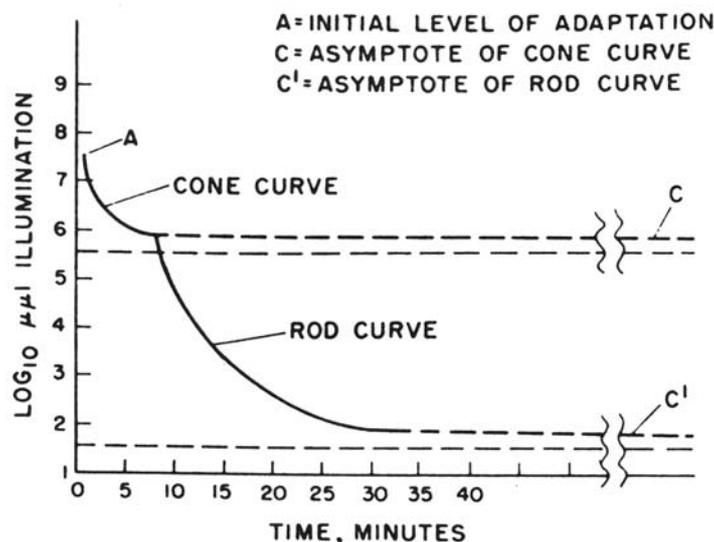# DARK ADAPTATION

1. The basic curve

The usual procedure in a dark adaptation experiment is to light adapt the observer with a bright light that is designed to bleach most of his photopigment. The observer usually looks directly at a large flashing test light (of about 420 nm wavelength) against a totally dark background, which can stimulate both rods and cones, and any adaptation measured with this test light should reflect the activity of both rod and cone systems. After extinguishing the adapting light the observer has to adjust (decrease) the intensity of the test light until he can barely see it, i.e. the detection threshold is determined. As dark adaptation progresses the observer continues to adjust the intensity of the test light in this manner, and the solid line of figure 1 shows the resulting dark adaptation curve. During the experiment, it is important that the room is perfectly "black" and that the subject is exposed to no ambient light.

Dark adaptation data are usually presented in graphic form with the abscissa giving the duration in the dark in minutes and the ordinate presenting the log of the threshold luminance (figure 1). As seen in the classical dark adaptation curves obtained by Hecht et al. (1935, 1937), the dark adaptation curve in figure 3.7 shows two distinct regions of recovery, dominated by the cones and the rods respectively. Most obvious is that over a period of about 35 minutes, threshold improves by about 6 log units. The initial phase of the curve is attributed to foveal adaptation, involving the cones, and is completed within about 8 minutes, during which the visual system increases its sensitivity by about 1.5 to 2 log units. The junction of the first segment curve represents near cessation of cone vision, referred as the rod-cone break. The final phase of the curve represents rod adaptation, which is more protracted (20-30 min), involves a sensitivity change in excess of 4 log units. Its completion depends on the intensity and the duration of light adaptation.


Figure 1: A typical dark adaptation curve. Threshold is plotted as a function of time in the dark. The two phases of the curve represent cone and rod adaptation, respectively (after McFarland et al, 1960). Note that $1\mu\mu L$ equals $3.183*10^{-9}$ cd/m^2.

Dark adaptation has been shown to vary with the duration and intensity of the pre-exposure the size of the test stimulus and the length of exposure of the test light Other factors affecting dark adaptation are the retinal position, the stimulus wavelength, pupillary size, and the test subjects themselves. Therefore, it becomes necessary to fully specify the test condition under which the dark adaptation was determined for the data to be meaningful.

Classical psychophysical evidence indicates that the rod and cone systems dark adapt independently (Hecht, 1937; Stiles, 1939; Rushton, 1961). The rod-cone break in figure 2 represents that point in time when rods become more sensitive than the cones. Prior to this point

the cones detect the stimulus; after this point the rods detect it. The **cone plateau** (at about 5-8 minutes) represents the threshold for the cone system, whereas the rod plateau represents the rod threshold. By repeating the dark adaptation experiment with the observer looking directly at a small test light (so its entire image falls on the all-cone fovea), it is possible to measure the adaptation of the cones only. In figure 2 the resulting dark adaptation curve, indicated by the dashed line, reflects only the activity of the cones. This curve matches the initial phase of the solid dark adaptation curve, but does not include the second phase.

An unfortunate complication with experiments on normal subjects relates to the difficulty in studying the rod-phase at early times when the cone system dominates. At any given time the more sensitive of the two systems (the cone system) will detect the stimulus, so that it is not easy to investigate the less sensitive system (the rod system). This problem was overcome by measuring dark adaptation in a rod monochromat, an observer apparently lacking any functional cone system, usually due to an inherited genetic defect. The dark adaptation curve of a rod-monochromat is shown by the dotted curve in figure 2. As soon as the adaptation light is extinguished, the rods begin to gain sensitivity and continue to do so until they reach their dark adapted level in about 30 to 40 minutes. The fact that the rods begin dark adapting immediately after the light is extinguished means that they are adapting during the cone phase of a normal person's dark adaptation curve; however, we do not see this rod adaptation because the cones are more sensitive. In addition, the rod monochromat's dark adaptation curve also shows the much slower adaptation of the rods compared to the cones. The rods take 20-30 minutes to achieve their maximum sensitivity, compared to only 5-8 minutes for the cones.
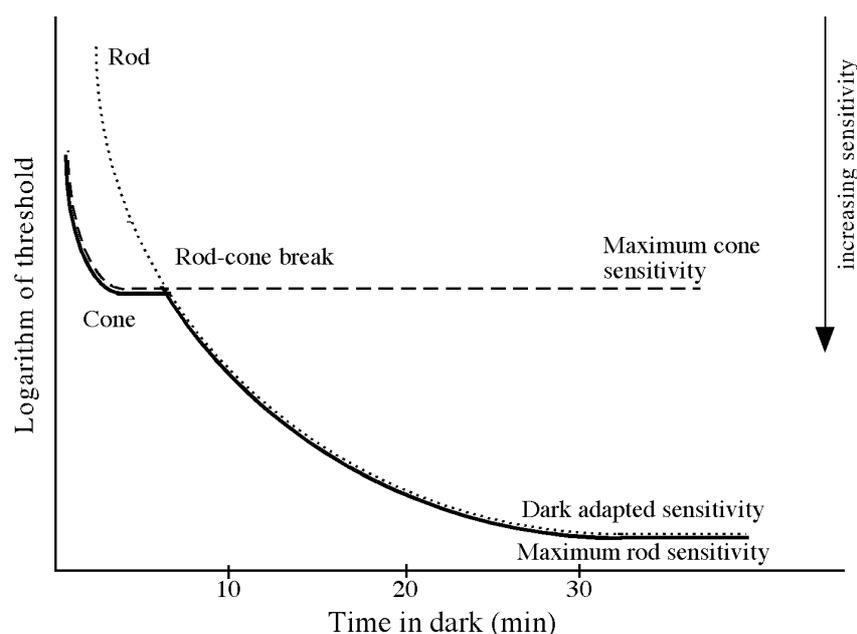
Figure 2: Dark adaptation curves. The solid line shows the two-stage dark adaptation curve for a normal subject, with a cone branch at the beginning and a rod branch at the end. The dashed line shows the dark adaptation of cones only, which can be achieved by using a small stimulus confined to the fovea. The dotted line shows the rod adaptation curve derived from a rod-monochromat observer.

As seen in figure 2, the difference in the range of illuminance over which rods and cones apparently operate adheres to the duplicity theory of Schultze (1866). According to this classical interpretation, there is a scotopic range of illuminance over which rod functioning is evident, and a photopic range where cone functioning dominates. Some authors also refer to a "mesopic" range over which the activity of either type of photoreceptor may become apparent. However, in the case of dark adaptation in normal observers threshold is determined by the activity of the more sensitive cones. It is believed that only some time after cone adaptation is complete will rods become more sensitive than cones and mediate detection of the target. However, recent evidence has shown that this may not be the case (see below).

2. Physiological basis of dark adaptation

The variation of intensity of light from the threshold of light detection through the maximal operating range of the eye at the upper limit of photopic vision is truly enormous and has been estimated to be anywhere between 8 and 12 log units. The mechanisms for adaptation to a lower prevailing luminance including darkness can be grouped into three gross divisions: (i) changes in the size of the pupil, (ii) changes in the steady-state concentrations of photosensitive pigments in the retina, (iii) changes in the level of neural activity in the cellular elements of the afferent visual system.

2.1 Changes in pupil size

The diameter of the pupil aperture changes in proportion to the number of incident quanta. In the average adult eye, the diameter of the pupil ranges from about 7.5 mm in the dark to 2.0 mm in bright light (see figure 3.9). It has been reported that at the level where the rods are fully saturated, it is about 2.4 mm. Therefore, the pupil area changes by a factor of about 10 from darkness to bright light. As the pupil becomes larger with decreasing luminance, it causes a greater retinal illuminance[1] for any stimulus (Woodhouse and Campbell, 1975). Normally, in most dark adaptation studies, where one is interested in retinal - rather than pupillary - function, the experiments are commonly conducted so that the changes in pupil size are not effective in changing the retinal illuminance. Anyway, even if the pupil diameter was uncontrolled, the shift is clearly too small (less than 1 log unit) to account substantially for the enormous changes in threshold that can occur during dark adaptation (approximately 6-7 log units). And more importantly, the 1 log unit influence of the pupillary reflex is ancillary to the light adaptation process itself. It involves a feedback mechanism with a time constant that is considerably slower than those governing light adaptation.
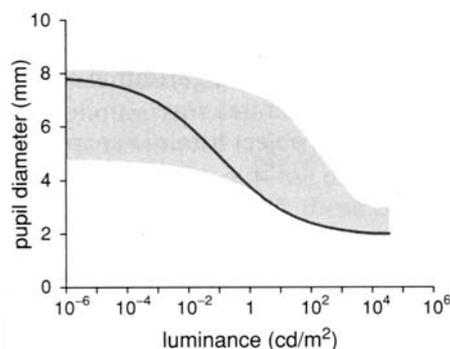
Figure 3: Estimate of average pupil diameter as a function of average luminance. The light grey region shows the extent of individual variation among twelve subjects (based upon Wyszecki and Stiles, 1982).

2.2 Photochemical theory

Hecht (1937) attempted to explain dark adaptation data in terms of hypothetical photochemical mechanism. He postulated that visual sensations were related to the bleaching of receptor photopigments, with the amount of unbleached pigment being the determinant of visual sensitivity. The differences between rods and cones reflected the sensitivity differences in the visual pigments that responded to light and to differences in the time constants that governed their regeneration. According to this simple photochemical hypothesis (Hecht, 1937), the amount of light absorbed from a just-visible stimulus would be constant, and hence threshold intensity should vary inversely with the concentration of rhodopsin remaining unbleached:

$$\vartheta/\vartheta_o = 1/(1-r) \qquad (1)$$

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[1] Retinal illuminance is defined as the intensity of an image formed on the retina and is proportional to the luminance of the object. Its unit is one troland (td) and is defined as the luminance of the object, expressed in cd/m^2, multiplied by the pupil area, expressed in mm^2.

where ϑ is the threshold when a proportion r of the rhodopsin is bleached, and ϑ_o is the fully dark adapted threshold.

2.3 Non-photochemical factors: Dowling-Rushton description

Later, the technique of retinal densitometry was developed, which made it possible to measure the actual concentration of visual pigment in the living human eye. Rushton (1961, 1965) was the first to actually relate the amount of rhodopsin bleached to psychophysical threshold in humans. At approximately the same time, Dowling (1960) related the sensitivity of the electroretinogram (ERG) in rats to the amount of bleached rhodopsin. Both sets of data showed that the state of long-term visual sensitivity generally related quite well to the amount of bleached photopigment and adhered to the following expression, which is known, therefore, as the Dowling-Rushton relation:

$$\log (I_t/I_o) = kB \qquad (2)$$

where I_t is the threshold intensity of the test flash in a given state of adaptation, I_o is the threshold intensity in the completely dark adapted eye, B is the proportion of photopigment that is bleached, and k is a proportionality constant. For humans the constant k is about 3 for cones and about 19 for rods. Rushton's (1961a, 1965a) and Dowling's (1960) results indicate one glaring error in Hecht's (1937) original photochemical theory; the relationship between visual threshold and bleached photopigment is logarithmic, not linear as stated by Hecht (1937) (see figure 4). According to equation 2, reducing the pigment concentration by 50% has a devastating effect on the ability to detect stimuli, as it increases the threshold by 10 log units. However, based purely on photopigment considerations (equation 1), a 50% bleaching is predicted to only double the threshold (see figure 4).
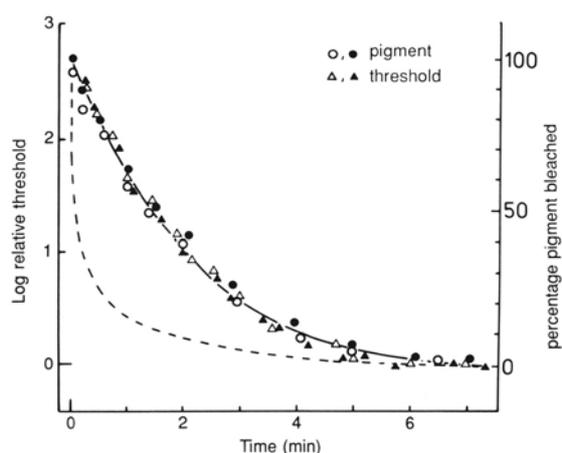
Figure 4: Recovery of sensitivity (circles) and regeneration of cone pigment (triangles) during dark adaptation. Open and closed symbols relate to different experiments. The dashed line indicates the expected threshold elevation due to pigment depletion only (after Rushton, 1965).

Therefore, Rushton's photochemical data showed that factors other than photopigment kinetics play a major role in dark adaptation. It is probably still acurate to state that photochemical considerations predict many aspects of data obtained during the "slower" phases of dark adaptation such as those indicated in figures 3 and 4. To a first approximation, photopigment concentration as described by the Dowling-Rushton relationship predicts visual detection threshold within a few seconds after an observer is placed in total darkness. This first approximation has been questioned on theoretical grounds and better mathematical fits have been obtained between photopigment concentration and threshold (e.g. Lamb, 1981). Moreover, neural factors must play a considerable role in long-term dark adaptation.

3. Suppresive rod-cone interactions

When dark-adapted rods and cones are exposed to a stimulus for which their sensitivities are very different, the threshold of visual detection is assumed to depend entirely on the response of the more sensitive receptor type. When rod and cone sensitivities are similar, however, both types have an opportunity to influence the threshold. Results of early summation experiments indicated that the signals from the rod and cone systems do not interact at all or only in a small excitatory manner at threshold (Ikeda and Urakubo, 1969; Drum, 1982; Benimoff et al, 1982). These summation experiments were based on bichromatic flashes, one component of which selectively stimulated the rods, while the other selectively stimulated the cones. Drum (1982) for instance, found that when rod and cone sensitivities were equal, the combined sensitivity was less than 0.2 log unit greater than it would have been for either rods or cones alone. In support of the above assumption, Stabell and Stabell (1976), by measuring the brightness of various monochromatic lights and the spectral sensitivities functions during dark adaptation, concluded that the effect of rod activity is absent during the cone-plateau period, and it starts contributing to the threshold response at about the cone-rod break of the dark adaptation curve.

This near-independence of threshold detection, as the above studies suggest, could be due to temporal phase differences between the rod and cone systems. In man, the rod signals may normally lag the cone signals by 100 msec in complete darkness (Foster, 1976), and by considerably more when the eye is light-adapted because cone signals speed up faster than rod signals with light adaptation. Such differences in the arrival time of rod and cone signals at say the retinal ganglion cells, could largely preclude the two sorts of signals from interacting.

However, numerous studies have challenged the classic duplicity theory of the retina, that rods and cones behave independently. Frumkes et al. (1973) used a psychophysical approach to show that rod- and cone-related signals could summate together to determine absolute threshold. They suggested that test threshold detection is mediated by the co-operative action of more than one mechanism. Some other experiments have demonstrated that cones may influence thresholds mediated by rods and vice versa (Foster, 1976; Frumkes and Temme, 1977; Temme and Frumkes, 1977; Frumkes et al., 1986). Furthermore, a growing amount of evidence has shown that cone-mediated responses to high frequency flicker are suppressed by rod dark adaptation, and enhanced by selective rod light adaptation (Goldberg et al., 1983; Coletta and Adams, 1984; Hess et al., 1992). This phenomenon is referred to as suppressive rod-cone interaction (SRCI).

Figure 5 illustrates the results of Goldberg et al.'s (1983) study. It shows the minimal intensity necessary to see flicker as a function of time in the dark. When the flickering was of 5 Hz and of medium or short wavelengths (yellow or green), threshold decreased throughout the entire period of dark adaptation. This function looks very similar to a typical dark adaptation curve, which shows a cone and rod portion. However, when longer wavelengths (red) were used, which would be likely to stimulate the cones, the intensity threshold initially decreased throughout the cone recovery stage, but was increased throughout the rod recovery period of dark adaptation. This effect was more pronounced with higher flicker frequencies. Moreover, figure 5 shows the results of the influence of light adaptation on cone-mediated flicker sensitivity; the intensity necessary to see flicker decreased with increasing intensity of the rod-stimulating adapting field. The above results indicate that rods tonically inhibit cone pathways in the dark: the enhancement of flicker produced by rod light adaptation is, hence, due to a removal of inhibition (Goldberg et al., 1983; Frumkes, et al., 1986).
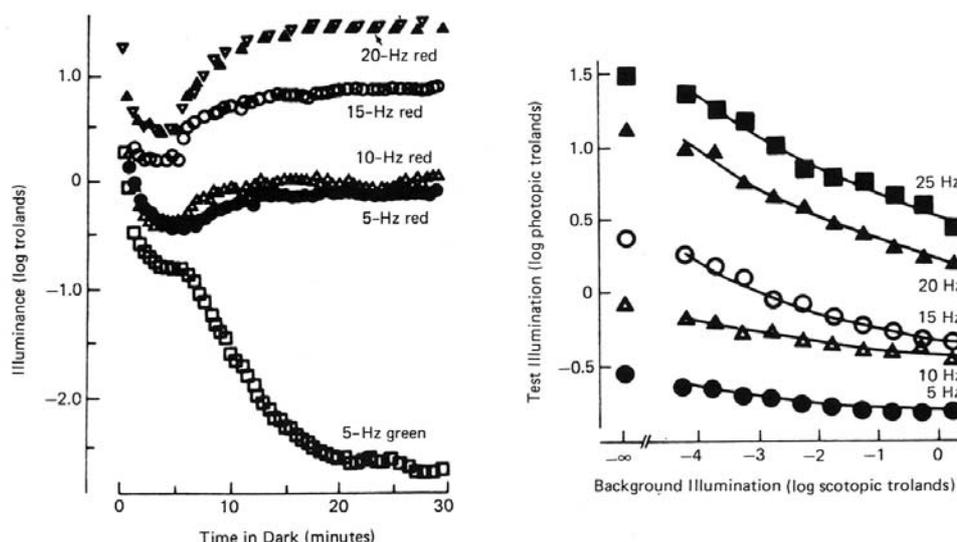
Figure 5: Influence of rod adaptation on cone-mediated flicker sensitivity. For the data presented on the left, flicker illuminance was adjusted throughout the time period of dark adaptation following 1 min exposure to 40000 td white light bleaching stimulus. Flicker was generated by a green stimulus of 5 Hz or by a red stimulus of the indicated frequency. For the data presented on the right, flicker illuminance thresholds were determined as a function of the illuminance of a continuously exposed adapting field of 512 nm wavelength (after Goldberg et al., 1983).

Hess et al. (1992) also assessed the relative rod-cone contribution for different temporal frequencies of stimulation and suggested that this combination depends on a number of factors: the temporal frequency of stimulation, the region of the retina and the level of illumination. At low rates of stimulation the combination of rod and cone signals is "passive" in that the most sensitive mechanism determines threshold. At medium to high rates of stimulation rod-mediated flicker signals inhibit more sensitive cone-mediated flicker signals, resulting in an overall sensitivity which is considerably worse than the capabilities of either system alone. In peripheral vision, no such temporal frequency specific interaction is seen and the more sensitive mechanism determines threshold regardless of the temporal frequency of stimulation (see figure 6).
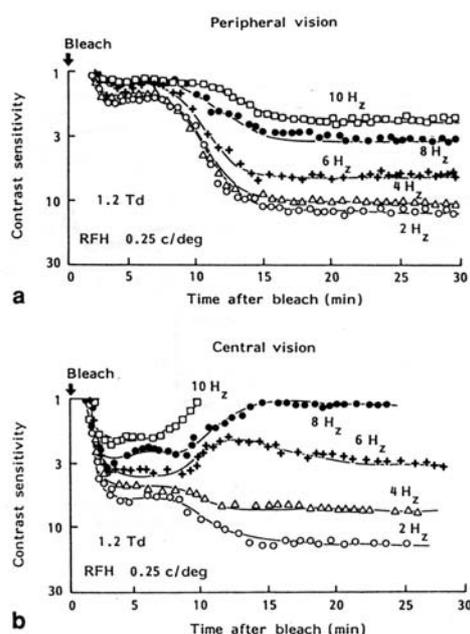

Figure 6 Contrast sensitivity is plotted against the time in minutes following a 6.7 log troland bleach for a range of temporal frequencies of stimulation. The spatial frequency is 0.25 c/deg and the mean illuminance is

1.2 td. The field size is 5 degrees and it is fixated either peripherally at 10 degrees (a) or centrally (b) (Hess et al., 1992).

The phenomenon of SRCI was also observed in several studies that monitored luminance thresholds for gratings of various spatial frequency content during the course of adaptation. For low spatial frequency gratings (presented at low temporal frequencies), thresholds measured in this way show a similar trend to conventional dark adaptation function, having distinct rod and cone phases. For spatial frequencies above the rod spatial resolution limit (i.e., 3.5 c/deg) the rod phase is absent. Studies by Brown (1954) and Brown et al. (1969) reported that the grating threshold reaches a plateau corresponding to the limit of cone sensitivity, while the more recent studies (Coletta et al., 1986; Naarendorp et al., 1988; Margrain and Thompson, 1997) postulated that threshold to high spatial frequency gratings rises again as the rods dark adapt, a phenomenon attributed to SRCI (see figure 7).

In particular, Margrain and Thompson (1997) showed that the slight rise of threshold after 5-10 minutes, when rods start dark adapting, becomes noticeable at intermediate spatial frequencies of 8.3 c/deg. This drop in sensitivity becomes more pronounced at higher spatial frequencies (14 c/deg), which is consistent with the findings of Naarendorp et al's (1988) study (see figure 7). At low spatial frequencies (0.6 c/deg) the threshold to detect the grating was qualitatively similar to the classical dark adaptation function.
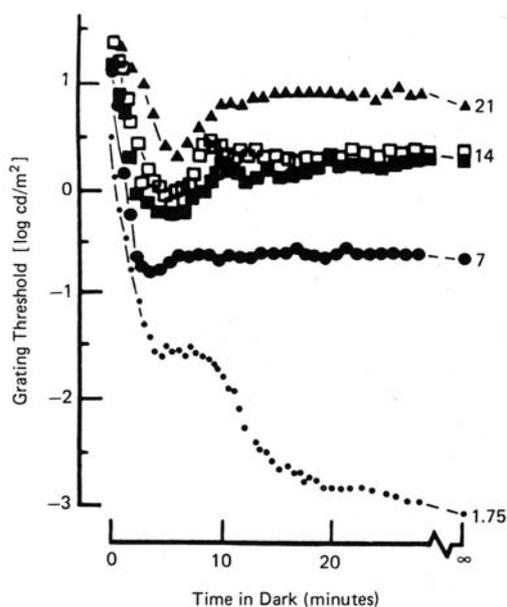

Figure 7 Grating luminance thresholds as a function of time in the dark. The different shaped symbols represent different spatial frequency gratings in c/deg as indicated. The open squares represent data obtained with 512 nm gratings, while the solid symbols represent data obtained with red gratings (after Naarendorp et al., 1988).

4. Effects of ageing on dark adaptation

Prior to the investigation of retinal adaptation under mesopic conditions, dark adaptation curves of subjects of different age were obtained. Figure 3.19 reveals that the dark adaptation curve varies considerably with age. When the level of luminance is suddenly reduced, the first phase is relatively short and is usually completed within the first 4-8 minutes, depending on the age of subjects. Both initial and final thresholds increase with age. According to figure 8 the drop in absolute foveal sensitivity between ages 19 to 76 is approximately 1 log unit, whereas the drop in absolute rod sensitivity is about 1.5 log units.

There are several reasons why these thresholds change with age. The radiation reaching the retina is significantly modified by ageing processes in the iris, the crystalline lens and to a smaller

extent, in the cornea. The retina itself undergoes changes that are likely to affect a number of visual functions. The extent to which changes occur in the visual pathways and the brain is still debated, but at least some of the tissues involved exhibit cell death.
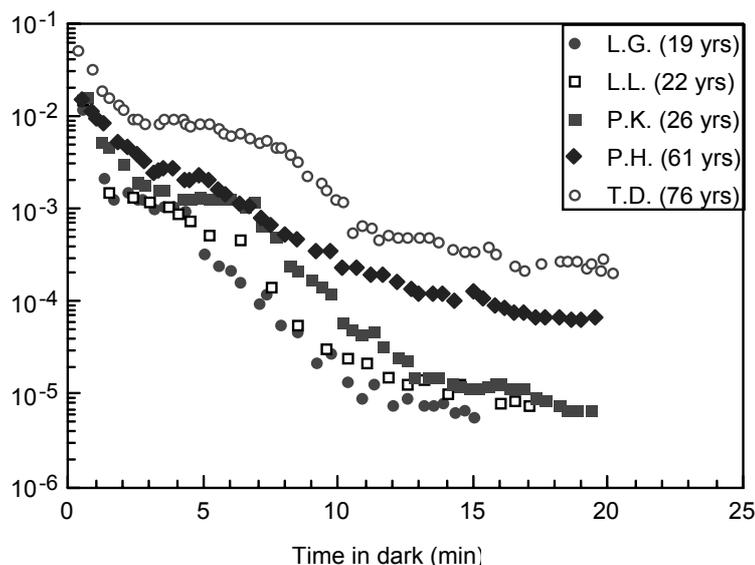
Figure 8: *Conventional dark adaptation curves showing the pronounced influence of age upon threshold of dark adaptation. The absolute sensitivity is much reduced and the gain in sensitivity is slower in the older observers. The size of the stimulus was 5 degrees and the retinas were bleached for 3 minutes.*

Studies of age difference in dark adaptation show a marked elevation in the final threshold of both the photopic (cones) and scotopic (rods) components of the curve. Rod thresholds increase progressively even when allowance has been made for senile miosis and lenticular absorption. McFarland and Fisher (1955) derived dark adaptation curves for observers aged 20 to 60 years and found a correlation of 0.89 between age and final threshold. McFarland et al. (1960) found a high correlation between age of observer and the thresholds of both rods and cones throughout the adaptation period (see figure 3.20). Domey et al. (1960) and Domey and McFarland (1961) derived a model for representing dark adaptation as a function of age and time. These authors attributed the observed differences in dark adaptation due to an age-related impairment of retinal metabolism, although a short-wavelength stimulus was used and no correction for pre-retinal absorption was considered.

However, Gunkel and Gouras (1963) postulated that the decrease in scotopic visibility is partially due to the ageing lens, but the magnitude of this effect is dependent on the spectral composition of the light used to test scotopic vision. If violet test lights are used, the rate of scotopic visibility with age is greatest and reflects predominantly lens senescence. If relatively long wavelength or even white lights are used, the measurable decrease of scotopic visibility with age is much less and reflects not lens but possibly pupillary changes. However, with yellow, low-pressure sodium street lighting, lenticular changes with age would be expected to have only minor effects on adaptation. Weale (1963) concluded that age differences in visual threshold are due in large measure to reductions in retinal illuminance associated with pupillary miosis and to increased lenticular opacity. The remainder of the loss may be attributable to changes in retinal metabolism and to degeneration of visual pathways (Weale, 1982).

Moreover, Birren and Shock (1950) found that although cone and rod thresholds showed a significant correlation with age, no significant correlation was found between the age and the rates of cone and rod adaptation. Their results are in agreement with Eisner et al. (1987), who found an elevation of 0.09 log units per decade, but no age difference in the rate of adaptation. This can be explained by the fact that, although loss of receptors at the fovea of the ageing eye produces a sensitivity loss (Vingrys and Cheng, 1995), it does not necessarily change the recovery rate of the remaining receptors (Marshall et al., 1979; Gartner and Henkind, 1981).

5. Retinal adaptation under mesopic lighting conditions

Figures 9a and 9b show results of retinal adaptation at different ambient illuminance levels (5.0, 1.0, 0.5 and 0.1 lux), as compared with the typical dark adaptation curve for subjects SP and LL. It is obvious that the retinal adaptation curve alters markedly with ambient lighting. In total darkness there is a clear discontinuity in the curve, which is attributed to two distinct regions of recovery, dominated initially by cone and subsequently by rod photoreceptor function. However, at upper mesopic levels (5.0 lux) the curve consists of one portion, undergoing a monotonic increase in sensitivity possibly attributed to cones only. Similarly, at 0.5 lux no break is evident, suggesting that the rod recovery is desensitised by the cone system, which dominates at these levels. If ambient illuminance is decreased to 0.1 lux (low mesopic levels) there is a slight inflexion followed by a second, rod-dominated phase of adaptation. Presumably, the discontinuity between the first and second segments, represents the transfer from cone to rod vision. Identifying the extent of this dichotomy is one of the main objectives of the present project.

Therefore, the data indicate that the visibility of the stimulus changes qualitatively on either side of 0.1 lux for these two observers. Note, also, that the maximal sensitivities under mesopic light levels are reduced at least 2 log units in comparison with complete darkness. It is evident from figure 9 that for a background illuminance of 0.1 lux the change-over point between the two parts of the adaptation curve is delayed by about 1 minute compared with that for absolute darkness. This implies that the rate of adaptation for cones is slower under high-mesopic than low-mesopic conditions.
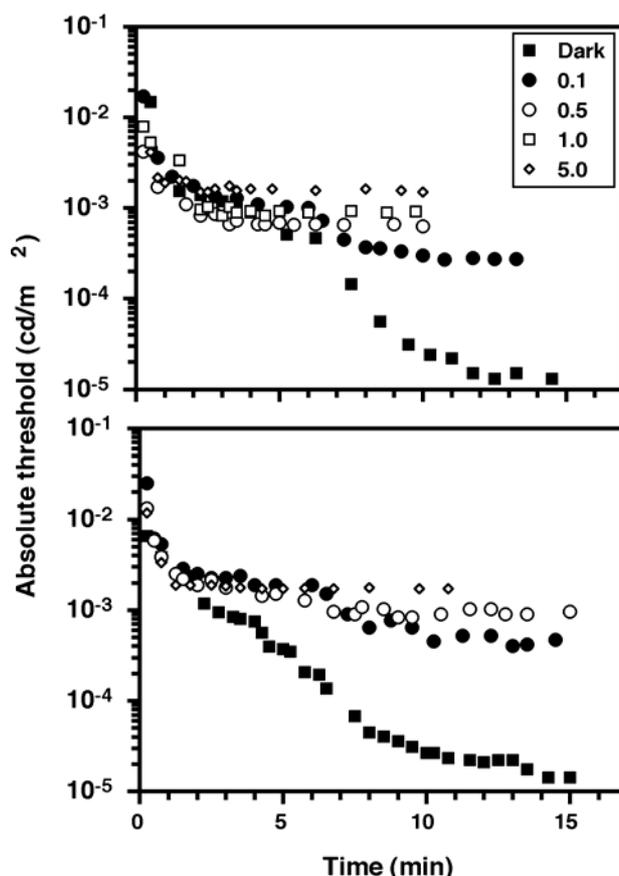
Figure 9: Retinal adaptation curves compared with the classical dark adaptation curve (filled squares) for two subjects. Four mesopic levels (5.0 - triangles, 1.0 - squares, 0.5 - circles and 0.1 lux - filled circles) of background illuminance are tested. Test field size is 3 degrees. Pre-test bleaching time is 1 minute.