

## DARK ADAPTATION, ABSOLUTE THRESHOLD AND PURKINJE SHIFT IN SINGLE UNITS OF THE CAT'S RETINA

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Granit (1943, 1944) observed that the threshold of retinal ganglion cells in the cat drops when they are allowed to dark-adapt after exposure to bright lights, and that there is a shift in spectral sensitivity analogous to the Purkinje shift in the human. The drop in threshold was rather small compared to that found in human dark adaptation, and the final threshold reached was not nearly as low as one would expect in an eye adapted for nocturnal vision. Pirenne (1954) has emphasized that there is a big discrepancy (a factor of  $10^2$ - $10^6$ ) between the lowest threshold obtained by electro-physiological methods and the much lower thresholds found by psychophysical methods in humans (Hecht, Schlaer & Pirenne, 1942). In addition, the existence of a random maintained discharge from retinal ganglion cells (Kuffler, FitzHugh & Barlow, 1957) raises some doubts about the relative parts played by the retina and the central nervous system in determining thresholds. We therefore set out to measure the absolute threshold of the large type of ganglion cell (Rushton, 1949) isolated by metallic micro-electrodes of the type used by Granit & Svaetichin (1939). The opportunity was taken of following threshold through the period of dark adaptation, and some observations of the Purkinje shift were made.

### METHODS

*Preparation of cat.* Anaesthetics affect the maintained discharge from the retina (Kuffler *et al.* 1957) and their effect on dark adaptation and absolute threshold is not known; ether-decerebrate cats with nerves III-VI crushed or cut intracranially were therefore used. These often keep in good condition with a still eye for about 12 hr. The experiment proper rarely started less than 2 hr after the inhalation of ether had ceased, and it often continued for more than 8 hr without any obvious change in behaviour, so we think that residual ether is not important. Additional anaesthetic (Granit, 1943, 1944) was not needed to keep the eye still.

*Preparation of eye.* For these experiments the eye had to be in the best possible condition; the technique of Talbot & Kuffler (1952), which avoids opening the eyeball, was therefore used. Briefly, the eye is held by a ring fixed to the attachment of conjunctiva to sclera, a hypodermic

needle is pushed through the sclera just behind the ciliary body, and an electrode is pushed through this needle until it touches the retina on the opposite side of the eye. The electrode is connected to a conventional physiological amplifier, loudspeaker, and oscilloscope. The electrode tip is observed through a combined ophthalmoscope and stimulator, and adjusted in position until good single units are obtained.

*Optical stimulator.* This was the multibeam instrument described by Talbot & Kuffler (1952), and subsequently slightly modified (Kuffler *et al.* 1957). The background light was used for light-adapting the preparation, as well as for illuminating the retina while a unit was sought. Its source was a tungsten filament lamp run at a variable voltage, and further adjustable in intensity and colour by the use of filters. It illuminated a circle on the retina of  $19^\circ$  diameter. The stimulus light was a glow modulator tube (Sylvania R1131C) driven from an electronic stimulator. This gave square-topped pulses of light of variable duration. The intensity was controlled by two Eastman circular neutral wedges, and the colour by Wratten filters. A perforated plate was placed in a position parfocal with the retina, and gave a range of concentric spots from  $14.5^\circ$  to  $36'$  in diameter (equivalent to 3.25 to 0.135 mm diameter on the cat's retina). These spots were placed at the centre of the receptive field of the ganglion cell isolated; this always lay close to the tip of the micro-electrode.

Light from the stimulator passed through a contact lens on the cat's cornea and the natural pupil which was dilated by division of the III nerve. Since the contact lens did not suit every cat, an additional spectacle lens was usually needed to focus accurately, but as it was of low power and close to the eye it did not change the magnification appreciably.

*Threshold measurement.* Two types of threshold measurement were made: (1) the 'threshold quantity' of light delivered to a small area in the centre of the receptive field in a brief flash, expressed in quanta (i.e. the number of quanta of wave-length  $510\text{ m}\mu$  which would be an equivalent stimulus to the non-monochromatic flash actually used), and (2) the 'threshold intensity' of a long flash of light covering the whole receptive field, expressed in quanta/sec.degree<sup>2</sup>. These could be compared with analogous measurements in man and in the normal intact cat.

The measurement of thresholds was complicated by the presence of a maintained, random, repetitive discharge of impulses from the ganglion cell, which occurred whether the retina was illuminated by light of constant intensity or was in total darkness. For reasons given elsewhere (Kuffler *et al.* 1957) we believe that this maintained discharge is not an artifact of the experimental conditions, but is a normal occurrence in the healthy retina. The way in which threshold and suprathreshold discharges modify this maintained discharge is described elsewhere (Fitzhugh, 1957), and for the purposes of this work the somewhat arbitrary judgement of the experimenter as to the 'threshold' setting had to be relied upon. This difficulty was not, however, so great as might be thought; the threshold was taken as the least strength of stimulus required to produce a perceptible change in the discharge in at least half the trials. First we used a loudspeaker to listen to the discharge and a conventional linear sweep to display it on a C.R.O.; later we also used an impulse interval meter (MacNichol & Jacobs, 1955). In this instrument each impulse appears as a dot on the screen. The abscissa is time, provided by a slow linear sweep synchronized with the flash; the ordinate of each dot depends on the interval since the preceding impulse, and in this application a convenient display was obtained when the ordinate was proportional to the logarithm of this interval. In this way every feature of a sequence of impulses lasting 3-4 sec can be made visible on a single sweep of 3-4 in. We found that this was a definite help in deciding whether a flash of light had affected the maintained discharge or not. Thresholds were repeatable to within about  $0.2\log_{10}$  unit, even if determined by different operators. Whenever possible repeat determinations were made.

#### *Calibration of light intensity*

*Density of wedges and filters.* These were measured in place in the apparatus using a Photovolt photoelectric photometer. The spectral transmission of the Wratten 75 filter used for absolute threshold measurements was measured on a Beckman spectrophotometer.

*Intensity of adapting light.* The light from the stimulator was projected through a lens of the same diameter as the cat's pupil on to a MgO surface and its intensity measured with a Macbeth visual comparison photometer. The intensity of the light reaching the cat's retina was calculated from this figure taking 13 mm for the posterior nodal distance of the cat's eye. No correction was made for losses in the cat's ocular media. This calibration applies wherever the intensities are given in f.c.

*Intensity of stimulus.* A method which avoided heterochromatic matching was used to calibrate the light from the glow modulator tube (Sylvania R1131C) used as stimulus for the absolute threshold measurements. The energy passing a Wratten 75 (blue-green) filter from a lamp standardized by the National Physical Laboratory was calculated from the known intensity and spectral emission of the standard and the known spectral transmission of the filter. This light fell on a Photovolt photomultiplier type photometer, and was used to calibrate it in energy units. This photometer was then used to measure the energy of light put out by the stimulator. The filtered light is not quite so effective for the scotopic eye as monochromatic light of  $510 \mu\mu$ , and the figures for energy were corrected for this, and expressed as equivalent quanta of this wavelength passing the cat's pupil.

*Errors.* The compact design of the combined ophthalmoscope and stimulator makes accurate photometry difficult, with the result that our errors may be rather large. For the absolute thresholds we do not think that the combined error can exceed  $0.4 \log_{10}$  units; this is made up as follows.

(i) The spectral emission of the stimulus light differs from that of the standard; this could only lead to a small error since the spectral dissimilarity was much reduced after the light had passed the Wratten filter, which was used for both lights, and the error was further reduced by putting a yellow filter in front of the photocell to make its spectral sensitivity curve more similar to that of the scotopic eye.

(ii) A rather big error arose from the fact that the glow modulator tube was found to increase its light output over a period of many minutes after being turned on; this change was attributed to warming up, and measurements with the Photovolt photometer showed that the output could double. It was left on continuously during calibrations, so that it was fully warmed up, but during threshold measurements it was only on during a small fraction of the time, and its light output may therefore have been only 50% of its value during calibrations.

(iii) When comparing the standard light and the stimulus light the wedge was at a low density; during the determination of threshold its optical density was greater by about 4. Unfortunately the calibration of this wedge is in some doubt because a repeat calibration at a later date gave densities about 10% lower than the original one. The calibration giving higher densities was used for the calculations, which means that this error tends to cancel (ii), and it is probably of the same order of magnitude.

An additional error is involved in the figures given for the Purkinje shift. The wedge was calibrated for blue-green (Wratten 75) light, but no separate calibration was done in the red-orange light (Wratten 29). These figures may, therefore, be subject to some consistent error, but from our experience of similar wedges we do not think that this exceeds  $\pm 0.2 \log_{10}$  units at most.

## RESULTS

### *Dark adaptation*

Fig. 1 shows the course of dark adaptation after light adaptations at 40 f.c. for 30 min. This was an on-centre unit, and after turning out the light the maintained discharge was silenced, but only for a short time; within 5 min it had returned, and was not obviously different from the maintained discharge in a light-adapted unit. The drop in threshold continued for 3 hr, and did not seem to be related to this temporary cessation of maintained activity. It will

be seen that the drop in threshold occurs in two stages. According to the classical duplicity theory the first stage would represent the dark adaptation of cones, the second that of the rods. In order to confirm this, dark adaptation was followed using red-orange (Wratten 29 filter) light as well as blue-green (Wratten 75) light. During the first stage both thresholds drop by about the same amount, but during the second stage the threshold to blue-green light drops much more than the threshold to red-orange light. It should be realized

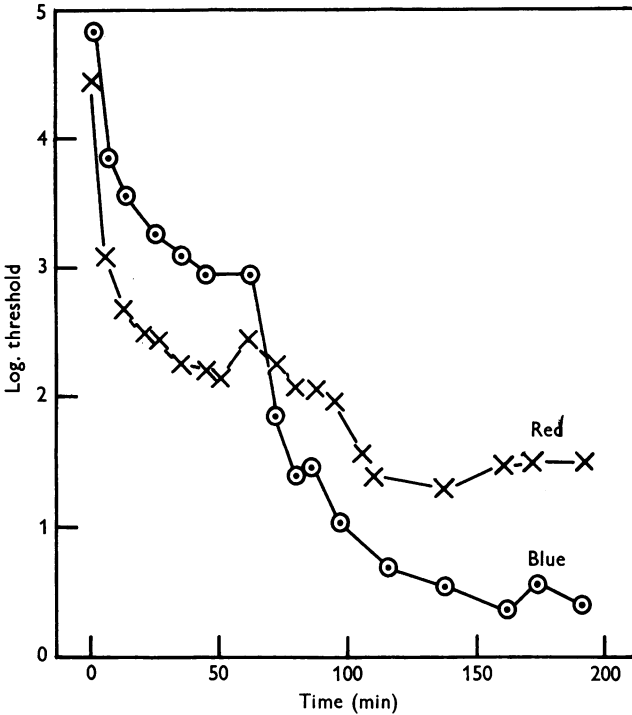


Fig. 1. Threshold (arbitrary units) of an on-centre unit (light-adapted for 30 min at 44 f.c. retinal illumination) to blue-green (Wratten 75, ⊙) and red (Wratten 29, ×) light. Stimulus duration 0.38 sec; diameter 2° 24'.

that the position of the whole of the red-orange curve relative to the blue-green curve is fortuitous, since it depends solely on the original choice of a filter which passed more light of photopic effectiveness but less of scotopic effectiveness, than the blue-green filter; nevertheless, a comparison of the amounts by which the threshold to the two different-coloured lights drops, gives a measure of the extent of the Purkinje shift, and confirms that the first stage of dark adaptation is mediated by cones, and the second by rods (Wald, 1941).

The shape and extent of this dark-adaptation curve are not unlike the curves for humans obtained in psychophysical experiments, but the time course is

definitely slower. The break in the human curve does not occur more than 15 min after the start of dark adaptation (Craik & Vernon, 1941), and there is little further drop in threshold after 40 min; here the break is at 60 min, and dark adaptation is barely complete by 160 min; in other words, dark adaptation is slower than in humans by a factor of about 4. This particular curve was, in fact, the most prolonged dark-adaptation curve that we obtained, but we have several in which the threshold was still going down after 100 min, and dark adaptation always took more than 70 min if the preceding period of light adaptation lasted longer than 5 min at an intensity greater than 4 f.c. This intensity of light would bleach visual purple at the rate of about 20%/min (Wald & Brown, 1953), so that a considerable fraction is likely to have been bleached out. We have done few dark-adaptation curves following weaker light adaptation, but it is clear that dark adaptation is quicker and covers a smaller range. In one case light adaptation was at 2 f.c. for 40 min, followed by 0.2 f.c. for 20 min; the threshold fell during dark adaptation through  $1.5 \log_{10}$  units, and the final threshold was reached in 20 min. In another case, light adaptation lasted for 20 min at 0.14 f.c., and the threshold fell to within  $0.4 \log_{10}$  units of its final value after only 3 min dark adaptation.

#### *Purkinje shift*

During dark adaptation the threshold to a red-orange stimulus does not drop as much as the threshold to a blue-green stimulus. If, in the experiment of Fig. 1, there had been no change in the spectral sensitivity of the eye, the threshold to the red stimulus would have dropped  $1.9 \log_{10}$  units further than it did, and this figure has been used as a rough measure of the Purkinje effect. Comparable figures have been obtained from six other units in five cats, and they all lie within the range  $1.8-2.3 \log_{10}$  units, though they were obtained under a considerable variety of conditions of stimulation; some of the figures for the photopic condition were differential thresholds, for example, and in other cases the unit was lost before it was certain that dark adaptation was complete. If the dominant wave-lengths for red-orange and blue-green stimuli were as far apart as 630 and 490  $m\mu$ , the comparable figure for the Purkinje effect in the human would have been  $2.45 \log_{10}$  units.

#### *Absolute thresholds*

Table 1 shows the range of absolute threshold values of eleven single units in seven cats. The stimulus for determining the threshold *quantity* of light was a flash of 5 msec duration which had passed through a Wratten 75 filter, having a maximum transmission at 490  $m\mu$ . The spots subtended  $1\frac{1}{4}^\circ$  or  $2\frac{1}{2}^\circ$  diameter, which is within the range where Ricco's law of complete summation is found to hold for the majority of units isolated by this technique (though occasionally smaller units are found). The stimulus spots were near the centre

of the receptive field. These thresholds are likely to be close to the lowest obtainable with this technique, and it will be seen that the lowest of them are not much higher than those found in humans by psychophysical techniques (Hecht *et al.* 1942). It was surprising to find that on-centre and off-centre units had substantially the same thresholds, on-centre units ranging from 264 to 3000 quanta, off-centre units from 232 to 2600. The threshold responses were not always simple (FitzHugh, 1957), but the occurrence of a few unusually short intervals between impulses seemed to provide the most sensitive index in the case of on-centre units, and the occurrence of a few unusually long intervals in the case of off-centre units.

TABLE 1. Absolute thresholds in equivalent quanta of 510  $m\mu$  (except where noted) entering the eye

Preparation used	Threshold quantity (no. of quanta)	Threshold intensity (quanta/sec. degree <sup>2</sup> )
Retinal ganglion cell in cat	Highest 3000	Highest 3300
	Average 1660	Average 1430
	Lowest 232	Lowest 520
Intact cat	—	(White light) 96
Human	50-150	23

The threshold *intensity* was determined with a blue-green stimulus spot subtending  $14\frac{1}{2}^\circ$  and lasting for 0.38 sec. This completely covered the receptive field, and the flash lasted longer than that part of the response (the unusually short or long intervals at the beginning of flash) which was used as a criterion of threshold response in this experiment. Enlarging the area or prolonging the duration of the stimulus would not therefore have lowered the threshold values to any great extent. Again there was no consistent difference between on- and off-centre units. In the table the figures for the intact cat are calculated from the data of Gunter (1951), obtained in conditioning experiments, and for man from Denton & Pirenne (1954). It will be seen that even our lowest figures for threshold intensity are considerably higher than those for the intact cat. If the figures for intensity in this table were expressed in terms of quanta per second *per mm<sup>2</sup> of retinal surface*, instead of *per degree<sup>2</sup> of solid visual angle*, the values for the cat would be larger, relative to those for man, by a factor of 2.2, since the cat's eye is smaller than man's. One degree<sup>2</sup> corresponds to 0.038 mm<sup>2</sup> of retinal surface in the cat, but to 0.085 mm<sup>2</sup> in man.

All our units were in the upper two quadrants of the cat's retina, which is the region overlying the tapetum; though we made no systematic search, we did not observe any correlation of threshold with position on the retina.

## DISCUSSION

The results reported here can be compared with previous results obtained on electrophysiological preparations of the retina, and they also need to be discussed in connexion with the results of psychophysical investigations of vision.

Granit (1943, 1944) has reported dark adaptation, Purkinje shifts and threshold values of single units isolated from mammalian retinæ, and our results confirm his findings qualitatively; quantitatively, however, there are some discrepancies. Granit's preparation showed a drop of threshold through  $2 \log_{10}$  units in about 1 hr, whereas our thresholds often dropped more than  $4 \log_{10}$  units and reached a plateau after 2 hr or more in the dark. Two facts suggest that our preparations differ from his in dark-adapting further, rather than in starting from a higher level of light adaptation; first, the lowest threshold he recorded in the cat was about 0.01 metre candle, which is a great deal higher than our values; and second, he used a light-adapting intensity of 2400 metre candles, which is considerably higher than the intensities we used. Another minor difference lies in the observed extent of the Purkinje shift. Granit reported that only 36% of his units showed the full shift of the maximum sensitivity from 500  $m\mu$  in the dark to 560  $m\mu$  after light-adapting. The remaining 64% only shifted as far as 520  $m\mu$ . Our observations on the Purkinje effect were not very extensive, but all the units tested showed a bigger effect than would have occurred had the shift of peak sensitivity been as small as this. It does seem possible that these quantitative discrepancies as to the amount of dark adaptation, the final sensitivity reached, and the extent of the Purkinje shift, all have some common explanation.

One further observation is of interest in connexion with recent hypotheses as to the nature of dark adaptation (Rushton & Cohen, 1954; Wald, 1954). It was found that dark adaptation was slow and prolonged, with easily separable rod and cone portions, *only* if the preceding light adaptation was intense enough and lasted long enough to bleach a considerable fraction of the rhodopsin in the retina. Under these conditions resynthesis must occur during dark adaptation, though one cannot tell if it is the rate-limiting process. If it is, then resynthesis must be considerably slower in the cat than in man, and there is some independent evidence that this is the case (Granit, Munsterhjelm & Zewi, 1939; Weale, 1953; Rushton & Campbell, 1954). Following adaptation to intensities which one would not expect to bleach out more than a small fraction of the retinal rhodopsin, dark adaptation is quick, and only extends over 1 or 2  $\log_{10}$  units. We have no data to show what changes are responsible for either the quick or the slow changes in threshold, but the fact that these retinal units show as big a drop of threshold during dark adaptation as the intact human subject leaves little room for central mechanisms in the explanation of dark adaptation.

Pirenne (1954) pointed out that electrophysiological preparations appear to be very insensitive compared to man and other animals when they are tested by psychophysical or behavioural methods. This discrepancy was the main reason for our interest in the absolute threshold of the units isolated by the micro-electrode technique: and it is satisfactory to find that, given sufficient care in obtaining a preparation which can be allowed to dark-adapt for 2-3 hr, and in which the effects of anaesthetics and poor circulation are avoided, thresholds are obtained which are very much lower than any previously reported. The smallest *quantity* of light, delivered in a small short flash, which changes the maintained discharge of the most sensitive ganglion cells to an extent detectable to the observer, is only two or three times the absolute threshold of the average human subject. Though one might expect the cat's eye to have a rather lower threshold than the human, we can safely claim that the more sensitive ganglion cells isolated by the micro-electrode technique respond to quantities of light of the same order of magnitude as those required by intact animals.

Pirenne (1954) originally made his comparison on the basis of threshold *intensities* rather than threshold *quantities* of light, and in this case a large part of the original discrepancy remains. Even the most sensitive units have thresholds about 50 times higher than those found by Gunter (1951), which confirm those found by Bridgeman & Smith (1942) and Mead (1942), and the difference would be increased if due allowance was made for the fact that these training experiments on cats were done using white rather than blue-green light.

There are several possible reasons for disagreement between electrophysiological thresholds and the thresholds of intact living cats. (a) The retinae of our preparations may not have been as sensitive as the retinae of normal cats because of the experimental interference; for instance, section of centrifugal fibres (if they exist in the cat) during decerebration may be important. (b) The units isolated may not be those with the lowest threshold, either because they are not the most sensitive type, or because they are not placed in the most sensitive region of the retina. (c) The method of judging a change in the maintained activity by listening to the loudspeaker and looking at the impulse interval meter trace may be insensitive compared to the normal analysis of impulses in the cat's C.N.S. This problem is discussed in another paper (FitzHugh, 1957), but seems unlikely to account for a big difference. (d) In electrophysiological experiments the discharge of a single unit is observed, whereas the normal living cat may use the discharge of many units simultaneously. We think that this factor might make a big difference to the threshold. First there is the possibility of 'probability summation' (Pirenne, 1943, 1951; Van der Velden, 1944; Bouman & Van der Velden, 1947; Denton & Pirenne, 1952); if a stimulus has only a small chance of firing

a given retinal unit, it may still have a large chance of firing *at least one unit* if it falls on a retinal area containing many similar units, or if it is maintained for a long duration. The fact that retinal ganglion cells have an irregular maintained discharge seems to render this concept in its simple form inapplicable, but such a background 'noise' raises the possibility of a more effective type of summation. A single fibre might carry to the central nervous system 'subthreshold' alterations in the pattern of its impulses: central summation of such subthreshold changes occurring in different fibres, or at successive instants of time, might cause some central threshold to be exceeded. If thresholds are determined centrally, then more information can be obtained from a large number of independently noisy visual communication channels, all being affected by the same signal, than from a single one. This factor would be most important in the case of large stimulus spots exciting many units and maintained for long durations; it is just under these conditions that there is the biggest discrepancy between our results for single units and those obtained on whole animals.

The situation can be summarized as follows. The thresholds of the retinal ganglion cells isolated by this technique are higher than those of the intact cat, but the difference is less than was previously thought, and it might result from the intact cat making use of information derived from many ganglion cells. This factor will be most important for large area stimuli but, because receptive fields overlap each other (Hartline, 1940; Barlow, 1953; Kuffler, 1953), it may also have an effect on the threshold for small sizes of stimulus spot.

#### SUMMARY

1. Dark adaptation, Purkinje effect and absolute thresholds have been studied by recording from ganglion cells isolated in unopened eyes of decerebrate cats.

2. After strong light adaptation, dark-adaptation curves showed a drop of threshold through more than  $4 \log_{10}$  units.

3. The curves showed rod and cone portions, and all units examined showed a large Purkinje effect.

4. Dark adaptation is much slower than it is in the human; it took up to three hours for absolute threshold to be reached.

5. In the most sensitive units the smallest *quantity* of light which perceptibly changed the maintained discharge was equivalent to about 250 quanta at  $510 \text{ m}\mu$ , measured at the cornea, which is about two or three times the human absolute threshold; the *average* value in eleven units was equivalent to 1660 quanta, which is roughly 15 times the human value.

6. The lowest light intensity (using long, large stimuli) which affected the maintained discharge was found to be about 500 quanta/sec. degree<sup>2</sup> in the

most sensitive unit, about 1500 quanta/sec. degree<sup>2</sup> for the average. For the human it is 23 quanta/sec. degree<sup>2</sup> (Denton & Pirenne, 1954).

7. On- and off-centre units have about the same thresholds, and dark-adapt similarly.

8. Reasons are advanced for expecting the thresholds of these retinal ganglion cells to be higher than the threshold of the intact cat.

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