

A SCOTOPIC 'BLUE SHIFT' OBTAINED BY ELECTRICAL MEASUREMENTS OF FLICKER RESONANCE

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In eyes containing rods and cones the well-known Purkinje shift of the luminosity curve or of the corresponding electrically determined sensitivity distribution of individual retinal elements consists in a shift towards the red end of the spectrum with light adaptation. This signifies that cones become responsible for vision. The visual purple (v.p.) absorption curve has its maximum around 5000 Å and in terms of the micro-electrode technique is represented by the scotopic dominator. In light adaptation, cones come to the fore. In terms of the same technique this means the appearance of a photopic dominator with maximum around 5600 Å. Not all elements in the cat's eye are capable of delivering a photopic dominator response upon light adaptation (Granit, 1947).

The red shift, which presupposes a considerable amount of light adaptation in the cat's eye (the animal we have used), stands in contrast to the fact that the first photochemical effect of light on the sensitive v.p. pigment actually is a shift of its spectrum towards the blue end. This was discovered by Lythgoe (1937), who called the photoproduct 'transient orange'. He found the substance to be exceedingly thermolabile. Lythgoe & Quilliam (1938*a, b*) then proceeded to study its absorption spectrum at low temperatures. Their results have been confirmed (see, for example, Collins & Morton, 1950*b*; Wald, 1951). It is not necessary to discuss further events and the formation of indicator yellow and colourless products.

It is unknown what these blue shifts may mean *in vivo*. The processes may be fast and too transient to measure, the products formed may act as yellow filters (Dartnall, 1948) or they may serve as photochemically active agents. There are, indeed, in the cat's eye, highly blue-sensitive elements (Granit, 1947; Donner & Granit, 1948) but this may mean that the micro-electrode by chance has struck an element that happens to contain a large number of 'blue cones'.

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In the absence of a blue shift, light adaptation insufficient to cause a red shift (i.e. before adaptation to cone level) might be expected to cause some narrowing of the scotopic sensitivity curve owing to the drop in v.p. concentration in modest light adaptation of the kind to be used below (but see Granit, Holmberg & Zewi, 1938; Hagins & Rushton, 1953, and below). Nevertheless, it seemed worth while, if the new method should prove accurate enough, to investigate this point in terms of what might be called physiological or retinal action spectra. This was the original aim of the work undertaken.

To become accessible to experimentation such problems require measurements of the average retinal response on a sensitive preparation. Electroretinography would be excellent if it could be made sufficiently fast and sensitive. As carried out in the standard way several hours are required to establish the form of a single spectral distribution curve, and even then a large number of values have to be obtained by interpolating between a limited number of measured quantities.

An approach to the problem outlined was opened up by the application by one of us (R.G.) of a resonance method to the measurement of flicker and fusion in the electroretinogram (e.r.g.). A great gain in speed, sensitivity and precision was obtained, and the results to be reported followed directly from the technical improvements introduced.

PRINCIPLES OF THE RESONANCE METHOD

A sensitivity distribution is experimentally defined by the amount of energy necessary at each wave-length to evoke a constant response. The results are generally plotted as reciprocals of the energy values (see Fig. 2). With the present method the constant response chosen is an e.r.g. flicker at a constant rate. A resonance meter (in this case a Vibration Analyser made by the General Radio Corp., U.S.A.) is set to resonate at the flicker frequency. The flickering electroretinogram is amplified and its magnitude indicated on an arbitrary voltage scale by the galvanometer needle of the resonance meter. One may choose the flicker fusion point as the constant index and diminish the intensity of the light in exposures of the flickering light lasting 3-4 sec at intervals of half a minute until the needle ceases to respond or, alternatively, keep the light permanently flickering and adjust the energy at each wave-length so as to maintain a constant deflexion of the indicator needle. The latter method is particularly fast, precise and convenient. The neutral wedge in the light beam may be adjusted while one watches the galvanometer of the resonance meter and brings the needle to the desired constant deflexion. The faster the constant flicker selected, the greater the amount of light needed to obtain a given index response. The level of adaptation is therefore dependent upon flicker frequency and is directly measured by the energy required for

a certain sustained flicker response at a wave-length corresponding to the peak of the v.p. absorption curve.

The maximum electroretinogram of the well dark-adapted cat's eye to a single flash is of the order of 1.2 mV. For this the intensities have to be

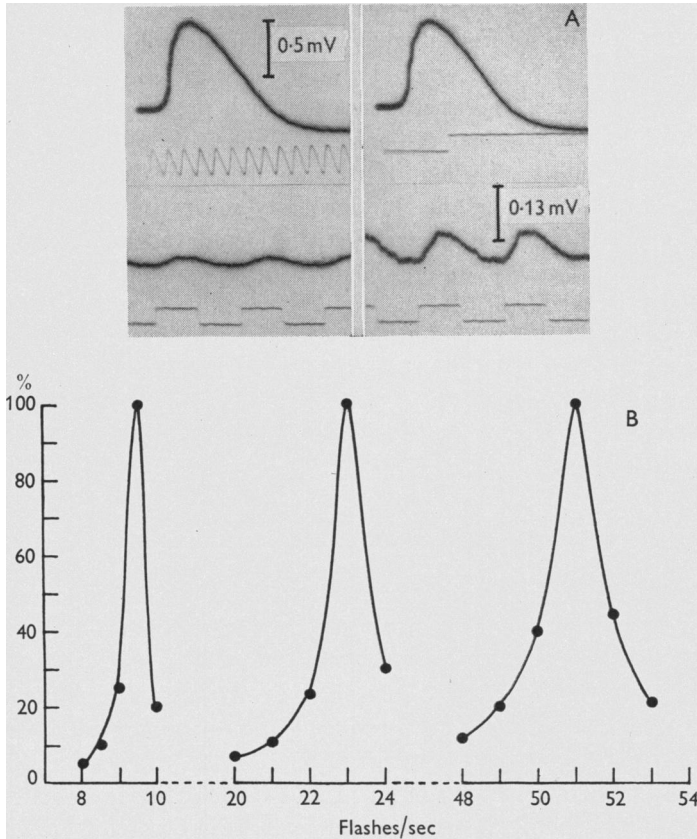


Fig. 1. A. Two photographs of the largest electroretinograms seen in these experiments in response to flashes at the maximum intensity of the Hilger-Tutton monochromator at 5000 Å. Note the characteristic wavy contour and absence of *a*-wave, for which stronger lights are required. Below, some flicker records. Time signal: 50 c/s, replaced by flash marker in three of the records. B. Some typical resonance bands of the vibration analyser with photocell connected and Velodyne run at constant speed as described in text.

strong and well above the cone range. With our Hilger-Tutton monochromator a maximum response of the order of 0.6 mV is obtained if the wave-length chosen falls around the top of the v.p. absorption curve (Fig. 1). This is still chiefly a rod electroretinogram, and modest light adaptation makes it too small to be very accurately measured in an ordinary record from a single flash.

Rod flicker runs up to frequencies around 25 flashes/sec (Granit, 1935; Enroth, 1952; Dodt & Enroth, 1953), and cone flicker in strong illumination up to values around 75–80 flashes/sec, both in retinal elements and in the electroretinogram (Enroth, 1952, 1953; Dodt & Enroth, 1953). Dodt (1951*a, b*) first showed electroretinographically on the human eye that such high flicker values can be obtained by using very strong stimuli. The figures given are from photographic determinations of fusion frequencies in amplified responses. The resonance method indicates scotopic flicker above the value at which amplification combined with photography makes good resolution possible and hence can be used at lower signal/noise ratios than would be possible in electroretinography at low intensities.

METHOD AND PROCEDURE

The electroretinogram of well dark-adapted cats was recorded in the customary way by silver-silver chloride cotton-wick electrodes taken to a condenser coupled amplifier, one lead on the cornea, and the other against the inside of the nose. Some animals were decerebrated, others received an intraperitoneal dose of pentobarbitone, 40 mg/kg, to which later small doses of dial were added intramuscularly, as needed. The decerebrated animals were given 5–10 ml. of a 20% solution of urethane; the third nerve was generally cut. The bulb was fixed by a few stitches to the surrounding tissue or sometimes to a metal ring. The pupil of the anaesthetized animals was immobilized by a few drops of homatropine and atropine. The light from the monochromator was adjusted to fill the pupil. As a check on the state of the eye the electroretinogram for wave-length 5000 Å was photographed before the experiment was begun.

The Hilger-Tutton monochromator was used in conjunction with a Philip's tungsten strip filament lamp run off high capacity storage batteries at a constant colour temperature of 2800° K. Neutral filters and a wedge served to vary stimulus intensity. When weak light-adaptation became necessary it was obtained from a 24 V matt bulb provided with an ordinary cup-like shade on a long flexible stand. The animal's box was opened on one side and the distance of the lamp adjusted while the response was observed on the resonance meter. So little of this light entered the eye that it never could be measured with our standard luxmeter in place of the eye. The ensuing depression in sensitivity could, however, be exactly measured through the rise in the energy necessary for a constant flicker response in the resonance meter (see below).

Leads from the amplifier were taken both to the vibration analyser and a cathode-ray oscillograph. The analyser, which has a frequency range of from 2 to 750 c/s, could be set to respond with a narrow or broad resonance band at the desired frequency. In actual practice the narrow band was found to give greater stability of the indicator needle of the vibration analyser. In order to have a ready check on the required precise coincidence of frequency in analyser and flickering beam the output from the photoelectric cell which indicated the flashes on the cathode ray was connected as an alternative input to the vibration analyser. Intermittent light was produced by a sectored disk (equal periods of light and darkness) turned by a Velodyne reversing motor-generator (British Air Ministry Type 74) electronically controlled and varied in speed by means of a potentiometer (Williams & Uttley, 1946), a technique used in this laboratory by Enroth (1952). To achieve the necessary long-term frequency stability in the experiments using permanent flicker it was found necessary to run the tachometer and amplifying valve circuits from batteries.

While observing the analyser's indicator needle with the photocell connected, the Velodyne potentiometer was set for resonance at the required frequency. Maximum deflexion of the needle signified that flash frequency and analyser setting were identical. In this way, identity of the two values could also be checked from time to time with minimum delay. An idea of the precision obtainable may be had from Fig. 1 which illustrates some such resonance bands.

Optimal accuracy was obtained in the later experiments when the eye was kept permanently flickering at constant speed and the wedge setting adjusted so as to maintain a constant needle deflexion as the wave-length was altered. It proved possible in the best animals to set the wedge to 1 mm in a single trial. This represents a change of transmission, T , of 3.75%. It is doubtful whether a cat can do better than that (see especially the curves of Fig. 3). However, the work was begun by determining fusion frequency with a small deflexion of the indicator needle as criterion for fusion. In these early experiments the eye was exposed to the flickering light for test periods of 3–4 sec in duration at intervals of 30 sec and a large number of values taken in such tests around the fusion point to determine it accurately. This method, in which dark adaptation is maintained between tests, requires more time and is less precise than the other one, though more accurate than the standard electroretinographic method. Between every two readings a control measurement at the maximum (5000 or 5100 Å) was inserted in order to have the general sensitivity level under control.

RESULTS

Permanent dark adaptation

A number of spectral sensitivity curves were first determined by the criterion of fusion frequency, as described above, in order to be able to compare them with the human scotopic luminosity curve and with the cat's curve as obtained by standard electroretinographic procedures (Wirth, 1953). These two curves agree fairly well with each other, as well as with Gunter's (1952) scotopic sensitivity curve obtained by behaviouristic tests. There is also, as shown by Gunter and by Weale (1953*a*), good agreement with the scotopic dominator (Granit, 1947; Donner & Granit, 1948) after appropriate corrections for absorption in lens and cornea as well as for tapetal reflexion. Since the eye was intact it seemed natural to use the human scotopic luminosity curve of Stiles & Smith (1944) for basic comparisons.

In Fig. 2 the curve drawn in broken lines is the human scotopic luminosity curve. The black dots are from four animals using the criterion of fusion at constant frequencies between 15 and 21.2 flashes/sec; the circles and the curve drawn through them are from six animals at constant frequencies between 7 and 8 flashes/sec. On four of the animals, both fast and slow flicker were used. Contrary to expectation, the curve obtained at the higher fusion frequencies agreed the better with the human scotopic luminosity curve. The other one was shifted to the blue side. Neither curve could be said to be definitely narrower than the human luminosity curve. Minor variations in visual purples are not uncommon (see for example, Collins & Morton, 1950*a*; Dartnall, 1953).

Since it seemed contrary to our expectations that the sensitivity distribution should be different in this particular fashion for low and high fusion frequencies a number of tests were made with the wave-lengths 4600, 4800 and 5000 Å alone at frequencies of 4, 8, 12, 16, 20 and 22 flashes/sec, some of the highest values occasionally being left out. The blue shift of the curve had an optimum around 8 flashes/sec. Sometimes the shift was less marked, sometimes more definite.

The results at the time suggested that there was a specific resonance to blue-sensitive elements at values around 7-8 flashes/sec. This may be a specificity of some time-constants of excitation or merely due to a favourable balance between rates of v.p. destruction and v.p. renewal at these particular light and dark intervals. Some unknown properties of the method (alternans rhythms, etc.) may also be held responsible for the blue shift.

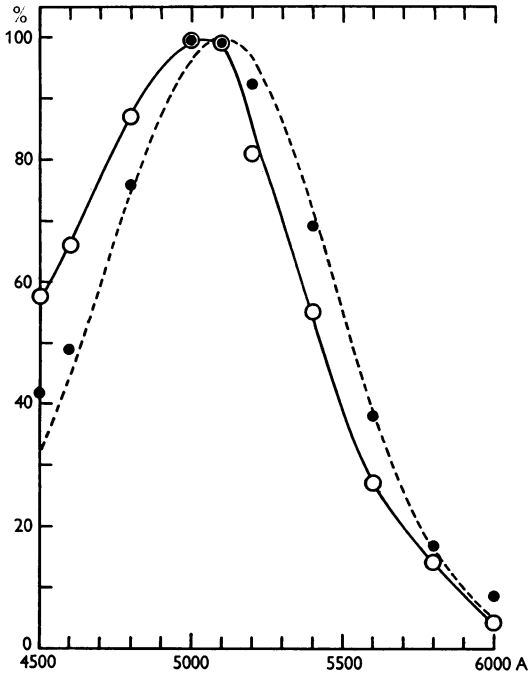


Fig. 2. Broken line (---) represents the human scotopic luminosity curve of Stiles & Smith (1944); \bigcirc — \bigcirc , averaged readings from six experiments at fusion frequencies of 7-8 flashes/sec, same from four experiments at fusion frequencies between 15 and 17 (3 animals) and 21.2 flashes/sec (1 animal).

As stated, the criterion of fusion with the resonance method lies above the value obtained by photographing flickering electroretinograms. This is partly a matter of sensitivity relative to useful amplification (see Methods), but the criterion itself may also be slightly different. The photographed fusion point has to be taken as the last value at which retinal flicker follows the flashes. At slightly higher values of intermittent illumination occasional wavelets drop out. The resonance method based, as it is, on the response of the needle of a slow galvanometer cannot respond to the disappearance of occasional responses when the method is used in this particular way.

Permanent flicker

The surprising discovery of a blue shift by the criterion of fusion at different flash frequencies applied to an eye kept in the dark was followed up by the method of permanent flicker which, of course, implies light adaptation to the stimulus. The possibility of alternans rhythms or missing responses will not

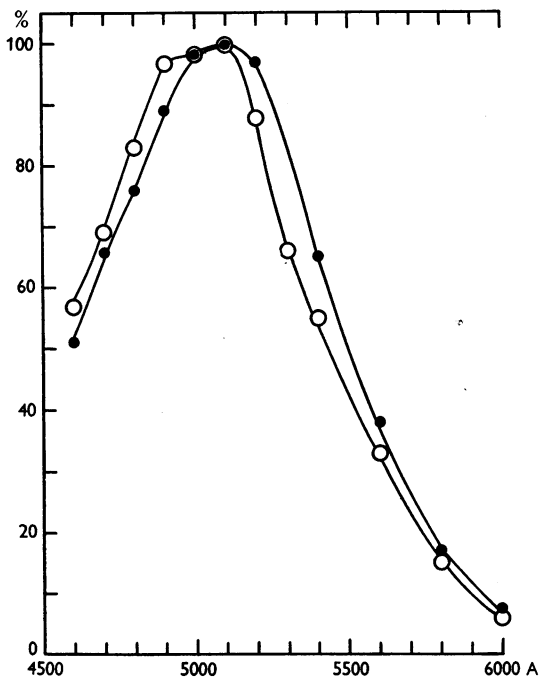


Fig. 3. ●, single readings for permanent flicker at 4 flashes/sec and constant deflexion on resonance meter; ○, same at 20 flashes/sec, except that the values for 4800 and 4600 Å are based on double readings.

enter with this method if one chooses a good deflexion of the resonance meter as the constant index to which the wedge has to be adjusted. The blue shift occurred again but now only at the higher frequencies.

Fig. 3 shows the result in a very satisfactory experiment on a decerebrate animal for 4 and 20 flashes/sec. All values, except two (see legend), were single settings of the wedge, and these were perfectly stable. The animal was equilibrated to the light adaptation involved (see below) in taking these two sets of readings. In this case the curve at 20 flashes/sec is shifted to the blue side and there is some indication of a little hump around 4900 Å, as if some other substance than the one responsible for the curve at 4 flashes/sec had been formed or merely risen above the threshold owing to the depression of v.p. sensitivity that occurred at the higher flicker rate.

Three decerebrate animals were studied systematically at increasing flicker frequencies. Wave-length 5000 Å was taken as 100%, the other wave-lengths being 4800 and 4600 Å. The results are put together in Table 1. In this table the level of sensitivity is also given by the logarithms of transmission ($\log T$) for wave-length 5000 Å. With this technique of permanent flicker and waiting

TABLE 1. Values for percentage sensitivity of the eye referred to wave-length 5000 Å, the general level of sensitivity being given in terms of the logarithm of transmission (T) of the same wave-length

	Flashes/sec						
	4	8	12	16	18	20	22
$\log T$	1.96	2.11	2.19	2.46	2.67	2.92	3.67
4800 Å	73	82	81	84	81	84	98
4600 Å	53	57	57	61	57	59	68
$\log T$	1.05	1.47	1.54	1.68	—	2.70	—
4800 Å	78	77	80	85	—	85	—
4600 Å	51	50	57	61	—	61	—
$\log T$	—	1.26	1.36	1.87	—	3.11	—
4800 Å	—	77	78	81	—	86	—
4600 Å	—	59	61	63	—	71	—

until a semi-stationary equilibrium had been established, the shift of the curves towards the blue end turned up at the higher frequencies suggesting that some light adaptation was necessary. This statement should be qualified by pointing out that the state of equilibrium is relative in that the sensitivity at the higher frequencies first drops quickly and then slowly. The curve at 20 flashes/sec was taken during the slow semi-stationary state. The results suggested that some light adaptation was essential for the blue shift to appear and that, inasmuch as some particular rate of stimulation was optimal, this may have been because of a favourable balance between breakdown and regeneration in the v.p. system.

Permanent slow flicker and light adaptation

The animal used in Fig. 3 was then exposed to light flickering at 4 flashes/sec, the relative level of sensitivity being 1.41 in terms of $\log T$ at 5000 Å. The filled circles in Fig. 4 are those of the curve of Fig. 3. Then the adaptation light was switched on and the level of sensitivity rapidly fell to $\log T = 2.62$. During the semi-stationary period the values at 4900, 4700 and 4600 Å were repeatedly taken with alternate control readings at 5000 Å in the usual fashion. The first set of values (○) was very high. Then sensitivity began to rise again, as often happened with some animals at certain adaptation intensities, while the work still went on. The next set of values (●) indicated a return towards the original readings although the level of sensitivity only had risen to $\log T = 2.52$. The values in the long wave-lengths were all taken in the later phase of the experi-

ment. Clearly it is impossible to take as many readings as one would like, even though the change in sensitivity is a fairly slow creep giving enough time to establish a few points accurately between tests with 5000 Å run as control.

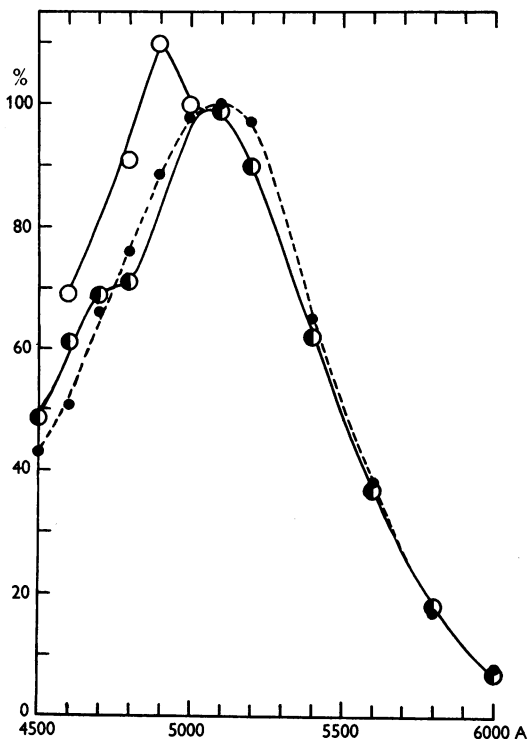


Fig. 4. ● - - - ●, curve from Fig. 3 taken at 4 flashes/sec; ○—○, early values after some light adaptation; ◐—◐, later values all recorded in permanent flicker at 4 flashes/sec, as described in text, with 5000 Å run as control at 100%.

Fig. 5 is mainly devoted to wave-lengths 5000, 4800 and 4600 Å during light adaptation in permanent flicker at 8 flashes/sec. The filled circles are the original values before light adaptation. The other values have been taken between 0.5 and 17 min of light adaptation, the early values being represented by open, the later ones by half-filled circles, 5000 Å always being 100%. The early fast drop in level of sensitivity was modest. It has hitherto been given as $\log T$, but it is perhaps of some interest in one instance to use sensitivity, which is $1/T$. The early fast drop then was from 393 to 55 in relative units. There was no secondary rise in level of sensitivity during the time the readings were taken.

DISCUSSION

It is clear then that, against expectation, it is impossible to demonstrate in the average response a narrowing of the v.p. curve or a definite red shift in modest light adaptation. There is, on the contrary, a blue shift which is large enough

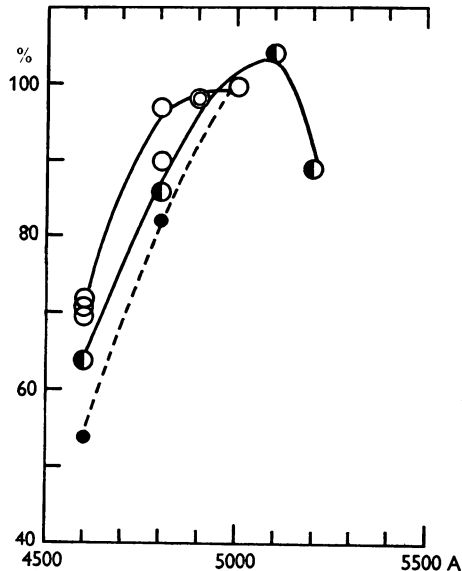


Fig. 5. As Fig. 4, but permanent flicker at 8 flashes/sec; ● - - - ●, readings in the fully dark adapted state; ○ — ○, immediately after slight light adaptation; ● — ●, later in light adaptation.

to express itself in the flickering electroretinogram. Very often this phenomenon is transitory but occasionally, at a suitable rate of flicker, it seems possible to establish a permanent blue shift, as in the first experiments using fusion frequency and full dark adaptation. It is difficult to say more about this phenomenon than that it proved feasible to bring it under some control and make it repeatable. Permanent flicker in the upper rod range of fusion frequencies alone, as well as permanent flicker in the lower rod range, if supported by some light adaptation, brought it forth in all experiments in which these procedures were tried. It might be added that it is doubtful whether any other method of measuring average sensitivity is fast and sensitive enough for this purpose. It is thus also concluded that the resonance method has emerged successful from its first trial on a specific problem.

What does the blue shift signify? In the first instance, perhaps, some relation between visual purple and blue-sensitivity, emphasized repeatedly by one of us in several papers (summarized by Granit, 1947). A hypothesis accounting

for the results will have to satisfy the following facts: (i) that the curve is shifted bodily to the blue side, (ii) that the shift appears to be of the order of only 100–150 Å, (iii) that in slight light adaptation the phenomenon is transitory and (iv) that it seems involved in a complex fashion in the phenomena of breakdown and regeneration of rhodopsin. In view of what is known about these processes, as studied in test-tubes, the substance may well be the *isorhodopsin* of Collins & Morton (1950*b*) of which Hubbard & Wald (1952) say that it 'has as yet no status in the living organism, and must for the present be regarded as an artefact' (p. 307). Its absorption maximum is given by the former authors as 4920 Å, by the latter as 4870 Å. Our suggestion implies that also in the living eye breakdown products of rhodopsin can regenerate both to *isorhodopsin* and the parent substance, visual purple itself. But we do not at the moment think this view the only one possible, merely highly plausible.

Our results run counter to notions based on blue-absorbing degradation products of visual purple serving as filters because these would cause red shifts. They are also of some interest in view of the recent method developed by Rushton (1952) for measuring v.p. concentration in the living eye by light reflected from the retina. It is known (Granit *et al.* 1938; Granit, Munsterhjelm & Zewi, 1939) that there may be considerable reductions in retinal sensitivity as measured electroretinographically without any equivalent reductions in v.p. concentration studied by timed extractions. The recent results based only on measurements by reflexion (Rushton, 1952; Hagens & Rushton, 1953) support the old work. If v.p. blue shifts of a transitory nature occur they may also signify the formation of fresh labile blue-sensitive systems (e.g. the pigment 467 of Dartnall, 1952) as v.p. sensitivity is depressed. In this case the postulated transient material, if the shift is small, may well be mistaken for visual purple if measured by reflexion.

Finally, it is interesting to recall that peripheral vision and vision in the dark have long been held to favour blue hues (see, for example, summary, Granit, 1947). This is again emphasized by the recent psychophysical results of Weale (1953*b*). Also, the rod-dominated eye of the guinea-pig is well provided with blue sensitive elements obtainable by the micro-electrode technique. These facts will also have to be considered but can hardly be accounted for by an explanation based on the assumption that *isorhodopsin* is formed in the living eye.

SUMMARY

1. A new method is described whereby flicker electroretinography for quantitative purposes is considerably improved by recourse to electrical resonance in order to emphasize any desired frequency of flicker within the rod and cone range.

2. It is used in the paper in order to measure the scotopic sensitivity distribution in the spectrum of the dark-adapted cat eye before and after modest light adaptation.

3. At certain flicker frequencies, the values depending upon how the resonance method is applied, the scotopic sensitivity distribution is found to be slightly shifted towards the blue end of the spectrum.

4. Light adaptation of the order used, so far from diminishing the width of the visual purple distribution of sensitivity, on the contrary causes a shift of the whole curve towards the blue end of the spectrum. This is in the opposite direction to the Purkinje shift.

5. A brief discussion is given of the known theoretical possibilities for obtaining 'blue shifts' large enough to influence an average response such as the electroretinogram.

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REFERENCES

- COLLINS, F. D. & MORTON, R. A. (1950*a*). Studies on rhodopsin. 1. Methods of extraction and the absorption spectrum. *Biochem. J.* **47**, 3-10.
- COLLINS, F. D. & MORTON, R. A. (1950*b*). Studies in rhodopsin. 3. Rhodopsin and transient orange. *Biochem. J.* **47**, 18-24.
- DARTNALL, H. J. A. (1948). Visual purple and the photopic luminosity curve. *Brit. J. Ophthalm.* **32**, 793-811.
- DARTNALL, H. J. A. (1952). Visual pigment 467, a photosensitive pigment present in tench retinae. *J. Physiol.* **116**, 257-289.
- DARTNALL, H. J. A. (1953). The interpretation of spectral sensitivity curves. *Brit. med. Bull.* **9**, 24-30.
- DODT, E. (1951*a*). Cone electroretinography by flicker. *Nature, Lond.*, **168**, 738.
- DODT, E. (1951*b*). Elektroretinographische Untersuchungen zur Analyse des Flimmerphänomens in menschlichen Auge. *Ber. dtsh. ophth. Ges.* 242-245.
- DODT, E. & ENROTH, CH. (1953). Retinal flicker in the cat. *Acta physiol. scand.* (in the Press).
- DONNER, K. O. & GRANIT, R. (1948). Scotopic dominator and state of visual purple in the retina. *Acta physiol. scand.* **17**, 161-169.
- ENROTH, CH. (1952). The mechanism of flicker and fusion studied on single retinal elements in the dark-adapted eye of the cat. *Acta physiol. scand.* **27**, Suppl. 100, 7-67.
- ENROTH, CH. (1953). Spike frequency and flicker fusion frequency in retinal ganglion cells. *Acta physiol. scand.* **29**, 19-21.
- GRANIT, R. (1935). Two types of retinae and their electrical responses to intermittent stimuli in light and dark adaptation. *J. Physiol.* **85**, 421-438.
- GRANIT, R. (1947). *Sensory Mechanisms of the Retina*. London: Oxford University Press.
- GRANIT, R., HOLMBERG, T. & ZEWI, M. (1938). On the mode of action of visual purple on the rod cell. *J. Physiol.* **94**, 430-440.
- GRANIT, R., MUNSTERHJELM, A. & ZEWI, M. (1939). The relation between concentration of visual purple and retinal sensitivity to light during dark adaptation. *J. Physiol.* **96**, 31-44.
- GUNTER, R. (1952). The spectral sensitivity of dark-adapted cats. *J. Physiol.* **118**, 395-404.
- HAGINS, W. A. & RUSHTON, W. A. H. (1953). The measurement of rhodopsin in the decerebrate albino rabbit. *J. Physiol.* **120**, 30*P*.
- HUBBARD, R. & WALD, G. (1952). Cis-trans isomers of vitamin A and retinene in the rhodopsin system. *J. gen. Physiol.* **36**, 269-315.
- LYTHGOE, R. J. (1937). The absorption spectra of visual purple and of indicator yellow. *J. Physiol.* **89**, 331-358.

- LYTHGOE, R. J. & QUILLIAM, J. P. (1938*a*). The thermal decomposition of visual purple. *J. Physiol.* **93**, 24-38.
- LYTHGOE, R. J. & QUILLIAM, J. P. (1938*b*). The relation of transient orange to visual purple and indicator yellow. *J. Physiol.* **94**, 399-410.
- RUSHTON, W. A. H. (1952). Apparatus for analysing the light reflected from the eye of the cat. *J. Physiol.* **117**, 47*P*.
- STILES, W. S. & SMITH, T. (1944). A mean scotopic visibility curve. *Proc. phys. Soc. Lond.* **56**, 251-255.
- WALD, G. (1951). The chemistry of rod vision. *Science*, **113**, 287-291.
- WEALE, R. A. (1953*a*). The spectral reflectivity of the cat's tapetum measured *in situ*. *J. Physiol.* **119**, 30-42.
- WEALE, R. A. (1953*b*). Spectral sensitivity and wave-length discrimination of the peripheral retina. *J. Physiol.* **119**, 170-190.
- WILLIAMS, F. C. & UTTLEY, A. M. (1946) The velodyne. *J. Instn elect. Engrs*, **93**, pt. 3A, 1256-1274.
- WIRTH, A. (1953). Electroretinographic evaluation of the scotopic visibility function in cats and albino rabbits. Proc. Symp. on physiology and pharmacology of receptors, Stockholm, December 1952, *Acta physiol. scand.* **29**, 22-30.