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# **The Photopic Spectrum of the Pigeon.**

By

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In a number of papers in this Journal (GRANIT, 1941—1942) I have described the spectral properties of receptors of different retinae, analyzed with the micro-electrode technique first used by GRANIT and SVAETICHIN (1939) with the frog's eye. In some types of retinae isolated elements have been obtained without difficulties, in others simultaneous activity of several units has been the rule. The eye of the pigeon belongs to the latter type, in fact, so much so that I never have succeeded in obtaining a restricted response from this retina with the same micro-electrodes which have given large single spikes from eyes of rats, guinea pigs, and cats, less regularly, well isolated spikes even from frogs which are not so favourable preparations as the mammals mentioned. It is tempting to believe that the ultimate cause behind this fact is that convergence towards the optic nerve, where recording takes place, is far less prominent in the pigeon's eye (CHIEWITZ, 1889) than in the others. This eye has both rods and cones but is dominated by cones (SCHULTZE, 1866).

The fact that a reasonable degree of isolation of the colour-sensitive elements could not be obtained with the pigeon prevented a detailed analysis of their spectral properties. Only the average photopic spectrum of the pigeon's eye has been obtained.

### **Methods.**

The pigeons were anaesthetized with a solution of 0.1 cc Avertin in 1.0 cc urethane (emulsion). About 0.4 cc of this mixture was injected intraperitoneally. The head was fixed with pins, cornea and lens re-

moved, and the micro-electrode inserted under the preparation microscope. Spontaneous activity was mostly present. The discharge to illumination consisted of massed impulses, amplified and led to cathode ray and loudspeaker. The threshold was determined in the different wave-lengths by listening to the discharge and observing it on the screen. The inverse value at the threshold was calculated in per cent of the maximum.

### Results.

The pigeons were light-adapted for 10—20 min. to the microscope lamp (2,400 m.c.) after which the return of sensitivity was followed for a number of wave-lengths. As in all other animals with both rods and cones the recovery of sensitivity followed in two steps, a first slowly rising phase during which the absorption of the cone system dominated, and a second phase during which a rapid and large rise of the sensitivity ( $1/\text{energy}$ ) took place. The latter phase led to a particularly great increase in the region of  $0.500 \mu$ . This change has been illustrated in previous work (GRANIT, 1941 b, 1942 a). Suffice it here to take 2 curves which also illustrate variations in a single experiment. These are shown

in fig. 1. The curve to the right was obtained immediately after light-adaptation but dark-adaptation was already making itself felt in the short wave-lengths before the experiment was completed. Somewhat later in the same experiment the whole curve has shifted to the left. Thus the pigeon has a Purkinje shift. Nevertheless it sometimes happens that the electrodes pick up the discharge from a region which does not

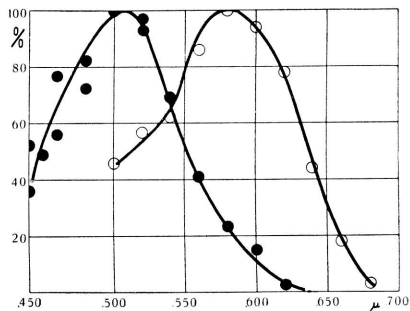


Fig. 1. Single experiment. Initially light-adapted pigeon first gave photopic distribution (open circles), later scotopic distribution of sensitivity (filled circles). Equal energy spectrum.

dark-adapt in this manner but merely slowly and moderately increases in sensitivity, the photopic distribution in the spectrum all the time remaining constant. One has probably then struck a rod-free area. In the rod-free eye of the Greek tortoise (GRANIT, 1941 a) all places behave in this manner. But in the pigeon

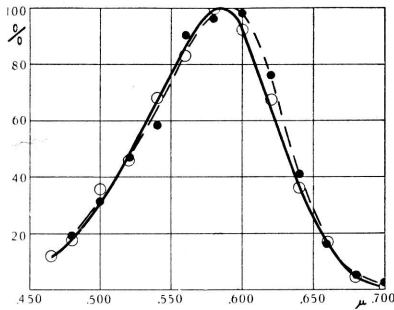


Fig. 2. Two experiments with light-adapted pigeons. Recording from places in the retina which did not dark-adapt in the course of the experiment. Equal energy spectrum.

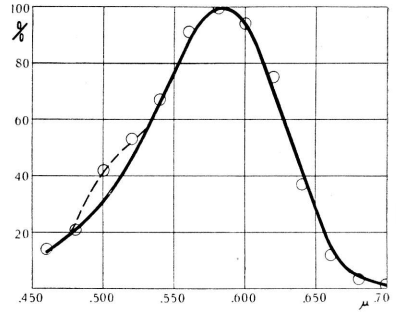


Fig. 3. Averages of 372 values from 27 series obtained from 20 light-adapted pigeons. Incipient dark-adaptation indicated by broken line. Spectrum of equal quantum intensity.

dark-adaptation as a rule begins after about 15—20 min. to affect the spectral distribution of the photopic eye. The beginning of this process is already found in the photopic curve of fig. 1.

These facts deserve to be pointed because methods based on training the animals, on pupillary reactions etc. cannot keep incipient dark-adaptation in check as well as the very much faster electro-physiological technique. The photopic maxima obtained by such methods can therefore easily become mixtures of photopic and scotopic curves. A photopic curve published by LAURENS (1923) with maximum in  $0.564 \mu$  is probably influenced by dark-adaptation.

In fig. 2 is illustrated two single experiments in which the increase in the short wave-lengths is absent. The maximum is found to be around  $0.580 \mu$ , or  $0.020 \mu$  further to the right than in the frog's eye.

We can then proceed to average the 27 series obtained from 20 pigeons, together based on 372 averaged values and a much greater number of individual readings. This curve, plotted against a spectrum of equal quantum intensity, is shown in fig. 3. The values are somewhat too high around  $0.500 \mu$  owing to the fact that it has not always been possible to avoid incipient dark-adaptation. Despite this the maximum must be placed around  $0.580 \mu$ . I should perhaps add that, excepting the easily recognizable tendency of the curves to be influenced by incipient dark-adaptation, I have never seen any animal in which the same photopic spectral distribution from case to case has recurred with such monotonous

regularity as the pigeon. Probably the reason for this is the great number of units that always were found to be simultaneously recorded. Every single curve is thus an average in itself.

### **Anomalous Nature of Purkinje Shift of the Pigeon.**

One of the main conclusions suggested by my analysis of the colour receptors with microelectrodes (cf. esp. GRANIT, 1942 a) is that animals with good colour vision always have a broad dominator band of spectral sensitivity and a number of narrow and steep modulator bands in different regions. I have assumed (GRANIT, 1941 c) that the broad dominator band mediates the perception of white and that the modulators serve to modulate this impression to colour by emphasizing their own spectral regions when stimulated. The broad band, which in the frog (GRANIT, 1942 a) and in the cat (GRANIT, 1942 unpublished) also is served by isolated units is the "carrier" of the Purkinje shift. For the system activated by visual purple in scotopic vision (maximum around  $0.500 \mu$ ) the photopic carrier of the Purkinje shift in frogs, cats and, to all appearance, also in man has its maximum around  $0.560 \mu$ . How are we now to understand that in the pigeon the dominator band, which in all animals is identical with the average photopic spectrum, turns up shifted  $0.020 \mu$  to the right with maximum around  $0.580 \mu$ ?

There is, to begin with, no reason whatever to assume the visual purple of the pigeon to be different from that of the frog. Beyond the single set of readings in fig. 1 I have not made any systematic observations on dark-adapted eyes, for the simple reason that GRAHAM, KEMP and RIGGS (1935) already have provided such data with the electroretinogram as index. LAURENS (1923), utilizing the pupillary reaction, and GRAHAM, KEMP and RIGGS have come to the conclusion, supported also by my observations, that the scotopic photosensitive system reproduces the absorption curve for visual purple. Visual purple has been extracted from the eye of the pigeon already by HESS (1912).

Why then this apparent exception from what seems to be a rule, namely, that when the visual purple is of the type with maximum around  $0.500 \mu$ , then the photopic dominator substance has its maximum around  $0.560 \mu$ ? Rather than to announce an exception from this rule, before compelled to do so by overwhelming evidence,

I would suggest that the difference is due to selective absorption by the intensely coloured oil globules of this eye. My assumption can be well supported by evidence.

The oil globules, discovered by HANNOVER (1840, 1843), were found by KÜHNE (1879) to consist of the red rhodophane, the yellowgreen chlorophane, and the orange xantophane. Their spectra have been determined by KRAUSE (1934), WALD and ZUSSMAN (1937) and by v. STUDNITZ and BUSCH (1941) in extracts

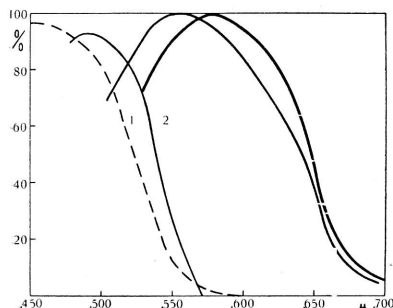


Fig. 4. *To the right:* HONIGMANN'S (1921) photopic curves for light-adapted chicken replotted on a percentage basis. The curve with maximum in  $0.560 \mu$  refers to young animals, the one with maximum in  $0.580 \mu$  to grown-up animals.

*To the left:* Absorption by the oil globules according to v. STUDNITZ and BUSCH (1941). 1, extract on all coloured droplets; 2, xantophane alone.

in  $0.560 \mu$ , the fully grown animals, however, gave one with maximum around  $0.580 \mu$ . His curves are shown redrawn in percent of the maximum to the right in fig. 4.

Now it is hardly probable that the photochemical substance has altered with age. His suggestion, that the density of the coloured filters has increased is altogether more reasonable. Their absorption maxima depend somewhat upon the solvent (see *e. g.* WALD and ZUSSMAN, 1937). I have inserted in fig. 4 two schematic curves, based on the data of v. STUDNITZ and BUSCH (1941), one for xantophane and the other for all substances extracted together with ether. It is clear that these filters tend to cut down sensitivity in the medium and short wave-lengths thereby pushing the photopic curve towards the red side. This gives a satisfactory explanation of the difference in the photopic curve of the pigeon as compared with the one found in frogs, cats and man.

from chicken retinæ which possess the same droplets as the pigeon's retina. With the chicken there have also been carried out important experiments by HONIGMANN (1921) on the scotopic and photopic sensitivity distribution, one of the few papers on such subjects in which adequate training methods have been combined with adequate physical technique. He found in the dark-adapted state the distribution required by visual purple. In the light-adapted state the young animals were found to give a photopic curve with *maximum*

WALD (1937) claims to have isolated from the eye of the chicken a substance which he calls »iodopsin» and assumes to be the cone substance with maximum in  $0.580 \mu$ . Quite apart from the fact that its spectrum cannot be regarded as settled by the work referred to, one would also like to reserve judgment as to the existence of this substance until further evidence has been presented.

### Colour Vision of the Pigeon.

From the work of HAMILTON and COLEMAN (1933) we know that the pigeon has good colour vision, a conclusion which also is suggested by the presence of a Purkinje shift. It is regrettable that technical difficulties have prevented a study of restricted units of activity in this animal, but to judge from experiments on other animals with colour vision (GRANIT, 1941—1942) the broad dominator band of this eye must also be modulated by narrow bands in different regions. Perhaps the oil globules add somewhat to the differentiation obtainable by these means.

### Summary.

The precise form of the photopic spectrum of the pigeon has been measured with the electrophysiological technique used with other animals in previous contributions to this problem.

The filtering effect of the coloured oil globules has been discussed in relation to the photopic spectrum.

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