted for reasons of simplicity.

6.1. Spectral sensitivity

Theoretical considerations

When N_i incident quanta of monochromatic light (wavelength λ) strike some simple receptor containing m molecules of an active absorbing pigment, the number of absorbed quanta N_a will be proportional to N_i and m, provided the quotient N_a/N_i is low:

$$N_a = a(\lambda) \, m \, N_i. \tag{6.1}$$

The proportionality constant $a(\lambda)$, the absorption spectrum, is a characteristic of the pigment concerned.

The N_a absorbed quanta will give rise to a signal R, which is assumed to be only a function of the total number of absorbed quanta N_a, irrespective of their wavelengths:

$$R = R(N_a). \tag{6.2}$$

The full curve in fig. 6.1 shows some assumed relationship between R and log N_a. The relationship between the signal R and the incident number of quanta N_i may be derived from this figure for each wavelength since, according to (6.1):

$$\log N_a = \log N_i + \log [a(\lambda) m]. \tag{6.3}$$

Thus, when substituting on the abscissa of fig. 6.1 log N_i for log N_a, the full curve shifts over a distance log $[a(\lambda) m]$ in a horizontal direction, which means that a set of parallel curves will result, the mutual distance of which is log $a(\lambda_i)$ — log $a(\lambda_k)$ (broken curves).

This makes it possible in practice to construct the curve relating log a to wavelength. For this purpose R must be measured for several wavelengths as a function of N_i. Then, some value of R is chosen and the value of log N_i necessary to attain this R is plotted as a function of the wavelength concerned (fig. 6.1).

The resulting absorption spectrum of the receptor is a relative one as the number of absorbed quanta is unknown. It may also be interpreted as an overall *spectrum of effectiveness* *) of the system, since it relates to wavelength the total number of incident quanta necessary to obtain a certain value for the
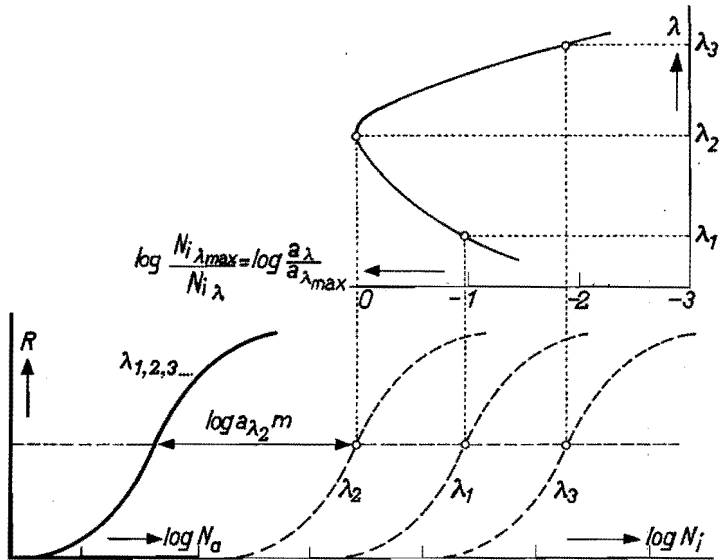
Fig. 6.1. Theoretical derivation of the absorption spectrum (upper graph) from curves that relate responses R to the number of incident quanta N_i for several wavelengths (broken curves). If one absorbing pigment is assumed, the broken curves are all parallel to the curve that relates the response to the number of absorbed quanta N_a (full curve on the left).

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*) In the literature the term "action spectrum" is often used instead. Some authors reserve this term for the true absorption spectrum, i.e. the spectrum of effectiveness corrected for all kinds of passive interaction. This is why we prefer a neutral term.

output R. Depending on the reaction R we shall speak of *pupillary spectrum*, *brightness spectrum*, etc. The *degree of effectiveness* P will more generally be defined as the reciprocal of the intensity of incident light necessary to obtain a certain response. This light intensity will be expressed either as a quantum flux Φ (quanta/second) or as a retinal illumination T (trolands).

For several reasons the picture given above is not universally applicable. If the density of the pigment is high, eq. (6.1) must be replaced by $\ln [N_i/(N_i - N_a)] = a(\lambda)m$. This means that only at low optical densities, defined $\log N_i/N_t = \log [N_i/(N_i - N_a)]$, in which N_t is the number of transmitted quanta, the influence of density on the shape of the absorption spectrum may be neglected. The influence of high densities makes itself felt in an absolute flattening or relative widening of the top of the absorption spectrum since the number of quanta available for absorption diminishes most for the wavelengths with high absorptions when the light gradually passes through the receptor. When studying photochemical reactions in vitro one can avoid this undesirable effect by measuring the optical density directly. From these measurements density spectra may be derived that do not depend on the density one is working with (see Dartnall [32]). In psychophysical experiments it is as yet not possible to measure the number of transmitted quanta. Fortunately, the density of the pigments in the retina is of the order of only 0·30 (Rushton [95,100]), so that the shape of the absorption spectrum is but slightly influenced by pigment density.

A second deviation occurs if the absorption spectrum changes under the influence of light by physical or chemical reactions. If the pigment is converted into some photoproduct that does not absorb any light, only the concentration of the pigment will be affected. However, if the resulting substance shows passive selective absorption, it will act as a colour filter and influence the relative absorption spectrum as measured. This screening action of photoproducts is of practical importance only when the optical density is high, which is not the case in the retina.

Thirdly, the photoproducts may regenerate into the initial photopigment under the influence of light. Then, the spectrum of effectiveness will differ from the absorption spectrum of the active pigment proper.

Finally, the photoproducts may show active absorption, which means that they themselves trigger nerve signals.

Reactions of this nature have been found in vitro (fig. 6.7) and it is quite possible that they also occur in the living retina.

The pupillary spectrum

For a centrally fixated disc subtending 18° we measured pupillary diameter D as a function of the total quantum flux Φ incident in the eye, for eight wavelengths. Figure 6.2 shows the results. On a logarithmic scale the curves are of a sigmoid shape, but the steep portions can readily be fitted by straight lines, which are found to be parallel. The satisfactory degree of parallelism indicates that the shape of the pupillary spectrum does not depend much on the pupillary criterion chosen. For a criterion of $D = 4·5$ mm these spectra have been constructed for two observers in the way indicated in the introduction (fig. 6.3, full curves). They show their maxima at 490 nm. Less accurate measurements performed earlier on five observers with a 26° field gave essentially the same results (fig. 6.4).

As has been argued on page 58, these pupillary spectra reflect the absorption spectra of the pigments in the light receptors. In the human eye, only one of
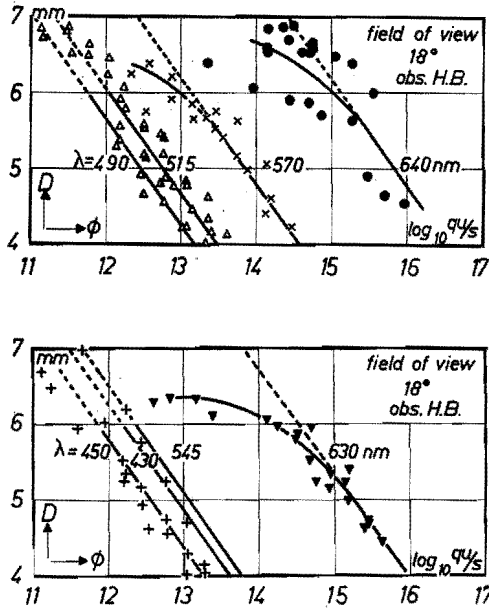
Fig. 6.2. Steady-state diameters of the pupil as functions of quanta flux Φ incident upon the eye, for eight wavelengths. For diameters below 5·5 mm, the results can be represented by straight parallel lines. For the wavelengths 430, 490 and 545 nm only the lines are shown.

these pigments, rhodopsin, has been isolated as yet. Its absorption spectrum, showing its maximum at about 500 nm, has been proved to coincide with the spectrum of the visual threshold in dim light (scotopic) conditions (max. 510 nm) after correction for selective absorption of the eye media (Crescitelli and Dartnall [30]). This scotopic visual threshold spectrum will be referred to as the "510" spectrum. Measurements of visual thresholds, critical flicker fusion and most other visual functions in daylight (photopic) conditions reveal a spectrum with a maximum at 555 nm *). By analogy with rhodopsin one might think of a pigment with an analogous absorption spectrum in the retinal cones which mediate photopic vision. This hypothetical pigment, however, has not been extracted yet. There are indications that the "555" spectrum is in fact a combination of three underlying pigments, which are supposed to mediate colour perception.

Apart from the pupillary spectra, fig. 6.3 also shows the "510" and "555" spectra, measured as scotopic and photopic visual thresholds for the same observers with the same apparatus. The pupillary spectrum does not show correspondence to the "555" spectrum. Better resemblance between pupillary

*) In the figures the scotopic and photopic spectra of the CIE standard observer will be used, the latter of which has been corrected in the short wavelengths as proposed by Judd [64].
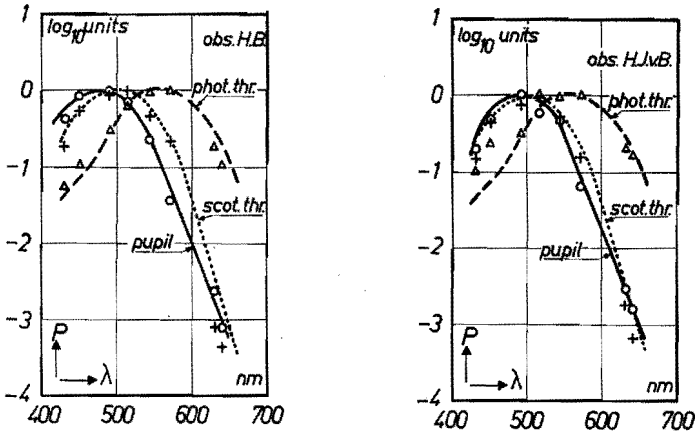
Fig. 6.3. Pupillary spectra (full lines) for a field of 18°. They are compared to visual threshold spectra for a scotopic field (1° at 9° nasal) and a photopic field (1° at the fovea). Two observers. The dotted and broken curves are the CIE scotopic and photopic spectra, the latter with the correction for short wavelengths as proposed by Judd [64]. Since the construction of the spectra has been performed for each separate session before averaging, these spectra deviate somewhat from the spectra that would be derived from the averaged curves of fig. 6.2.

spectra and the "510" spectrum may be noted, though the pupillary spectra are higher at extreme wavelengths. Since, as has been argued, many factors may influence the shape of spectra, we would like to stress the correspondence between the pupillary spectrum and the "510" spectrum rather than propose the existence of a new retinal pigment with a maximum absorption at 490 nm. Accepting the differences between both curves as an effect of second order, we shall discuss the implications of the first effect, viz. that pupillary activity would seem to be mediated by the pigment rhodopsin which also governs scotopic vision.

Fig. 6.4. Pupillary spectra for a central 26° field. Five observers.

In chapter 3 it is mentioned that the intensities at which a similar pupillary spectrum was found by Wagman and Gullberg [129]) were above the range of scotopic vision. In fact, the illumination at which we obtained static contractions are 3-7 log units above cone threshold and accordingly in the range of photopic, cone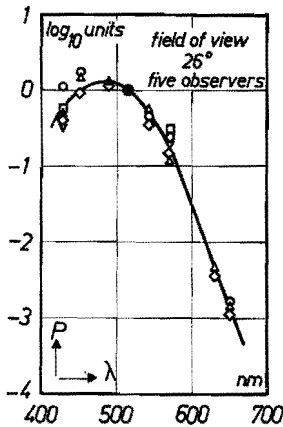-mediated vision. This implies that pupil size is controlled by the rod pigment rhodopsin whereas at the same time visual functions (brightness, colour) are governed by cone pigments.

In our experiments we used a central field of 18°. For pupillary reactions of the dynamic type, it has generally been recognised that the illuminated retinal area is not restricted to the portion corresponding with the outer field of view. For steady-state reactions, Campbell and Alpern [24,6]) suggested a similar effect: due to scattering processes within the eye, the parts of the retina outside the directly illuminated area would receive indirect illumination at a much lower intensity level than the direct illumination. Since in vision rods exert their activity at low levels of illumination, indirect illumination may be held responsible for the rod-dominated pupillary response, by supposing that the cone signals from the directly illuminated area are crowded out by the rod signals from the much larger, indirectly illuminated areas. In that case, the rhodopsin spectrum of the pupil can be accounted for and the attractive basic assumption of a close parallelism between vision and pupillary reactions can be maintained.

In order to obtain direct experimental evidence on this point, we again measured the pupillary spectrum, now illuminating the total retina homogeneously by way of an Ulbricht sphere. Some results are shown in fig. 6.5. For the long wavelengths, the maximum illumination available (about 4 log phot. td) turned out not to be sufficiently high to cause a substantial contraction of the pupil. For the other wavelengths steep parallel curves were obtained, from which the spectrum of effectiveness was found (fig. 6.6). The pupillary spectra are
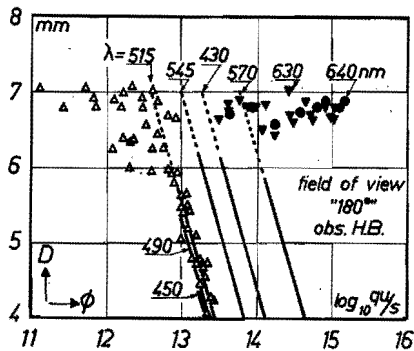

Fig. 6.5. Pupillary diameter D versus quanta flux Φ for a "180°" field. The intensities for the wavelengths 630 and 640 nm were not sufficiently high to produce significant contractions. Experimental points are only shown for the wavelengths 515 nm ($\triangle$), 630 nm ($\blacktriangledown$) and 640 nm ($\bullet$).
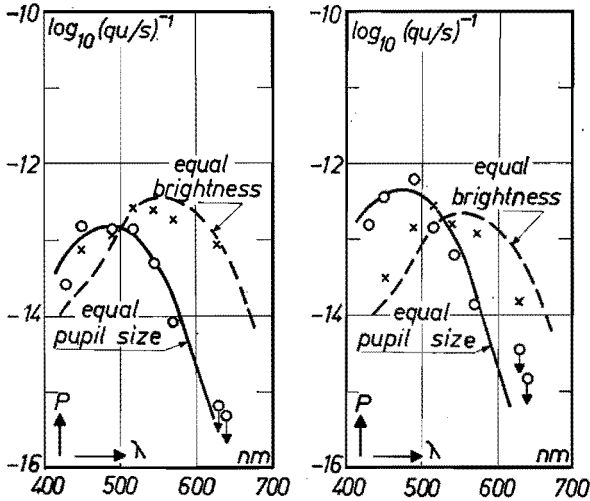
Fig. 6.6. Pupillary spectra for illumination of a "180°" field (full curves). The extension of the field does not influence the position of the maximum which remains at 490 nm. The results are compared to brightness spectra, obtained from performing successive heterochromatic brightness matchings with a wavelength of 515 nm of the indicated intensity. Broken curves: CIE photopic spectrum.

compared to brightness spectra, constructed from the fluxes necessary to reach a (rough) successive heterochromatic brightness match with a 515 nm illumination at about equal intensity level as is required by the pupil to contract to a value of 6 mm. The pupillary spectra (full curves) still resemble the "510" spectrum whereas the brightness spectrum resembles the "555" spectrum of photopic vision (broken curves).

Our conclusion is that if the retina is illuminated homogeneously, pupil size and brightness impression are controlled by different pigments, which are the rod pigment rhodopsin for the pupil and the cone pigments for vision. This throws doubt on the hypothesis that stray light gives an explanation of the occurrence of similar differences that were found with an 18° field. Postponing a discussion of the quantitative role of stray light to the next chapter, we shall now consider the possible origin of the relatively small differences between the pupillary spectrum and the "510" spectrum.

Pupillary spectrum and scotopic brightness spectrum; detailed discussion

Guided by the photopic intensity level at which the pupillary spectra were obtained, we originally supposed the pupillary spectrum to be composed of two spectra, for which purpose the "510" spectrum and the detection spectrum for blue (max. 460 nm) could be linearly added to get a reasonable approximation of the pupillary spectrum [14a]. Since then, we have obtained evidence contrary to this hypothesis. As the "blue cones" show a directional sensitivity, the hypoth-

esis predicts that such a directional sensitivity should also be found for the pupillary responses to short-wavelength illumination. This was not found experimentally, as will be shown in sec. 6.2.

A different explanation of the enhancement for the shorter wavelengths of the pupillary spectrum as compared to the "510" spectrum was proposed by Campbell and Alpern [24]. They are of the opinion that these differences arise from the dominating role of the indirect illumination which, in the case they considered, arose from direct illumination of the central 26° of the retina. As has been said, the spectrum of effectiveness is a characteristic of the receptive pigment. Why then should the shape of the resulting spectrum be influenced by the direct or indirect way the light passes before being absorbed by the pigment? The answer given by Campbell and Alpern is that the magnitude of the fundus component (the light scattered and reflected from structures in and behind the retina) is in itself dependent on wavelength, due to selective light absorption by pigments and blood layers. Thus, the indirect light coming from the fundus has passed a colour filter and when this light is absorbed by rhodopsin, the spectrum of effectiveness for the pupil will show deviations from the absorption spectrum of rhodopsin. A similar explanation has been put forward by Dodt and Walther [37] to account for analogous deviations in the spectrum of the electro-retinogram (ERG) in rabbits. Campbell and Alpern, assuming the fundus to reflect the light diffusely, calculated the wavelength dependence of fundus reflection from measurements of the portion that leaves the eye through the pupil. By subtracting this filter characteristic from the pupillary spectrum, a corrected curve resulted which coincided with the "510" spectrum.

A recent analysis of the fundus component of the indirect light by Vos [127] has raised some doubt about the hypothesis on which this explanation is based. According to Vos the fundus component is very complex in origin, so that a uniform wavelength dependency for all angles is by no means certain. Thus, the measurements of fundus reflection as performed by Campbell and Alpern would not be representative of the fundus reflection in other directions. If the indirect light scattered by cornea and lens is also taken into account (these components show hardly any dependence on wavelength according to DeMott and Boynton [36]), it seems reasonable to suppose that the influence of the coloured component of the indirect light is small as compared to the components that do not show spectral selectivity. In that case the correspondence of the corrected pupillary spectrum to the "510" spectrum would be accidental.

The explanation of the differences between the spectra in terms of indirect illumination, reflected from the fundus, also requires that the indirectly illuminated peripheral retina contributes more to pupillary contraction than does the directly illuminated central area of 26°. In the literature about distribution over the retina of static pupillary contribution one finds either a central maxi-

mum with a considerable decrease towards the periphery or an almost homogeneous sensitivity in the central 60° (see sec. 3.3). The last hypothesis alone does not contradict the supposed influence of indirect illumination. So far, however, ideas about the influence of direct and indirect illumination are far from clear. In the next chapter we will discuss this problem in greater detail.

On page 59 we have indicated other processes which may effect the spectrum of effectiveness. According to reviews by Dartnall [32,33] the rhodopsin is converted rapidly by light absorption into metarhodopsin (transient orange $\lambda_{max} = 486$ nm), which in vitro may be converted into a mixture of rhodopsin (502 nm) and iso-rhodopsin (492 nm) by light absorption or by thermal isomerisation. It may also be converted thermally into retinylidene-opsin (indicator yellow, $\lambda_{max} = 365$ or 440 nm dependent on the pH). Part of Dartnall's diagram is shown in fig. 6.7. One or more of the substances mentioned might act as an active pigment, though such a behaviour has not been found as yet. It may be noticed that all these substances show an absorption spectrum that is shifted to the short wavelengths as compared with rhodopsin, similarly to the pupillary spectrum. If iso-rhodopsin could act as an active pigment, the pupillary spectrum might be easily explained. It is, however, not certain that iso-rhodopsin exists in the living retina.

A shift would also be accounted for if rhodopsin were regenerated by light absorption from its photoproducts such as transient orange which shows its maximum absorption at 486 nm. If so, the short wavelengths would then favour the regeneration of rhodopsin and thus might lead indirectly to the rhodopsin mechanism giving a higher response to the illumination. This explanation was already proposed in 1938 by Granit, Therman and Wrede [52] in order to explain the spectrum of the electro-retinogram (ERG) of the frog, which also shows an enhancement in the short wavelengths, in agreement with the human spectrum (Riggs, Berry and Wayner [93]).

The relative importance of the processes that accompany the bleaching of rhodopsin will increase with larger concentrations of decomposition products, which in turn are dependent on the level of illumination of the rhodopsin. As will be shown in sec. 6.3 the illumination levels at which the pupil reacts to static light are rather high, so that a substantial portion of rhodopsin will be bleached. As only steady-state reactions are considered, the concentration of the various photoproducts may be expected to have reached a state of equilibrium, provided the reaction kinetics are not too slow.

In conclusion we may state that an explanation of the differences between the pupillary spectrum and the "510 "spectrum, based upon cooperation between rods and "blue cones", must be rejected. The explanation by Campbell and
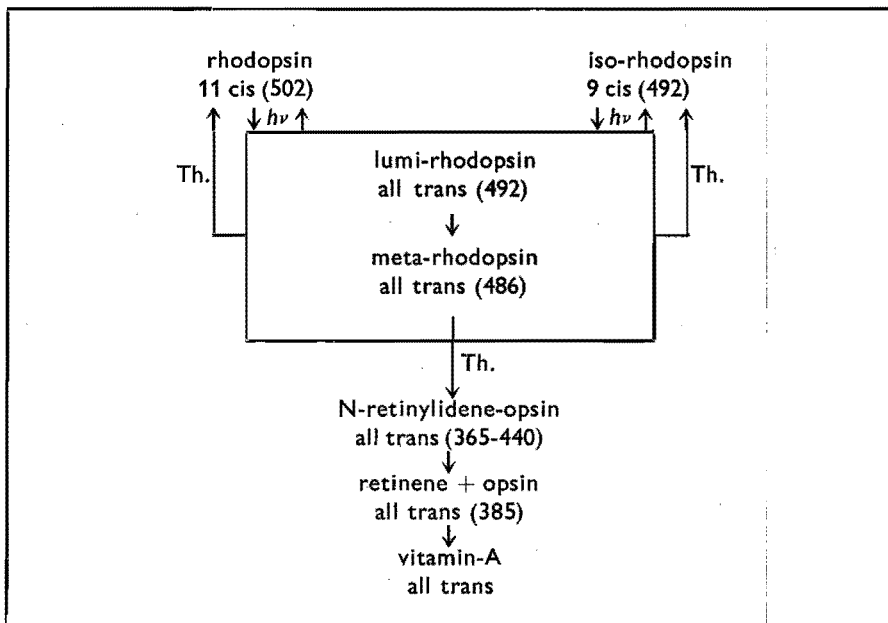
rhodopsin   iso-rhodopsin
11 cis (502)   9 cis (492)

↑ ↓$h\nu$↑   ↓$h\nu$↑ ↑

Th.   lumi-rhodopsin   Th.
   all trans (492)

↓

meta-rhodopsin
all trans (486)

Th.
↓
N-retinylidene-opsin
all trans (365-440)
↓
retinene + opsin
all trans (385)
↓
vitamin-A
all trans

Fig. 6.7. Rhodopsin reactions in vitro (after Dartnall [32,33]); Th. = thermal reaction, $h\nu$ = light-induced reaction.

Alpern [24]), in terms of selective fundus reflection, meets some strong counter arguments if it refers to indirect illumination. If the light reflected by the fundus and absorbed in the directly illuminated area itself would be held responsible, it is difficult to explain why the "510" spectrum would not also be modified, unless illumination caused an increase of the local blood flow. A third hypothesis remains open, viz. that the photoproducts of rhodopsin, most of which show an increased absorption for short wavelengths, take part in pupillary contraction either by light-induced regeneration or by active absorption. Lastly, the existence of some other active pigment with maximum absorption at 490 nm cannot be ruled out.

The reported influence of cones

In the foregoing part we assumed the pupillary spectrum to originate from the rod pigment rhodopsin. In the literature, however, there are spectral data indicating that the cones also participate in steady-state reactions of the pupil. This cone effect presents itself as an increased effectiveness for long wavelengths as compared to the "510" spectrum. Alpern and Campbell [6]) report, for an 8° field, a pupillary spectrum which can be explained on the basis of an addition of the logarithm of the rod and cone signals. The data of Wagman and Gullberg [129]), though spreading considerably, show a similar long-wavelength

increase of about 1·5 log unit for a 16·6° field. Our experiments with an 18° field (fig. 6.3) reveal an increase of about 0·4 log unit.

In order to decide whether the size of the field is of critical importance we carried out measurements with a 5° field for two wavelengths (515 nm and 640 nm); since the spectral data were the same as for the 18° field no such importance could be established.

Can methodological differences possibly account for the deviating results? Campbell and Alpern took photographs of the pupil after 30 and 60 seconds adaptation to the illumination. Wagman and Gullberg did the same after 10, 20, 30, 45, 60 seconds. In our experiments, we waited until the pupil looked steady and quiet for some 10 seconds, which required variable time intervals. In chapter 5 it has been shown that transient contractions are slower for long wavelengths than for short ones. This may have caused the increased effectiveness of the static pupil for the long wavelengths that was found with the photographic method, though the successive intensity steps in Campbell and Alpern's experiments amounted only to 0·5 log unit. As a second methodological difference it will be remembered that increased oscillations and blinks all cause a systematic decrease in pupil size. If these decreases are somehow fed by cone activity, they may account for the increased degree of effectiveness for the long wavelengths found with the photographic method. Though we have no definite proof that this is the correct explanation of the different findings, it seems at present the most probable one.

In saying this, we are aware of the fact that we have offered no explanation for the 0·4 log unit difference between the pupillary spectrum and the "510" spectrum in the long wavelengths which persists in our experiments. Possibly, slow transients have also played a part in our experiments. A decision on this point may be expected by measurements of pupillary spectra when the retinal image is stabilised, in which case pupillary contraction persists (Gerrits and De Haan [47]), though visual impressions disappear completely.

6.2. Directional sensitivity

In 1933 Stiles and Crawford [120]) found a considerable decrease in brightness sensation when the point of entry of a pencil of light at the pupil was shifted from the centre to the pupil edge. Since then it has become accepted that this effect is due to a directional sensitivity of the retinal cones. This directional sensitivity may be understood from the geometrical properties of the cones. The retinal rods do not show such a directional sensitivity, though for angles of incidence larger than occurring in normal vision such an effect may also be present (see the recent survey by Vos and Walraven [128]). Usually, the effect is expressed in terms of $\eta(d)$, defined as the quotient of the illumination at the direction of incidence that shows a maximum efficiency, and the illumination at a distance d mm (in the plane of the pupil) from this point, required for an

equal effect. For rods $\eta = 1\cdot0$, irrespective of d; for cones $\log \eta = -0\cdot05\ d^2$ (Stiles [111]), giving $\eta = 0\cdot17$ for $d = 4$ mm.

Within the framework of a division of retinal receptors into rods and cones, this effect offers a possibility of classifying pupillary receptors in either or both of these categories. Accordingly, we can see whether these results agree with the conclusion most readily drawn from spectral measurements, viz., that the rod pigment rhodopsin mediates the steady-state response of the pupil.

When measuring any directional sensitivity present, the direction of incidence on the receptors must be controlled accurately. This can only be achieved if the effects on the pupil are caused by direct illumination as opposed to indirect light that is scattered entoptically, though any directional sensitivity present shields the receptors against light from unfavourable directions. We chose a rather large field of view (22°) which was centered on the fovea. We measured the pupillary reactions for various points of entry of the light in the plane of the pupil. The results at three wavelengths are shown in fig. 6.8. Though the brightness of the field changes considerably when the point of entry in the plane of the
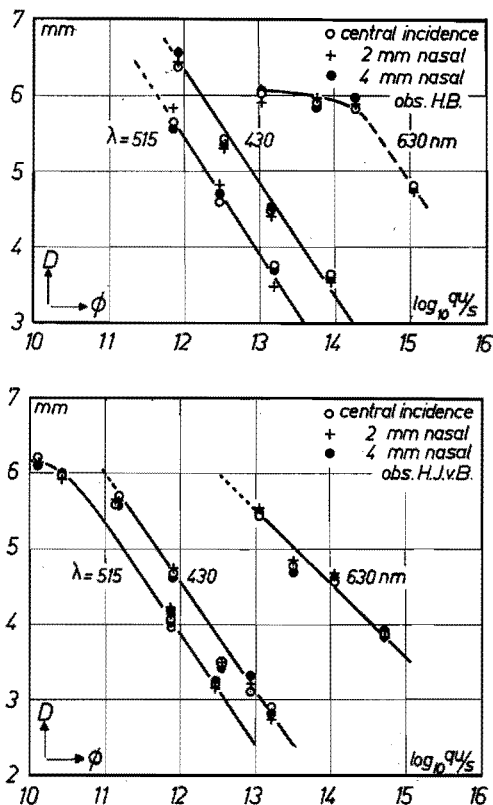

Fig. 6.8. The influence on pupil size of variations in the point of entry of the light in the plane of the pupil. Three wavelengths, two observers. No significant differences occur.

pupil is moved, pupil size does not show any significant change. The relative light fluxes necessary for eliciting a pupil size of 4·5 mm are shown in fig. 6.9. For the purpose of comparison the visual thresholds of the photopic and the scotopic systems have been measured with the same apparatus. It may be concluded that pupillary contraction does not depend on the direction of incidence on the receptors, up to about 10° difference from perpendicular incidence, η being $1·0 \pm 0·2$ for $d = 4$ mm.

As additional evidence, a comparison has been made between an open-loop situation (widened pupil) and a closed-loop situation (natural pupil) for
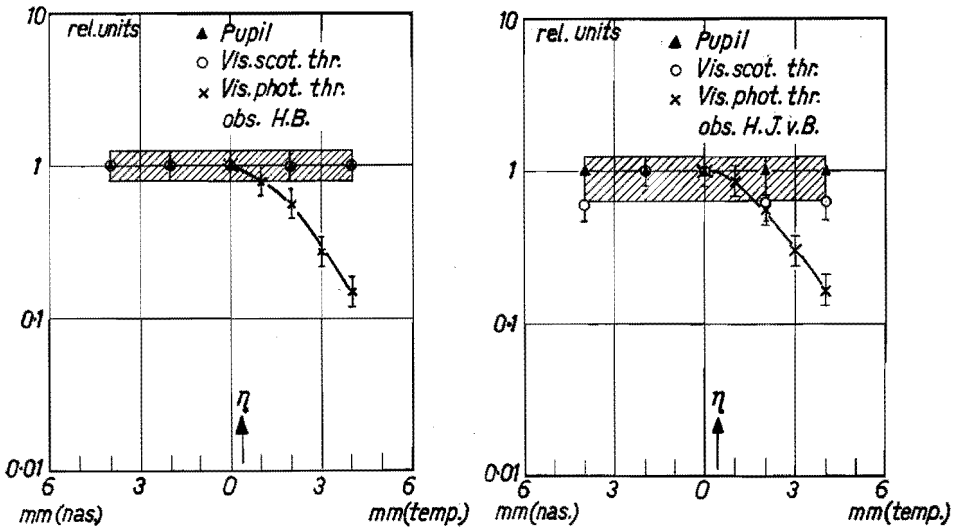

Fig. 6.9. Directional sensitivities for the static pupillary contraction, as compared to those of the scotopic and photopic visual thresholds. Two observers.

illumination of a "180°" field. Since the effects of the peripheral parts of the pupil contribute most to a possible directional-sensitivity effect, any directional sensitivity present must be expected to show itself most clearly in the case of a small natural pupil. In fig. 6.10 the two kinds of measurement are compared. The result is that there is no significant difference between the two types of experimental conditions. The broken line indicates the results that would have been expected for the widened pupil if the directional sensitivity of the pupillary receptors had been analogous to that of the retinal cones. Thus, these measurements agree with the previous ones in that no directional sensitivity is present.

In the literature, only two papers on the directional sensitivity of static pupillary receptors seem to exist. Spring and Stiles [111] measured the effect for a 52° field, using white light of about 3 log phot.td. They found as an average value $\eta = 0·5$, which they consider not significantly different from unity. For
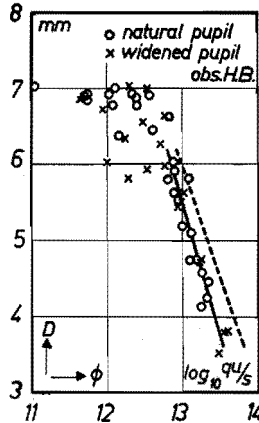
Fig. 6.10. Comparison between illumination through the natural pupil (○) and through the widened pupil (×) for a "180°" field (515 nm). If there were directional sensitivity in accordance with that of the cones, the crosses would be expected to coincide with the broken line. In fact, no such effect occurs.

a foveal field of 1°, Alpern and Benson [5]) found a directional sensitivity in accordance with that of the cones.

In order to see whether the size of the field is of any influence, we tried to measure the effect for a 1° field. However, up to illuminations of 6 log scot.td we found no substantial static contraction. Therefore we turned to a 5° field (515 and 630 nm), for which the differences between pupillary diameters at central incidence and at 4-mm nasal incidence were less than 0·10 mm, corresponding to a value of $\eta = 1 \cdot 0 \pm 0 \cdot 2$. Since Alpern and Benson restrict the significance of their results because of possible blinkings, lid closures, etc., it seems possible that transients have contributed to their results (see discussion in sec. 5.1).

6.3. Illumination level

It may be open to doubt whether the level of retinal illumination at which pupillary contractions occur must receive explicit attention in a chapter devoted to the properties of pupillary receptors. It is by no means sure that the lower threshold and the upper (saturation) threshold of pupillary contractions are governed by processes in the receptors. Yet the range of retinal illuminations in which pupillary reactions occur provides information about a property of the pupillary receptors.

The retinal illuminations that cause steady-state contractions are lowest when the whole retina is illuminated homogeneously. For such a "180°" field the illumination needed for a certain diameter can be derived from fig. 6.5. Figure 6.11 shows again the spectra of effectiveness. They may now be compared with the effectiveness spectra for the criteria of a visual threshold in fully dark-

adapted conditions, a colour threshold (as roughly measured), and a successive heterochromatic brightness match with a 515-nm field. All data have been collected with a "180°" field. Since the pupillary spectrum resembles the scotopic one, it is convenient to express the level of retinal illumination in scotopic trolands. We then obtain a value of —4·0 log scot.td for the visual threshold and a range for pupillary contractions from +2·5 to at least +4·5 log scot.td.

Are the illumination levels at which the pupillary system is active, above the saturation level of the rods (which may be defined as the illumination level
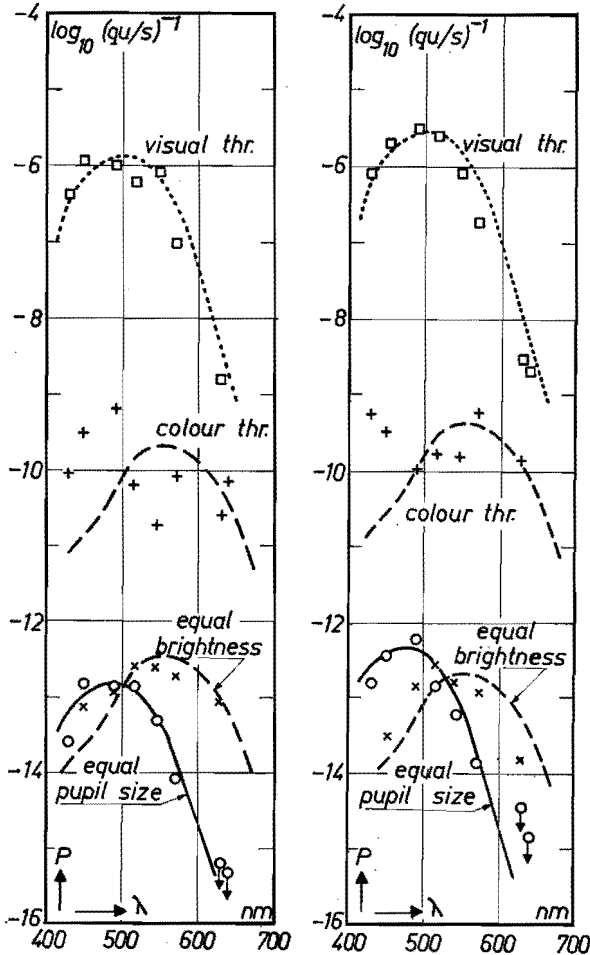
Fig. 6.11. Visual and pupillary spectra (left, observer H.B.; right, observer H.J.v.B.). The data indicate:
□ visual thresholds of the fully dark-adapted eye (flashes 100 ms);
+ colour thresholds, roughly measured;
× equal brightnesses, measured by successive, heterochromatic matches;
○ equal pupil size (observer H.B., criterion 6·0 mm; observer H.J.v.B., 5·0 mm).
The dotted and broken curves indicate scotopic and photopic spectra, respectively.

above which a further increase of illumination does not effect the output)? Aguilar and Stiles [4]) and Rushton [97]) have measured the saturation level of the scotopic system. For this purpose it is necessary to isolate it from the photopic system, because in normal vision the photopic system takes over at illuminations far below the saturation level of the scotopic system. Aguilar and Stiles achieved this end by a careful choice of wavelength, size and position of the field, and point of incidence at the pupil, while Rushton was able to work with a rod monochromat as a subject. Their results (fig. 6.12) are well in agreement: up to a steady illumination of 2 log scot.td, the retinal illumination needed for an
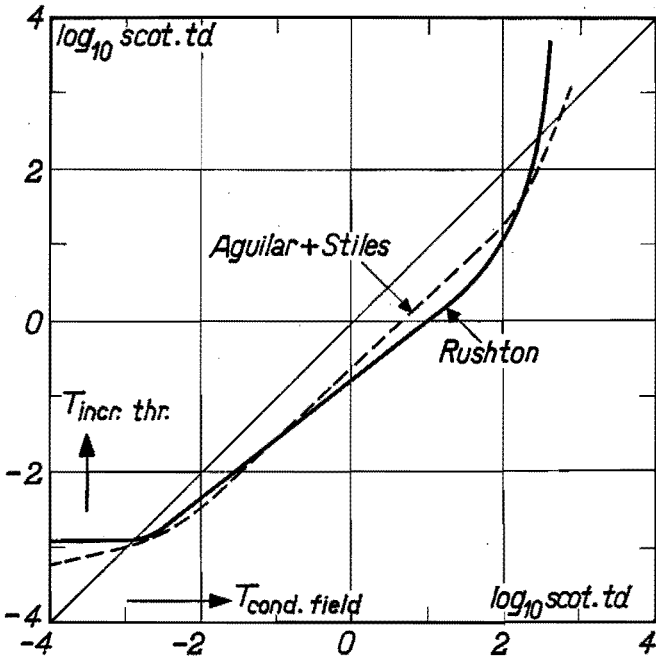
Fig. 6.12. Visual increment thresholds in relation to the illumination of a conditioning field, for the scotopic visual system. Saturation occurs at a steady illumination of some 1000 scotopic trolands.

increment threshold increases about in proportion to the steady illumination, while for higher steady illuminations it rises much more rapidly, indicating total saturation at a conditioning illumination of about 3 log scot. td. From these results we may see that the static pupillary processes start at an illumination level where the visual scotopic system becomes saturated (fig. 6.13).

The saturation level of the scotopic visual system should be distinguished from the illumination level at which rhodopsin is bleached. Campbell and Rushton [22]) investigated the concentration of rhodopsin in the living eye by measuring the amount of light reflected from the fundus of the eye and leaving the eye again

through the pupil. This light passes the retina twice and contains information about the pigment densities. According to Rushton [97,99], the concentration p of unbleached rhodopsin is related to the retinal illumination T (scot. td) of a steady conditioning field according to the formula $p/(1-p) = 40\,000/T$, Figure 6.14 shows this relationship. It may be seen that rhodopsin is not bleached substantially at the level of the extrapolated pupillary threshold (2·7 log scot. td), whereas for illuminations of about 4 log scot. td, at which level the 18° pupillary spectra were measured, 20% of the rhodopsin is bleached away. This makes clear that a rhodopsin origin of static pupillary contraction is quite possible.

Therefore, rather than explaining why rods serve pupillary reactions at illumination levels as high as 4 log scot. td, an explanation is called for to account for the fact that the visual scotopic system is saturated at illuminations as low as 3 log scot. td, at which 97% of the rhodopsin is still unbleached. This has actually been attempted by Fuortes, Gunkel, and Rushton [45], who suggest that the saturation of the scotopic system is due to saturation of the rods (as opposed to rhodopsin), rather than to cone-rod suppression, or even rod-rod suppression. Up to the present, however, the evidence available on this point is scanty. At any rate, the signals for the steady-state pupil bypass the scotopic bottleneck,

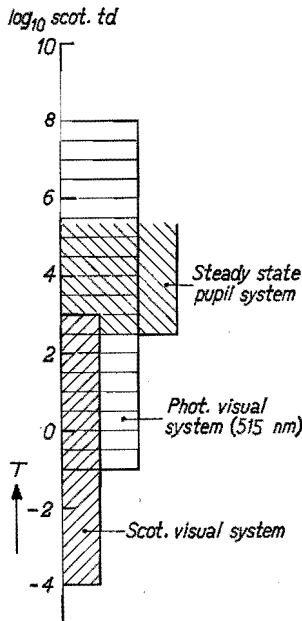Fig. 6.13. The illumination range where steady-state contractions of the pupil occur, as compared to the ranges for the scotopic and photopic visual systems. The steady-state contraction starts at an illumination where the scotopic visual system becomes saturated. The photopic range cannot appropriately be expressed in scotopic units; the indicated range holds only for the wavelength of 515 nm.
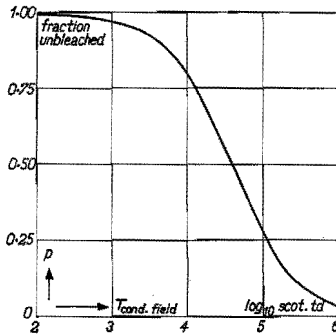
Fig. 6.14. Fraction p of unbleached rhodopsin as a function of the illumination of a steady conditioning field according to Rushton's relationship $p/(1 - p) = 40\,000/T$.

which implies that at least some of the rods do not saturate at 3 log scot. td. This is in agreement with the measurements of Elenius and Lehtonen [39]), who reported the spectrum of the standing potential of the eye to correspond with the rhodopsin spectrum at an intensity level of about 3 log scot. td.

Since pupillary contraction diminishes brigthness impression, it is conceivable that it is part of a more general adaptation mechanism. If so, the correspondence between the saturation level of scotopic vision and the level at which the static pupil starts contracting then suggests the hypothesis that scotopic vision might be inhibited by the same rod signals that account for pupillary contraction.

6.4. Conclusions

The spectrum of effectiveness for steady-state reactions of the pupil shows a maximum at about 490 nm. In principle, this spectrum is a characteristic of the absorbing pigment involved. When comparing it to visual-brightness spectra for the scotopic (max. 510 nm) and photopic (max. 555 nm) systems, the degree of correspondence between the pupillary spectrum and the scotopic spectrum points to a common rhodopsin origin. The differences between these two spectra may be explained by assuming some influence of light absorption by photo-products rather than by an appreciable influence of selective fundus reflection. Contrary to some findings reported in the literature, our spectral data do not reveal any significant influence of cones.

The direction of incidence of the light on to the receptors was found not to influence pupillary contraction. Rod-mediated scotopic vision does not show any such influence either, whereas cone-mediated vision shows a considerable dependence.

The retinal illuminations on which the pupil showed substantial contractions were found between 2·5 and 4·5 log scot.td or higher. At these illumination levels vision is purely photopic. Under isolated conditions, the scotopic visual system is saturated at about 3 log scot. td. In the literature much lower illumination

levels are reported for obtaining steady-state contractions. This can be explained, partly at least, from methodological differences.

All the experimental evidence collected by us is in agreement with the hypothesis that retinal receptors which mediate the steady-state light reaction of the pupil are almost exclusively rods. The illumination levels at which these rods are active are above the range of scotopic or mesopic vision and in the range of purely photopic vision.

7. ORGANISATION OF THE RECEPTIVE FIELD FOR STEADY-STATE REACTIONS

7.1. Introduction

In the previous chapter it has been established that the receptors for steady-state reactions of the pupil are rods. In this chapter we shall consider, the processes by which the signals from many rods converge to one steady-state response of the pupil. This problem was introduced in chapter 1 as the organisation of the pupillary receptive field.

A logical way to investigate this is first to measure pupil size as a function of light intensity for a small illuminated field in various retinal positions, and then to try to find out how different parts of a larger field interact in causing the one contraction. From these experiments it is hoped to learn the nature of the processes that lead from light absorption to pupillary contraction and the basic parameters by which a certain retinal position can be characterised. Experiments of this type have been reported in the literature (see sec. 3.3) and our results (sec. 7.2) are in agreement with them.

Unfortunately, the results do not permit a straightforward analysis such as is suggested above. In trying to overcome this difficulty one may inquire into the influence of intra-ocular stray light, which hampers the interpretation of the experimental data. For it is not quite correct to attribute the pupillary response to the directly illuminated field alone, since indirect illumination may have contributed to a particular pupillary response to an unknown extent. We shall devote a separate section to this indirect illumination (sec. 7.3). In the light of recent data from the literature we shall seek to establish the circumstances under which indirect illumination would contribute substantially to the response.

In experiments with central fields of various sizes it has been found that steady-state contractions depend in first approximation on total light flux. This effect can be explained on the assumption of a linear integration of the signals. However, this assumption cannot explain the dependence on illumination, which is of a logarithmic nature. Moreover, it cannot be combined with the gradients in retinal contribution found when the retina is explored with a small spot, as has long been recognised. Accordingly, we have to assume that the receptive system is a non-linear one. This non-linearity can be accounted for by one logarithmic operation in a chain of otherwise linear processes. On the basis of experimental results in which the influence of indirect illumination can be neglected, we shall put forward a theoretical description in which such a logarithmic intensity dependence and a retinal weight function are assumed (sec. 7.4). We hope to show that the main findings can be reasonably explained (sec. 7.5), on the understanding that the indirect illumination is taken into account. Special attention will be paid to the central retinal area where rod density falls to zero.

It would be attractive, of course, to translate the descriptive formula into anatomical and physiological terms. Since this may be done in more ways than one, we shall consider the limitations of the isomorphies explicitly (sec. 7.6). In this connection, we hope to show how the adequacy of the description may be further tested.

In order to compare the influences on pupil size of various field configurations, we have to adopt a certain measure. As such we shall again use the degree of effectiveness P which has been defined in sec. 6.1 as the reciprocal of the light intensity that causes the pupil to contract to a certain diameter D. Light intensity will now be expressed as retinal illumination T (scotopic trolands abbreviated to scot.td) as this is the stimulus to which the receptors react. The simplest outcome that one can think of is that the differences between values of P, occurring at various configurations of the field, are independent of the criterion of D. If so, the curves relating diameter to illumination can then be represented by a standard curve and only one parameter. As a matter of fact, the results do not fulfil this condition. Thus, each of the curves to be compared has to be characterised by two or more parameters. However, for the outline of the problems involved, one criterion ($D = 6$ mm) suffices. We shall give more detailed information about the experimental results later. For reasons of clarity, the experimental points will be shown in part of the graphs only.

In all experiments reported in this chapter, monochromatic light has been used with a wavelength of 515 nm. Usually, configurations to be compared were offered to the observers in one session. Most experiments have been carried out by two observers. Their results were in reasonable agreement. As a rule, the outcome of only one of them (H.B.) will be shown.

7.2. Influence of position and size of the retinal field

The influence of retinal position has been studied by measuring degrees of effectiveness for a 2° field offered to the observer in various retinal positions. Preliminary experiments showed this effectiveness to be roughly symmetrical around the fovea. We therefore carried out a larger series of experiments for the nasal side of the retina alone. The results are shown in fig. 7.1. The effectiveness shows its maximum at a foveal position and decreases smoothly towards the retinal periphery to a total amount of one log unit. The half-width of the curve is about 23°. These results conform to similar measurements performed by Crawford (see p. 23), though in our experiments we needed higher illuminations.

One would like to regard each of the measured values of the effectiveness as an inherent property of the retinal area on which the light spot in the visual field is imaged. If so, fig. 7.1 would then represent an intrinsically retinal weight
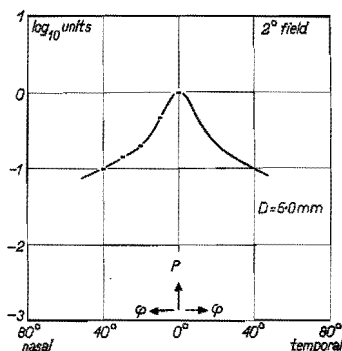
Fig. 7.1. Degrees of effectiveness *P* (relative to maximum) for several retinal positions of a 2° field. The effectiveness decreases towards the periphery. Criterion *D* = 6·0 mm, observer H.B.

function. As further experiments showed, this interpretation encounters some difficulties.

In chapter 6 we reached the conclusion that the pupillary receptors are rods. Rod density is low in the foveal area and even zero in the central fovea. Accordingly, one might expect a low value of the pupillary effectiveness. On the contrary, we found a maximum when the field was presented foveally. Although there is no *a priori* need to expect a direct proportionality between pupillary effectiveness and rod density, there do not seem to be any grounds either for expecting a maximum effectiveness in places without rods. A solution may partly be found if we consider the influence of indirect illumination, since this may have interfered with the detection of a possible foveal minimum of the retinal contribution to pupillary contraction. This will be further discussed on p. 101.

One expects the resolving power of an exploring field to be of the order of the size of the field, which was 2° in the above experiments. When larger fields are used as a test field, the curve of fig. 7.1 is supposed to flatten due to the smoothing effect of the increase of field size. Figure 7.2 shows measurements for both a 2° and a 20° test field which, for purposes of comparison, have been presented relative to their maximum values. Contrary to expectation, the curve for the larger field shows a steeper decline towards the periphery. This anomalous increase of resolving power suggests that the curves of fig. 7.2 are not representative of the directly illuminated areas. In the next section we shall consider the bearing of indirect illumination on this problem.

The unexpected differences between fields of 2° and 20° with respect to pupillary contraction raise interest in a further exploration of the influence of field size. What would be the pupillary contractions when fields of various sizes were presented to the eye, all centered on the fovea? If all parts of the retina contributed linearly and to the same extent, one would expect the contraction to depend on total light flux only (*integration*). If so, the degree of
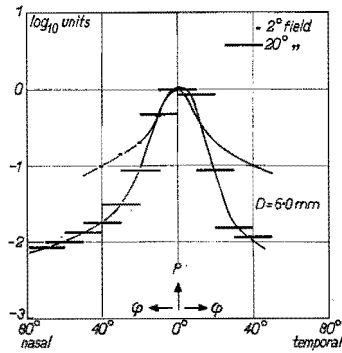
Fig. 7.2. Degrees of effectiveness P (relative to maximum) for several retinal positions of 2° and 20° fields. The decrease in effectiveness for the 20° field is much steeper than for the 2° field. Criterion $D = 6.0$ mm, observer H.B.

effectiveness (expressed as reciprocal trolands) would then increase linearly with the area of the field. In the case of a decrease of retinal contribution from the fovea towards the periphery, as is suggested in fig. 7.2, one might suppose that redistribution of a given light flux from a small central spot with a high effectiveness to a larger area where average effectiveness is much lower, will cause a decrease in pupillary contraction. If so, the light flux required for a constant-response criterion must then increase for larger fields (*under-integration*). Finally, situations may occur in which the required light flux decreases with the size of the field (*over-integration*). In a double logarithmic representation of degree of effectiveness versus field area (fig. 7.3) *), integration is indicated by a line of unity slope. Under-integration makes itself manifest by a slope flatter than 45° and over-integration by a slope steeper than 45°.

The experimental results obtained by illumination of fields ranging from a diameter of 2° to a "180°" field, are shown in fig. 7.4. Starting with the smallest
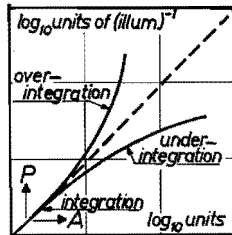

Fig. 7.3. Representation of the effects of over-integration, integration and under-integration in a double logarithmic plot of effectiveness P versus field area A.

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*) From a physical point of view it is not attractive to use a logarithmic area scale. It has been chosen here because it enables one to visualise area functions over a large range of areas.

field, the curve of effectiveness shows integration between 2° and 5° diameter, over-integration between 5° and 22°, and under-integration for still larger fields. In this way, the effectiveness for a full visual field in which the large ineffective retinal periphery is involved, lies on one integration line with a 2° field, imaged on the very effective fovea.
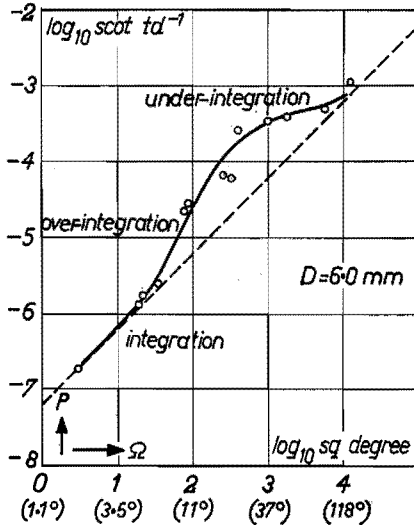

Fig. 7.4. Degree of effectiveness P as a function of field area of central fields, represented by the solid angle Ω. The effects of integration, over-integration, and under-integration occur consecutively from small towards large fields. Observer H.B.

The results reported in the literature (see p. 23) deviate only slightly from the data presented here. Usually, the data almost coincide with an integration line, though Luckiesh and Moss [80] found that the effectiveness showed a maximum for an 18° field. Apart from these data, all results were obtained at intensities lower than those needed in our experiments.

The expectation, based on fig. 7.2, that only under-integration can occur, has turned out to be incorrect. It rested on the view that the influence of an increase in illuminated area cannot be balanced by a proportional decrease in illumination level, due to the lower average effectiveness of the larger area. However, this expectation in turn implies a presumption, viz. that area and illumination are interchangeable, which is the case if the pupillary system is a linear one. If the system contains non-linear elements (due to adaptation, saturation, etc.) an increase in illuminated area may influence pupillary contraction much more than would a proportional decrease in illumination level. Therefore, the assumption of non-linearities may provide a key to the solution of the problem how the

results with fields of one size in different positions can be combined with the results obtained with fields of various sizes.

In illustration of this we shall compare the change in output of some linear system with that of some non-linear system when a given light flux is redistributed over a tenfold area, of which the added areas contribute only one third of the area first illuminated.

If we illuminate an homogeneous area A of a linear system with an illumination T, the response will be $R_1 = a.A . 10T$. Spreading the same light flux over the area $10A$ will result in an illumination T, in which case the response diminishes to $R_2 = a.A.T + \frac{9}{3} a.A.T = 4 a.A.T$ (under-integration).

Now we repeat this procedure with elements that respond in proportion to the logarithm of illumination and, as before, linearly to area: $R = \beta$. area. log illumination. In this case $R_1 = \beta.A.\log 10T/T^*$ (T^* is a constant) and $R_2 = 4 \beta.A.\log T/T^*$. The change in response now amounts to $R_2 - R_1 = \beta.A$ [3 log $T/T^* - 1$]. Depending on the value of T/T^*, this difference will be either positive (over-integration), zero (integration), or negative (under-integration).

Although it has long been recognised that the pupillary system is a non-linear one, the implications on the organisation of the receptive system do not seem to have met much consideration. What kind of non-linearities are to be expected?

With regard to the receptive system, it is generally admitted that a linear dependence on illumination does occur at low illuminations only. For higher illuminations the amplitude of the responses is usually proportional to the logarithm of the illumination. For example, fig. 7.5 shows experimental data of static pupil size, which can be satisfied by the equation

$$C = D_0 - D = B \log (1 + T/T^*). \tag{7.1}$$

This expression combines a linear relationship if $T \ll T^*$, viz. $C = 0.43 \, BT/T,^*$ with a logarithmic one if $T \gg T^*$, viz. $C = B \log T/T^*$. It will constitute the basic equation of the theoretical description in sec. 7.4. The parameter T^*
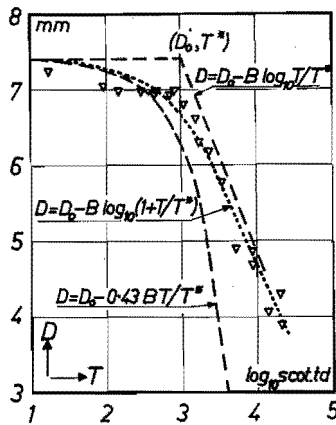

Fig. 7.5. Description of experimental results by the equation $D = D_0 - B \log (1 + T/T^*)$. Both asymptotic equations $D = D_0 - 0.43 \, BT/T^*$ and $D = D_0 - B \log T/T^*$ have been indicated; $D_0 = 7.4$ mm, $B = 2.6$ mm/log unit, $T^* = 3.0$ log scot. td. Field 48°, observer H.B.

represents the illumination level of the transition from a linear to a logarithmic relationship in the situation of full adaptation to the illumination. We will refer to T^* as the *point of transition*. At high illuminations, saturation effects must be expected from bleaching of pigments, etc. These are not included in the equation.

The occurrence of non-linearities are not restricted to the receptive system. In the motor system, the pupillary muscles show, at least partly, a non-linear characteristic. The minimum diameter of the pupil is about 1 mm but for pupillary diameters below some 4 mm a decrease of pupil size must involve an increasing mechanical compression of the surrounding sphincter muscle, which restricts any linear behaviour to diameters exceeding these 4 mm. This non-linearity has no impact on the conclusions reached in the preceding section, thanks to the use of a constant criterion of pupillary response. Though we have no evidence about other non-linearities concerning steady-state reactions, their presence should not be ruled out.

In order to collect evidence as to the degree of linearity of the centres that combine signals from different retinal areas, we have checked whether the contraction C_{A+B} in response to simultaneous illumination of two different fields A and B, equals the sum of C_A and C_B obtained in response to separate illumination of the fields. Figures 7.6 and 7.7 show for two cases the diameters D
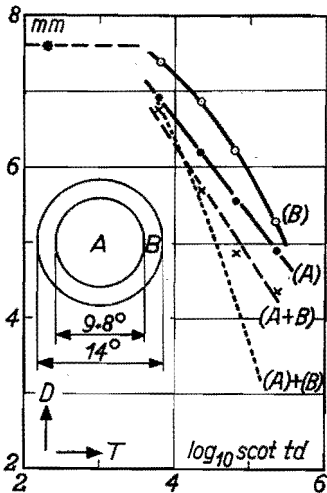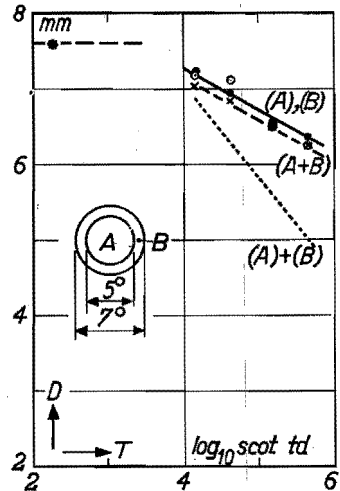
Fig. 7.6   Fig. 7.7

Pupillary diameter D as a function of retinal illumination T. Comparison of the contractions occurring when two fields are presented simultaneously (broken lines, marked $(A + B)$) to the sum of the contractions occurring when the two fields are presented separately (dotted lines, marked $(A) + (B)$). The contractions have been taken relative to the diameter in the dark which amounted to 7·6 mm. For low illuminations $C_{A+B} = C_A + C_B$ whereas for higher illuminations $C_{A+B} < C_A + C_B$. This is indicative of some non-linear behaviour. These results are representative of many situations that have been tested.

as measured separately for a certain field A and another field B, as well as for field $A + B$. For easy comparison, the dotted lines give the sum of the contractions C_A and C_B taken relative to the pupil diameter in the dark (7·6 mm). It will be seen that the additivity law $C_{A+B} = C_A + C_B$ applies reasonably well for small contractions or low illuminations, whereas for higher contractions or high illuminations $C_{A+B} < C_A + C_B$, which implies a definite deviation from linearity. This result is representative of all fields of view tested. We have summarised various data in an appendix.

However, when both fields are offered to one eye, our experiments do not give conclusive evidence, since the indirect illuminations of the fields A and B may overlap. If so, the true illumination then differs from the one desired, in which *different* retinal areas should be illuminated simultaneously. Since the influence of indirect illumination, which limits the value of these experiments, increases with the level of direct illumination, the experimental results do not oppose the assumption about a possible addition of the contributions from different retinal areas. In the theoretical description of the receptive system that we hope to put forward in sec. 7.4, we shall adhere to this assumption and deal linearly with the factor area. Illumination will be considered to be a nonlinear, logarithmic parameter.

7.3. Indirect illumination

One of the factors, the influence of which could only qualitatively be accounted for in the past, is the indirect light that is scattered or reflected within the eye. A pupillary contraction does not reveal whether it arose from directly illuminated areas, from indirectly illuminated areas, or from both. Usually, the indirect light illuminates large areas at low levels. This indirect illumination may exert considerable influence on the pupil. In general, the influence of indirect illumination may be expected to be relatively large when the direct illumination reaches ineffective retinal areas. Following this line of thought, Heddaeus [54] and Hess [57] attributed the contractions, occurring when peripheral retinal areas were illuminated, to stray light reaching the sensitive central area *) (see also sec. 3.3). Since we want to know when and to what extent indirect light plays a part in pupillary contraction, we shall briefly discuss some quantitative data on the retinal distribution of indirect illumination which have become available in the past ten years.

Retinal distribution of indirect illumination

The indirect light in the eye stems mainly from three sources (fig. 7.8). The

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*) These ideas were developed for the interpretation of experiments on dynamic pupillary thresholds. They are of basic importance for all kinds of overall reaction of the retina.
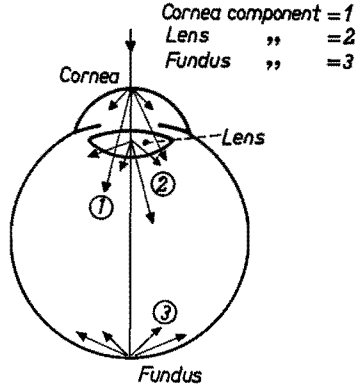
Fig. 7.8. Intra-ocular sources of indirect illumination.

cornea (1) and the lens (2) show a good deal of scattering. The origin of this scattering may be attributed to minor irregularities of the surfaces that separate the various media and also to small inhomogeneities of the refractive index within the lens. The fundus (3) reflects and scatters some light. According to Vos [127], the fundus component may in its turn be analysed as consisting of three processes: (a) the retina scatters some light, (b) the pigment epithelium behind the receptor layer reflects some light more or less diffusely, and (c) the sclera shows diffuse reflection, this light, however, being absorbed for the greater part by the pigment epithelium.

The retinal distribution of the light for any directly illuminated configuration can be calculated from the intensity distribution around the retinal image of a point source. On excised eyes of steer, sheep, cat, and pig, DeMott and Boynton [36] measured directly for a point source the amount of stray light coming from cornea and lens as a function of the angular distance from a point image. Their results are shown in fig. 7.9 (full line), which indicates the logarithm of the fraction of total light flux scattered within a solid angle of one square degree at an angle θ from the direction of incidence. According to a calculation on the basis of these data, 31 % of the total light flux would be scattered over angles larger than 2°, for which angles the measurements yielded reliable data. Much care was taken to account for possible post-mortem changes which were shown to be only slight. Within 0·1 log unit the intensity level of the stray light turned out to be uniform over the visible spectrum. Within reasonable limits these results agree with similar measurements carried out earlier by Boynton, Enoch, and Bush [17] on one excised human eye, but they are some 0·7 log units above the level of total indirect illumination that had been assumed from indirect experiments on the increase of visual thresholds due to a glare source.

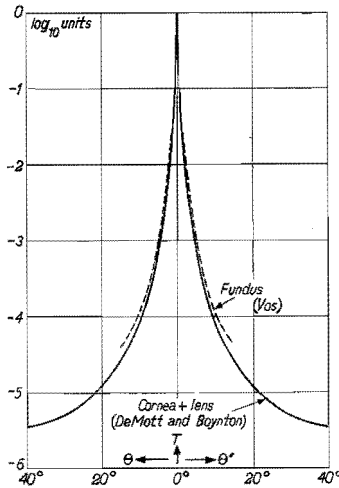The magnitude of the fundus component for a point source has been studied

Fig. 7.9. The distribution of indirect retinal illumination around a point image, according to data from DeMott and Boynton [36]) (cornea and lens components) and Vos [127]) (fundus component). The ordinate values represent the fraction of total incident flux per square degree retinal area. The absolute level of Vos' data has been increased by $1 \cdot 1$ log unit in order to show the correspondence between the two distributions.

by Vos [127]). The dotted line in fig. 7.9 shows his results, the absolute level of which has been increased by $1 \cdot 1$ log unit for easy comparison. The data are valid for a non-foveal point source as the fovea is a singular point, due to the smaller depth of the retina there. Vos arrives at the conclusion that the fundus component is slightly higher than the cornea + lens component. Despite the differences in physical origin, the shape of the distribution of illumination from the fundus component turns out to resemble very nearly that of cornea and lens.

It is certain that there are widespread individual variations in the amount of indirect illumination. The main source of this variation stems from ageing effects. It is well known that the amount of scattering from the lens increases with age and it is possible that this holds for other processes as well. Since of the three components contributing to indirect retinal illumination the angular distribution is more or less similar, it seems likely that the relative retinal distribution of indirect light around a point source does not show any important dependence on age. Yet, the absolute level may show considerable individual variations.

In order to obtain information about this absolute level for the eyes of our observers, we performed two kinds of experiment. First, we tried to compare subjectively the intra-ocular indirect illumination with a series of stray illuminations added from outside the eye. Secondly, we compared intra-ocular stray light

with extra-ocular homogeneous veils on the criterion of producing equal increases in visual threshold.

When looking at a bright monochromatic point source, one observes indirect light as a regular pattern of tiny points around the bright point source. When adding extra-ocular stray light one is able to compare the brightness of intra-ocular indirect illumination to brightness increases of the extra-ocular amounts that are invisible, just visible, comparable to, or much more intense than, intra-ocular scatter. By comparing these observations with the physical scatter distributions of the added stray light, an estimation of the magnitude of the intra-ocular stray light can be obtained. According to a suggestion by Schouten [105], extra-ocular stray light has been produced by means of scatter filters. These filters consist of two sheets of slightly frosted glass between which a thin layer of oil is present. By taking different proportions of machine oil and linseed oil, various refractive indices and accordingly various amounts of scattering were effected. The scatter filters were mounted in a disc to ensure a rapid change. The disc was placed about $2\frac{1}{2}$ cm in front of the eye. Depending on pupil size, the retinal area of this extra scattered light subtended about 20° of the visual field. The physical distributions obtained with two of the discs are shown in fig. 7.10. The extra amounts of stray light from these discs were "just visible" and "comparable to intra-ocular scatter", respectively. When comparing these distributions with the curve of DeMott and Boynton (fig. 7.9) it can be con-
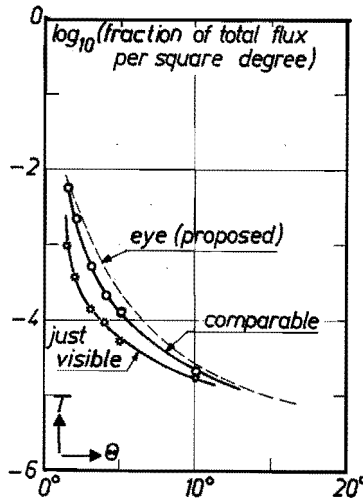

Fig. 7.10. Physical distributions of stray illumination that have been measured for two scatter filters (full curves). The dotted curve represents the intra-ocular distribution of indirect illumination, as proposed for the right eye of observer H.B. Ordinate values in fraction of incident flux per square degree.

cluded that for this observer the level of indirect illumination must be expected to be somewhat below that curve.

Next, we measured the extent to which a visual threshold (test field) is increased by a conditioning glare source at certain distances from the test field. Assuming that no direct inhibition effects of the glare source on to the test field occur *), the increase of threshold is effected via the straylight veil. If so, one can then express the influence of the glare source in terms of "equivalent veil", i.e. the illumination of a large field overlapping the test field, necessary to obtain the same increase in visual threshold. As a test field we used a 100 ms flash of 1° diameter, projected on the retina 9° nasally to the fovea. The conditioning fields were steady 2° fields of various intensities, at distances of 5° and 10° from the test field (fig. 7.11), and a large field overlapping the test field. In the
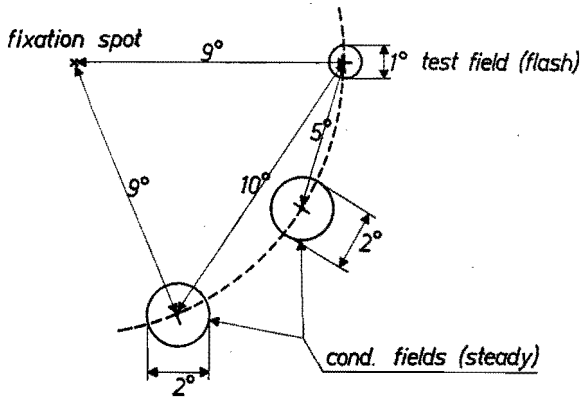
Fig. 7.11. Field configuration that has been used for measuring equivalent veils of a 2° conditioning field at distances of 5° and 10° from a 1° test field.

scotopic intensity range (0 to 3 log units increase of threshold as compared to the dark-adapted eye) we found as a result that the equivalent veil, expressed as a fraction of total light flux per square degree retinal area, amounted to —3·5 ± 0·2 log units (5° distance) and —4·5 ± 0·2 log units (10° distance), respectively (observer H.B., fig. 7.12). For observer H.J.v.B. the results were 0·3 log units lower. These values are 0·5 and 0·8 log units below the data of DeMott and Boynton and correspond reasonably well to the subjective estimate according to the first method (see fig. 7.10).

For the light distribution around a point image for observer H.B. we shall

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*) The main argument in favour of this assumption is the linearity of the processes involved, which is easily accounted for by physical scattering. From a theoretical point of view direct neural effects are not excluded from playing a part provided they are linear over a large range of intensities. For retinal distances below a few degrees, nervous inhibition effects are known to play an important part.

Fig. 7.12. Proposed retinal distribution of indirect illumination around a point image for the right eye of observer H.B. The curve has been obtained by adjusting the absolute level of the curve of DeMott and Boynton (fig. 7.9), by a decrease of 0·5 log unit. The two points indicate the results of the experiment on equivalent veils.
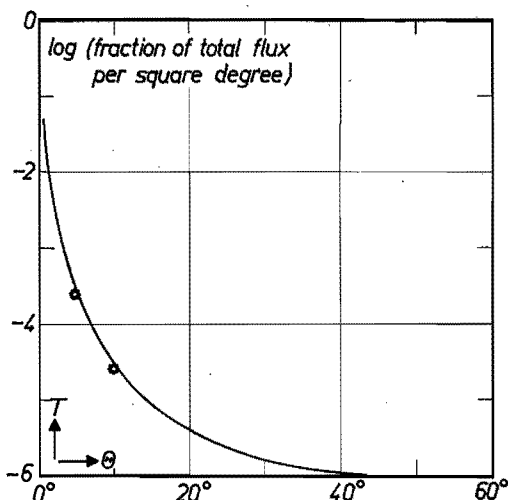
use the data of DeMott and Boynton, decreased by 0·5 log units in order to adapt the absolute level to the eye under consideration. An evaluation shows this distribution (fig. 7.12) to correspond to a total amount of 10 % light scattered and reflected at distances greater than 2° from the direct point image. Once the distribution around a point image is known, the distribution for any field may be calculated. Assuming one value for the total light flux, the dotted lines of fig. 7.13 indicate, for example, the retinal light distribution for discs of 2° and 20° and for a ring with inner and outer diameters of 22° and 35°, respectively *). The coincidence of the curves for large eccentricities stems from the gradual flattening with distance of the point-image distribution curve.

Application to the pupil

Referring to figs 7.2 and 7.4, the black horizontal lines in fig. 7.14 show the direct retinal illuminations that turned out to make the pupil contract to 6·0 mm. This illumination refers to discs of the indicated size in different retinal positions as well as to concentric discs of various sizes, centred on the fovea. The curved lines indicate the distribution over the retina of the indirect illumination **) for some of these cases according to fig. 7.13.

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*) We have disregarded the detailed gradients at the edges of the direct fields since these have no impact on the pupillary problem involved.

**) The troland has been defined only for objects in the outer world which are imaged on the retina. We shall extend the use to illuminations stemming from intra-ocular sources. For this indirect illumination, the troland will be defined as the product of extra-ocular luminance (cd/m²) and pupillary area (mm²) that would produce a retinal illumination equivalent to the indirect illumination under consideration.
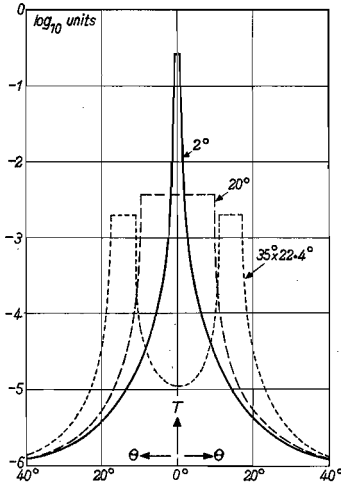
Fig. 7.13. Distribution of retinal illumination for discs of 2° and 20° and for a ring with diameters 22° × 35°, as have been calculated from the distribution around a point image according to fig. 7.12. No attention has been paid to the detailed gradients at the edges of the fields.
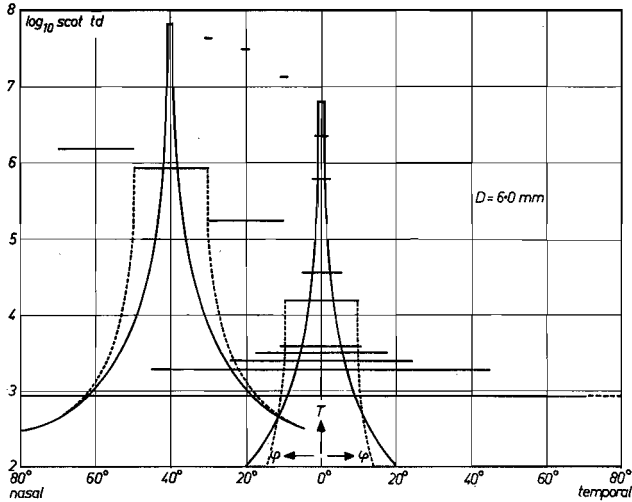
Fig. 7.14. Steady retinal illuminations, required for a pupillary diameter of 6·0 mm for various field configurations, as indicated in the figure. For fields of 2° and 20° in positions $\varphi = 0°$ and $\varphi = 40°$, the distributions of retinal illumination have been drawn (according to fig. 7.13).

It is interesting to note that 2° and 20° peripheral fields ($\varphi = 40°$) illuminated at such a level that they produce equal pupillary contractions, produce equal indirect illuminations in the central area. This indirect illumination of the centre

is 0·5-1 log unit below the direct, homogeneous illumination of a large central field (35° or more), necessary to obtain this contraction. The quantitative evaluation, therefore, supports the idea that the central area may contribute substantially to contractions on peripheral illumination, which approximates the views of Heddaeus [54] and Hess [57]. In the case of centrally fixated fields of 2° and 20°, the indirect illumination is also spread over the retina. The area where this indirect illumination contributes to pupillary contraction will be more restricted than in the case of peripheral fields, since for central fields the direct illumination is lower whereas the effectiveness of the areas struck by indirect illumination decreases with increasing distance from the focused image. In particular for fields larger than 20° and occupying the central area, the spread of the illumination may probably be neglected with respect to pupillary contraction.

To obtain also direct experimental evidence as to the role of the indirect illumination for a central 2° field, we carried out some experiments in which, from outside the eye, we increased the amount of stray light in two steps (fig. 7.15). The extra amounts of scatter were "just noticeable" (1) and "comparable to intra-ocular scatter" (10), respectively, when looking at a point source. The physically measured distributions of illumination as well as the proposed intra-ocular scattering function were already shown in fig. 7.10. In fig. 7.15 the contractions resulting from a 2° foveal field are shown to have definitely increased by the small amounts of scatter. This supports the idea that for small retinal fields the direct illumination contributes considerably to pupillary contraction. It may be noted that the direct illuminations required for these contractions are
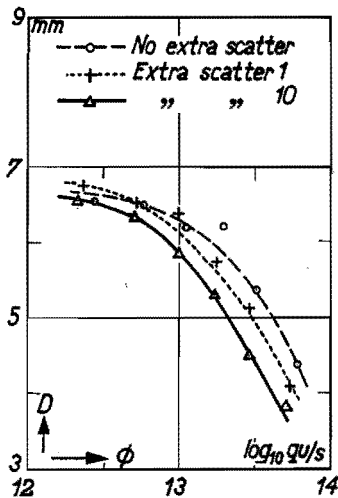

Fig. 7.15. Pupillary diameter D as a function of quantum flux for a foveal field of 2°. Small increases in indirect illumination from outside the eye cause significant increases in contraction. The physical distributions of the extra scatter are shown in fig. 7.10.

of the order of 7 log scot.td, indeed very high values (fig. 6.13). In such circumstances it is but logical to suppose an overall response to originate not only from the directly illuminated area. This may provide an explanation of the fact that no dip in effectiveness is found when only the fovea (without rods) is illuminated. If this foveal dip exists, its existence may well be masked by indirect light reaching the surrounding rods.

In sec. 7.2 we found an anomalous increase in resolving power when substituting an exploring field of 20° for a field of 2°. There we suggested that indirect illumination might be partly responsible for this effect. We may now conclude that no justification can be found for attributing the measured degree of effectiveness to only directly illuminated areas. Especially for peripheral positions of the fields, the results seem to provide information on the retinal distribution of indirect illumination rather than on the degree of effectiveness of the directly illuminated areas. Accordingly, the idea that resolving power increases with decreasing size of the field may be fallacious since the retinal area that produces the pupillary response may have a much larger size than the direct field and even a different position. This may cause distortion of the experimental results on any supposed retinal sensitivity function, which may well affect the curves for the smaller fields more than for the larger ones.

The problem of "over-integration" cannot be understood by considering merely the influence of indirect light. On the contrary, if we suspect the indirect light of playing an important role for small fields especially, the true local degree of effectiveness in the small central fields is still lower than indicated in fig. 7.4 and the over-integration is accordingly higher. For a proper understanding of this over-integration, the essential influence of non-linearities must be taken into account.

In conclusion we may say that the spread of excitation by indirect illumination causes a general tendency towards integration effects, in which the pupillary response is governed only by total light flux. Experimentally, this tendency has been found for many field configurations as will be clear from the data provided in the appendix. Since these effects may have originated from the blurring influence of indirect illumination, they need not necessarily be attributed to linear effects within the receptive system itself.

7.4. Proposed theoretical description

From the foregoing discussion it has become clear that non-linear processes may play an essential role in the pupillary receptive system. Unfortunately the spread of excitation by indirect illumination interferes with the information about the retinal localisation of the activity that causes the pupil to contract. If it is desired to collect basic data as to the variations of intrinsic parameters over the retina, situations should be compared in which the influence of indirect illumination is either very small or constant.
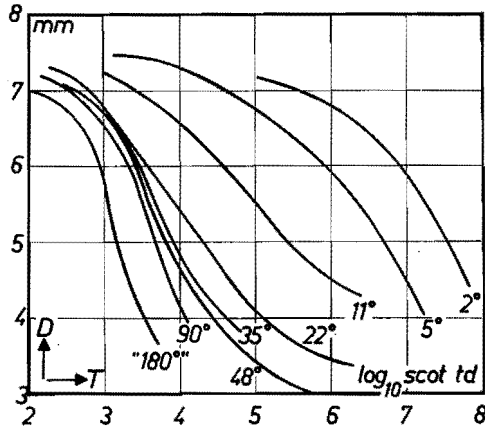
Fig. 7.16. Pupillary diameter D versus retinal illumination T for central discs of various sizes. The lines have been drawn freehand through the experimental points, which will be partly shown in fig. 7.20.

Figure 7.16 shows pupillary diameter as a function of retinal illumination for a large range of field sizes, which in all cases were centred on the fovea. We shall assume that for the five fields larger than 20° the influence of indirect illumination is negligibly small. The experimental data of these five fields can be fitted by the formula *)

$$C = D_0 - D = B \log (1 + T/T^*) . \qquad (7.1)$$

Assuming $D_0 = 7 \cdot 4$ mm, the values of the two parameters B and T^* are shown in table 7.I. It may be noted that, within experimental error, the transition

TABLE 7.I

Values of B and T^* when describing the experimental data for five large central fields (diameter $2\,a$) by the equation $D = D_0 - B \log (1 + T/T^*)$ (eq. (7.1)

$2\,\alpha$ (degrees)	B (mm/log unit)	T^* (log scot.td)
22·4	1·6	2·9
35·0	2·2	3·0
48·4	2·6	3·0
90·0	3·2	3·0
"180"	4·2	2·8

---

*) To account for the non-linear behaviour, we chose a logarithmic function, which may be applied to many physiological processes. The main reason for this choice was the mathematical simplicity of the description. Of course, the conclusions to be reached will apply equally to curves of similar shape, though of different mathematical formulation.

point T^* is independent of the size of the field (2·9 log scot.td). The only
variable is B, representing the gradients of the curves if $T \gg T^*$. It is found to
increase with field size. We shall now work towards a generalisation of eq. (7.1).
For this purpose we assume that the gradient in response to a homogeneously
illuminated field is built up from several independent contributions $w.\Delta A$
of areas ΔA (w is a weight function). Then $B = \Sigma w.\Delta A$ and accordingly

$$C = [\log (1 + T/T^*)] \Sigma w.\Delta A. \tag{7.2}$$

We now omit the conditions of uniform illumination and of a large field. We
then arrive at the hypothesis that, for any retinal distribution of illumination
the resulting pupillary contraction C can be described by the equation

$$C = \Sigma [\log (1 + T/T^*)]. w.\Delta A. \tag{7.3}$$

Since the retina shows a great deal of centro-symmetry around the fovea we
shall turn to polar coordinates (φ, ψ). We shall adhere to the general practice
of representing them by the coordinates of an incident ray in the outer field
of view that projects to a particular point of the retina. Thus, φ is the angle
between this ray and the visual axis $(0 \leqslant \varphi \leqslant 90°)$ and ψ is the angle between
this ray and the horizontal plane through the visual axis $(0° \leqslant \psi < 360°)$.
Retinal areas ΔA are then expressed by the solid angle $\Delta \Omega$ that they occupy
when seen from the nodal point (fig. 7.17):

$$\Delta \Omega = (\sin \varphi). \Delta \varphi. \Delta \psi \text{ square degrees } (\varphi \text{ and } \psi \text{ in degrees}). \tag{7.4}$$

The retinal area ΔA, corresponding to one solid angle $\Delta \Omega$ increases somewhat
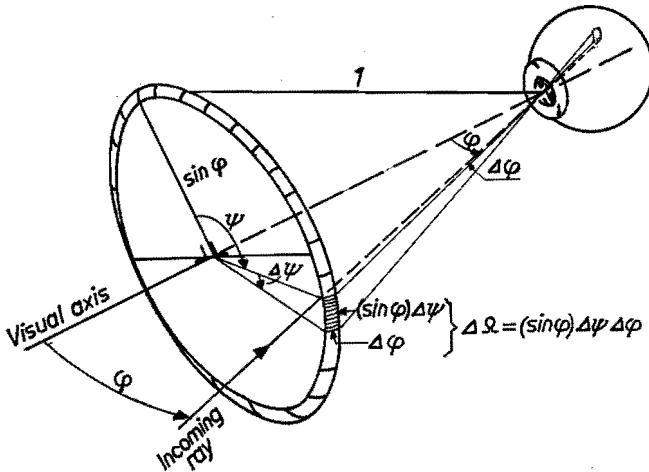with φ.

Fig. 7.17. Description of a retinal position by means of polar coordinates (φ, ψ). A small
retinal area ΔA is represented by its solid angle $\Delta \Omega = (\sin \varphi) . \Delta \varphi . \Delta \psi$.

Before evaluating this equation numerically, we shall adopt a physical model whose behaviour is described by eq. (7.3). This will be done to specify what the essential assumptions are. We assume this model to consist of photoreceptors of one type, located on the inner surface of a hemisphere (fig. 7.18). For low illuminations, each receptor reacts linearly to its illumination whereas
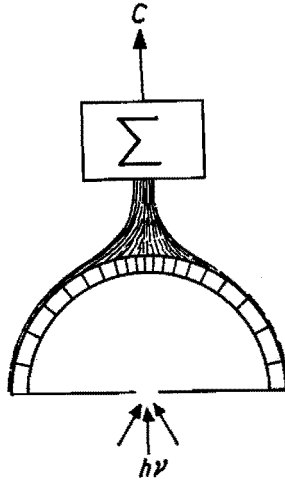
Fig. 7.18. Physical model that obeys the proposed theoretical description of pupillary contractions, see eq.(7.3). The light is absorbed by logarithmic photoreceptors, whose response C_i is assumed to be proportional to log $(1 + T/T^*)$. The density distribution of these logarithmic elements equals the weight function w. The integrator Σ adds all incoming signals C_i. Its output C represents pupillary contraction.

for high illuminations its output is proportional to the logarithm of the illumination. The density of the logarithmic receptors is assumed centro-symmetrical around the main axis. The light enters through a small hole in the centre of the hemisphere. Behind the receptive surface we assume an integrator Σ, which adds all the outputs of the photoreceptors. The output of this integrator represents the contraction C.

Thus we assume:

(1) A logarithmic receptor i has an output

$$C_i = \log (1 + T/T^*). \tag{7.5}$$

(2) The output C of the integrator consists of the sum of outputs of the individual photoreceptors:

$$C = \Sigma \, C_i. \tag{7.6}$$

This means that the contribution ΔC from a small uniformly illuminated area

represented by its solid angle $\Delta\Omega$ will be

$$\Delta C = w \cdot \Delta\Omega \cdot C_i, \tag{7.7}$$

if w represents the density of the logarithmic receptors. The equation of this model becomes

$$C = \Sigma \left[\log \left(1 + T/T^* \right) \right] . w . \Delta\Omega, \tag{7.8}$$

which is equivalent to eq. (7.3).

In order to carry out numerical calculations of D as a function of T on the basis of eq. (7.3), the retinal illumination $T(\varphi, \psi)$ has been evaluated from the light distribution in the outer field of view and the intra-ocular light distribution around a point image as proposed in fig. 7.12. We chose the following numerical values of D_0, T^* and w.

D_0. We chose a constant value $D_0 = 7\cdot4$ mm. In actual experiments the diameter in the dark varies between $7\cdot0$ and $7\cdot9$ mm (observer H.B.).

T^*. On the strength of the experiments for the five large fields (fig. 7.16) we chose a constant value of the point of transition T^* ($2\cdot9$ log scot.td). This facilitates the evaluation of the description in several respects, e.g. the retinal distribution of only one parameter (w) need be derived from the experiments. Some implications of this choice will be considered on p. 107. In fact, we have some indications that T^* shows a higher value in the central area.

w. We took a centro-symmetrical *weight function* $w = w(\varphi)$ (fig. 7.19) that passed smoothly through the average values $\overline{w} = B/\Omega$ that must be
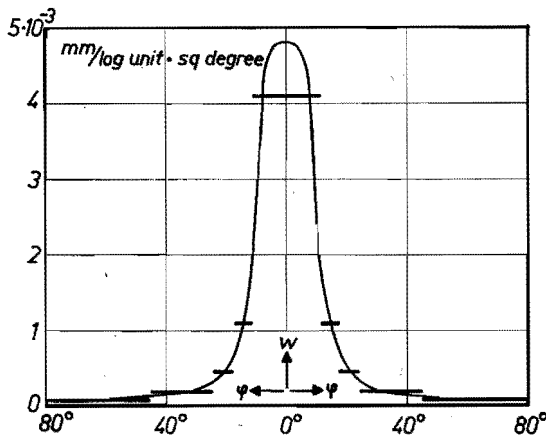

Fig. 7.19. Proposed retinal weight function, drawn smoothly through the average weight factors $\overline{w}$ that permit an adequate description of the experimental curves for central fields of 22°, 35°, 48°, 90°, and "180°" (table 7.II). For these large fields the spread of excitation by indirect illumination is assumed to be negligible.

assumed to fit the experimental data for the five central discs with diameters 22°, 35°, 48°, 90°, and "180°". This was done by subtracting these slopes, thus obtaining theoretical values for the rings between the discs (table 7.II). Of course, it would be more attractive to use direct experimental values for the rings instead. However, when applying the rings, any influence of indirect illumination causes systematic deviations, which seem worse than some increase in accidental deviations.

Thus, the only pupillary data used for adapting the theoretical description to the experiments are the values of D_0 and T^* and the values of B obtained with five large central discs.

TABLE 7.II

Theoretical contributions of retinal rings derived by subtraction from the experimental values obtained for discs (see table 7.I)

	2 a (degrees)	Ω (sq. degr.)	B (mm/log unit)	$B/\Omega = \overline{w}$ (mm/log unit sq. degr.)
discs	22·4	390	1·6	
	35·0	950	2·2	
	48·4	1 820	2·6	
	90	5 990	3·2	
	"180"	13 000	4·2	
	↓	↓	↓	
rings	0 -22·4	390	1·6 →	4·1 .10⁻³
	22·4-35·0	560	0·6	1·1 .10⁻³
	35·0-48·4	870	0·4	0·46.10⁻³
	48·4-90	4 170	0·6	0·15.10⁻³
	90 -"180"	7 000	1·0	0·14.10⁻³

7.5. Comparison of theoretical description with experimental results

The theoretical evaluation enables us to calculate numerically the contractions in response to any retinal light distribution, the indirect illumination from scattering processes included. In this section we shall compare the outcome of these calculations to actual experimental data.

The calculations have been done by numerically summing the values $\Delta C = [\log(1 + T/T^*)] \cdot w \cdot \Delta\Omega$, in which the summation areas $\Delta\Omega$ were chosen such that within these areas the illumination parameter $\log(1 + T/T^*)$, either from direct or from indirect illumination, as well as the weight factor w

could be represented reasonably well by one value each. The number of separately considered areas varied from 1-10, in the case of central fields, to 10-30 for peripheral fields, where the centres of illumination and of weight function do not coincide. An example of the calculations will be given on p. 100.

The outcome for central fields of various sizes is shown in fig. 7.20. The lines represent theoretical predictions whereas actual experiments, for each field size obtained in 2-7 sessions, are shown by the points. The agreement for the fields of 22° and above arises from the fact that these experiments have been used to shape the weight function of the theory. For the smaller fields, the theoretical curves approximate experimental data, deviations being within some 0·5 mm contraction or 0·5 log units illumination. In the calculations, the relative contributions from the directly illuminated fields themselves decrease sharply from the 22° field towards smaller fields. For fields smaller than some 7° a substantial contraction is predicted only if the indirect illumination, which occupies much
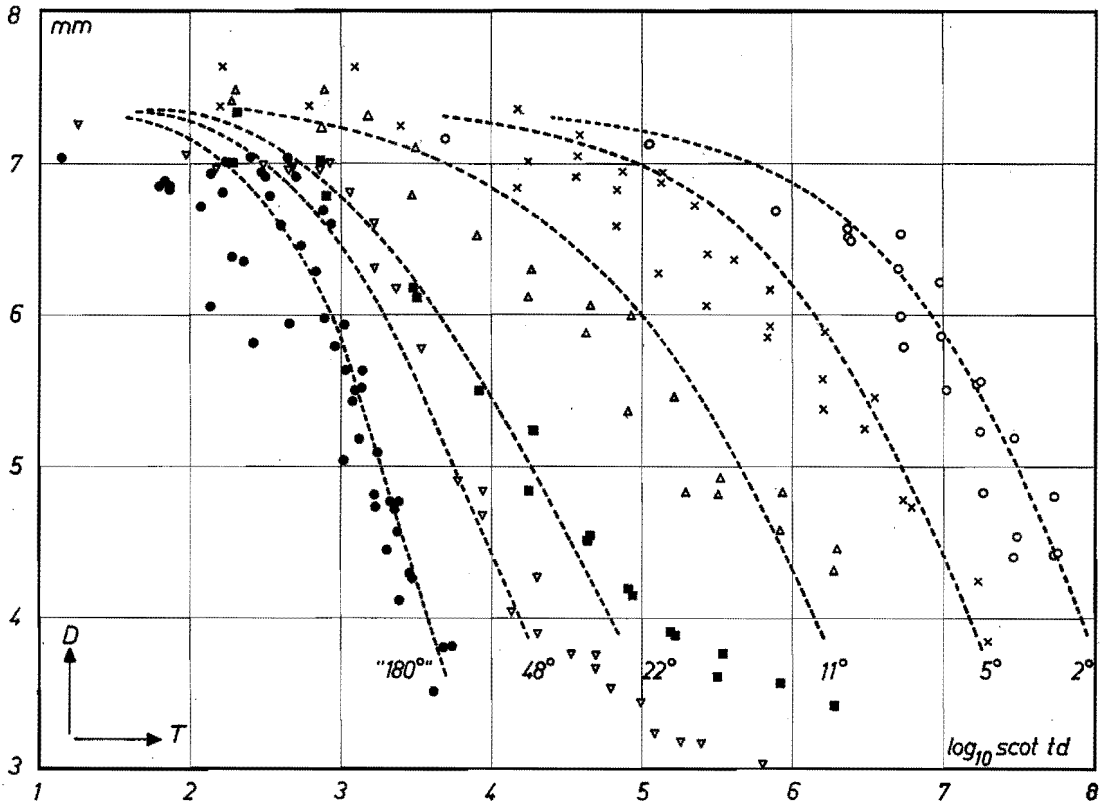

Fig. 7.20. Experimental and theoretical diameters for central fields of various sizes. The dotted curves show the results evaluated from the theoretical description according to eq. (7.3), which has been adapted for five fields larger than 20°. The theoretical description takes into account direct as well as indirect illumination. Observer H.B.
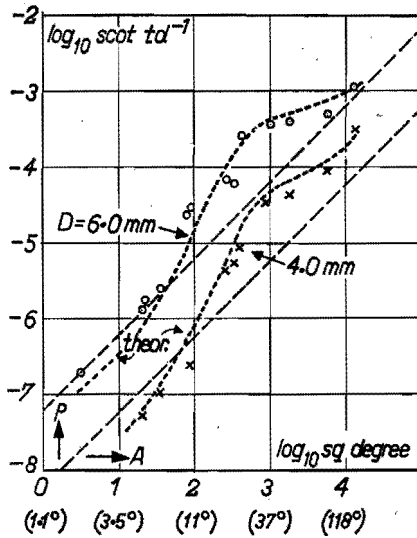
Fig. 7.21. Experimental and theoretical degrees of effectiveness for central fields of various sizes. Criteria $D = 6\cdot0$ and $D = 4\cdot0$ mm, observer H.B. The effects of integration, over-integration, and under-integration are adequately described by the theoretical equation (7.3).

larger areas, is of sufficient intensity. For fields smaller than $5°$ (20 square degrees) the contribution of the directly illuminated areas is even negligibly small. This implies that the only important variable is total light flux, since for small fields the distribution of indirect illumination over the retina is dependent on total light flux only, except in the very neighbourhood of the direct fields, which occupy areas too small to contribute substantially to the resulting contraction. These phenomena are shown more clearly in fig. 7.21 where, similar to fig. 7.4, the degree of effectiveness $P(\equiv T^{-1})$ is presented as a function of the area occupied by the direct field. The $45°$ slope predicted for small fields represents adequately the effect of integration found in the experiments which, according to the theory, is due to the prevailing influence of indirect illumination. The effect of over-integration for fields between $5°$ and $22°$ results from an increase of the contribution of the directly illuminated area, which causes an increase of pupillary contraction to such an extent that the illumination level can be permitted to decrease more than proportionally for an equal-response criterion. For fields larger than $22°$, the considerable decrease of weight function towards the retinal periphery makes itself felt as under-integration.

For fields of constant size, imaged at various distances from the fovea, theoretical description and actual experimental outcome are shown in figs 7.22 and 7.23 for two field sizes. Deviations from the experiments are within $0\cdot7$ log units ($1\cdot3$ mm), the description generally giving lower values for the contractions, especially for peripheral illumination. The integration effect implies
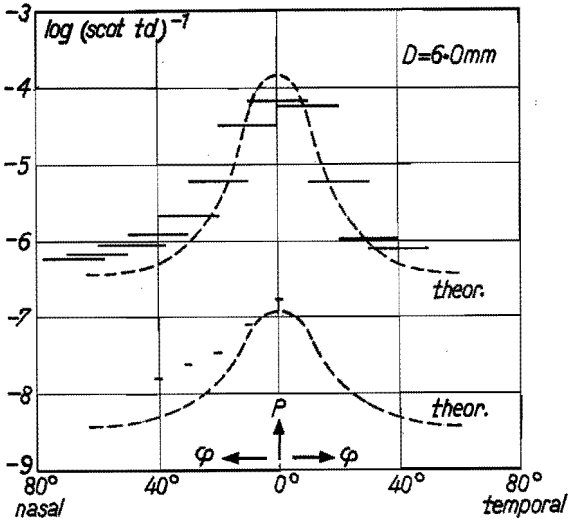
Fig. 7.22. Experimental and theoretical degrees of effectiveness for fields of 2° and 20° at various retinal positions. Criterion $D = 6\cdot0$ mm. Observer H.B.
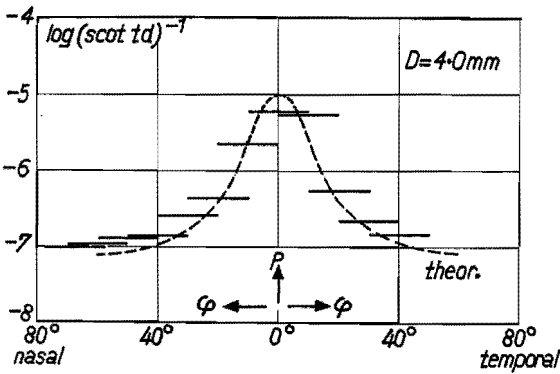
Fig. 7.23. Experimental and theoretical degrees of effectiveness for a field of 20° at various retinal positions. Criterion $D = 4\cdot0$ mm. Observer H.B.

that, independent of field size, the only relevant variable is total light flux. For peripheral positions of the fields this is indicated in fig. 7.22 by the difference of 2 log units between the illuminations required for the 20° and the 2° fields since the areas involved differ by a factor of 100. In the theoretical description this effect is due to the low values of peripheral weight factors, which set a low limit to the contributions of direct illumination even for a field of 20° (300 square degrees). Again, if the contribution of direct illumination is low, the contractions obtained are a result of indirect illumination of much larger areas, which mainly depends on total light flux. For positions of the fields closer to the fovea, the local weight factor gradually increases and the direct illumination accounts for

the effect of over-integration, which for central fields has already been discussed. The calculations have been carried out also for some ring-shaped fields. The deviations between the experiments and the description were comparable to those of the configurations presented.

As an example of the calculations we shall compute semi-quantitatively contractions from eq. (7.3) (p. 93) for four different situations. For central fixation we shall compare a 2° retinal field, illuminated directly with 6·0 log scot.td to a 20° field, illuminated with 4·0 log scot.td. The total light fluxes are equal in both cases. For a peripheral position ($\varphi = 40°$) the same fields will be compared for retinal illuminations of 8·0 log scot.td (2° field) and 6·0 log scot.td (20° field).

The summation of eq. (7.3) will be carried out roughly by dividing the retina into three parts only:

(1) The directly and uniformly illuminated area, contributing $C_1 = [\log (1 + T/T^*)] \cdot \overline{w}_1 \cdot \Omega_1$.

(2) The indirectly illuminated area within $\theta = 20°$ from the centre of the direct field; $C_2 = \overline{[\log (1 + T/T^*)]} \cdot \overline{w}_2 \cdot \Omega_2$.

(3) The indirectly illuminated area at distances greater than 20° from this centre. For the 2° and the 20° field to be compared these illuminations are equal as we use equal light fluxes (see fig. 7.13); $C_3 = \overline{[\log (1 + T/T^*)]} \cdot \overline{w}_3 \cdot \Omega_3$.

Equation (7.3) then becomes $C = C_1 + C_2 + C_3$.

The numerical calculations are shown in table 7.III. The values of $\log (1 + T/T^*)$ can be taken from fig. 7.13, those of w from fig. 7.19. It may be of help to remember that $\Sigma w \cdot \Delta \Omega$ summated over the total retina is a constant representing the value B obtained for a uniformly illuminated retina. The values of C_3 for 2° and 20° fields are essentially equal, since the same retinal areas are illuminated with equal illuminations.

It is shown in the table that for central fields, the larger theoretical contractions result from the 20° field. This is due to direct illumination. Though direct illumination for the 2° field is higher by two log units, its solid angle Ω is too small to produce any significant contraction. This indicates that, if equal contractions are required, the light flux for the 2° field must be chosen higher (over-integration). For the peripheral position ($\varphi = 40°$), the computed contractions are found equal. The reason is that in the directly illuminated areas the weight function is very low, whereas the indirect illumination now accounts for a substantial contraction. Since C_3 is larger than C_2, equal contractions are now produced by equal light fluxes, irrespective of the direct field (integration).

When combining these rough results for central and peripheral fields, it becomes clear that the 20° field shows a steeper decline of effectiveness towards the periphery than does the 2° field, the main reason being that only for the smaller field is the direct illumination of no importance for the resulting contraction.

In conclusion we find that the theoretical description deals adequately with the effect of over-integration, which can be fully understood from the non-linear characteristics in the receptive system. In combination with these non-linearities, the blurring influence of indirect illumination can account for the anomaly that resolving power increases when larger fields are applied. The integration effects that have been found for fields smaller than 20 square degrees in the retinal centre towards 300 square degrees in the retinal periphery can also be explained by the influence of the indirect illumination, which operates on a system in which contributions from large areas are favoured.

Quantitatively, the deviations between the proposed theoretical description and the actual experiments are of the order of 0·7 mm contraction or 0·5 log units of illumination, which must be considered too large to be accidental. This

TABLE 7.III

Rough calculations of the contractions for 2° and 20° fields in central ($\varphi = 0°$) and peripheral ($\varphi = 40°$) positions, according to eq. (7.3): $C = \Sigma\ [\log (1 + T/T^*)]\ .\ w\ .\ \Delta\Omega$. For the two fields, the light fluxes have been chosen equal so as to show the effects of over-integration ($\varphi = 0°$) and integration ($\varphi = 40°$). $T^* = 2·9$ log sect.td.

central fields $\varphi = 0°$

		diameter 2°			diameter 20°		
		C_1 $\theta \leqslant 1°$	C_2 $1° < \theta < 20°$	C_3 $\theta \geqslant 20°$	C_1 $\theta \leqslant 10°$	C_2 $10° < \theta < 20°$	C_3 $\theta \geqslant 20°$
T	log scot.td	6·0	2·5	0·7	4·0	2·2	0·7
$\log [1 + T/T^*]$	log units	3·1	0·15	0·0	1·1	0·1	0·0
$\overline{w}$	mm/log unit sq. degree	4·8.10⁻³	1·8.10⁻³	0·17.10⁻³	4·2.10⁻³	1·0.10⁻³	0·17.10⁻³
Ω	sq. degrees	3·1	1·3.10³	11.10³	0·31.10³	1·0.10³	11.10³
$\overline{w}\ .\ \Omega$	mm/log unit	0·01	2·3	1·9	1·3	1·0	1·9
$\log [1 + T/T^*]\ .\ \overline{w}\ .\ \Omega$	mm	0·03	0·35	0·0	1·4	0·1	0·0
C			⎣—0·4 mm—⎦			⎣—1·5 mm—⎦	

peripheral fields $\varphi = 40°$

		diameter 2°			diameter 20°		
T	log scot.td	8·0	4·5	2·7	6·0	4·2	2·7
$\log [1 + T/T^*]$	log units	5·1	1·6	0·2	3·1	1·3	0·2
$\overline{w}$	mm/log unit sq. degree	0·13.10⁻³	0·17.10⁻³	0·36.10⁻³	0·15.10⁻³	0·17.10⁻³	0·36.10⁻³
Ω	sq. degrees	3·1	1·3.10³	11.10³	0·31.10³	1·0.10³	11.10³
$\overline{w}\ .\ \Omega$	mm/log unit	0·00	0·22	4·0	0·05	0·17	4·0
$\log [1 + T/T^*]\ .\ \overline{w}\ .\ \Omega$	mm	0·00	0·35	0·8	0·15	0·22	0·8
C			⎣—1·2 mm—⎦			⎣—1·2 mm—⎦	

order of magnitude of these deviations is small enough to be attributed to a somewhat different weight function, a somewhat different distribution of indirect illumination, and a non-linear behaviour somewhat different from a $\log (1 + T/T^*)$ function. In fact, the differences seem too small to justify a detailed investigation of their origin.

The central area

The evidence collected in chapter 6 suggested that the pupillary receptors are rods. The measurements reported in the present chapter, however, revealed a maximum of the effectiveness in the fovea, where rod density is very low. On p. 90 it has been suggested that this discrepancy may be understood if the indirect illumination is taken into account: the foveal position of a direct image

may favour contraction because the indirect illumination and the rod distribution are centrosymmetrical around the same point. Hitherto, we have paid no further attention to this problem because a detailed discussion seemed more appropriate.

Les us consider theoretically the contraction in response to illumination of a small field, as a function of the distance φ from the fovea, assuming a foveal maximum of the weight function. We are interested in the function $C = \Sigma [\log (1 + T/T^*)] . w . \Delta\Omega$ (eq. (7.3)) especially with regard to variations of φ. Figure 7.24 shows schematically the relative distributions of $\log (1 + T/T^*)$, which is symmetrical around the illuminated spot, and of w, which is symmetrical around the fovea. Since we are interested in the influence of variations of φ, we shall simplify the problem by omitting the variable ψ for a moment, thus obtaining the one-dimensional function $C' = \underset{\varphi}{\Sigma} [\log (1 + T/T^*)]. w . \Delta\varphi$. If we shift the illumination centre towards the fovea, C' will increase due to the greater amount of overlap of both functions (see fig. 7.24) until a maximum value is reached for a foveal position of the field. It can easily be shown that the same conclusion holds for C in the two-dimensional situation. Now we introduce a foveal dip in the weight function occupying an area of 2 square degrees, other factors remaining equal. This foveal area contributed to the response to an amount of $C = [\log (1 + T/T^*)] \times 5.10^{-3} \times 2 = 10^{-2} \log (1 + T/T^*)$ mm. Clearly a contribution of some 0.01 mm is far beyond experimental detectability. Consequently the omission of this small contribution can have no practical influence on the conclusion that the maximum value of the effectiveness will be reached for a foveal position of the direct field. We conclude that, according to the theory, the maximum value of the effectiveness that has been found for a foveal position of the field does not imply that the retinal weight
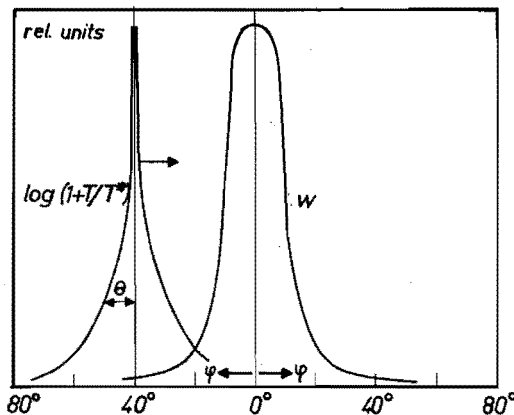

Fig. 7.24. Relative distributions of $\log(1 + T/T^*)$ for a $2°$ field and weight function w. The summated product $C' = \Sigma [\log (1 + T/T^*)] . w . \Delta\varphi$ will show its maximum for $\varphi = 0$, also when the contribution of the central fovea is zero.

function shows a foveal maximum. If the area of the assumed central dip is gradually enlarged, a situation will be reached in which the maximum value of the effectiveness shifts detectably towards the parafovea.

The difficulty in obtaining information on the magnitude of local weight functions of small retinal areas may also be illustrated by considering illuminations that are symmetrical around the fovea. For each ring of width $\Delta\varphi$, the solid angle $\Delta\Omega$ amounts to $(\sin \varphi) \Delta\varphi \Sigma \Delta\psi = 360 (\sin \varphi) \Delta\varphi$ square degrees. Accordingly, we can write $C = \Sigma [\log (1 + T/T^*)] . w . 360 (\sin \varphi) \Delta\varphi$. Figure 7.25 shows $w . 360 \sin \varphi$ as a function of φ. Even if the weight function is as-
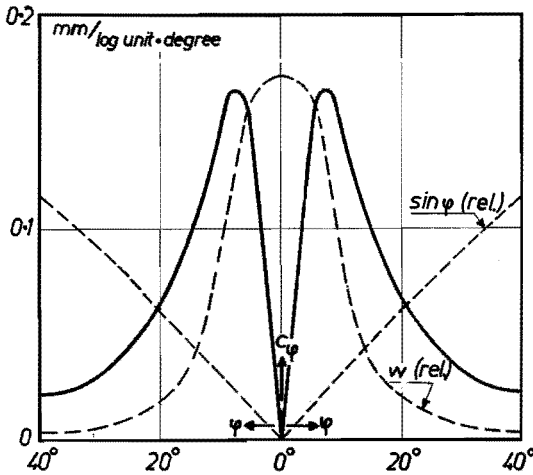
Fig. 7.25. The function $C_\varphi = 360 . w . \sin \varphi$, which represents the contributions to pupillary contraction of rings (width $1°$), centred on the fovea. Despite a foveal maximum of w, the contribution of the fovea will be negligible.

sumed to show its maximum value at $\varphi = 0$, the contribution of the central area is very small as compared to that of rings with more peripheral locations, which effect is due to the increase with φ of the areas involved.

Despite these theoretical difficulties, we shall try to find out whether the weight function shows a maximum or a minimum at the fovea. To reach the most favourable circumstances we must escape as far as possible from the disturbing influence of the indirect illumination. This can be achieved by such choice of the direct fields that the indirect illuminations show a high degree of balance for the situations to be compared. For this reason we chose sets of concentric discs and rings occupying equal retinal areas, and illuminated them equally.

Two sets of concentric fields have been used. The radii of the larger set amounted to $0°$-$4·9°$, $4·9°$-$7·0°$, $7·0°$-$8·5°$, and $8·5°$-$9·8°$. The dimensions of the smaller set were twice as small (fig. 7.26). For two of the cases the
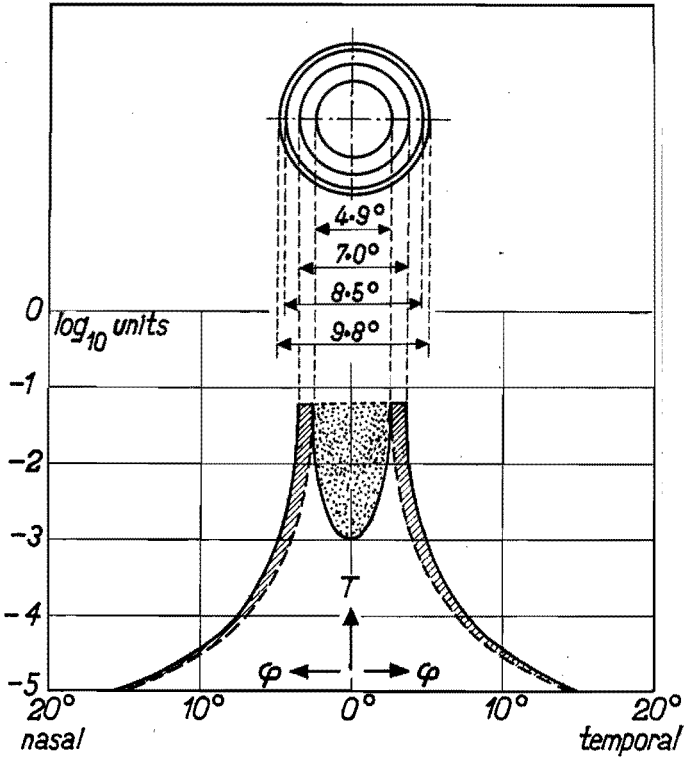
Fig. 7.26. Set of concentric disc and adjacent rings, occupying equal retinal areas. The retinal light distributions (according to fig. 7.12) for two of these fields are shown by the lower curves. The dotted and hatched areas indicate the differences between these illuminations, which, for the indirect illumination, are restricted to relatively small retinal areas.
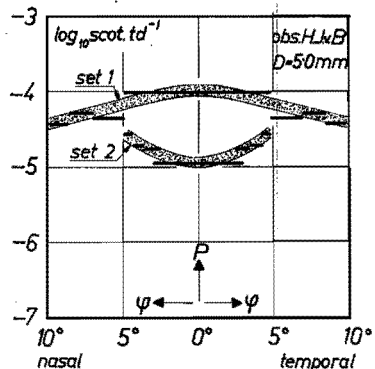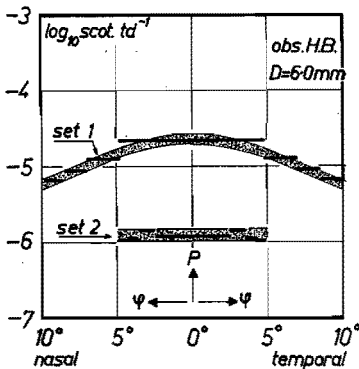
Fig. 7.27. Degrees of effectiveness P, measured for sets of concentric disc and adjacent rings of equal areas. For the smaller set, the results of observer H.B. do not show any significant difference, whereas those of observer H.J.v.B. show a small but significant foveal dip. The comparison within each set is more accurate than the comparison between the two sets. Averages of three experimental series.

retinal light distribution derived from fig. 7.12 is also shown. The differences are now restricted to a small area and any differences in experimental outcome may therefore be attributed to the hatched areas we are interested in. The various fields of each set have been presented successively to three observers in six intensities. The relative accuracies within one set are higher than the absolute accuracy of each set. For two observers, the degrees of effectiveness are shown in fig. 7.27 *). Both of them show a central maximum for the larger set. For the smaller set, observer H.B. shows no differences between the four situations. This means that either the contributions of the differently illuminated areas are equal or that they are very small. Observer H.J.v.B. shows a significant dip of effectiveness in the centre. This supports the idea that for him a central dip may exist in the true retinal contribution to pupillary contraction.

As a second experiment on the contribution of the central area we measured the effect on the pupil of the omission of a small central area from a large homogeneously illuminated field. The retinal illumination remains practically the same everywhere except for the omitted central area. We chose an illuminated field of 25° and omitted consecutively the central 4, 8 and 12 degrees. The outcome is shown in fig. 7.28. Omission of the central 4° produced a small, not significant decrease of the contraction. The ring of 25° × 8° gave a clear decrease of contraction of the order of 0·4 mm, whereas for the 25° × 12° ring this decrease was about 1 mm. The theoretical description requires that the omitted central area must be of the order of 30 square degrees (diameter 6°) before a
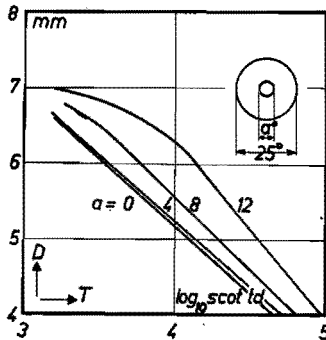
Fig. 7.28. The influence on pupil size when the central 0°, 4°, 8°, and 12° are omitted from a 25° field. Curves drawn through the averages of three experimental series. Observer H.B.

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*) The method rests on the principle of equal illuminations which may produce different contractions. For reasons of uniformity with other presented data, the curves of fig. 7.27 show the differences of illumination that cause equal contractions instead. Such presentation does not influence the position of maxima and minima. The transformation between $\Delta \log T$ and ΔC can be obtained by application of the experimental value $\Delta C / \Delta \log T = 0.9$ mm/log unit.

detectable 0·2 mm difference in pupillary contraction occurs. The results are in agreement with this expectation. The influence of indirect illumination can also be controlled to some extent by applying large homogeneously illuminated conditioning fields on which the test field is superimposed. We have not explored this third method.

7.6. Theoretical description and physiological processes

The chief aim of the description was to find out whether, given a certain decrease of weight function from the fovea towards the periphery, the cooperation of direct and indirect illumination, operating on a system that behaves linearly except for one non-linear, logarithmic transformation, might account for the observed effects for different configurations of the field. The general correspondence between the actual experiments and the theoretical description which has been adjusted in one parameter (w) and two constants (D_0 and T^*) justifies this assumption. The correspondence does not prove that the pupil reacts in the way suggested by the describing equation. However, if we assume for a moment that the description represents static pupillary processes correctly, we must make some additional observations concerning the degree of isomorphy between the elements of the describing equation on the one hand and anatomical and physiological data on the other.

(a) The logarithmic relationship $C \sim \log(1 + T/T^*)$ has been introduced in a purely descriptive way. It corresponds with the input-output relation of a logarithmic element in the situation of full adaptation to the illumination. This relationship resembles closely that proposed by Rushton [96] to express the contribution of receptors to excitation pools in the frog's retina. The available evidence suggests that the signals generated in retinal receptors are proportional to the illumination [41]. In other layers of the retina, electro-physiological potentials show a logarithmic dependence on illumination (Rushton [98], Fatehchand, Svaetichin et al. [40,121]). For this reason, the elements which perform the logarithmic transformation are most readily localised close to the receptor layer.

We did not assume any saturation effects of the receptive system at high illuminations, though from the considerable extent of bleaching that occurs above retinal illuminations of 5 log scot.td (fig. 6.14) deviations from the assumed logarithmic relationship are to be expected. In the experiments such effects would be expected to present themselves as a decrease of the slopes $\Delta D/\Delta \log T$, which effect can be distinguished from muscular saturation effects only if it occurs at pupillary diameters larger than some 4 mm. Our experiments gave no clear indications of such an effect.

What fields would be most favourable to experimental detection of possible

saturation effects of the receptive system? It seems that central fields of medium size offer the best prospects. For either small or peripheral fields, the small contribution of the directly illuminated area to pupillary contraction may easily escape from experimental detection because of the larger contribution by indirect illumination. For very large central fields, pupillary diameters are already very small at relatively low retinal illuminations, which causes muscular saturation effects to come into play below the saturation level of the receptive system. A close inspection of fig. 7.20 reveals that for a field of 11° some decrease of slope occurs at $D = 4·8$ mm, $T = 5·5$ log scot.td. Though the effect is but slightly expressed, it may represent an indication of the expected saturation of the receptive system.

In the descriptive formula a saturation effect may be introduced by substituting $\log [(1 + T/T^*)/(1 + T/T_s)]$ for $\log (1 + T/T^*)$, where T_s is presumably of the order of 5 log scot.td. The theoretical upper limit of the contribution of a retinal area $\Delta\Omega$ then amounts to $[\log (T_s/T^*)] . w . \Delta\Omega$.

(b) The weight function is analogous to the density of the logarithmic receptors of the physical model of p. 94. More generally, it represents the density of logarithmic elements involved, each of which may receive inputs from several linear receptors. The relative density distribution of the logarithmic elements belonging to the receptive field of the static pupil, is represented by the weight function $w(\varphi)$. If we therefore compare the density distribution of retinal rods to the proposed weight function (fig. 7.29), it is not surprising that the two functions are different (in fact, the weight function can be approximated by the quotient of rod density and φ, as may be derived from fig. 7.25). As an analogy, one would not expect the retinal distribution of scotopic visual functions to agree with the distribution of rods, which represents only the most distal layer. For example, Mandelbaum and Sloan [81] showed scotopic visual acuity to have a retinal distribution different from rod distribution.

> It is conceivable that in some higher centre of the pupillary receptive system signals from different logarithmic elements are multiplied by different factors. By such a selective multiplication the observed weight functions would be influenced in essentially the same way as by a density function of logarithmic elements. If so, the relative weight function is then isomorphous with the product of density function and selective multiplication. The absolute values depend on non-selective transformations, such as muscle sensitivity, as well.
>
> Could it possibly be that there are only a few logarithmic elements present? Within the receptive field of each logarithmic element, integration is assumed and this hypothesis affords a simple explanation for the integration that actually occurs for disc-like fields smaller than 20 square degrees in the retinal centre, and smaller than at least 300 square degrees in the retinal periphery. We have not developed this idea in detail. To do so, it will be necessary to assume T^* as varying over the retina, since the number of possible values of the slope B would be very much limited which, in itself, would leave no room for the differences of effectiveness as they actually occur.

(c) In the description we assumed a constant value of the point of transition T^* for the whole retina. The point of transition reflects an essential property of the
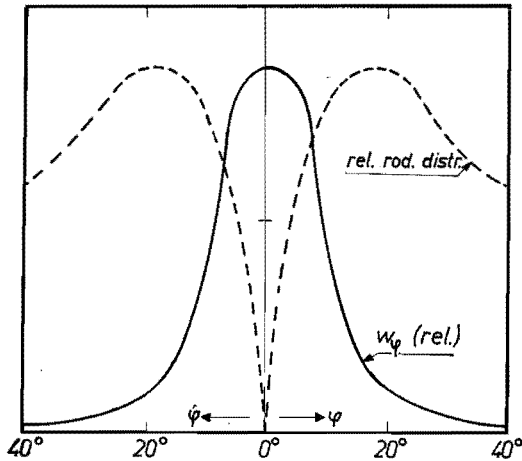
Fig. 7.29. Comparison of the weight function, corresponding with the density distribution of logarithmic elements, to the density distribution of retinal rods, according to Oesterberg [86]).

logarithmic elements, viz. the value of their input at which the output-input relation changes from a linear one to a logarithmic one. If we assume all logarithmic elements to be equal, the retinal illumination at which this input value is reached will depend on the number of connected rods or on the amount of absorbing pigment from which a logarithmic element receives signals. This leads to an isomorphy between the value of $1/T^*$ and the amount of pigment that feeds a logarithmic element (provided other operative coefficients are equal). According to this view, the constant value of T^* that has been assumed supposes logarithmic elements to be fed by equal amounts of rhodopsin.

A different assumption would be that each of the retinal rods feeds one logarithmic element. If so, $1/T^*$ would then show a retinal distribution given by the quotient of rhodopsin density r and density w of logarithmic elements. Since in first approximation, $w \sim r/\varphi$, as a result $1/T^* \sim \varphi$. We have not evaluated this assumption, but the indication of a relatively small contribution to pupillary contraction of the central area that was found for observer H.J.v.B. (fig. 7.27) may be explained by an increased value of T^* due to the low density of rhodopsin rather than by a decreased density of logarithmic elements.

We draw the conclusion that the experiments permit a certain degree of freedom of choice with regard to the retinal distribution of T^*. The simplest interpretation of the calculations is that it indicates the reciprocal of the amount of rhodopsin by which a logarithmic element is fed. According to this interpretation, our assumption that T^* is a constant corresponds with a constant amount of rhodopsin for each logarithmic element.

(d) In the theoretical description we took into account a spread of excitation around the illuminated area due to indirect illumination. An essential property

of this indirect illumination is that it depends linearly on the illumination of the direct image. It is quite conceivable that, in addition to this effect, the excitation in the retinal layers is spread out to a certain extent. If such a retinal effect were proportional to the illumination, its effect on the pupil would simply be added to the effect of indirect illumination. Any similar inhibition effect would act in the opposite direction. It is an open question yet whether these kinds of process play a part in the retina.

Further outlook

If the proposed description reflects some essential features of steady-state pupillary processes, it is to be expected that it is of somewhat wider importance than for merely summarising certain approximate reactions of the pupil to steady illuminations, for one or two observers. We may briefly indicate some further possibilities, which we have not explored, for checking whether this expectation is borne out.

(a) In our experiments only one eye was illuminated. The description suggests that all processes in the pupillary loop are linear, except for one of the first steps which is a logarithmic one. If this is correct, the contractions $(D_0 - D)$ in reaction to illumination of both eyes may be expected to be twice those of only one eye. The experiments of Reeves [92] seem to be in rather good agreement with this expectation.

(b) Several pathological effects can possibly be interpreted in the essential terms of the description. This may also apply to the influence of various drugs on the pupil, which would be expected to influence only D_0 and the absolute value of the weight function.

(c) Individual differences in pupillary reactions are known to be considerable. For example, fig. 7.30 shows pupillary diameters of five observers in reaction to illumination of a central 26° field (515 nm *).
In terms of the description their origin might be found in:
(1) the initial diameter in the dark D_0, which is known to show large individual differences, depending on age, psychological factors, etc.;
(2) differences in the point of transition T^*. For the eight observers for whom we have data available, the values of T^* were in the range of 2·3 to 3·0 log scot.td;
(3) the absolute level of indirect illumination, which shows considerable dependence on age;
(4) the weight function w. It seems reasonable to suppose that the absolute values of $w(\varphi)$ show greater individual differences than do the relative ones.

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*) For shorter wavelengths the deviations from the straight lines are less pronounced and for longer wavelengths more pronounced than for the indicated 515-nm curves.
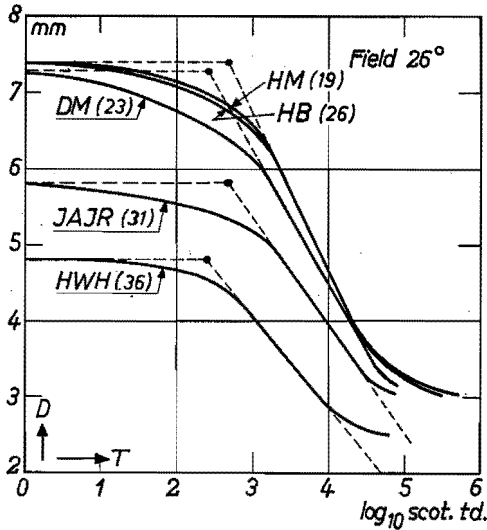
Fig. 7.30. Pupillary diameter as a function of retinal illumination for five observers, whose ages are given. The initial diameter D_0 and the slope B seem to decrease with age.

These differences are reflected in the slopes B of fig. 7.30, the extremes of which differ by a factor two. There is an indication of a correlation between D_0 and B, both showing a decrease with increasing age.

7.7. Conclusions

When the position on the retina of some illuminated field is varied, a maximum contribution to pupillary steady-state contractions is found for a central position of the field and a gradual decrease towards the retinal periphery. This decrease is more pronounced for a larger field than for a smaller one. When the size of centrally fixated discs is varied, keeping constant the total light flux entering the eye, a maximum contraction is found for a field of some 22°. Towards both smaller and larger sizes, the total light flux necessary for reaching an equal contraction slightly increases (maximum 1 log unit difference).

Even when taking into account the indirect illumination from intra-ocular scatter, these combined results cannot be understood from a linear system. However, if one logarithmic transformation is introduced — from retinal illumination T to $\log(1 + T/T^*)$ — the various findings can be explained. A formula, worked out on this basis, describes the experimental results quantitatively within an average deviation of 0·5 mm diameter or 0·5 log unit of illumination.

According to this theoretical description, there are two parameters that depend intrinsically on retinal position: the weight function w and the point of transition T^*. The weight function is assumed to be centro-symmetrical around the fovea and shows a maximum in the fovea or parafovea, amounting to 5.10^{-3} mm contraction for each log unit of illumination and square degree

of retinal area. In the far periphery, about two per cent of this value is reached. The point of transition has been assumed as constant (2·9 log scot.td), but there are indications of a higher value in the central area. The minimum of retinal contribution to pupillary contraction that probably exists in the fovea is masked by the co-occurrence of a maximum influence of indirect illumination. The integration effects that have been found for fields smaller than 20 square degrees in the retinal centre and 300 square degrees in the retinal periphery, can be fully explained by the influence of the indirect illumination, which operates on a system in which contributions from large areas are favoured.

A translation of the parameters of the description in terms of physiological properties of anatomical units can be performed in more ways than one. In the most simple translation, the weight function w is interpreted as the density of logarithmic elements, located close to the retinal receptors, whereas the point of transition T^*, which has been assumed to be constant, is isomorphous to the reciprocal of the amount of rhodopsin that feeds such a logarithmic element.

The organisation of the receptive field for pupillary steady-state reactions may be described as follows: the light absorbed by retinal rods causes a linear signal in the receptors. These signals are conducted to logarithmic elements, the input of which is the sum of the receptor signals concerned. The density distribution of the logarithmic elements shows a general decrease from the retinal centre towards the periphery. After the logarithmic transformation, the signals from the various logarithmic elements are added. The resulting signal constitutes the motor signal for the pupillary muscles which govern pupillary diameter in linear dependence on their motor signal.

It may be expected that the study of individual variations especially may add new evidence concerning the problems to which this chapter has been devoted.

8. PROPERTIES OF PUPILLARY RECEPTORS FOR FLASH REACTIONS

8.1. Introduction

In this chapter we shall consider some properties of the retinal receptors that mediate pupillary reactions to flashes. The transients to which these reactions belong may be considered as constituting the light reflex proper. The main differences from the static experiments discussed in the preceding chapters are:

(a) The introduction of the time parameter offers more opportunities for experimentation. Short light flashes, step functions and sinusoidal variations in illumination are the stimuli most widely used. Our own experiments have been done with flashes only. With respect to interpretation, however, it is even more difficult than in the steady-state case to know the part of the loop from which the observed essentials of the pupillary response originate. The condition that the motor part of the loop should be in the same state of activity under the various illuminations to be compared, is more difficult to fulfil, since it requires the time functions of the responses to be similar.

(b) Much greater use can be made of conditioning fields. In this way some properties of the receptive system may be investigated with the help of test stimuli which themselves do not change the condition of the receptive system. The static pupillary response to the conditioning field can easily be distinguished from the dynamic response to the test stimulus. It is of great help to the experimenter in these investigations that the transient responses require several log units less illumination than the steady-state responses.

Since rather unexpected results were obtained for the steady-state reactions, it also seemed useful to investigate one type of dynamic reaction. In the literature we find that the receptors for the dynamic pupillary reactions show a general correspondence with the receptors for the visual-brightness function, which are rods and cones. On the basis of the arguments put forward in chapter 6, these receptors may be characterised by spectral sensitivity due to their absorbing pigments, and directional sensitivity arising out of their geometrical properties. Besides, the influence of adaptation is characteristic of the system involved. With respect to this factor it is likely that neuro-organisational rather than photochemical processes play a part, since bleaching effects occur only at high levels of illumination.

Since the interpretation of the spectral data is not so straightforward as it is for the steady-state reactions, the subdivision of this chapter must needs be different from that chosen in chapter 6. In this chapter we shall consider separately the flash reactions of the pupil for a central 18° field, in which rods dominate (sec. 8.2), and a foveal 1° field where only cones are present (sec. 8.3). For the interpretation of the results it is essential to consider how the cooperation between rod and cone signals takes place. With respect to this, we shall

discuss the applicability of some simple hypotheses (sec. 8.4). The pupillary reactions mentioned in this chapter are concerned with flash reactions only. Flash duration was 100 ms in all experiments. Prior to the experiments, the eye was 30 minutes dark-adapted.

8.2. Central field of 18°

The spectrum

Flashes of eight wavelengths were offered to the observer's 30 minutes dark-adapted, right eye. The field was a central disc, the diameter of which subtended 18°. For some wavelengths the amplitudes of the resulting contractions as a function of quantum flux are shown in fig. 8.1; C_{max} turns out to be propor-
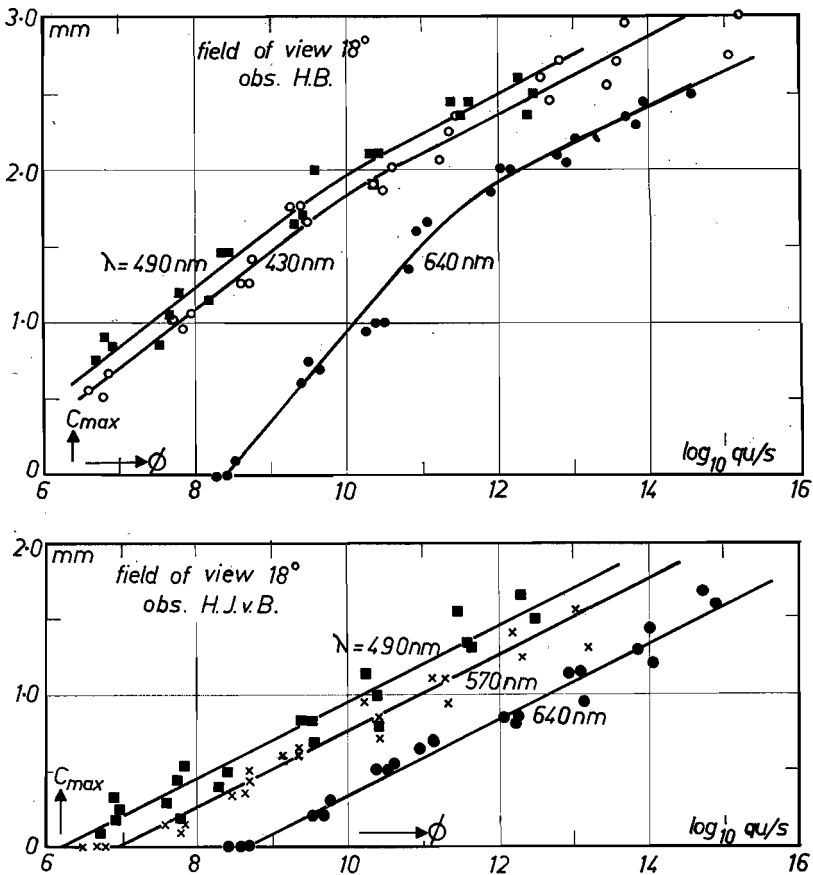

Fig. 8.1. Amplitudes of contraction C_{max} in response to 100-ms flashes of a large variety of intensities. Two observers. For observer H.B., the lines for short wavelength are not parallel to those for long wavelength which points to the participation of more than one absorbing pigment.

tional to the logarithm of the incoming flux over a large range of intensities (3-5 log units). For the greater part the lines are parallel. As was argued on page 58 this means that the pupillary spectrum may be attributed to one absorbing pigment only. Contrary to this, the gradients for the longer wavelengths (630, 640 nm) of observer H.B. were found to be significantly higher than those for the other wavelengths (see fig. 8.1). Consequently, the spectrum here is dependent on the pupillary criterion chosen. This result shows that more absorbing pigments are involved than just one.

Pupillary spectra of two observers are shown in fig. 8.2 for the criteria C_{max}

Observer H.B.   Observer H.J.v.B.
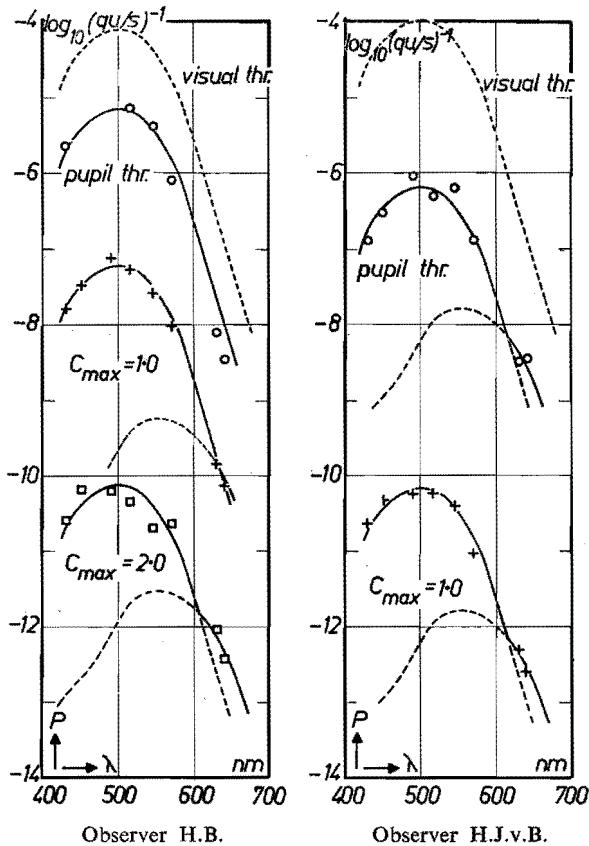
Fig. 8.2. Spectra for the indicated criteria. The curves are composed of scotopic and photopic spectra of the CIE standard observer, the latter with the short-wavelength correction proposed by Judd [64]). The absolute level of the scotopic spectrum has been adapted to the short wavelengths whereas the photopic spectrum has been adapted to the long wavelengths. This implies the hypothesis that a certain response is either scotopic or photopic. Field 18°.

to be 0·0 mm (extrapolated pupillary threshold), 1·0 mm and 2·0 mm. For purposes of comparison the visual-threshold spectrum under the same experimental conditions has also been given (broken curve). The visual spectrum

is of normal scotopic nature with its maximum around 510 nm. As the pupillary spectra show a close resemblance to the visual-threshold spectrum, the latter has been shifted so as to make clear the extent of correspondence with the pupillary data. Except for the long wavelengths the agreement is quite satisfactory, which confirms Schweitzer's [107] results.

Since the long wavelengths of visual scotopic spectra are known to be easily influenced by cone processes, it seems logical to find out whether for these wavelengths the photopic spectrum may be applied to the pupillary results. This is found to be the case (fig. 8.2). It is, however, not surprising that the spectrum fits the two experimental points since many curves may fit two points. We therefore need additional evidence. As a hypothesis we shall put forward that the pupillary spectra reflect the absorption spectra of those pigments that also mediate the scotopic and photopic brightness functions, which spectra will be referred to again as "510" and "555" spectra, respectively.

> Though the experimental points are reasonably well represented by the proposed combination of "510" and "555" spectra, it may be doubted whether this is the only possibility of combining these spectra to make a satisfactory fit. The analysis chosen assumes that for each wavelength only the highest effectiveness of the two spectra survives. Other simple possibilities are either linear addition: "510" + "555", or logarithmic addition: log "510" + log "555". Each of these possibilities has its own characteristic properties. Postponing a discussion on this point to sec. 8.4, let us provisionally accept the proposed analysis. Its relevance seems relatively safe with respect to visual and pupillary thresholds as normally thresholds are assumed to be determined by the most sensitive of the components only.

Selective suppressions

The hypothesis about the two spectra is open to experimental verification. The sensitivities of scotopic and photopic functions are known to be suppressed selectively by conditioning fields of properly chosen wavelength and intensity. One may also take advantage of the directional sensitivity of the receptors of the photopic system only. According to the hypothesis, pupillary contractions are supposed to be influenced in about the same manner as the visual functions are. To verify the hypothesis, we have superimposed 430 nm (blue) and 640 nm (red) flashes on a steady 450 nm conditioning field of the same dimensions as the test flashes (17°). This conditioning field will greatly affect the visual scotopic sensitivity whilst leaving the photopic sensitivity unaffected as long as the intensities applied are not too high. According to our hypothesis we must expect the pupillary contractions at the 430-nm flashes to diminish whereas the contractions at the 640-nm flashes will be almost unaffected, determined as they are by the "555" spectrum, except for very small contractions (fig. 8.2).

Figure 8.3 shows the resulting contractions for five intensities (including zero) of the conditioning field which most influences the smaller contractions in response to 430-nm flashes. When the flash illumination exceeds the steady illumination of the conditioning field by about 1·2 log unit, the latter is found
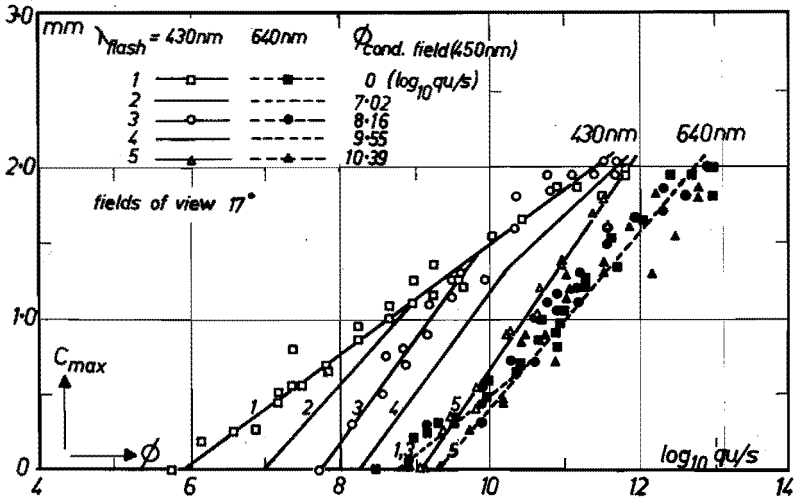
Fig. 8.3. Influence of a 450 nm conditioning field in five intensities on the pupillary responses to flashes in two wavelengths.

The responses to short wavelengths (open symbols) change considerably as long as the flash intensity does not exceed the illumination of the conditioning field for more than 1·2 log unit. The influence of a conditioning field expresses itself as an increase in threshold illumination and as an increase in initial slope.

The long wavelength responses (black symbols) are hardly, or not at all, affected by the conditioning field, which points to a different (photopic) origin.
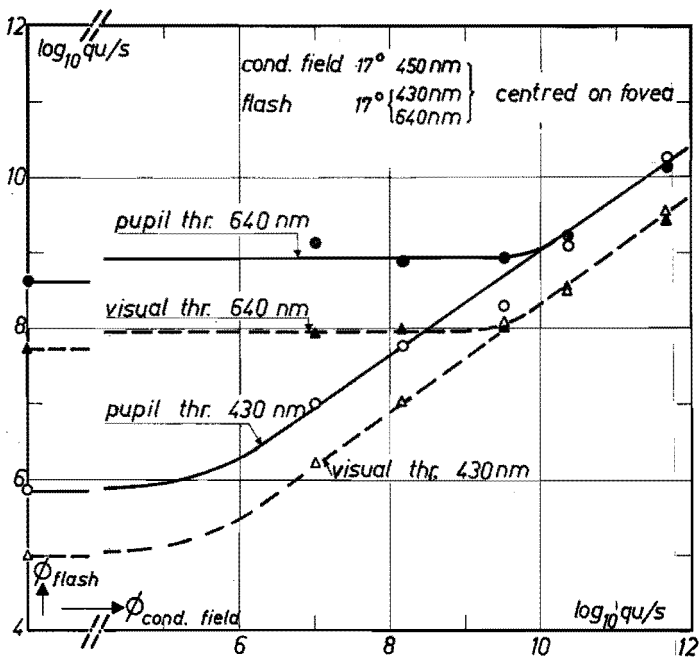
Fig. 8.4. Pupillary and visual thresholds as functions of the quantum flux of a steady conditioning field (450 nm). Apart from an intensity difference the curves show much correspondence.

Fig. 8.5. Directional sensitivities of pupillary receptors. The 515-nm responses do not change when the point of entry in the plane of the pupil is changed from a central to a $4\cdot0 \pm 0\cdot5$ mm nasal position, whereas the 630-nm responses change for $0\cdot4 \pm 0\cdot3$ log units at contractions of about 1 mm. Though the accuracy is low, the data are in accordance with the analysis of fig. 8.2, suggesting that both rods and cones are involved in these pupillary contractions.

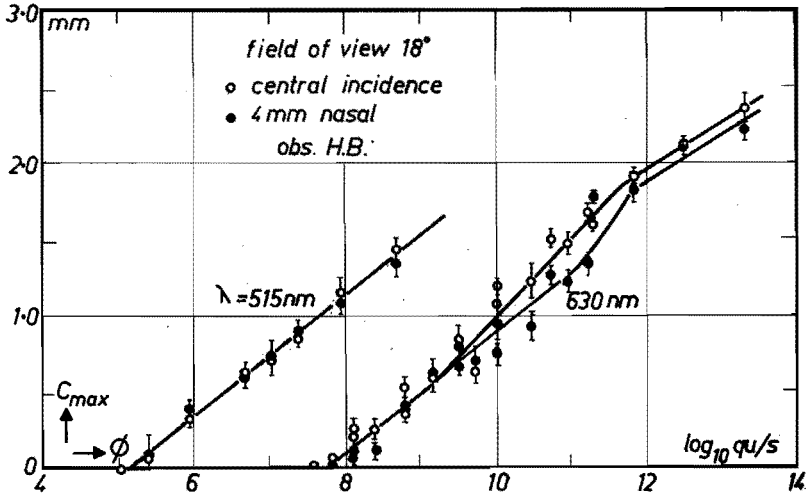to have no influence on the contractions. Thus, the slopes of the curves increase with increasing conditioning intensity. The contractions to the 640-nm flashes are only slightly affected, as expected. Figure 8.4 has been constructed from these data. It compares, for both wavelengths used, the flash intensities necessary to reach the visual and the pupillary thresholds, as a function of the quantum flux of the conditioning field. The visual and the pupillary thresholds are found to be affected in the same way and almost to the same extent.

Since the cones, which supply the photopic system, show a directional sensitivity, our hypothesis predicts that varying the point of entry in the plane of the pupil will influence the long-wavelength responses, while leaving the short-wavelength responses unaffected. For the wavelengths 515 nm and 630 nm, flashes of central entry and of $4\cdot0 \pm 0\cdot5$ mm peripheral entry (temporal) have been compared (fig. 8.5). The pupillary response to a 515-nm flash turns out to be independent of the point of entry, whereas the 630-nm response is affected for contractions between 1 and 2 mm, to the amount of some 0·4 log units. In the case of a pure-cone response this difference would be 0·8 log units (fig. 6.9). Due to the uncertainty of 0·5 mm in the point of entry, the value of 0·4 log units offers qualitative rather than quantitative evidence of a directional sensitivity.

We may conclude that for an 18° field both the influence of the conditioning field and that of the point of entry are in accordance with the hypothesis that

the "510" as well as the "555" spectra play a part in the flash responses of the pupil.

8.3. Foveal field of 1°

It may be expected that the activity of cones will come out more clearly when only the central fovea is illuminated, since this area does not include rods. To this end, we performed similar experiments with a 1·1° foveal field, the centre of which coincided with a small, weakly illuminated fixation mark.
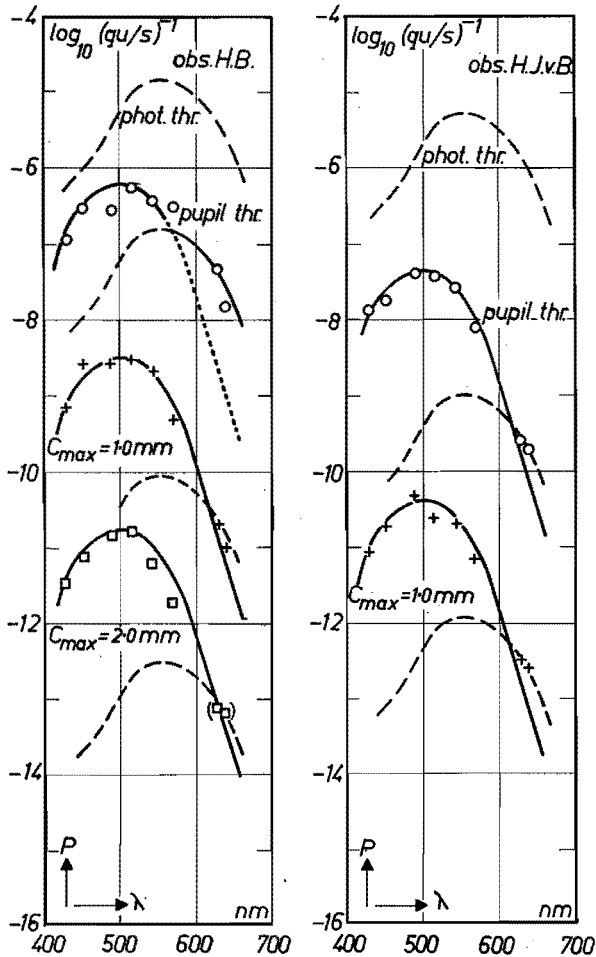

Fig. 8.6. Pupillary spectra for illumination with a flashed foveal field of 1·1°. Two observers. Similarly to fig. 8.2, the scotopic and photopic spectra have each been adapted to one side of the wavelength scale. Even for the pupillary threshold, there is a dominating contribution of rods.

The spectrum

Figure 8.6 shows spectra of two observers. The kind of analysis applied is the same as in the 18° case. It is remarkable that the main factor is still the "510" spectrum, though observer H.B. also shows a "555" component, the influence of which gradually diminishes with higher flash intensities, contrary to expectations. The most probable explanation is that the "510" spectrum arises from indirect illumination, absorbed by rods in the foveal surroundings. Is this indirect illumination of sufficient intensity to do so?

On the basis of the intensity distribution of the indirect light as proposed in fig. 7.12 and of measurements of absolute scotopic visual thresholds, we constructed fig. 8.7. It shows the flash intensity (flux) of a foveal 1° field (515 nm) at which the visual scotopic threshold at a distance φ to the fovea is exceeded. It may be concluded that the values of the fluxes necessary to obtain a pupillary response to such a foveal flash (larger than 6 log qu/s) cause parafoveal illuminations that are well above the visual threshold. Thus, the increase of the role of the "510" spectrum with increasing flash intensities may be explained as due to the increasing size of the retinal areas involved.
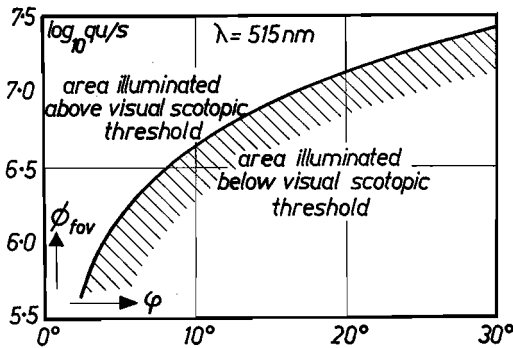
Fig. 8.7. The flux Φ of a foveal field (515 nm) at which the indirect illumination at a distance φ exceeds the absolute visual threshold. The distribution of indirect retinal illumination has been taken from fig. 7.12.

Selective suppressions

In order to see whether our analysis of the pupillary reactions in terms of direct, foveal cone illumination and indirect parafoveal rod illumination holds, we have selectively suppressed one or other of the two influences. The influence of the indirect illumination may be expected to be diminished selectively by a large conditioning field of short wavelength which reduces the sensitivity of the "510" component. Figure 8.8 shows the outcome of such an experiment. A 1·1° foveal flash was presented at two wavelengths: 430 and 640 nm. The visual and pupillary thresholds have been measured at several intensities of an 18°, 450-nm conditioning field. It will be seen from the figure that the two visual thresholds

and also the 640 nm pupillary threshold are affected to the same extent, whereas the 430 nm pupillary threshold is affected much more *). When the conditioning field is of sufficiently high intensity, the indirect light acting on the rods becomes sub-threshold. In that case a pure pupillary "555" spectrum may be expected. This expectation was tested experimentally by measuring the pupillary-threshold spectrum at an intensity level of 2·3 log scot.td of the conditioning field (in fig. 8.8 indicated by the black arrow), which, according to fig. 8.4, raises the visual scotopic threshold by some 4 log units. The resulting spectrum is shown in fig. 8.9. For purposes of comparison the pupillary-threshold spectrum in the dark-adapted eye (fig. 8.6) has been given again. The pupillary thresholds are now found to be reasonably covered by the "555" spectrum drawn. A similar, more accurate experiment with similar outcome was published earlier by Alpern and Campbell [6]).

We have also tried to suppress the "555" component selectively. For this purpose we used a 630-nm foveal conditioning field of the same dimensions as
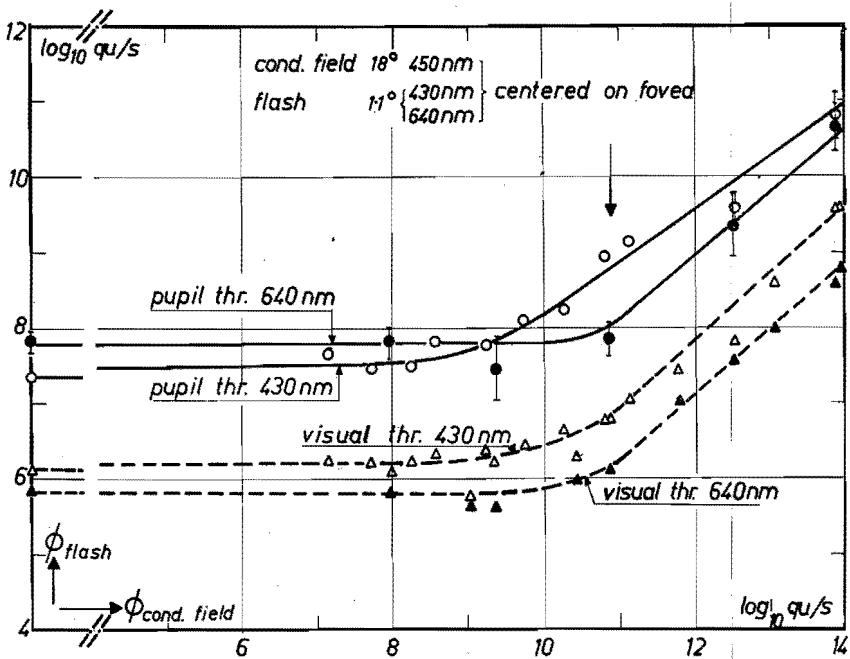
Fig. 8.8. Influence of a large 450-nm conditioning field on visual and pupillary thresholds for 1·1° foveal flashes. The visual thresholds are of photopic (cone) origin and the correspondences between the curves suggest a similar origin of the pupillary thresholds. The rod component of the pupillary 430-nm responses is readily suppressed by the conditioning field. Observer H.B.

*) It seems likely that the indirect flash illumination also exerts some influence outside the 18° conditioning field. For this reason it would have been better if we had chosen a larger conditioning field.
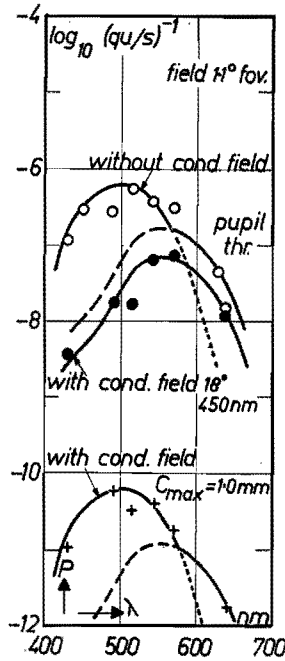
Fig. 8.9. Selective suppression of the rod component of the pupillary spectrum for fovea flashes by means of a 450 nm, 18° conditioning field with an intensity of 2·3 log scot.td (in fig. 8.8 indicated by the arrow). Observer H.B.

the flash field. It is to be expected that the scotopic sensitivity in the parafovea is hardly influenced by this field. When applying flashes of 515 nm super-imposed on such a conditioning field, the indirect light is visible at lower flash intensities than is the direct, focused light. Figure 8.10 shows the influence of such a conditioning field on the contraction amplitudes obtained with flashes
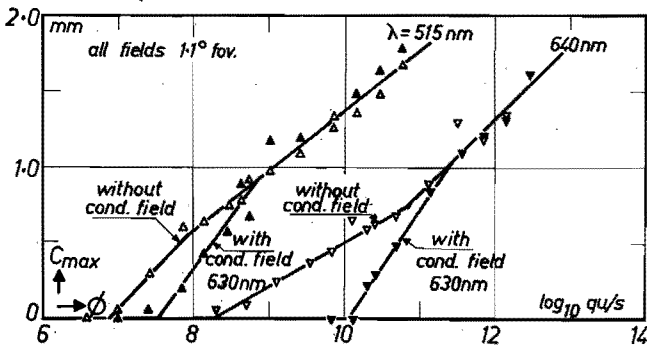
Fig. 8.10. Selective suppression of the cone component of the pupillary spectrum for foveal flashes by means of an overlapping steady conditioning field of long wavelength (630 nm, 3·2 log phot.td). Observer H.B.

of 515 nm and 640 nm. The 640-nm pupillary threshold is found to be affected much more than is the 515-nm threshold. Moreover, the 515-nm and 640-nm curves, which were not parallel in the dark-adapted state, are made parallel by the conditioning field. This may be taken as evidence that one of the component spectra has been ruled out.

As a second experiment with a view to suppressing the "555" spectrum selectively we have compared central and 4-mm peripheral entries in the plane of the pupil, to make use of the directional sensitivity of the cones. Figure 8.11 shows
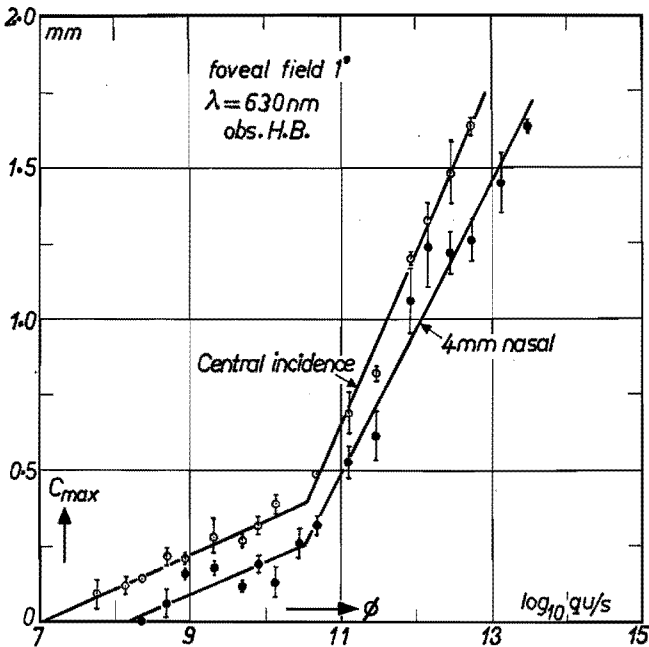
Fig. 8.11. Directional sensitivities of pupillary receptors for a 1° foveal field. The upper curve is for central incidence in the plane of the pupil, the lower one for entry at 4·0 ± 0·5 mm nasal incidence. For contractions smaller than 0·3 mm, the difference of 1·1 ± 0·4 log units points to a purely cone origin.

the results. Though the gradient of the curves is only slight, it is clear that the 630 nm curve has been shifted by about one log unit, thus revealing clearly its cone origin.

The experimental results with foveal flashes are, therefore, in general agreement with the assumptions that the pupillary "510" component is due to indirect illumination reaching neighbouring rods, whereas the "555" component is due to cone activity.

8.4. Interaction between rod and cone signals

Since we have now ascertained that both rods and cones play a part in reactions of the pupil to flashes, the question arises how the signals of the two kinds of receptor combine or interfere in producing one pupillary response. Before discussing this question, it may be of help to mention briefly some data concerning this interaction in vision.

Vision

If a visual response is neither purely scotopic nor purely photopic, it is called mesopic, which means that both scotopic and photopic systems are somehow involved. The existence of mesopic vision is in fact a correction to the duplicity theory, since essentially this theory distinguishes only two kinds of vision, requiring inhibition effects to account for their separation. It is not yet possible to obtain a clear impression of mesopic vision from the literature. The intensity range is limited downwards by the photopic threshold ($-1 \cdot 5$ log phot.td) and upwards by the scotopic saturation level (3 log scot.td). Generally, inhibition effects will restrict this range of mesopic vision much further.

Most studies concerning mesopic vision have been carried out on the basis of visual-threshold determinations. The visual threshold is found to be governed by the system which in itself shows the lowest threshold under the experimental conditions. Deviations from this rule only occur under conditions where the two systems happen to show roughly equal threshold values. Under these conditions the mesopic interval is very small indeed.

For illuminations above threshold it has been established that vision is mesopic over a much larger intensity range. It is uncertain, however, how the cooperation between the two systems takes place. We know something about the illumination levels at which the photopic system overrules the scotopic system (several photopic trolands), though it is uncertain whether the process can be adequately accounted for by units of cone illumination. There is evidence in favour of a much larger mesopic range in the retinal periphery (Weale [132], Smith Kinney [108], Clarke [26,27], Mandelbaum and Nelson [82]). Apart from complete inhibition as is assumed by the duplicity theory in its pure form, there are indications of various kinds of interaction, such as limited inhibition (Clarke [26]) and logarithmic addition (Rushton [96]).

The pupil

With respect to vision it is not necessary to use only threshold criteria, though it is the usual procedure. The pupil lends itself directly as an indicator in above-threshold conditions. It may be remarked here that any application of pupillary results to visual impressions must rest on a firm basis of direct experimental evidence.

In the preceding parts of this chapter we have readily made use of the hypothesis that the maximum contraction of the pupil in response to flashes is brought about by either rod or cone activity. This hypothesis received preliminary support from the experimental results to the effect that contractions, which on the basis of spectral information must be attributed to one system, did not change when the sensitivity of the other system was affected. In this part we shall pay special attention to this phenomenon and try to make a differential diagnosis from two other simple possibilities. Though the hypothesis applied in the previous section comes out as the most satisfactory one, the available evidence does not permit a definitive conclusion.

When illuminating some field of constant size with a monochromatic flash, the flux being Φ quanta/second, the signal from the rod part will depend on the value $s'\Phi$ if $s' = s'(\lambda)$ is the relative spectral sensitivity on quantum basis of the rod pigment. Similarly, the cone system will contribute some function of $s\Phi$. The interaction between rod and cone signals may be very complicated. This short discussion will be restricted to three simple processes by which the interaction may be assumed to occur:

(1) Linear addition of rod and cone signals ("linear addition"):

$$R = R\,(s'\Phi + a\,s\Phi). \tag{8.1}$$

Linear addition does not imply that no non-linear transformations are permitted. They can, however, occur only after linear combination of rod and cone signals.

(2) Addition of the logarithms of rod and cone signals, shortened to "logarithmic addition":

$$R = R\,(\log s'\Phi + \beta \log s\Phi). \tag{8.2}$$

(3) Complete suppression of the smaller of the two signals ("either-or" hypothesis):

$$R = R\,(s'\Phi) \quad \text{if } s' > \gamma\,s,$$
$$R = R\,(s\Phi) \quad \text{if } s' < \gamma\,s. \tag{8.3}$$

This is the kind of analysis used in the preceding sections.

These 3 hypothetical interactions between rod and cone signals will now be compared regarding their implications on:

(A) the spectrum,
(B) the relations between C_{max}-log Φ curves for various wavelengths,
(C) the influence of conditioning fields,
(D) the influence of direction of incidence on the receptors.

(A) *The spectrum*

(1) For "linear addition", the constant-response spectrum $P(\lambda)$ (log units) will take the form of $\log\,[(s' + as)/(1 + a)]$. When negative values of a are ex-

cluded, the λ_{max} of such spectra will be found somewhere between 510 nm and 555 nm, dependent on a. Figure 8.12 shows these spectra for $a = 0, \frac{1}{2}, 2$ and ∞. The black points have been taken from typically mixed pupillary spectra in figs 8.2 and 8.6. They agree with spectra characterised by $a = 1/20$ and $a = 1/2$, respectively.

(2) "Logarithmic addition" will give rise to a spectrum $P_\lambda = (\log s' + \beta \log s)/(1 + \beta)$. In this case too, λ_{max} will be somewhere between 510 nm and 555 nm. Figure 8.13 shows these spectra for $\beta = 0, \frac{1}{2}, 2$ and ∞. The black points are similar to those in fig. 8.12. For no values of β the agreement is quite satisfactory for short as well as for long wavelengths.
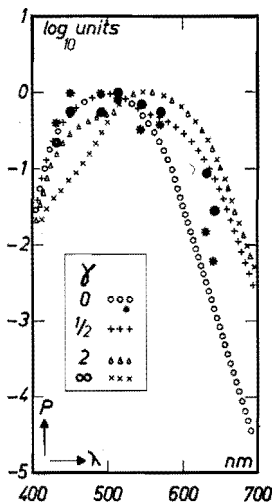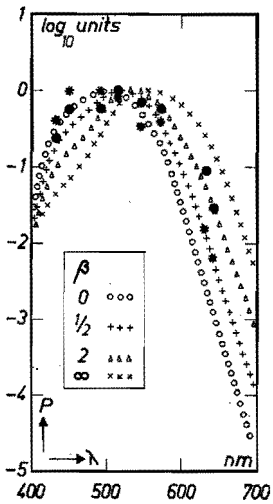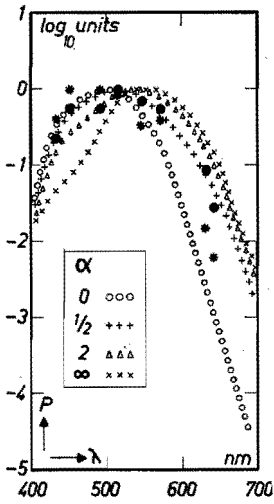
Theoretical spectra according to three hypotheses of interaction between rod and cone signals. The black symbols represent experimental data taken from figs 8.2 and 8.6.

Fig. 8.12. "Linear addition"   Fig. 8.13. "Logarithmic addi-   Fig. 8.14. "Either rods or
$a = 0, \frac{1}{2}, 2$ and ∞.   tion" $\beta = 0, \frac{1}{2}, 2$ and ∞;   cones" $\gamma = 0, \frac{1}{2}, 2$ and ∞.

(3) In the "either-or" case the spectrum will be $P_\lambda = \log s'$ when the scotopic response s' exceeds the photopic response γs; at wavelengths for which $s' < \gamma s$, the spectrum will take the form $P_\lambda = \log s$. Figure 8.14 shows these spectra for $\gamma = 0, \frac{1}{2}, 2$ and ∞. The black points agree with spectra characterised by $\gamma = 1/20$ and $\gamma = 1/2$, respectively. Thus, differential diagnosis from linear addition will be difficult. In this respect, the situations in which $\beta \approx 1$, resp. $\gamma \approx 1$ offer the best possibilities.

Though the number of wavelengths used and the accuracy of the measurements are too low to permit a definite choice of one out of the three hypothesis, it seems that hypothesis (2) of "logarithmic addition" is somewhat less suitable than the two other ones.

(B) *The relationships between C_{max}-log Φ curves for various wavelengths*

(1) and (2) In a C_{max}-log Φ plot the curves for the various wavelengths will be parallel if α or β are constants (see sec. 6.1). If α or β itself varies with intensity, this prediction no longer holds. If so, α or β has then to be some function of $(s'\Phi, s\Phi)$. These more complicated cases lie outside the limited scope of this discussion.

(3) In the "either-or" case, the curves for various wavelengths take one out of two possible shapes depending on the sign of the difference between $s'\Phi$ and $\gamma s\Phi$.

The experiments (figs 8.1, 8.6 and 8.10) show that two different slopes may occur, which finding is in accordance with the "either-or" hypothesis only.

(C) *The influence of conditioning fields*

In general a conditioning field will affect both systems differently.

(1) and (3) If the rod system is affected unilaterally, the wavelength responses for which the cone contribution exceeds the rod contribution will change slightly ("linear addition") or not at all ("either-or" hypothesis). Effects on only-cone-prevailing responses will occur when the cone system is affected unilaterally. In general, a conditioning field will only affect responses that belong to one side of the spectrum.

(2) If "logarithmic addition" occurs, this corresponds to a change in β. At all wavelengths this will cause a substantial difference in the responses. The spectrum will change according to the change of β.

From the results (figs 8.3 and 8.10) it may be seen that quite often only one side of the spectrum is affected. This cannot be explained by "logarithmic addition". Both "linear addition" and the "either-or" hypothesis may account for the results.

(D) *The influence of the direction of incidence on the receptors*

A change in direction of incidence will decrease the cone absorption, the contribution of the cones $s\Phi$ now becoming $\eta s\Phi$ $(1 \leqslant \eta \leqslant 0)$; η decreases with increasing obliqueness of incidence. To counteract this decrease in response, log Φ must be increased by Δ log Φ.

(1) In "linear addition", Δ log Φ will amount to $-\log(s' + \alpha s)/(s' + \eta\alpha s)$, the long wavelengths being affected more than the short ones.

(2) For "logarithmic addition", independent of wavelength, Δ log $\Phi = -[\beta/(1 + \beta)]$ log η.

(3) In the "either-or" case, the responses for which the scotopic contribution exceeds the photopic one will be unaffected, whereas the responses for which the photopic contribution exceeds the scotopic one, will be affected to the full

extent ($\Delta \log \Phi = -\log \eta$). The responses can change from cones to rods when the obliqueness of incidence is increased.

The few experiments in which the direction of incidence has been varied (figs 8.5 and 8.11) do not firmly support any of these hypotheses. In fig. 8.5, $\Delta \log \Phi$ seems to depend on λ, which would count against logarithmic addition. Since one can be sure that only the cone absorption is changed by variations in the direction of incidence, this is an important method for further analysis, provided the position of the point of entry of the incident light in the plane of the pupil is maintained very precisely. In our experiments this precision was of the order of 0·5 mm which is not good enough to permit of an accurate analysis.

In conclusion as to the three hypotheses, we find that the "either-or" hypothesis (3) fits the experimental results best, whereas some predictions on the basis of "logarithmic addition" differ from the experimental results. It may be remembered here that Alpern and Campbell [6]) showed that the predictions (A) and (D) of the "logarithmic addition" hypothesis hold good for a pupillary-threshold criterion, when the eye is stimulated with sinusoidal variations in light intensity superimposed on a steady conditioning field. Some of the visual spectra of Clarke [26,27]) also have the appearance of "logarithmic addition", whereas some of his other spectra are rather of the "linear addition" type.

It may be noted that a combination of the hypotheses (1) and (3), or (2) and (3), by introduction of separate thresholds for the rod and cone systems, removes some of the counter-arguments. Still, hypothesis (3) itself is capable of dealing adequately with our results. The difficulty in assuming some kind of combination is that the number of extra assumptions, or parameters, is increased which in turn decreases the value of a possible correspondence between the set of hypotheses and the experimental results. For this reason we preferred the simple "either-or" hypothesis, in spite of the obvious simplifications involved.

We shall illustrate the adequacy of the "either-or" hypothesis by means of an example of a response, which on reasonable grounds would be judged to be a mixed rod-cone response, that does not change when the contribution of the rod component is decreased by a conditioning field. Figure 8.15, derived from fig. 8.3 is such a case. It shows the influence of a conditioning field (450 nm) on the 640-nm responses of the pupil for 17° fields of view. The contributions of the rods (dotted lines) may be evaluated from the 430-nm responses (full lines) by a 2·4 log units shift reflecting the differences in scotopic sensitivity. If no conditioning field is present (lines marked 1), the responses smaller than 1 mm can be attributed to rod activity. Application of a conditioning field changes the rod contribution (full lines marked 3 and 5). If no cones were present, the experi-
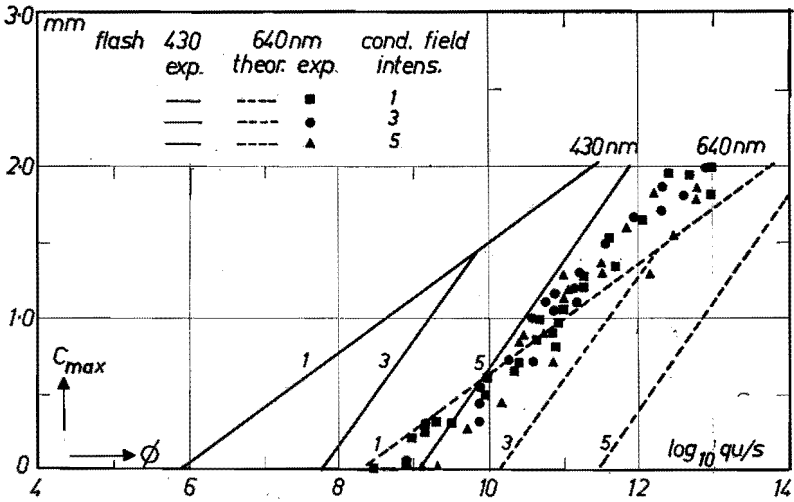
Fig. 8.15. Though a proper conditioning field decreases the scotopic contribution to 630-nm responses for a 17° field (broken lines drawn parallel to the full 430-nm lines), the experimental contractions (black symbols) are hardly affected.

mental 640-nm responses would show the same shift (dotted lines marked 3 and 5). The drastic decrease in rod contribution, however, has hardly any influence on the 640-nm responses. The conclusion is that either the cone response prevents the rod response from being influenced by the conditioning field, or that in the absence of a conditioning field the 640-nm responses (> 0.5 mm) are due to cone activity only. The latter conclusion is the simpler one and illustrates the applicability of the "either-or" hypothesis.

It must be emphasised that the above discussion only dealt with the contraction amplitude C_{max} of the responses and not with total time functions. Therefore, the conclusion that rods and cones may be considered mutually exclusive in feeding the contraction amplitude of the pupil to a flash, cannot be extended to the total time function of the flash responses. Lowenstein and Loewenfeld [76] have presented evidence of a large increase in contraction time when the illumination level increases from scotopic to photopic levels.

Since arguments have been put forward in favour of an addition of the logarithms of scotopic and photopic signals in other reports about pupillary responses, measured in different experimental conditions, the problem as to how rod and cone systems interact with respect to the pupil is still rather complicated. A careful analysis of directional sensitivities of the total time functions of the responses (latency times included) under the various circumstances may possibly lead to a better understanding.

8.5. Conclusions

Pupillary reactions to light flashes are mediated by two kinds of receptor,

viz. rods and cones. This conclusion is based upon the pupillary spectra that reflect the absorption spectra of rod and cone pigments and on some data concerning the directional sensitivities of the receptors themselves. Since the two kinds of receptor are active under almost the same circumstances as in vision (apart from the influence of indirect illumination) it is very likely that they issue from the same retinal networks as are involved in vision. For this reason it seems permissible to extend the terms "scotopic" and "photopic" of vision to the receptive systems for pupillary flash reactions.

The evidence collected about the interactions between the scotopic and the photopic receptive systems of the pupil (mesopic reactions) is most simply explained by the hypothesis that either the scotopic or the photopic system is active, which implies that they are mutually inhibitive. For other pupillary reactions it is known that logarithmic addition of rod and cone signals occurs. In these respects too, the transient reactions of the pupil correspond to the visual ones, where various kinds of interaction have been shown to exist.

9. ORGANISATION OF THE RECEPTIVE FIELD FOR FLASH REACTIONS

9.1. Introduction

In the preceding chapter it has been shown that a light flash incident upon the dark-adapted eye makes the pupil contract in accordance with the spectra and the directional sensitivities of rods and cones. Both kinds of receptor could be isolated by a proper choice of wavelength and conditioning field. In this chapter we shall study the organisation of the receptive field under these circumstances, i.e. the processes intermediate between the absorption of light by a great many receptors and the subsequent pupillary contraction. Again, we shall distinguish between scotopic responses mediated by rods (sec. 9.2) and photopic responses mediated by cones (sec. 9.3).

As before, the outcome of the experiments will be presented in terms of pupillary effectiveness P, i.e. the reciprocal of the retinal illumination T (scotopic or photopic trolands), necessary for reaching a certain contraction amplitude C_{max}, for which we have chosen the values 0·0 mm (threshold), 0·5 mm and occasionally 1·0 mm.

In chapter 8, the available evidence pointed to a common receptor origin of visual reactions and pupillary contractions, though in the latter the photopic contribution was easily masked by the scotopic one, initiated by indirect illumination. The common receptor origin makes it of interest to compare the pupillary effectiveness to the analogously defined effectiveness for the criterion of a visual threshold. Those visual threshold data in the scotopic section (sec. 9.2) that are supposed to be caused mainly by cones cannot appropriately be expressed in units of scotopic trolands; they will be shown in brackets.

The degrees of effectiveness for pupillary flash reactions may also be compared to those for steady-state reactions which have been amply discussed in chapter 7. Despite obvious analogies between steady-state and flash reactions with regard to the influence of position and size of the illuminated field, no satisfactory description of the flash reactions have been obtained. On the basis of chapter 7, we shall indicate what kind of additional factors may be assumed to exert influence. In sec. 9.4 we shall touch upon possible origins of the large individual differences.

9.2. The scotopic receptive field

In order to isolate the scotopic responses from the influence of the photopic system we used flashes of 515 nm in the dark-adapted eye, in which situation even small foveal fields reveal a rod spectrum (fig. 8.6), due to indirect illumination of the parafovea. By analogy with the study of the steady-state receptive field we will use various fields:

(a) discs of a certain size in various positions of the horizontal meridian;
(b) concentric sets of disc and adjacent three rings, occupying equal retinal areas (fig. 7.26);
(c) concentric discs of various sizes, centred on the fovea.
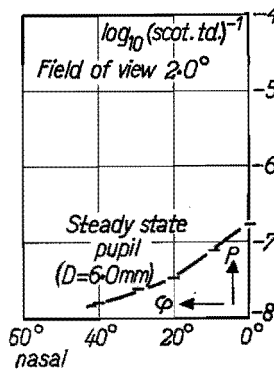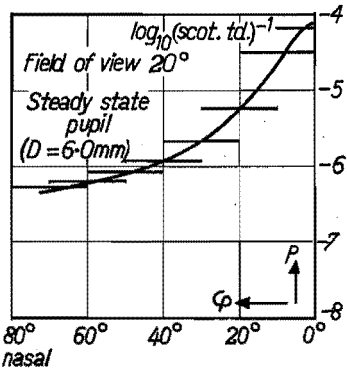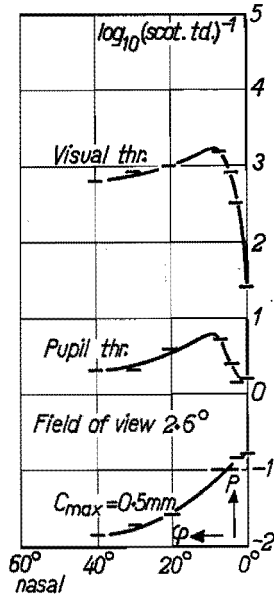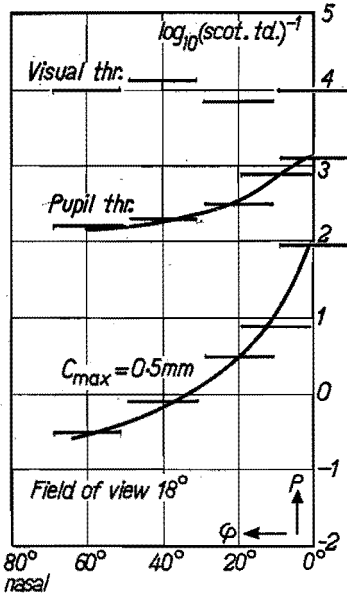
Fig. 9.1. Degrees of effectiveness P (i.e. the reciprocal of the retinal illumination required for a certain response criterion) required for a certain response criterion) for discs of 18° in various retinal positions, for the criteria of (from top to bottom): the absolute visual threshold, a pupillary threshold, a pupillary contraction of 0·5 mm and a steady-state diameter of 6·0 mm; λ = 515 nm, flashes 100 ms; observer H.B.

Fig. 9.2. Similar to fig. 9.1, now for a field of only 2·6°. The foveal dip in effectiveness disappears for higher response criteria, which effect is attributed to the increasing influence of indirect illumination.

(a) Fields presented in different retinal positions

Figure 9.1 shows the measured degrees of effectiveness for retinal discs with a diameter of 18°, projected on the retina in various positions of the horizontal meridian (nasal side). The visual threshold comes out almost independent of this position, but the pupillary threshold increases from the centre towards the periphery by about one log unit as appears from the corresponding decline in effectiveness. This gradient is even more marked for a criterion $C_{max} = 0.5$ mm (2·5 log units) which indicates that in the central area the intensity gradient $\Delta C_{max}/\Delta \log T$ is larger than in the periphery. It is remarkable that the shape of the 0·5-mm curve very much resembles that found for the steady-state criterion $D = 6.0$ mm (lower graph), the main difference being a shift of retinal illumination as high as 6 log units.

When repeating the experiments for a smaller field (2·6°), a different result is obtained (fig. 9.2). The visual-threshold curve shows a central dip due to the well-known dip in rod density (the dip of the blind spot at about 18° nasally to the fovea has not been explored). The pupillary-threshold curve also shows such a dip, though its depth is less than for the visual threshold. Thus, the pupillary-threshold behaviour for the 2·6° field is more or less analogous to the visual threshold, where the indirect illumination does not interfere and the resolving power is accordingly higher than for the 18° field. Surprisingly, the curve for $C_{max} = 0.5$ mm does not show a central dip. This curve adheres to the steady-state results where, especially for smaller fields, the indirect illumination masked the contribution of the directly illuminated fields.

The transition with increasing illumination from a foveal minimum towards a foveal maximum may at first sight be connected to the transition from scotopic to photopic intensities. If so, the increasing influence of the foveal cones would then be responsible for the foveal maximum of the 0·5-mm curve. This cone component, however, should express itself clearly in the spectrum, which, according to fig. 8.6, is not the case. Therefore, it seems out of question that the foveal maximum is due to the influence of cones. It seems more appropriate to seek an explanation in indirect illumination. Though the fovea itself may be least effective with regard to the direct illumination, its central position may be very favourable to the effect of indirect illumination, as has been explained in sec. 7.5 (fig. 7.24). Therefore, the transition from a central minimum towards a central maximum in fig. 9.2 can be most readily attributed to the influence of indirect illumination which spreads over progressively increasing areas with increasing light intensity. This explanation is analogous to that proposed for the steady-state experiments.

On this basis a possible explanation can be offered for the discrepancy between the results of Harms [53]) and Schweitzer [107]) (see p. 27). In moving a flashed point source over the dark-adapted retina, Harms found a minimum contraction when the light was focused on the blind spot, and a maximum for a foveal position. Schweitzer confirmed

the minimum for the blind spot, but found another minimum for the fovea. The experimental data indicate that Harms' observers required higher illuminations than Schweitzer's. The indirect illumination for Harms' observers was accordingly higher and could give rise to the foveal maximum as in the 0·5-mm curve of fig. 9.2. One of our observers who showed a high pupillary threshold, showed no foveal minimum for a pupillary-threshold criterion either. The clearly expressed minimum contraction for light focused on the blind spot, gave confidence to Harms that indirect illumination did not contribute substantially to the contractions. However, due to the symmetry of the retina around the fovea, a foveal position of the direct illumination may be much more favourable to the contribution of indirect illumination than may any other retinal spot. This is, in fact, the two-dimensional extension of the explanation which has been proposed for the one-dimensional case on p. 102 (fig. 7.24).

(b) Concentric sets of disc and adjacent rings; the central area

If the above explanation applies, we must expect that the central dip in pupillary effectiveness may be better explored by using concentric sets of disc and adjacent rings occupying equal retinal areas. According to the discussion on p. 103 this method is a balancing method with respect to the indirect illumination since the indirect illuminations are equal except in the immediate neighbourhood of the directly illuminated fields. Four of these sets have been used in which the areas of the fields ranged from 1·2 to 75 square degrees.

The outcome of the experiments is laid down in fig. 9.3 *). Except for the smallest set, the visual and pupillary thresholds now show the same effects though their intensity differences become larger when the area decreases. Unlike fig. 9.2, fig. 9.3 shows a pronounced foveal dip for $C_{max} = 0·5$ mm also, though in both cases the retinal areas involved amount to 5 square degrees. We take this as evidence in favour of the hypothesis that the indirect illumination may obscure an existing central dip in retinal contribution.

The results for the smallest set (1·2 square degrees) are different. This set explores the differences on the very edge of the fovea. The visual threshold shows a large gradient, but the differences in pupillary threshold are but slight. This is not surprising, since rod densities in this region are very low, due to which factor the contraction of the pupil depends almost exclusively on the indirect illumination, which is very much the same for these fields.

The shapes of the $C_{max} = 0·5$ mm curve and the curve for the steady-state reaction $D = 6·0$ mm show clear differences. The dynamic dip is clearly expressed whereas in the steady-state experiments no such dip appears.

(c) Concentric discs centred on the fovea

Application of discs of various sizes, all centred on the fovea, gives the results shown in fig. 9.4 (double logarithmic plot). As has been explained on p. 79

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*) The concentric discs provide a balancing method for the indirect illumination only if the direct illuminations are equal. For purposes of easy comparison with the other figures, fig. 9.3 shows illumination values for an equal pupillary response instead. An approximate transformation to equal illuminations is obtained by applying $\Delta C_{max}/\Delta \log T = 0·4$ mm/log unit.
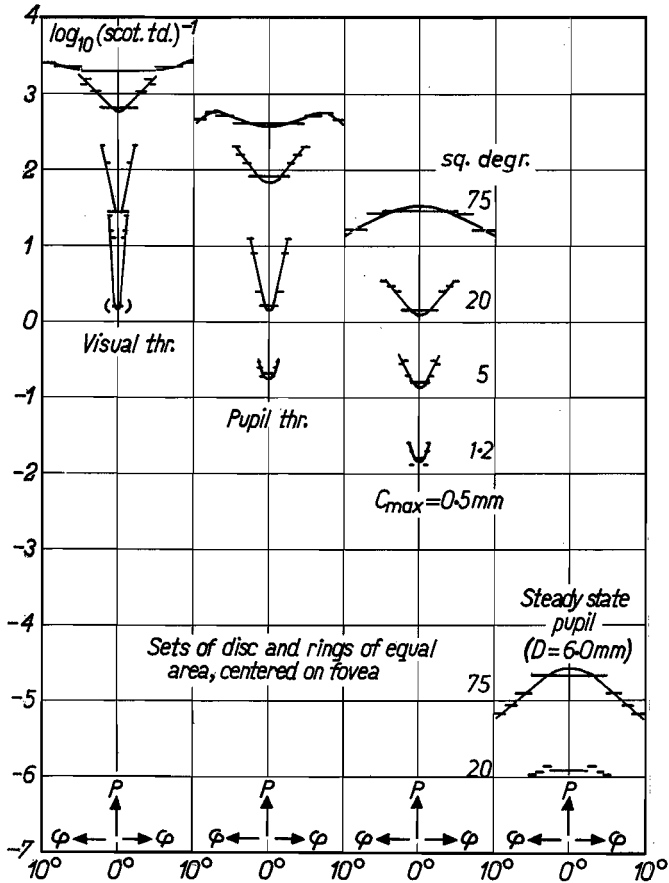
Fig. 9.3. Degrees of effectiveness P for sets of disc and adjacent rings of equal area (four areas). Response criteria as indicated. For these fields the influence of indirect illumination is balanced to some extent, which may explain why the central dip is present also for a response criterion of $C_{max} = 0.5$ mm. Observer H.B.

(fig. 7.3), a slope of 1 in these graphs indicates that the response is dependent on total light flux only (integration). A slope greater than unity indicates that the total light flux necessary for a certain response decreases when the size of the field increases (over-integration). Slopes less than unity indicate an increase in total light flux with increasing field size (under-integration). A horizontal line indicates a situation in which the effect depends only on the illumination, independent of the area exposed.

The large degrees of over-integration for the visual as well as for the pupillary curves should be noted. For the visual threshold this effect is known to be connected with the gradients of rod density in the parafovea. With increasing area more densely rod-packed edges are exposed. Combined with a certain amount of extra summation due to the area itself becoming larger, this explains

the over-integration for the visual threshold. The pupillary threshold shows a similar curve (though, in agreement with Schweitzer's results [107]), the distances between the pupillary and the visual curves become larger for smaller fields). This may indicate that the basic processes for the pupillary and the visual thresholds are similar. On the other hand, the steady-state curve ($D = 6$ mm) and the flash-response curves are also similar, which would point to a common origin in the contribution of indirect illumination. In order to decide which of the two similarities is the essential one, we have compared visual and pupillary thresholds in a retinal area where rod density does not show such large gradients.

The triangles in fig. 9.5 show the visual thresholds for a 9° nasal position of the centre of the discs. The open circles show the pupillary degrees of effectiveness
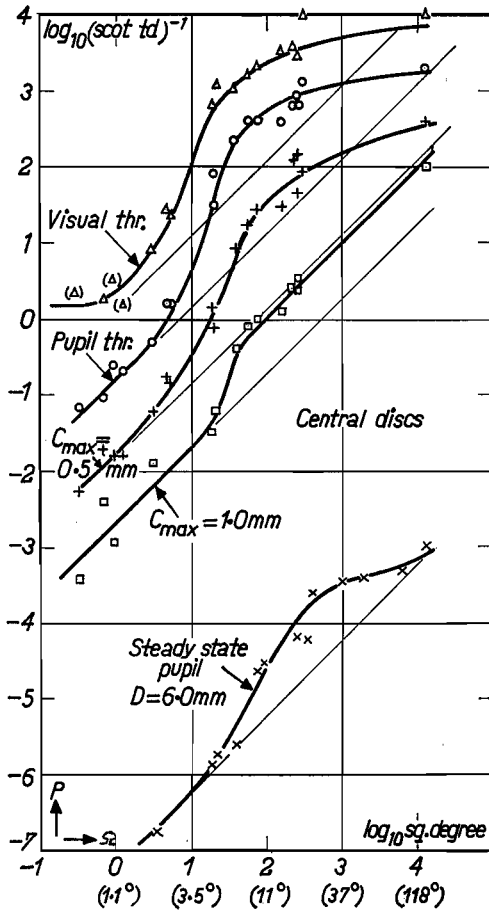

Fig. 9.4. Degrees of effectiveness P as a function of solid angle Ω of the field for centrally fixated fields of various sizes. Observer H.B. A large effect of over-integration occurs for fields between 2° and 7°. For the characteristics of this double logarithmic plot we refer to fig. 7.3. Visual-threshold data between brackets are supposedly of photopic origin.

for this parafoveal localisation. The latter turn out to be similarly dependent on the size of the field as in the case of a foveal centre (full lines). Since the visual and the pupillary curves have lost their similarity, it may be concluded that the pupillary over-integration depends primarily on the effect of area itself. Possible local differences in rod density are outweighed by the contribution of indirect illumination.

Tentative theoretical description

In the preceding part we have ascertained that the flash responses and the steady-state responses of the pupil show a great deal of correspondence, apart from the large intensity shift. In particular, we have confirmed that in both cases the indirect illumination influences the results similarly. It is attractive to see
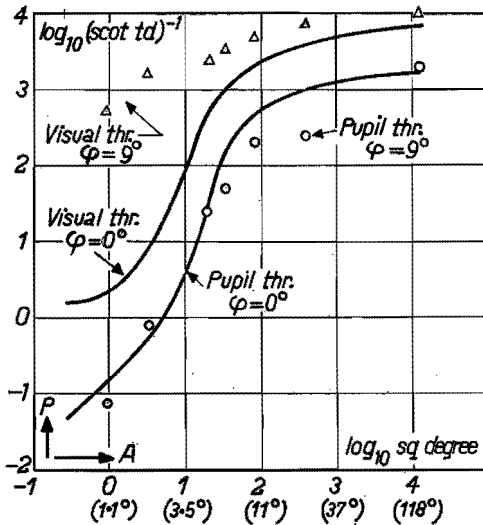
Fig. 9.5. Comparison between peripheral and central positions of the fields with respect to the effect of over-integration. For a 9° peripheral position of the field centres, the pupillary data (O) show over-integration, which effect is not found for the visual thresholds (△). The full lines have been taken from fig. 9.4 and show the over-integration for both criteria that occurs for a central position of the fields. Observer H.B.

whether this qualitative analogy can be extended to a quantitative description, which for steady-state reactions has been proposed in chapter 7.

Apart from the quantitative introduction of the distribution of indirect illumination, the essentials of the steady-state description were:

(a) only one non-linear transformation performed by logarithmic elements, viz. from the retinal illumination T to $\log (1 + T/T^*)$;

(b) two position parameters w and T^*; the weight function $w(\varphi)$ could be interpreted as the density distribution of logarithmic elements in the retina,

whereas $1/T^*$ was isomorphous to the total amount of rhodopsin that feeds one such element (p. 108).

Unfortunately, we have not been able to find a satisfactory description of the flash responses of the pupil. Notwithstanding, we shall work out an equation similar to the steady-state equation, since it may offer insight into the system under consideration. Analogous to the equation (7.3) for steady-state reactions, we shall try to describe the contraction amplitude of the pupil in reaction to flashes as

$$C_{max} = \Sigma \left[\log \left(1 + T/T^* \right) \right] . w . \Delta\Omega. \qquad (9.1)$$

(a) The *logarithmic transformation* is essential. First, it explains easily that for a great many situations the contraction amplitude C_{max} is proportional to the logarithm of the illumination. Secondly, the effect of over-integration requires some non-linear transformation, for which the common logarithmic one is convenient. Contrary to the steady-state contractions, the flash reactions of the pupil are proportional to the logarithm of the illumination for very small contractions also. For this reason it seems indicated to substitute $\log T/T^*$ for $\log (1 + T/T^*)$. If so, T^* then indicates the pupillary threshold. However, from a more general point of view, $\log (1 + T/T^*)$ seems more appropriate. We shall adhere to this latter expression.

It may be noticed that for illuminations $T \gg T^*$, $\log (1 + T/T^*)$ may be taken as $\log T/T^*$. If the condition $T \gg T^*$ is assumed to apply in all situations in which pupillary contractions occur, it is implied that T^* has a value lower than the illumination level of the pupillary threshold. If so, T^* can then be found by backward extrapolation to a hypothetical contraction value C_0 which must be exceeded before any contraction of the pupil can be observed. Accordingly, formula (9.1) is changed into

$$C_{max} = C_0 + \Sigma \left[\log \left(1 + T/T^* \right) \right] . w . \Delta\Omega, \qquad (9.2)$$

where C_0 may be interpreted as a threshold somewhere in the pupillary motor system, which must be exceeded by the signal from the receptive system before any contraction of the pupil occurs.

The introduction of a threshold in the motor system may account for the fact that at constant flash illumination, a mere increase in the illuminated area suffices to make the pupil react. Thus, the signal produced by illuminating only parts of the larger field are either extinguished or so small that the resulting pupillary contraction escapes from experimental detection. In the latter case, the pupillary threshold as determined is no threshold in the strict sense. As an example one may compare central fields of $7°$ and $3.5°$, both illuminated by a 100 ms flash of 0.1 scot.td. The $7°$ field produces a pupillary contraction of 0.5 mm (fig. 9.4). For fields smaller than $3.5°$, irrespective of their position, no detectable contraction occurs.

When carrying out the proposed backward extrapolation for some fields (fig. 9.6), a value $C_0 = -0.4$ mm, $T^* = -3.8$ log scot.td is found to be convenient for a variety of fields, provided they are not too small. For central discs smaller than $10°$, a proper choice of T^* will be discussed below.

(b) The theoretical *weight function* w is expressed in the gradient $B = \Delta C_{max}/\Delta\log T$, which for homogeneously illuminated fields equals $\Sigma w \cdot \Delta\Omega$. In the steady-state experiments, the influence of indirect illumination was supposedly so large that the fields offered at various distances from the fovea could not be considered to provide information about the local contributions of the directly illuminated areas. For the flash reactions of the pupil, the well-defined thresholds for the $18°$ field in various positions are found to be so low (fig. 9.1) that for illuminations slightly above these threshold values
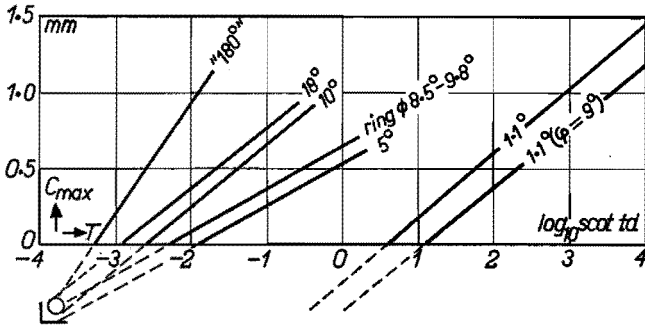
Fig. 9.6. Amplitudes of contraction C_{max} as functions of retinal illumination T for an arbitrary selection of scotopic fields (flashes 100 ms). If the equation $C_{max} = C_0 + B$ log $(1 + T/T^*)$ is applied, it follows that $C_0 \approx -0.4$ mm and $T^* \approx -3.8$ log scot.td. Observer H.B.

the indirect illumination will have little influence. Figure 9.7 shows experimental results for some positions of this $18°$ field. From this figure it may be concluded that the initial slopes B decrease with increasing distance from the fovea (table 9.I). Accordingly, the weight function w must be supposed to show its maximum in the fovea or parafovea, whilst decreasing towards the periphery (fig. 9.8, table 9.I), in a manner similar to the steady-state weight function. It is of importance to consider the initial slopes only, since for higher illuminations the indirect illumination may have contributed to the contractions (which applies to small fields as well).

From fig. 9.6 it appeared that the point of transition T^* may be considered as approximately constant when applying large fields. These large fields do not provide information about the distribution of T^* within these fields. It may be expected that T^* shows different values in the central area, where large gradients of rod density occur. In this central area, we found a clear dip in the retinal
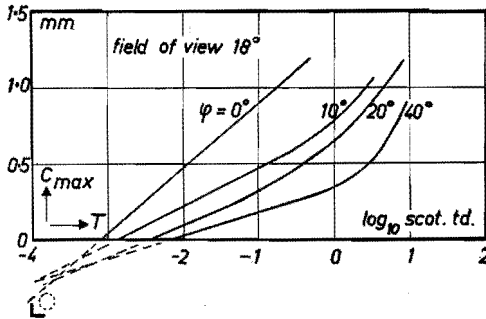
Fig. 9.7. Amplitudes of contraction C_{max} as a function of retinal illumination T obtained for a field of 18° at various distances to the fovea. Observer H.B.

TABLE 9.I

Values of initial slope B, weight factor $\bar{w} = B/\Omega$ and point of transition T^* as derived from measurements with a scotopic 18·5° field (270 square degrees) in various retinal positions φ. The describing equation is $C = C_0 + B \log(1 + T/T^*)$ with $C_0 = -0.4$ mm

φ (degrees)	B (mm/log unit)	$\bar{w} = B/\Omega$ (mm/log unit .sq. degr.)	T^* (log scot.td)
nas. 0	0.41 ± 0.05	$1.6 \;.\, 10^{-3}$	-3.9 ± 0.1
10	0.27 ± 0.05	$1.0 \;.\, 10^{-3}$	-4.1 ± 0.2
20	0.20 ± 0.05	$0.7 \;.\, 10^{-3}$	-4.0 ± 0.3
40	0.15 ± 0.05	$0.55 . \,10^{-3}$	-4.3 ± 0.6
60	0.12 ± 0.05	$0.4 \;.\, 10^{-3}$	-4.8 ± 1.0
temp. -10	0.30 ± 0.05	$1.1 \;.\, 10^{-3}$	-3.9 ± 0.3
-20	0.15 ± 0.05	$0.55 . \,10^{-3}$	-4.3 ± 0.6

Fig. 9.8. Tentative weight function w for scotopic pupillary contractions. The function has been worked out from the experimental values of the initial gradients $B = \Delta C_{max}/\Delta \log T$ for a 18° field in various retinal positions. The horizontal lines show the values $\bar{w} = B/\Omega$ of table 9.I.

contribution to pupillary contraction (fig. 9.3). In formula (9.2) this can be expressed either by a dip in the weight function or by an increase in T^* value. According to p. 108 T^* is isomorphous to the amount of rhodopsin that feeds one logarithmic element (the density of these elements being w). The density of rhodopsin in the retinal centre is very low and its distribution function runs parallel to the visual thresholds measured in this area (Campbell and Rushton [22]). Now it appeared from fig. 9.3 tha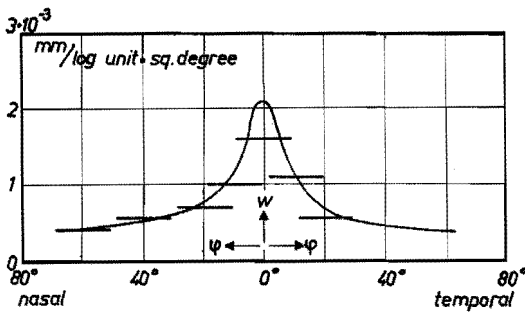t the visual thresholds and the pupillary contractions showed a clear correspondence provided the indirect illumination was balanced. For these reasons it seems logical to attribute the low contributions to pupillary contractions of the central area to increased values of T^*. If so, in first approximation, the retinal distribution of T^* in the central area will be inversely related to the density distribution of rhodopsin.

Now that we have evaluated the retinal distributions of w and T^*, one important aspect of eq. (9.2) still remains to be discussed. This concerns the supposed *summation* of signals from different retinal areas. For the steady-state reactions we tested the relationship $C_A + C_B = C_{A+B}$ for various field configurations. For low illuminations it was found to hold, but for high illuminations we found a lack of summation: $C_A + C_B > C_{A+B}$. Since this effect could be explained from the influence of indirect illumination, it did not plead against the assumed linear summation. As regards the reactions to flashes, we found generally that the sum of C_A and C_B did not even approximate to C_{A+B} for illuminations that were much too low to cause a substantial spread of indirect illumination. Thus, the hypothesis that signals from different retinal areas are added is incorrect.

For example, we shall show one of the experiments which was designed as a test for the assumed summation. In order to escape from the influence of time factors, we chose the fields A and B at equal distances from the fovea, ensuring minimum disturbing influence of overlapping indirect illumination by choosing them in opposite directions from the fovea. As a matter of fact, we used two discs of $6 \cdot 3°$ diameter at $9°$ nasally (A) and temporally (B) to the fovea. The indirect illuminations around these fields do not overlap substantially at illuminations below 0 log scot.td. Figure 9.9 shows the results which may be represented by straight lines. For the combined situation ($A + B$), the contractions are larger and the threshold lower than for A or B separately. However, the summation is far from complete. Since only small contractions are involved, it seems unlikely that this effect is due to scale compression on the side of the iris muscle. We conclude that the signals are combined non-linearly in the sense that an effect of inhibitive interaction occurs.

The lack of summation may also be illustrated by a calculation of the slope B that must be expected for a "180°" field if equation (9.2) applies. From fig. 9.8 it may be evaluated that $B = \Sigma w \cdot \Delta \Omega \approx 5$ mm/log unit. The experimental value is $0 \cdot 7$ mm/log unit.
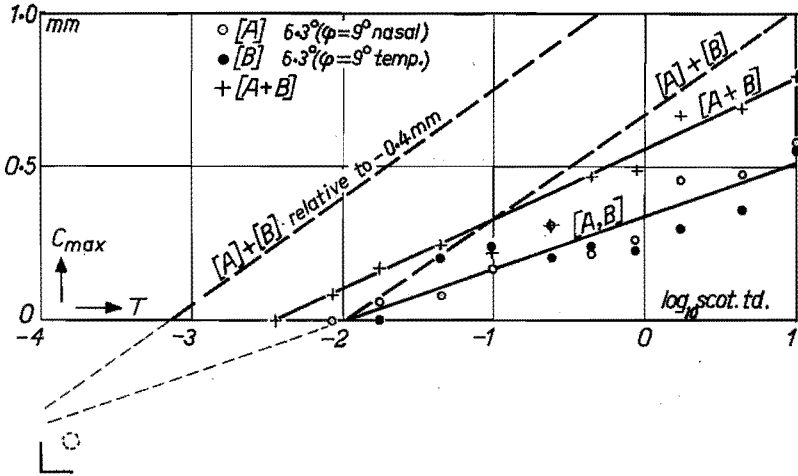
Fig. 9.9. Experimental evidence against the summation principle. The experimental results for a field $(A + B)$ do not correspond with the sum of the fields (A) and (B) separately (broken lines). The fields A and B were of equal size $(6.3°)$ and at equal distances to the fovea $(\varphi = 9°)$ in opposite directions.

What factors may limit the summation? First, one can think of the restriction of the experiments to the amplitude of the contraction. There is much evidence for a decrease in latency times with increasing illumination and with decreasing distance from the fovea (Lowenstein and Loewenfeld [76], Alpern, McCready, and Barr [8]). Even if the time functions of the flash responses were to show differences of latency times only, large fields would cause flatter time functions of the contractions than would small fields, this implying that large fields suffer from too low C_{max} values as compared to the sum of their component areas, as has been indicated schematically in fig. 9.10.

Next, there are clear indications that for flash reactions the signals from different retinal areas are combined non-linearly, e.g. by inhibition effects of

Fig. 9.10. Decrease ΔC_{max} of the amplitude of contraction that may result from possible differences in latency intervals of the responses. Complete summation has been assumed.

signals from intensely illuminated areas on signals from weakly illuminated areas. Another possibility is a non-linear relationship between innervation and amplitude of contraction, though the large intensity range in which C_{max} is proportional to the logarithm of the illumination does not suggest such a scale compress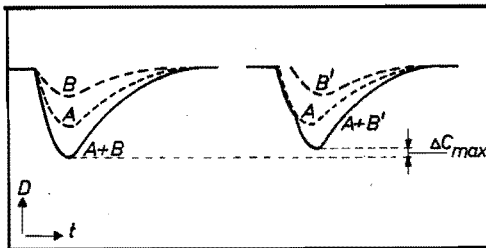ion. Using C_{max} values of 1·5 mm, Baker [12] found a non-linear summation effect for the combination of signals from both eyes. This shows that the non-linear processes are not restricted to the retina.

When summarising the value of the proposed description, we may say that the great differences in pupillary contraction that occur for a wide variety of illuminated fields can be accounted for qualitatively. Apart from the factors that have been used for the description of steady-state reactions, there is an indication that a negative value of C_0 may exist, which would correspond to a threshold in the motor system. The formula falls short in describing the results quantitatively, because the assumed linear summation of signals from different retinal areas does not apply. This may tentatively be attributed to the influence of two factors: (1) The dependence of latency interval on retinal position and illumination — this may be indicated by a factor $X_1 = X_1(\varphi, T)$ — and (2) inhibitive interaction between various illuminated areas to be indicated by $X_2 = X_2(\varphi, \psi, T)_{i-j}$.

Though in principle this lack of summation invalidates the theoretical considerations that have been given, the qualitative explanation of several observed effects makes one confident that some essential features may have been detected.

Since we have not carried out any further research with respect to these factors, we cannot evaluate our views in more detail. We shall therefore leave the problem at this point and turn our attention to the applicability of this discussion to the organisation of the receptive field for photopic reactions.

9.3. The photopic receptive field

Now that the difficulties for the description of the scotopic receptive field have been outlined we may confine the discussion of the analogous situation for the photopic receptive field. For some fields of view the results will be presented and the applicability of the discussion for the scotopic receptive field to the photopic one will be considered.

The cone processes were isolated by applying a large conditioning field of short wavelength, which raised the scotopic visual threshold by about 2 log units without affecting the photopic visual thresholds. A wavelength of 640 nm was chosen for the flashes. The classification of the pupillary responses into the photopic category was judged from spectral information and from the influence of the intensity of the conditioning field on the responses, on the hypothesis that either the scotopic or the photopic system is active (see sec. 8.4).

Fields presented in different retinal positions

Figure 9.11 shows the degrees of effectiveness that have been found for a 2·5° field in various positions on the horizontal meridian. The effectiveness is at its maximum in the fovea and decreases gradually towards the periphery. This descent is steeper for the pupillary threshold (2 log units) than for the visual threshold (1 log unit). The half-width of the curve for $C_{max} = 0·5$ mm is only about 1°.

We have tried to explore the steep foveal maximum somewhat further. In the corresponding scotopic experiments it was favourable to use sets of concentric discs and rings of equal areas, since the indirect illuminations at already short distances outside the discs or rings were equal, with the result that their influences balanced in first approximation. In the photopic experiments, how-
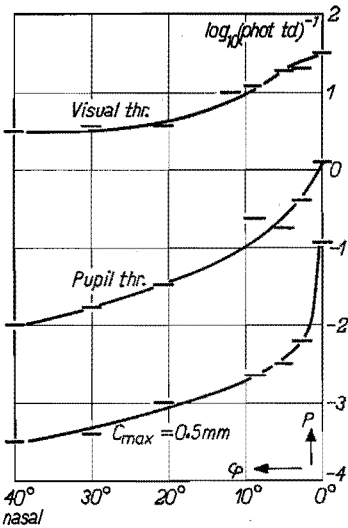
Fig. 9.11. Photopic receptive system. De-grees of effectiveness P for discs of 2·5° in various retinal positions. Flashes 100 ms, 630 nm; observer H.B.
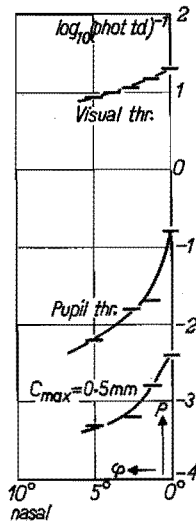
Fig. 9.12. Similar to fig. 9.11, now for a field of 1°.

ever, the influence of indirect illumination will probably come mainly from the fovea itself, where both cone density and pupillary contribution show a sharp peak. Hence, the balance of indirect illuminations at some distance from the fovea is of little concern and the application of these discs and rings offers no advantage. We therefore repeated the experiments with a somewhat smaller field (1°). Figure 9.12 shows for this case the half-width to be about 1°, so that no steeper descent was obtained than in the case of the 2·5° field. For the smaller

field, the illuminations required to obtain a certain pupillary contraction must be chosen progressively higher. This will promote the contribution of indirect illumination and thus blur existing differences between the directly illuminated areas, more than in the case of the 2·5° field.

Discs, centred on the fovea

For a small number of foveally centred fields the degrees of effectiveness are shown in fig. 9.13. The visual thresholds turn out to be almost independent of field size, which is due to the fact that the highly sensitive fovea, where only cones are present, is included in all fields. For the pupil a somewhat larger area (diameter 5°) dominates the response, any further increase of the illuminated field being almost without influence. This suggests that the areas outside this central 5°, however large, offer no contribution to the contraction amplitude C_{max}.

However, peripheral areas contribute substantially to the response when illuminated directly as was illustrated by fig. 9.11. Since the direct illuminations are too low to permit a disturbing influence of indirect illumination, we are forced to conclude that in central illumination the peripheral contribution to C_{max} is either masked or suppressed. Masking will result when pupillary responses from peripheral illumination are much slower than the responses from central areas. Suppression of peripheral signals by signals from the centre is also possible.
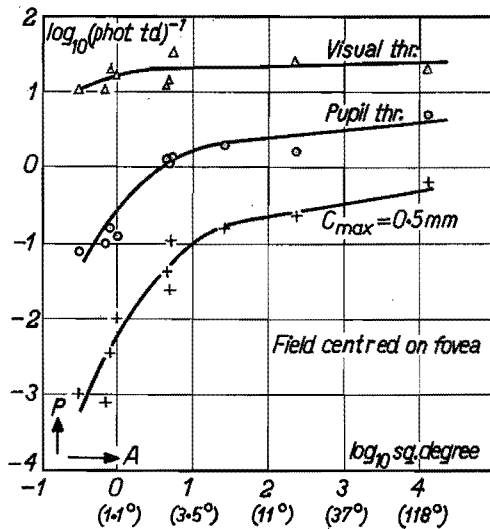
Fig. 9.13. Photopic receptive system. Degrees of effectiveness for central fields of various sizes. Any increase of field size beyond 5° has little influence on the results. Observer H.B.

Discussion

Our photopic results are analogous to the scotopic ones in that time functions as well as inhibition effects need further study. Nevertheless, we shall discuss some aspects of the application of eq. (9.2), now for the photopic case. In order to see whether the photopic results may be approximately described by the equation

$$C_{max} = C_0 + \Sigma \left[\log \left(1 + T/T^* \right) \right] . w . \Delta \Omega, \tag{9.2}$$

fig. 9.14 shows the measured contraction amplitudes as a function of illumina-
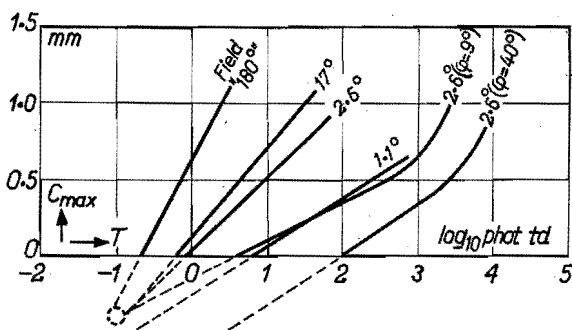
Fig. 9.14. Contraction amplitudes C_{max} as a function of retinal illumination T for an arbitrary selection of photopic fields.

tion (now expressed in log photopic trolands) for a number of fields. Backward extrapolation gives a point of intersection around $T = T^* = -1 \cdot 0$ log phot.td, $C_{max} = C_0 = -0 \cdot 4$ mm. The fact that C_0 shows the same value as in the scotopic case may be taken as an additional indication that in the motor system such an internal threshold may exist.

In order to construct an appropriate weight function w we used the equation $\Sigma w . \Delta \Omega = B$. Figure 9.15 shows amplitudes of contraction for fields of $2 \cdot 5°$
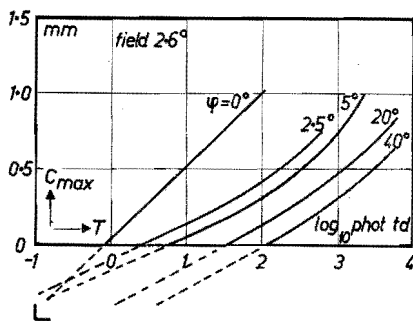
Fig. 9.15. Experimental curves obtained for a field of $2 \cdot 5°$ at various distances φ to the fovea. Photopic circumstances, observer H.B.

in some retinal positions. The initial slopes are shown in table 9.II. This gives rise to a weight function with a sharp foveal peak (fig. 9.16), which very much resembles the cone-density distribution according to Oesterberg[86]. As regards the distribution of T^*, fig. 9.15 leads to the conclusion that T^* shows a constant value within a distance of $10°$ from the fovea and a gradual increase towards larger eccentricities.

TABLE 9.II

Values of initial slope B, weight factor $\bar{w} = B/\Omega$, and point of transition T^* as derived from measurements with photopic fields of $2\cdot6°$ and $1\cdot1°$, in various retinal positions φ. The describing equation is $C = C_0 + B \log (1 + T/T^*)$ with $C_0 = -0\cdot4$ mm

φ (degrees)	B (mm/log unit)	$\bar{w} = B/\Omega$ (mm/log unit .sq. degr.)	T^* (log phot.td)
field 2·6° ⎰ 0	0·48 ± 0·05	0·090	—0·9 ± 0·3
2·6	0·25 ± 0·05	0·047	—1·1 ± 0·3
5	0·25 ± 0·05	0·047	—1·0 ± 0·3
9	0·22 ± 0·05	0·041	—1·0 ± 0·3
20	0·25 ± 0·05	0·047	0·0 ± 0·3
40	0·25 ± 0·05	0·047	+0·6 ± 0·3
field 1·1° 0	0·28 ± 0·05	0·30	—0·6 ± 0·3

Fig. 9.16. Tentative weight function w for photopic pupillary contractions, constructed from the experimental values of the initial gradients $B = \Delta C_{\max}/\Delta \log T$ (see table 9.II). The horizontal dashes show the values of $\bar{w} = B/\Omega$. The dotted line indicates the distribution of cone density, according to Oesterberg [86].

Comparison between scotopic and photopic interpretations

Setting aside the uncertainties that arose from the lack of summation for a moment, we shall compare the interpretations of the scotopic and photopic receptive field, especially with respect to the absolute values of w and T^*. In the scotopic situation the maximum value of w was some 2.10^{-3} mm/log unit .square degree (fig. 9.8), whereas in the phot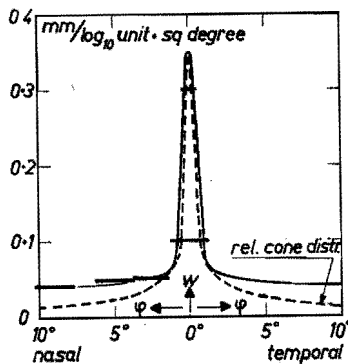opic situation w amounted to a maximum of about 0.3 mm/log unit.square degree (fig. 9.16) which is a hundred times higher than the scotopic value. The scotopic value of T^* was about -3.8 log scot.td; the photopic value amounted to -1.0 log phot.td. In terms of quantum flux at the wavelength of the respective maximum sensitivities, the photopic value of T^* is some 3000 times higher than the scotopic one.

According to the discussion in sec. 7.6, $1/T^*$ is isomorphous to the total amount of pigment that feeds one logarithmic element, whereas the absolute level of the weight function w is related to the density of logarithmic elements. In these terms, the differences between the scotopic and photopic values of T^* indicate that the amount of pigment that feeds one photopic logarithmic element is 3000 times less than the amount that feeds a scotopic logarithmic element. The differences between the absolute values of the weight functions w indicate that the density of logarithmic elements in the photopic system exceeds that of the scotopic system by a factor 100. The difference between the values 3000 and 100 may tentatively be interpreted in terms of overlapping receptive fields of scotopic logarithmic elements.

Thus, the photopic situation is characterised by a high density of logarithmic elements, each of which is fed by a small amount of pigment. In the scotopic situation a low density of logarithmic elements is combined with a large amount of pigment for each. It is satisfactory to note that these tentative evaluations agree with anatomical and physiological data on nervous connections within the retina. The similarity of the shapes of the photopic weight function and the cone-density function may be connected with the one-to-one relationship of the central cones to the optic-nerve fibres by way of the bipolar cells (Polyak [88]).

More information about time functions and inhibitive interactions must be available before it can be decided to what extent this line of approach enables one to collect essential or merely circumstantial knowledge of the organisation of the scotopic and photopic receptive fields.

9.4. Individual differences

The light reactions of the pupil show large individual differences. Drischel [38]) devoted a special study to them, reaching the conclusion that these differences were connected with a relative prominence of either the parasympathetic (contracting) system or the sympathetic (dilating) system, which he supposes to be mutually inhibitive. It would be a step forward if such relative prominence

could be characterised by a small number of variables only. We have not carried out any special research into this question. In order to get an impression as to the general value of the results, some experiments were carried out by some more observers. We shall briefly discuss the relevancy of these data to the problem of individual differences.

Figure 9.17 shows the scotopic pupillary reactions for an 18° field in
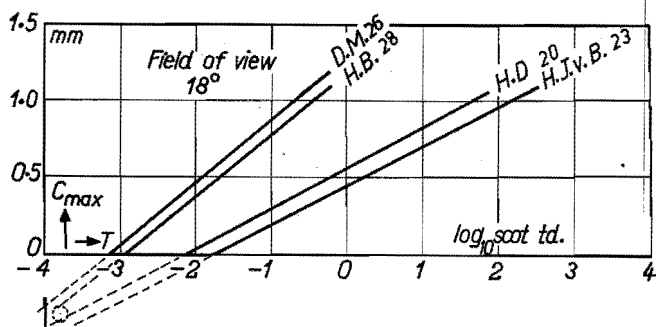
Fig. 9.17. Pupillary-contraction amplitudes C_{max} as a function of retinal illumination for four observers of the indicated ages. Scotopic field of 18°, $\lambda = 515$ nm, flashes 100 ms.

the case of four observers. In order to decide whether the kind of analysis proposed earlier in this chapter may be applied, the lines for the four observers have been extrapolated backward. Though the results do not suggest a point of intersection, the various 18° lines are rather close together around the point which we suggested as a kind of threshold (—3·8 log scot.td, —0·4 mm). The differences between the observers concern mainly the slopes of the curves, and are most easily attributed to differences in the pupillary motor system. Comparisons in fig .8.2 and in fig. 8.6 also show that the various spectra with two observers are dependent on the illumination level more than on the actual pupillary criterion involved.

Hence, our evidence, collected for young observers, points to the motor system of the pupillary loop as the main source of the individual differences for pupillary flash reactions. This would be in agreement with the view that differences in the autonomic nervous system are involved. These might express themselves in the contractions mainly as a kind of multiplication factor. Here too, our evidence is indicative only. The influence of drugs, the influence of age, and the influences of various diseases are also related to the problem of individual variations, these problems having undergone but little quantitative investigation as yet.

9.5. Conclusions

Though a satisfactory description of the organisation of the receptive field for

pupillary flash responses has not been achieved, some factors seem rather well established. The receptive system may be divided into a scotopic portion, the receptors of which are rods, and a photopic portion fed by cones. The central dip in rod density and the central maximum in cone density are reflected in the reactions of the pupil. Apart from this central area, the scotopic and photopic contributions to pupillary flash reactions decrease towards the retinal periphery.

With respect to the differences between the scotopic and photopic systems, the scotopic values of the transition point T^* (a measure of absolute sensitivity) are much lower than the corresponding photopic values. The contribution to pupillary contraction per unit retinal area and log unit illumination (a measure of differential sensitivity) for the scotopic responses is substantially lower than for the photopic responses. These two findings may be combined when the differential sensitivity is assumed to depend on the density w of logarithmic elements whereas the absolute sensitivity depends on the total amount of pigment available for each of such elements. Then, the scotopic system combines a low density of logarithmic elements with a large receptive field of each, whereas the photopic system shows a high density of logarithmic elements each of which is supplied from a small receptive field.

It seems fairly certain that processes of this sort also account for the differences between scotopic and photopic visual thresholds. If large areas are illuminated, the intensities needed for a threshold response of the pupil are only slightly higher than for visual thresholds. With respect to these factors, the organisation of the pupillary system shows correspondence to the organisation of the visual system. When considering the influence of retinal area there is no correspondence between visual and pupillary data. A visual impression is a localised response, which is little influenced by the actual size of the illuminated field. The pupillary contraction is an overall response. When the illuminated area is increased, one finds a general increase in contraction-intensity gradient and, up to a field size of 20° for the scotopic system and 5° for the photopic system, progressively lower thresholds.

Despite differences of several log units in illumination, there is much correspondence between scotopic flash responses and steady-state responses of the pupil, as far as the influence of area is concerned. The flash response is, however, more complicated. First, it is characterised by two parameters (contraction and time), whereas the steady-state response has only one parameter (contraction) On reasonable grounds it is to be expected that intense or central illumination sets aside the influence of simultaneous dim or peripheral illumination on the amplitudes of the contraction. Secondly, the contributions from different retinal areas suppress one another in the case of flash responses. For steady-state responses it was not necessary to assume such inhibiting effects. We have not carried out any special investigation with respect to these two factors. For the

two reasons mentioned, the indirect illumination may be expected to be of somewhat less influence on the flash responses than on the steady-state responses, though it also dominates the flash responses in the case of a highly illuminated small or peripheral field.

There are some indications for a threshold somewhere in the motor system regarding pupillary flash responses. Individual differences in this motor system probably constitute the main factor in the large individual differences that occur in flash responses.

10. GENERAL CONCLUSIONS

In the foregoing chapters we have made an analysis of the receptive systems for both the steady-state and the flash reactions of the pupil with regard to the properties of the receptors and the organisation of the receptive field. In this last chapter we shall try to fit our main findings into a somewhat wider framework by a comparison with the receptive systems of the retina for visual brightness impression. For this purpose we have condensed most results in table 10.I, to which we have added some relevant data from the literature on the visual system. With regard to the restrictions of validity of our own conclusions we refer to previous chapters in which more detailed information is also to be found.
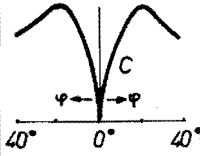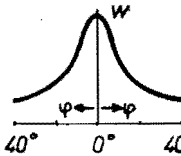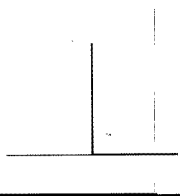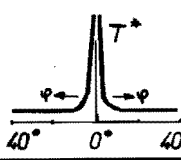
The main parameters that play a part will now be discussed briefly. This may serve as a comment on the rows in table 10.I. as well.
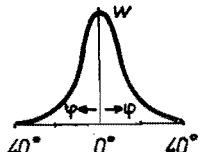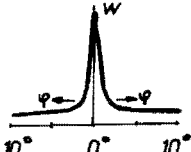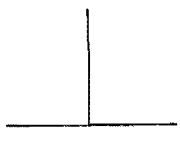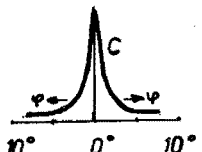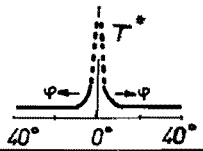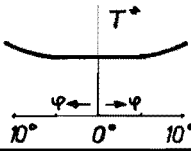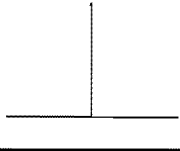
(a) The *spectrum* provides information on the pigments in the receptors that absorb incident light quanta. The absorption spectrum is a characteristic of the pigment involved and can be traced in all reactions caused by these light absorptions. The receptors that contain the pigments provide for a linear transformation from the absorbed number of quanta into a nervous signal.

(b) In cones, the absorption rate is largely dependent on the direction of incidence of the light. Since rods do not show this effect, the *directional sensitivity* is a characteristic of the receptor type involved. From both spectral data and directional sensitivities the conclusion has been reached that in conditions of adaptation to dim illumination, rods are the receptors for vision as well as for pupillary flash reactions. In conditions of adaptation to bright illumination, steady-state reactions of the pupil and the steady component of the ERG too are mediated by rods whereas vision and pupillary flash reactions are mediated by cones. There are indications that usually only one kind of receptors is involved in a pupillary flash reaction.

(c) The *intensity range* for the various phenomena, expressed in units appropriate to the receptors involved, show interesting differences. The minimum amount of light needed by a rod to produce a signal is only one quantum. At visual-threshold level, the average rate of quanta absorption is about one quantum per rod per 15 minutes. At the saturation level of the scotopic visual system (3 log scot.td) the rod pigment rhodopsin is still almost completely unbleached. This indicates that the saturation of the scotopic visual system is not caused by bleaching of rhodopsin, but by processes in a further stage of the transmission, either in the rods or in the neural circuitry involved in scotopic vision. The steady-state reaction of the pupil is still governed by rods at intensity levels definitely above the level of scotopic saturation. This shows that at least part of

TABLE 10.I. Comparison of certain properties of the visual system to corresponding properties of the pupillary system. For explanation see text. $\Delta C \equiv C - C_0$.

			RECEPTORS rods	VISION brightness B (scotopic)	PUPIL flash response (scotopic)
spectrum	a	$\lambda_{max}(nm)$	500	510	500
directional sensitivity	b	$\eta(d = 4\ mm)$	1·0	1·0	1·0
intensity range	c	$T_{min} \mid T_{max}$ (log trolands)	1 qu $\mid$ > 5	$-4 \mid +3$	$-3·5 \mid$ > 2
descriptive formulae	d		$R = cT$	$\log B = n \log T/T^*$	$\Delta C = $ $= \Sigma X_1 X_2 w [\log (1 + T/T^*)] \Delta \Omega$
weight function	e	$w(rel.)$	[graph]		[graph]
point of transition	f	$T^*(rel.)$		[graph]	[graph]
influence condit. field	g			$\left.\begin{array}{c}T^* \\ n\end{array}\right\}$ increase	$\left.\begin{array}{c}T^* \\ w\end{array}\right\}$ increase
main individ. variable	h				$\Sigma w\ \Delta \Omega$

(Rows e and f grouped under the vertical label RETINAL DISTRIBUTIONS)

PUPIL steady-state response	PUPIL flash response (photopic)	VISION brightness B (photopic)	RECEPTORS cones
490	550	550	550
1·0	0·10	0·16	0·16
2·5 | ⩾ 5·0 log scot. td ⟷ log phot. td	0·5 | > 4	—1·5 | 8	1 qu | > 8
$C = \sum w \times [\log(1+T/T^*)]\Delta\Omega$	$\Delta C = \sum X_1 X_2 w \times [\log(1+T/T^*)]\Delta\Omega$	$\log B = n\log T/T^*$	$R = cT$
w ($40°$ $0°$ $40°$)	w ($10°$ $0°$ $10°$)	(line)	C ($10°$ $0°$ $10°$)
T^* ($40°$ $0°$ $40°$)	T^* ($10°$ $0°$ $10°$)	(line)	
	$\left.\begin{array}{c} T^* \\ w \end{array}\right\}$ increase		
$\dfrac{D_0}{\sum w\,\Delta\Omega}$ level indir. illum.	$\sum w\,\Delta\Omega$		

the rods are not saturated at 3 log scot. td, suggesting that the origin of scotopic saturation lies in the neural circuitry involved. Signals for pupillary steady-state reactions bypass this saturation effect, which shows that they pass a functionally separate network.

The conditions in which rods or cones prevail in pupillary flash reactions are roughly the same as those for scotopic and photopic vision, respectively. This is true only if the influence of indirect illumination by entoptical scatter is left out of account. If we restrict the terms scotopic and photopic to retinal illumination (as opposed to the light distribution in the outer field of view) they may be applied to pupillary flash reactions as well.

(d) The *tentative descriptive formulae* for the dependence of the various phenomena on position, area, and illumination of the retinal field, show some differences as well as a notable correspondence. One of the differences is that brightness impression is a localised response whereas the reactions of the pupil are overall responses. The pupillary formulae combine a linear dependence on illumination for illuminations below the point of transition T^* with a logarithmic dependence for illuminations above T^*. Primarily, the weight function w is isomorphous not to a certain portion of contributing receptors, but to the density of logarithmic elements which are different from, but probably located close to the light receptors. Such a logarithmic operation may be held responsible for the fact that a great many phenomena, such as pupillary contractions of static and dynamic types, the amplitudes of the electro-retinogram ERG (Armington [10], Troelstra and Schweitzer [123]), local potentials in the retina of various type (Fatehchand, Svaetichin et al. [40,121], Rushton [98]), and latency times (Roufs [94]) are proportional to the logarithm of the illumination. Only for the potentials of the receptors themselves does a linear dependence on illumination seem to exist (Fatehchand, Laufer and Svaetichin [41]).

Concerning the pupillary reactions, the formulae provide an explanation of the fact that whereas the retinal contributions show a gradual decrease from the fovea towards the periphery, yet centrally fixated fields show an integrative effect over a wide range of areas, that is, the contraction is largely dependent on total light flux, irrespective of the size of the field. This explanation is based on two hypotheses: (1) a logarithmic operation by which the effect of an increase in area predominates over that of an increase in illumination, and (2) a contribution per unit retinal area that decreases from the centre towards the periphery. For small fields, the spread of illumination over large areas (indirect illumination) is supposed to be the main cause of the response. For larger fields, the direct illumination takes over, but the decrease in contribution per unit area towards the periphery counteracts the influence of the increase in area. In this way the integration effect derives from the combination of two independent processes in a non-linear system, viz. the spread of excitation by indirect illumination

and the decrease in contribution per unit of retinal area towards the periphery. When considered separately, the integration effect might misleadingly suggest a linear system. The approximate integration also occurs for other overall responses of the retina, such as the ERG (Boynton and Riggs [16], Crampton and Armington [28]), where the influence of indirect illumination is generally accepted.

(e) The *weight function* $w(\varphi)$ is directly connected with the density distribution of the assumed logarithmic elements. The weight functions are high in the central area and decrease towards the periphery, which is likewise true for responses fed by rods. This indicates a dominance of logarithmic elements in the central area, which may tentatively be connected with the dominance of this central area in the visual system. The large degree of correspondence between the weight function for photopic pupillary flash responses and the density distribution of cones points to a direct proportionality (one to one?) between the densities of receptors and of logarithmic elements. Possibly, Polyak's [88] finding that retinal fibres leading to pupillomotor centres arise mainly from the central area, has a bearing on this effect.

In table 10.I the weight functions (contribution per unit area per log unit illumination) have been presented as being relative to their maxima. In fact, the photopic maximum of the weight function is about a hundred times higher than the scotopic maximum. This indicates a far higher density maximum of photopic logarithmic elements than of scotopic logarithmic elements. The analogous weight functions for the brightness impression B have not been filled in. For reasons of analogy, the exponents n of Stevens' power law [119] come into consideration. Whether and to what extent n varies over the retina is however not known. It must be emphasised that the value of n depends on a supposed exponential transformation from $\log B$ to B as well.

(f) The *point of transition* T^* is inversely related to the amount of pigment that feeds one logarithmic element. In the formulae, the value of T^* has been assumed to be constant except for rod responses in the central area. Since the influence of threshold values that vary with the distance to the fovea has not been explored, the proposed formulae may be regarded only as an indication that there could well be such an organisation. The threshold for scotopic reactions is about three log units lower than for photopic reactions, and since pigment densities in rods and cones are of the same order of magnitude (Rushton [95,100]), the number of receptors converging on to one logarithmic element is far higher for the scotopic than for the photopic system.

(g) *Conditioning fields* generally exert the same influence on brightness impression as on pupillary flash reactions. Thresholds as well as gradations

increase, the latter only in case the flash illumination does not exceed the illumination of the conditioning field too much. Theoretically, an increase in the gradation $\Delta C_{max}/\Delta \log T$ corresponds with an increase in the density of logarithmic elements. This may tentatively be connected with the decrease in the integration area for visual thresholds and with the increase in visual acuity, that occur under the influence of a conditioning field (Van den Brink and Bouman [18], Bouman and Ten Doesschate [15], Barlow [13], Glezer et al. [48,49]).

(h) *Individual variations* of visual functions are generally smaller than variations of pupillary reactions, which are considerable. With regard to this factor the evidence collected in this study is only of a preliminary nature. The origin of these variations may most readily be localised in the motor system. Concerning the reactions of the pupil to steady illumination, part of the individual variations reported in the literature must be attributed to different degrees of transients and fluctuations.

It seems appropriate to add a few lines on the value of the distinction "steady-state" versus "flash" reactions of the pupil, which latter can probably be generalised to a wider area of dynamic pupillary reactions. For fundamental reasons it seems indicated to maintain operationally the distinction between modes of behaviour of an unknown system under different circumstances until sufficient evidence has been collected to the effect that basically the same kind of processes occur. With respect to steady-state versus flash reactions, the evidence as yet available justifies a strict distinction. According to spectral and directional sensitivities, different kinds of receptor are involved. Further, they operate at intensity levels differing up to 6 log units, the pupil being very unsensitive to steady illumination though showing a high sensitivity to flashes. The retinal distribution of activity shows differences too. Finally, the individual variations of the contractions in the two circumstances may vary even in opposite directions.

We end this chapter by summarising very briefly the main results. The identity of the receptors that mediate pupillary light reactions has been established as being rods for steady-state reactions, and rods and cones for flash reactions. Pupillary reactions to flashes show such a correspondence with visual brightness impression that it is permissible to extend the concepts scotopic and photopic of the duplicity theory of vision to pupillary flash reactions. In the organisation of the receptive field of the pupil, one can distinguish between:
 (a) the influence of retinal illumination, which appears to be of logarithmic nature;
 (b) the influence of retinal position, by means of two parameters: (1) a weight factor (w) that corresponds to the density of logarithmic elements and

(2) a point of transition T^* from linear to logarithmic behaviour of these elements, the reciprocal of which is isomorphous to the amount of pigment that feeds one such element;

(c) the influence of illuminated area which for steady-state responses can be taken as linear.

For flash reactions we must add some unknown time-interval function as a third position parameter and further an inhibitive interaction between various illuminated areas. These two factors have not been investigated.

Pupillary steady-state responses have to be distinguished from flash reactions because of clear differences between the receptive systems involved.

This study has indicated some avenues of further research, which might lead to a better understanding of the pupillary system. Apart from the two factors indicated above, this mainly concerns the individual differences, the influence of age and the influence of various drugs. It is suggested that some of the proposed relationships may find a wider application to visual processes.

Appendix I. Conversion between light units

Electromagnetic radiation may be expressed physically in terms of its quantum flux Φ (qu/s). In the case of light, we are dealing with radiation that can be absorbed in the retinal receptors. Then this quantum flux must be weighed according to the absorption spectrum concerned. It has been agreed to use the photopic spectrum ($\lambda_{max} = 556$ nm) and the scotopic spectrum ($\lambda_{max} = 507$ nm) of the CIE standard observer. For each wavelength, these CIE data are expressed as proportions of absorbed energy flux, taken relative to its maximum. A small correction factor (λ_{max}/λ) provides for a conversion to proportions of quantum flux. Having carried out this weighing procedure, we arrive at the light flux F which is expressed as photopic and scotopic lumens, respectively. From this light flux all other light units are derived, such as luminous intensity I in candela (emitted lumens per steradian), luminance B in cd/m^2 (emitted lumens per steradian per square metre emitting area) and illumination E in lux (incident lumens per square metre).

Given the luminance of an object in the visual field, the illumination of the retina depends on the product of luminance L and pupillary area A. It is conveniently expressed in trolands T, where $T \equiv L.A$ (L in cd/m^2, A in square mm). The dimension of the troland is not illumination, which reflects the difficulties one may run into when applying light units to imaging systems.

In this study we have used two units mainly, viz. the flux Φ entering the eye (in qu/s) and the retinal illumination T in photopic or scotopic trolands. In order to facilitate transformations, we give some formulae and conversion factors below.

Formulae

Units: F is expressed in scotopic or photopic lumens, Φ in quanta per second, T in scotopic or photopic trolands, Ω in square degrees.

$F \longleftrightarrow \Phi$ $F = \Phi/b$ with $b = b(\lambda)$. Hence $\log F = \log \Phi - \log b$.

$T \longleftrightarrow F$ $T = F.c/\Omega$ with $c = 3 \cdot 3.10^9$. Hence $\log T = \log F + 9 \cdot 52 - \log \Omega$.

$T \longleftrightarrow \Phi$ $T = \Phi(c/b)/\Omega$. Hence $\log T = \log \Phi - \log b/c - \log \Omega$.

$a \longleftrightarrow \Omega$ A circular field of diameter $2\,a°$ occupies a solid angle $\Omega = 2\pi$ $(1 - \cos a)$ sterad. $= 2\pi (1 - \cos a)$. 3280 square degrees.

Conversion factors

λ (nm)	log 556/λ	phot. log b	scot. log b'	phot. log b/c	scot. log b'/c
		$\log F = \log \Phi - \log b$		$\log T = \log \Phi - \log b/c - \log \Omega$	
507	0·04		15·18		5·66
556	0·00	15·64		6·12	
430	0·11	17·47	15·81	7·95	6·29
450	0·09	16·97	15·47	7·45	5·95
490	0·05	16·27	15·21	6·75	5·69
515	0·03	15·83	15·20	6·31	5·68
545	0·01	15·64	15·46	6·12	5·94
570	—0·01	15·68	15·92	6·16	6·40
630	—0·06	16·28	17·76	6·76	8·24
640	—0·06	16·46	18·11	6·94	8·59

2α (degr.)	Ω (sq.degr.)	$\log \Omega$
1	0·78	—0·11
2	3·14	0·50
5	19·6	1·29
10	78	1·89
20	310	2·50
45	1 580	3·20
90	6 000	3·78
180	20 500	4·31

Appendix II. Experimental steady-state data

In chapter 7 we developed a theoretical description that dealt reasonably with the steady-state contractions obtained experimentally. Only part of the available data is shown in that chapter. Since the data may be of interest to other investigators, they have been condensed in the table below.

For each test field we fitted the experimental points by a curve of the form $D = D_0 - B \log (1 + F/F^*)$, which describes the steady-state diameter D (mm) as a function of the light flux F (scot. lumens) incident on the eye; D_0 is an individual variable and B and F^* are the parameters characteristic of each particular curve. The values of B and F^* are not quite independent since the effect of an increase in F^* may be compensated to some extent by an increase in B. Attention may be drawn to the fact that the almost similar formula (7.3) (p. 93), viz. $D = D_0 - \Sigma [\log (1 + T/T^*)] \cdot w \cdot \Delta\Omega$ gives a *theoretical* description, in which T^* and w are supposed to be intrinsically retinal parameters. The formula applied here gives a purely *experimental* description.

A conversion from luminous flux F to retinal illumination T is obtained by applying the formula $\log T$ (trolands) $= \log F$ (lumens) $+ 9 \cdot 52 - \log \Omega$ (square degrees). For this reason the values of $\log \Omega$ have also been listed below.

distance φ from fovea (degrees)	field diameter 2α (degrees)	Ω (log sq. degr.)	observer H.B. $D_0 = 7 \cdot 4$ mm			observer H.J.v.B. $D_0 = 6 \cdot 4$ mm		
			measured down to D (mm)	B (mm/ log unit)	F^* (log scot. lumen)	measured down to D (mm)	B (mm/ log unit)	F^* (log scot. lumen)
					central discs			
2	0·5	4·5	1·8	−3·0	3·5	1·4	−4·0	
5	1·3	4	1·4	−3·4	3	1·2	−4·6	
7	1·6	4·5	1·4	−3·5				
8·5	1·8	5·5	2·0	−4·1				
10	1·9	4·5	2·0	−3·7	3·5	1·4	−4·8	
11	2·0	4·5	1·0	−4·6	3	1·2	−5·2	
14	2·2	4	2·0	−3·8				
17	2·4	4	2·2	−3·8				
18	2·4	4	1·6	−3·0				
20	2·5	4	2·2	−3·6	3	1·2	−4·1	
22	2·6	4	1·6	−4·0	3	1·6	−4·4	
25	2·7	4	1·8	−4·1				
35	3·0	4	2·2	−3·5	3	2·0	−3·9	
48	3·3	4	2·6	−3·2	3	3·6	−3·5	
90	3·8	4	3·2	−2·7	3	4·4	−3·2	
"180"	4·3	4	4·2	−2·4	3	5·6	−2·2	

φ (degrees)	2α (degrees)	Ω (log sq. degr.)	observer H.B. $D_0 = 7.4$ mm			observer H.J.v.B. $D_0 = 6.4$ mm		
			measured down to D (mm)	B (mm/log unit)	F* (log scot. lumen)	measured down to D (mm)	B (mm/log unit)	F* (log scot. lumen)
			discs in various retinal positions (φ)					
nas. 0	2	0·5	4·5	1·8	−3·0			
nas. 10	2	0·5	6	2·0	−2·5			
nas. 20	2	0·5	5·5	2·8	−2·0			
nas. 30	2	0·5	5·5	2·6	−1·9			
nas. 40	2	0·5	6	2·8	−1·7			
0	7	1·6	4·5	1·4	−3·5			
10	7	1·6	5	2·0	−2·5			
20	7	1·6	5	2·8	−1·8			
nas. 30	7	1·6	5·5	3·0	−1·5			
40	7	1·6	5·5	3·2	−1·3			
60	7	1·6	5·5	4·0	−1·1			
0	20	2·5	4	2·2	−3·6	3	1·2	−4·1
10	20	2·5	4	2·0	−3·0			
20	20	2·5	4	2·6	−2·4	3	2·0	−2·9
nas. 30	20	2·5	4·5	2·6	−2·1			
40	20	2·5	4·5	2·4	−2·0	3	2·8	−2·2
60	20	2·5	5·5	2·8	−1·6			
10	20	2·5	4	2·2	−4·0			
temp. 20	20	2·5	4	2·4	−2·6			
temp. 30	20	2·5	4	4·0	−1·6			
40	20	2·5	4	3·4	−1·6			
			annuli around fovea					
	2 - 5	1·2	5·5	1·4	−3·6	4	1·6	−4·2
	5 - 7	1·3	5·5	1·0	−3·8	3·5	1·8	−4·3
	7 - 8·5	1·3	5·5	0·8	−4·0	3·5	2·0	−4·3
	8·5-10	1·3	5·5	1·4	−3·3	3·5	2·2	−4·2
	10 -14	1·9	4·5	2·2	−3·4	3	1·8	−4·2
	14 -17	1·9	5	2·0	−3·2	3	1·6	−4·4
	17 -20	1·9	5·5	2·0	−3·1	3	2·2	−3·8
	4 -25	2·7	4	1·8	−4·1			
	8 -25	2·7	4	2·4	−3·8			
	12 -25	2·6	4	2·8	−3·2			
	22 -35	2·7	4	2·2	−2·9	3	2·8	−2·7
	35 -48	2·9	4	2·6	−2·2	3	2·0	−2·9
	22 -48	3·1				3	2·2	−3·0
sector ψ (degrees)			ring sectors					
0 — 30	10 —20	0·7	6	0·6	−5·1			
0 — 60	10 —20	1·0	6	1·0	−4·2			
0 — 90	10 —20	1·2	5·5	0·8	−4·4			
0 —180	10 —20	1·5	4·5	1·8	−3·6			
0 —360	10 —20	1·8	4	2·0	−3·4			
0 — 30 and 180—210	10 —20	1·0	5·5	1·2	−4·0			

Summary

The physiological basis of the pupillary light reactions is constituted by light absorption in the retinal receptors and subsequent transformation of the signals generated, by the nervous circuitry involved in the retina, and, after having passed the optic nerve, in the midbrain also. These processes cause stimulation of the pupillary muscles. Probably, time functions of pupillary movements are controlled by the double innervation of the sphincter muscle.

This study is concerned with processes between the light absorption and the resulting pupillary reaction. Subjects of investigation have mainly been the properties of the receptors and the organisation of the receptive field, which comprises the manner of convergence of many receptor signals to one pupillary reaction. We distinguish the equilibrium diameters of the pupil at constant illumination (steady-state reactions) from the pupillary reactions in response to transient illumination (transient reactions) of which only the reactions to flashes have been investigated here. As a response criterion for these flash reactions we chose the amplitude of the contraction. When measuring steady-state diameters of the pupil, large fluctuations and transient reactions must be avoided as they cause a systematic reduction of the diameter (chapter 5). For this reason the pupil has to be inspected during the measurements. We achieved this by applying the entoptical method which allows the observer to perform the inspection himself (chapter 4).

It is generally supposed that the light receptors which mediate pupillary reactions are identical with those that mediate visual brightness impression, viz. rods for scotopic vision in dim light conditions and cones for photopic vision in bright light conditions. As regards the transient reactions of the pupil this view is supported by the experimental evidence available, but this cannot be said of steady-state reactions (chapter 3). For the pupillary steady-state receptors our experiments (chapter 6) reveal a spectrum with maximum sensitivity at a wavelength of 490 nm. This has been obtained at clearly photopic illumination levels as appears from the maximum of the measured brightness spectrum at 555 nm. It also appears that variation in direction of incidence on the receptors, which exerts a definite influence on brightness (Stiles-Crawford effect), does not affect steady-state contractions. These data led us to the conclusion that rods are responsible for the steady-state contractions of the pupil at illuminations at which cones control brightness impression. The illumination levels concerned (above 500 scot.td) lie in a range in which the scotopic visual system is saturated. We could not find any influence of cones on steady-state contractions.

To what extent do the various retinal areas contribute to steady-state contractions? When offering some steadily illuminated field in various retinal positions the resulting contraction shows its maximum at a central position of the field and decreases gradually at more peripheral positions, as has been known

for long. However, these contractions cannot be attributed only to directly illuminated areas since indirect illumination by scattering processes within the eye may have contributed as well. When stimulating the retina with central fields of various sizes, a decrease in contribution to the retinal periphery does not occur. Then pupillary contraction is found to depend approximately on total light flux, irrespective of the size of the field. Our experiments revealed a maximum contraction for a field of 22°.

Starting from the outcome of experiments carried out with large retinal fields, in which the indirect illumination does not interfere, we have developed a formula that describes the steady-state contraction of the pupil of one observer for any retinal light distribution, including indirect illumination (chapter 7). In this description we suppose the linear signals of several receptors to be conducted to a logarithmic element, the output C_i of which is related to retinal illumination T as $C_i = \log(1 + T/T^*)$. The pupillary contraction C is found by simple summation: $C = \Sigma\ C_i$. According to this description, the contribution per unit of retinal area depends on two parameters: the density w of logarithmic elements and the point of transition T^*, which characterises the transition from linear to logarithmic behaviour. We assumed a centro-symmetrical density $w = w(\varphi)$ which shows a high value in the central 20 degrees of the retina (corresponding to 5.10^{-3} mm contraction per log unit illumination per square degree retinal area) and a rather steep decrease towards the periphery of the retina. The point of transition T^* has been assumed to be constant (800 scot.td). For a variety of configurations of the field, the calculated steady-state contractions turned out to approximate the experimental values to some 0·5 mm. The non-linear term in the description causes an increase in area to prevail over an increase in illumination. This phenomenon favourably affects the contribution of indirect illumination. The description indicates that contractions in response to central fields smaller than 20 square degrees and peripheral fields smaller than 300 square degrees are almost wholly due to indirect illumination.

We have also investigated the kinds of receptor which play a part in pupillary reactions in response to flashes of light. Both spectral data and directional sensitivities support the hypothesis that rods as well as cones do contribute. Provided the influence of indirect illumination is taken into account, the pupillary receptors are similar to the brightness receptors. The influence of steady conditioning fields on both functions is also similar. For these reasons the terms "scotopic" and "photopic" of the duplicity theory of vision may be applied as well to pupillary flash reactions. The hypothesis that pupillary flash reactions are controlled either by rod or by cone signals fits the experiments somewhat better than the hypotheses that linear or logarithmic additions of these signals occur (chapter 8).

We have not succeeded in finding an adequate description of the organisation

of the receptive field in flash reactions, expressed as the contractions descended from isolated retinal areas and the manner by which separate simultaneous contributions to pupillary reaction are combined (chapter 9). Many phenomena observed in flash reactions resemble closely those of steady-state reactions, for which a theoretical description has been obtained. This suggests that the processes occurring in both kinds of pupillary reaction are more or less analogous.

The experiments reveal that the foveal minimum of rod density can be traced in the scotopic flash reactions of the pupil, as well as the steep foveal maximum of cone density in photopic reactions. The maximum scotopic contribution per square degree retinal area has been found to be some 2.10^{-3} mm contraction per log unit increase in illumination, whereas the photopic maximum is a hundred times higher. The illumination threshold for scotopic reactions is considerably lower than for photopic reactions. When interpreting these data in terms of the steady-state description, we find for the scotopic situation a low density of logarithmic elements, each of which receives signals from many rods, whereas the photopic situation is characterised by a high density of logarithmic elements, each of which is connected to only a few cones. Contrary to steady-state reactions, the available data indicate no independent contributions to flash reactions of different retinal areas. A second complication is that the time function of the contraction cannot adequately be represented by the amplitude only. These two factors have not been investigated any further.

We have a number of indications that some threshold is included in the motor part of the pupillary system equivalent to a contraction of some 0·4 mm amplitude. The considerable individual differences of pupillary contractions are probably due to differences in the motor system. For steady-state and for transient reactions these individual differences seem independent. Steady-state reactions require far higher illuminations than transient reactions, the differences exceeding 6 log units in certain cases. When combining this with the different receptor origins, the maintenance of the distinction between steady-state and transient reactions seems indicated.

It is suggested that some elements of the description proposed for pupillary processes may apply to other processes in the visual system as well (chapter 10).

Samenvatting

De reacties van de pupil op licht berusten fysiologisch op lichtabsorptie door receptoren in het netvlies en verwerking van de ontstane signalen door zenuwnetwerken eerst in het netvlies en na het passeren van de oogzenuw in de middenhersenen, wat leidt tot een activering van de pupilspiertjes. Vermoedelijk wordt het tijdsverloop van pupilbewegingen beheerst door de tweevoudige innervatie van de sphincterspier.

Deze studie is gewijd aan processen die optreden tussen lichtabsorptie en de resulterende pupilbeweging. Er is voornamelijk aandacht geschonken aan de eigenschappen van de receptoren en aan de organisatie van het receptieve veld van de pupil, waaronder wordt verstaan de wijze waarop vele receptorsignalen convergeren tot één pupilreactie. Onderscheid wordt gemaakt tussen de evenwichtsdiameters van de pupil bij constante belichting (statische lichtreacties) en de pupilbewegingen na veranderingen in de belichting (dynamische lichtreacties), waarvan hier alleen de reacties op lichtflitsen zijn onderzocht. Als criterium voor deze laatste reacties is de amplitude van de contractie gekozen. Het meten van de statische pupildiameter wordt bemoeilijkt door fluctuaties en door dynamische lichtreacties. Deze storende factoren veroorzaken een systematische verkleining van de pupildiameter (hoofdstuk 5). Bij het meten van statische pupildiameters dient de pupil daarom voortdurend geïnspecteerd te worden. In de metingen is dit bereikt door gebruik te maken van de entoptische meetmethode, waarbij de waarnemer deze inspectie zelf verricht (hoofdstuk 4).

In het algemeen wordt verondersteld, dat de lichtreceptoren van het pupilsysteem en die van de visuele helderheidsindruk identiek zijn, namelijk staafjes bij lage lichtintensiteiten (scotopisch zien) en kegeltjes bij hoge lichtintensiteiten (fotopisch zien). Voor dynamische pupilreacties vindt deze hypothese in de literatuur experimentele rechtvaardiging, maar voor de statische lichtreactie is dit in mindere mate het geval (hoofdstuk 3). Uit onze onderzoekingen (hoofdstuk 6) blijkt dat het spectrum van de statische pupilreceptoren een maximum vertoont bij een golflengte van 490 nm bij fotopische lichtintensiteiten, waarbij de helderheid maximaal bleek te zijn voor licht van 555 nm. Bovendien blijkt dat een verandering van de invalsrichting van het licht op de receptoren wèl invloed heeft op de helderheid (Stiles-Crawford effect), maar niet op de statische pupilcontractie. Deze experimentele gegevens leiden ertoe om aan te nemen dat bij fotopische lichtintensiteiten, waarbij de helderheid door kegeltjes wordt bepaald, staafjes verantwoordelijk zijn voor de statische pupilcontractie. Het betreft hier lichtniveau's hoger dan 500 scot.td, waarbij het scotopische visuele systeem verzadigd is. Het is niet gelukt om enige invloed van kegeltjes op de statische pupilcontractie te vinden.

Er is onderzocht in welke mate de verschillende netvliesgedeelten bijdragen tot de statische pupilcontracties. Als het netvlies wordt afgetast met een licht-

vlek is de pupilcontractie maximaal bij belichting van het centrum, terwijl naar de netvliesranden de contractie geleidelijk minder wordt, zoals reeds lang bekend is. Door de algemeen veronderstelde invloed van indirect licht dat binnen het oog verstrooid is, kunnen deze resultaten niet kwantitatief worden betrokken op de direct belichte netvliesgebieden. De afneming naar de netvliesranden blijkt niet indien het netvlies wordt gestimuleerd met centrale velden van verschillende grootten. In dat geval blijkt de pupilcontractie in eerste benadering afhankelijk te zijn van de totale lichtflux, ongeacht de veldgrootte. In onze eigen experimenten (hoofdstuk 7) werd bij gegeven lichtflux een maximale contractie gevonden voor een centraal veld van 22°.

Uitgaande van experimenten met grote velden waarin het indirecte licht geen storende rol speelt, is door generalisering een formule gevonden, die voor één proefpersoon de statische pupilcontractie beschrijft voor elke lichtverdeling op het netvlies. Hierbij moet kwantitatief rekening worden gehouden met de indirecte belichting. De veronderstelling is, dat signalen van een aantal receptoren worden toegevoerd aan een logarithmisch element, dat bij een retinale verlichtingssterkte T een uitgangssignaal levert van $C_i = \log (1 + T/T^*)$. Door sommatie $C = \Sigma\, C_i$ wordt dan de statische pupilcontractie C gevonden. De bijdrage per oppervlakte-eenheid netvlies wordt dan bepaald door twee intrinsieke parameters: de dichtheid w van logarithmische elementen en het overgangspunt T^* dat de overgang van lineair naar logarithmisch gedrag karakteriseert. In de beschrijving is een centrosymmetrische dichtheidsfunctie $w(\varphi)$ (gewichtsfunctie) aangenomen, die hoog is in de centrale 20° (met een bijdrage per vierkante graad netvliesoppervlak van 5.10^{-3} mm contractie per decade lichtintensiteit) en sterk afvalt naar de periferie van het netvlies. Het overgangspunt T^* is over het netvlies constant verondersteld (800 scot.td). De op deze wijze berekende pupilcontracties blijken voor zeer verschillende configuraties van het gezichtsveld gemiddeld tot op 0·5 mm overeen te komen met de experimenten. Door de niet-lineaire term in de beschrijving prevaleert de invloed van een vergroting van het belichte oppervlak boven die van een verhoging van de lichtintensiteit. Dit bevordert de bijdrage van de indirecte belichting, die volgens de beschrijving geheel overheerst bij centrale velden kleiner dan 20 gr² en bij perifere velden kleiner dan 300 gr².

Ook voor pupilreacties op lichtflitsen is nagegaan welke receptoren een rol spelen (hoofdstuk 8). Zowel de spectrale gegevens als de gevonden richtingsafhankelijkheden zijn in overeenstemming met de hypothese dat staafjes èn kegeltjes een bijdrage leveren en wel op analoge wijze als bij de helderheidsindruk het geval is, mits voor de pupil rekening wordt gehouden met de indirecte belichting. Deze analogie geldt ook voor de invloed van continu belichte conditioneringsvelden. Op grond van deze analogieën is het geoorloofd om de termen scotopisch en fotopisch uit de dupliciteitstheorie van het zien ook toe te passen op de reacties van de pupil op lichtflitsen. De hypothese dat de con-

tractie-amplitude bepaald wordt òf door staafjessignalen òf door kegeltjessignalen vindt een wat betere aansluiting bij de experimenten dan de hypothesen dat er hetzij een lineaire dan wel een logarithmische samenvoeging van staafjes- en kegeltjessignalen zou plaatsvinden.

Tevergeefs is getracht een adequate beschrijving te vinden voor de organisatie van het receptieve veld van de pupil voor reacties op lichtflitsen, in termen van de bijdragen van geïsoleerde netvliesgebiedjes tot de contractie-amplitude en de wijze waarop afzonderlijke bijdragen worden samengesteld (hoofdstuk 9). Vele verschijnselen bij flitsreacties herinneren sterk aan die bij statische reacties, die wèl toegankelijk bleken voor een theoretische beschrijving. Dit wekt de verwachting dat de optredende processen voor beide soorten pupilreacties analoog zijn.

Experimenteel blijkt dat het minimum van de staafjesdichtheid in de fovea (het netvliescentrum) duidelijk wordt weerspiegeld in de scotopische pupilreacties, evenals het scherpe foveale maximum van de kegeltjesdichtheid in de fotopische pupilreacties. Per vierkante graad netvliesoppervlak blijkt de bijdrage tot de contractie scotopisch maximaal ongeveer 2.10^{-3} mm contractie per decade intensiteitsverhoging te zijn, terwijl het fotopische maximum honderd maal zo hoog is. De drempel voor scotopische reacties is aanzienlijk lager dan voor fotopische reacties. In termen van een beschrijving analoog aan die voor het statische geval duidt dit voor de scotopische situatie op een lage dichtheid van logarithmische elementen die elk signalen ontvangen van vele staafjesreceptoren, terwijl voor de fotopische situatie een grote dichtheid van logarithmische elementen zou bestaan, die elk vanuit slechts weinig kegeltjesreceptoren gevoed zouden worden.

De beschikbare gegevens wijzen er echter op, dat voor flitsreacties niet mag worden aangenomen dat verschillende netvliesgebieden onafhankelijk bijdragen tot de pupilcontractie. Bovendien is het vrijwel zeker dat de contractieamplitude lang niet altijd éénduidig is gerelateerd aan het tijdsverloop van de contractie. Deze beide factoren zijn niet in het onderzoek betrokken.

Er zijn aanwijzingen dat in het motorische systeem van de pupilbaan een drempel is opgenomen die equivalent is aan ongeveer 0·4 mm contractieamplitude. De grote individuele verschillen in pupilreacties moeten vermoedelijk worden gezocht in het motorische gedeelte van de pupilbaan. Deze verschillen lijken voor statische en dynamische reacties onafhankelijk te verlopen. Voor statische reacties van de pupil zijn veel hogere lichtniveau's nodig dan voor dynamische reacties; het verschil kan zelfs meer dan zes decaden bedragen. In combinatie met de reeds vermelde verschillen in receptoren pleiten deze gegevens vooralsnog voor een strikte handhaving van het onderscheid tussen beide soorten pupilreacties.

Het lijkt niet onwaarschijnlijk dat voor sommige organisatieprincipes van het receptieve systeem van de pupil, in het visuele systeem een ruimere toepassing kan worden gevonden (hoofdstuk 10).

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STELLINGEN

bij het proefschrift van H. Bouma

19 januari 1965

I

Een systematische daling van het aantal verkeersongevallen kan slechts dan worden bereikt wanneer konsekwent wordt erkend dat de verantwoordelijkheid daartoe berust, niet bij de verkeersdeelnemers, maar bij de overheid.

II

Regering en parlement maken onvoldoende gebruik van de aanwezige informatie betreffende het verbeteren van de verstandhouding tussen de volkeren.

III

Vanwege het sociale karakter van wetenschappelijke en technische activiteiten mag van de Nederlandse publiciteitsmedia worden gevraagd dat zij het in dezen gevoerde beleid kritisch gaan begeleiden.

IV

Teleologische beschouwingen in de biologische wetenschappen zijn zowel misleidend als overbodig.

V

Door het aanbrengen van niet-lineaire elementen kan een grotere flexibiliteit van overigens lineaire receptieve systemen worden bereikt.

VI

De veronderstelde analogieën tussen de menselijke informatieverwerking en die van bestaande technische systemen laten onvoldoende ruimte voor adaptatie en verwachting, welke in het menselijke waarnemingsproces essentieel zijn.

VII

De Nederlandse klinkers zijn niet eenduidig te beschrijven met de in hun spectrum voorkomende formantfrekwenties.

VIII

Bij de bestudering van de mate waarin zintuiglijke indrukken naar hun intensiteit worden beïnvloed, zijn numeriek schatten en gelijkstellen gelijkwaardige meetmethoden.

IX

Uit een dimensiebeschouwing volgt dat de psychofysische instelmethode een waarde voor de verschildrempel levert welke middelevenredig is tussen het juist waarneembare verschil en de gemiddelde stapgrootte aan het eind van het instelproces.

X

De toonhoogte van samengestelde akoestische signalen wordt bepaald door het tijdpatroon. Indien de spectrale componenten meer dan één kritieke bandbreedte uiteenliggen spelen tenminste twee tijdpatronen een rol.

XI

Het mesopische zien is nog te weinig benut voor een kwantitatieve psychofysische bestudering van in het netvlies optredende processen.

XII

Een optimaal medisch gebruik van pupilbeïnvloedende farmaca wordt bemoeilijkt door een gebrek aan gegevens omtrent de beïnvloede fysische parameters.