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THE SPECTRAL SENSITIVITY OF THE PIGEON'S RETINAL ELEMENTS

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Spectral sensitivity curves for the pigeon have been determined during both dark- and light-adaptation by various methods. In the scotopic state Laurens (1923) analysing the pupillary reaction, Graham, Kemp & Riggs (1935) using the electroretinogram as an index, and Granit (1942) working with the microelectrode, have provided data showing the similarity between the scotopic sensitivity curve and the absorption spectrum of visual purple, the presence of which in the pigeon's retina had earlier been demonstrated by Hess (1913). Under photopic conditions the eye is maximally sensitive at 5800 Å, a displacement of 200 Å towards the red end of the spectrum as compared with the corresponding curves of several other vertebrates (Granit, 1947). This displacement has been recorded both in training experiments on hens (Honigmann, 1921) and in electro-physiological work using the optic nerve discharge as an index (Granit, 1942). The diminished sensitivity at short wave-lengths has been explained as due to the selective absorption of the coloured oil globules of the cones. Schultze (1866), had earlier pointed out their possible significance for vision since they are placed as filters in front of the light-sensitive external limbs of the cones. Since the scotopic sensitivity of the pigeon's retina reproduces the visual purple curve there is, according to Granit (1942), no reason to believe that the observed shift in the spectral location of photopic sensitivity is caused by differences in the photochemical substances involved but rather is explained by the absorbing action of the oil globules.

Granit (1942) recorded from the pigeon's retina only the massed discharge from a great number of elements. In the photopic state he always got the broad dominator curve. However, Hamilton & Coleman (1933) showed that the pigeon has good colour vision which led Granit to assume that narrow modulator bands must be present in this eye too. The experiments described in the present paper were carried out in order to test this hypothesis and to examine in more detail the effect of the coloured globules.

METHODS

The general arrangement of the experiments was the same as used by Granit in his micro-electrode investigations on the retinae of various animals (cf. Granit, 1947).

The pigeons were anaesthetized with 3–4·5 ml. of 20% urethane given intraperitoneally. The head was rigidly fixed with pins to a large piece of cork provided with an excavation to suit the head. Cornea and lens were removed from the eye and the micro-electrode inserted with a Zeiss slide micro-manipulator. The micro-electrodes used were of the type described by Svaetichin (1951); silver solder drawn out in glass tubes to the diameter wanted. It was found that electrodes with a tip diameter of about 10 μ were the most suitable for the present purpose; finer ones were also tried.

The recording equipment consisted of a condenser-coupled amplifier with a direct coupled cathode-follower input stage, cathode-ray and loudspeaker stage.

As light source a 200 W microscope lamp (125 V d.c.) was used, the constancy of the current being controlled by an ammeter (accuracy 1%) and a suitable slide resistance. Practically monochromatic light was obtained by the use of metal-interference filters (Schott and Gen.), inserted in the light beam made parallel by a collecting lens and provided with a photographic shutter. The transmission maxima and the corresponding band-widths of the filters (difference in Å between the wave-lengths with 50% of max. transmission) are given in Table 1. The intensity of the stimulating light was adjusted by means of a neutral wedge and neutral filters of known density. Finally, the light was focused on the opened eye of the pigeon through a system of lenses and mirrors that could be adjusted for each experiment separately. The intensity of the light at different wave-lengths and for different wedge settings was calibrated with a photocell of accurately known spectral sensitivity and a suitable galvanometer.

TABLE 1. Spectral properties of metal interference filters used

Wave-length of max. transmission (Å)	Band-width (Å)
4180	125
4410	160
4620	104
4790	95
5030	140
5250	120
5430	88
5580	125
5820	81
5960	120
6130	50
6380	170
6790	220

Generally the pigeons were left to dark-adapt 1–2 hr after the operation or were light-adapted with white light (1500 m.c.) from the microscope lamp. When the experiment was started the electrode was pressed down until it touched the retina and a response to light was obtained. Even with 10 μ electrodes the first discharge recorded was always composed of a great number of active units, the spikes being very small in size. When the electrode was pressed further down fairly large (20–50 μV) spikes were recorded and the discharge was restricted to a single or only a few active units. The probable explanation of this is that the micro-electrode first recorded the discharge from the layer of nerve fibres passing to the optic nerve on the surface of the retina and when pressed down struck one or a group of the ganglion cells present in the following layer. In fact the giant ganglion cells have been shown by Rushton (1949, 1953) to produce the discharge recorded with micro-electrodes from the retina of the cat. If isolation was satisfactory the threshold measurements were started. Light flashes of about 2 sec duration were used, the photographic shutter being operated by hand. The wave-lengths were always taken in a random order. Wave-lengths of 5030 or 5820 Å were used as reference points to check fluctuations in the general sensitivity of the element investigated (Donner & Granit, 1949). Small changes in thresholds with the reference wave-length were corrected for; experiments with large and rapid fluctuations were rejected.

In all, thirty-six pigeons were used for the experiments.

RESULTS

General observations

The usual type of discharge recorded when the electrode had been successfully inserted is shown in Fig. 1, which also shows the average degree of isolation obtained in these experiments. The record shows discharges in response to a light flash of about 2 sec duration from the same light-adapted element at relative intensities 0·05 and 1·5 (5820 Å). The threshold of the on-effect was at 0·035. The size of the spikes corresponds to 20–25 μV. All elements recorded were of this type giving both on- and off-effects. Usually the sensitivity of the components was approximately the same both during light- and dark-adaptation. This is clearly seen in Fig. 1 which also shows that an increase in the intensity of the stimulating light did not to any great extent rebalance the on- and off-effects as, for instance, recorded in the dark-adapted cat's retina (Granit, 1944; Donner & Willmer, 1950). Although the record in Fig. 1 is taken from a light-adapted eye, dark-adapted elements behaved in an essentially similar manner. This is probably due to the dominance of the cones in those parts of the retina investigated (the electrode was always placed as centrally as possible).

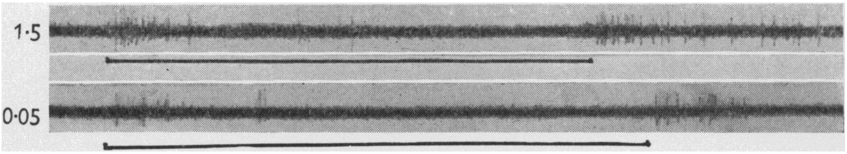

Fig. 1. The discharge of a typical element of the pigeon's retina at the relative intensities 0·05 and 1·5. Wave-length 5820 Å, light-adaptation. Black line below records indicates period of illumination = approximately 2 sec.

Spontaneous activity was rarely present; it was noted that in those cases where it occurred the reason probably was the pressure exerted by the electrode. This absence of spontaneous activity made it uncertain whether the element in question was still under the electrode during darkness. This often led to the loss of the element.

It cannot, of course, be definitely stated that the type of discharge shown in Fig. 1 (large spikes) was actually produced by single active units. It is, however, likely that most of the experiments refer to the properties of single elements since at the threshold it was always much easier to discriminate between a few relatively large spikes and the small impulses in the background; especially when a loudspeaker stage making it possible to cut off the small impulses was used. At higher intensities these, due to their great number, tended to disturb the record much more. Of course Granit's (1947, p. 304) remarks on the certainty with which a given record may be said to represent the discharge of a single unit apply to the present experiments too.

Massed discharge from the dark-adapted retina

It is known from previous work (Laurens, 1923; Graham *et al.* 1935) that the overall sensitivity of the pigeon's retina in the scotopic state is governed by visual purple. This provided a means of checking the reliability of the calibrations and of investigating if metal interference filters could be successfully used instead of a monochromator. Thus some experiments were performed with dark-adapted eyes and electrodes having a tip diameter of 30μ, recording the discharge from a great number of active units. The averaged results from four such determinations are given in Fig. 2 (circles) and compared with the visual purple absorption curve as given by Hecht, Shlaer & Pirenne (1942). The agreement is satisfactory, although there is a slight tendency towards higher values in the yellow and red parts of the spectrum. This may be explained as due to some influence of the numerous cones. It can thus be stated that the apparatus and the experimental procedure used were able to produce results with an accuracy sufficient for experiments of this type.

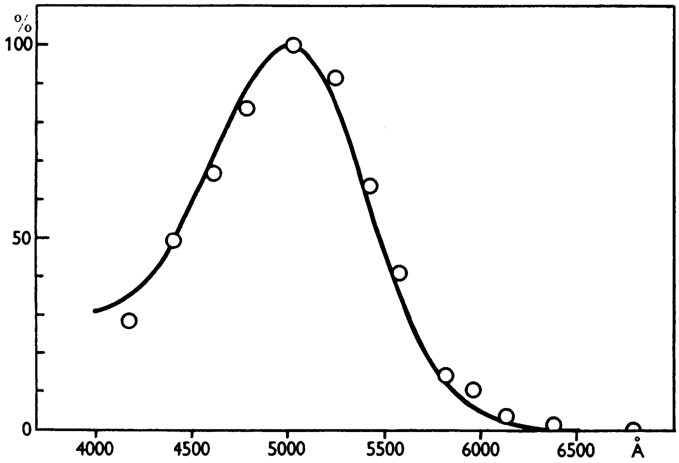

Fig. 2. Scotopic sensitivity of massed discharge (circles) as compared with the visual purple absorption curve given by Hecht *et al.* (1942) (full line). Average of four experiments. Equal quantum intensity spectrum.

The spectral sensitivity of single elements

In the great majority of elements sensitivity curves other than that of visual purple were obtained; also in the dark-adapted state. In a few cases the elements showed a maximum sensitivity at 5000 Å, but the curve was generally narrower than that shown in Fig. 2. Such sensitivity curves were also recorded by Donner & Granit (1949) from the dark-adapted cat's eye. Granit (1941 *a*) describes modulator curves from the retina of the rat with their maximum at 5000 Å and probably due to the activity of rods.

It is not surprising that visual purple curves were so rarely obtained from isolated elements when the electrode was placed in the central parts of the retina. The situation is quite different when recording the discharge from a great number of units where the more sensitive components—the rods—must be expected to determine the sensitivity. Furthermore, in the latter experiments the discharge probably originated from the more peripheral parts of the retina where the rods are more numerous. This was because the discharge from the nerve fibres passing from the periphery to the optic nerve on the surface of the retina were probably recorded when larger electrodes are used.

It soon became evident that two main types of sensitivity curves were the ones most commonly obtained, both in the photopic and scotopic states: (*a*) broad curves with their maximum sensitivity around 5800–5900 Å, and (*b*) sensitivity curves with one or more narrow peaks located with a few exceptions either at 4800, 5400–5500 or 5900–6100 Å (Table 2).

The broad curves closely resembled the photopic dominator curve recorded by Granit (1942) usually from light-adapted retinae but also during dark-adaptation. The main difference consisted in the occurrence of humps in the regions of modulator activity. Fig. 3 gives the average of three typical elements, two of them from a light-adapted retina and one during dark-adaptation. The broken line gives the average curve of Granit (1942). It is probable that the humps on the dominator curves as seen in the case of single elements are obscured when recording the average photopic sensitivity of the retina thus explaining the difference observed. An irregular dominator curve was also obtained by Granit (1943) when recording the spectral sensitivity of isolated elements in the light-adapted retina of the cat. Granit (1945) points out that the irregularity can be explained on the assumption that the dominator represents the sum of modulator activity.

The other type of sensitivity curves recorded in the present experiments were much narrower than those described above—typical modulator curves in Granit's terminology. In most elements only one narrow peak of this type was recorded, but curves with two or even three peaks were also obtained. Three typical curves obtained from single elements are shown in Fig. 4. The middle curve (◑ - - - - ◑) was recorded during light-adaptation, the other two during dark-adaptation. The curve with its maximum around 6000 Å shows the simplest type of curve recorded. In dark-adapted eyes a small hump around 5000 Å was often seen (e.g. Fig. 4, left curve). Again, during light-adaptation there was a certain tendency towards an increased sensitivity at 5500–6000 Å that may be explained as the influence of the photopic dominator. A curve of this type is the middle curve in Fig. 4. This was one of the few experiments in which the spike could be maintained so long that it was possible to record the sensitivity both during dark- and light-adaptation. In

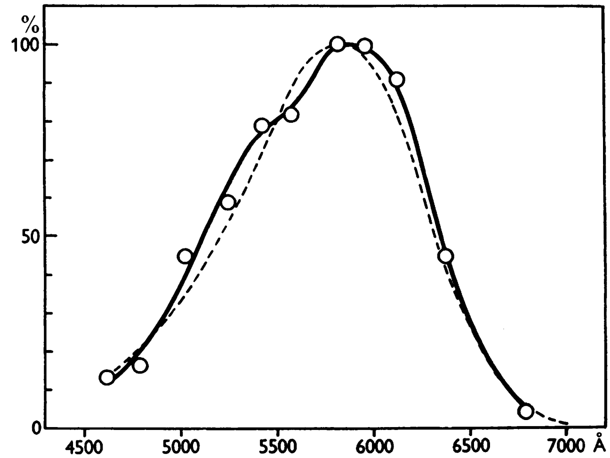

Fig. 3. Average of three elements giving the photopic dominator response (○——○) as compared with the averaged curve for pigeons determined by Granit (1942) (- - - - -). Equal energy spectrum.

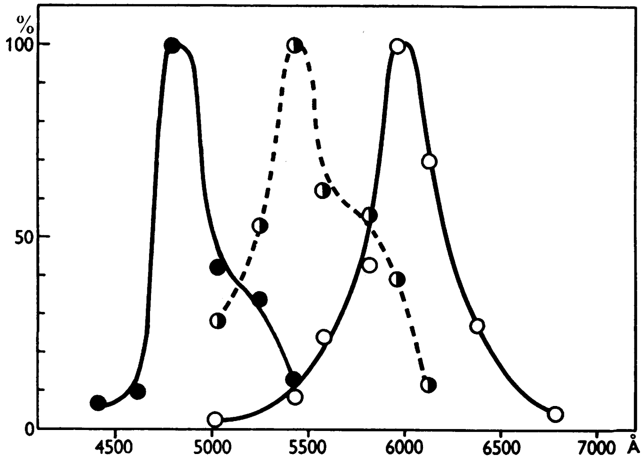

Fig. 4. Typical modulator curves obtained from single elements. The middle curve (◑ - - - ◑), recorded during light-adaptation, the other two during dark-adaptation. Equal energy spectrum.

the dark-adapted state the sensitivity curve had a secondary hump at 5000 Å which disappeared during light-adaptation. Instead a new hump turned up as shown in Fig. 4. The maximum sensitivity was, however, not shifted by the light-adaptation but remained at 5430 Å.

Another characteristic feature was the asymmetrical shape of the curves as, for instance, is well illustrated in Fig. 4, left curve. Thus the sensitivity of the elements often decreased much more rapidly towards the short wave-lengths than towards the red end of the spectrum.

TABLE 2. Occurrence of modulator maxima in experimental material

Wave-lengths used	Dark-adaptation	Light-adaptation	Σ
4180	—	—	—
4410	1	2	3
4620	2	—	2
4790	4	3	7
5030	—	—	—
5250	3	3	6
5430	6	4	10
5580	3	2	5
5820	1	1	2
5960	2	4	6
6130	3	2	5
6380	—	1	1
6790	—	—	—

It was found that narrow modulator curves like those shown in Fig. 4 were recorded both from light- and dark-adapted retinae and that they occurred mainly in three spectral regions. Table 2 gives the location of the maxima of all modulator peaks observed, irrespective of whether the same element showed one, two or three sensitivity maxima. It is obvious that the modulator peaks are grouped around the wave-lengths 4790, 5430 and 5960–6130 Å, and that there is no significant effect due to the state of adaptation. The dispersion of the peaks to other neighbouring wave-lengths does not, however, give a quite correct picture of the material concerned since in most cases where the sensitivity was highest at a wave-length next to, say 5430 Å, it was very nearly the same in the latter wave-length too, thus indicating that the actual sensitivity maximum was located somewhere between the two. Thus it was always easy to decide which of the three types a modulator unit belonged to. In addition it must be remembered that the curves with more than one peak are also included. In these cases the sensitivity maxima may have been slightly shifted by nervous interaction.

The modulator curves of the simple type shown in Fig. 4 have formed the basis for a further analysis. Elements of this type have been averaged and the results are given in Figs. 5–8, together with the spectral sensitivity of the modulators of the frog's retina (broken line) as determined by direct threshold measurements by Granit (1941 *b*). The frog modulators have the same spectral location as those found in the cat's retina (Granit, 1945, 1947) but the latter are somewhat narrower. Both eyes, in addition, give the same photopic dominator curve. The results from the frog's eye have, however, been chosen for comparison since the modulator units from the cat's retina were determined by experiments with selective adaptation while in case of the frog the same method as used in the present work was applied. Thus errors owing to different methods are less probable explanations of the divergent properties of the pigeon modulators as compared with those of other vertebrates.

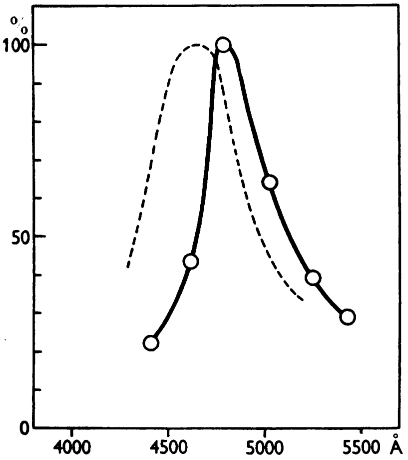

Fig. 5.

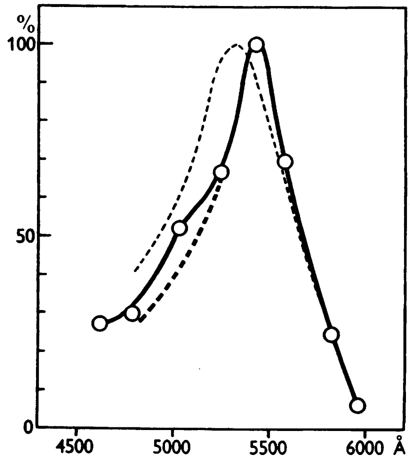

Fig. 6.

Fig. 5. Averaged curve for blue modulator (○——○). Four elements. Broken line in this, and Figs. 6–8 indicates modulator curves of frog (Granit, 1941*b*). Equal quantum intensity spectrum.

Fig. 6. Averaged curve for green modulator (○——○). Six elements. Equal quantum intensity spectrum.

Fig. 5 gives the average of four elements all recorded in the scotopic state. All four curves had their maximum at 4790 Å. As seen from Table 2, three modulator peaks at 4410 Å and two in 4620 Å were also obtained. These have all been seen in experiments where the curve recorded has been composite, giving other peaks as well. The curves maximally sensitive at 4620 Å closely resemble those giving a peak at 4790 Å in that the sensitivity at this wavelength is nearly as high as in 4620 Å, indicating that they are of same origin. Those curves again with a sensitivity maximum at 4410 Å give a low sensitivity to 4620 and 4790 Å, being thus clearly different in nature. Only three elements, however, show this property. The existence of a modulator unit in the pigeon's retina with its maximum sensitivity at approximately 4400 Å is thus indicated but cannot be definitely demonstrated on the basis of the present material. It may be mentioned that in the dark-adapted cat's retina

Donner & Granit (1949) were able to show the presence of a region of modulation around 4200 Å.

In Fig. 6 the average of six elements is given; two of them were recorded from a light-adapted eye and the rest during dark-adaptation. One of the light-adapted and two of the dark-adapted elements gave the maximum sensitivity at 5430 Å. Two elements had their maxima at 5580 Å but gave the relative sensitivities 97 and 81 % respectively at 5430 Å, thus indicating that the actual maximum was located somewhere between these two wave-lengths.

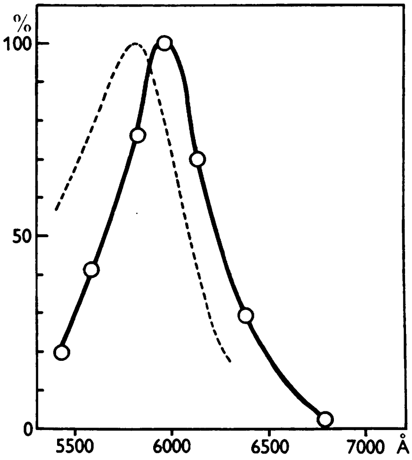

Fig. 7.

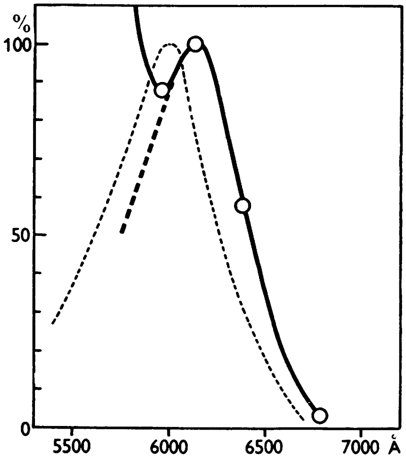

Fig. 8.

Fig. 7. Averaged curve for yellow modulator (O——O). Three elements. Equal quantum intensity spectrum.

Fig. 8. Averaged curve for secondary hump observed at 6130 Å. Six elements. Equal quantum intensity spectrum.

The last element had its peak at 5250 Å, but at 5430 Å the sensitivity was still 94 % of the maximum. It may thus be stated that although in this region modulator maxima in the experiments were found to occur at 5250, 5430 and 5580 Å they were relatively constant in position, the maximum probably being located between 5400 and 5500 Å. This circumstance is also illustrated by Fig. 6, the averaged curve being very narrow. The curve has a small hump at 5000 Å, which most probably is caused by rod activity. The broken line in this region indicates the assumed course of the pure modulator curve. This curve has been used when calculating the absorption of the coloured oil globules.

Fig. 7 gives the average of three elements, two of them light-adapted, and one dark-adapted. Two were maximally sensitive at 5960 Å and one at 5820 Å. The latter curve gave the relative sensitivity 95 % at 5960 Å. Excepting these elements averaged in Fig. 7, a secondary hump with its maximum at 6130 Å was observed in many elements with a more complicated sensitivity curve. It is uncertain whether these humps represent the activity of a modulator unit different from that in Fig. 7 or if the humps indicate the activity of the same unit but slightly shifted by nervous interaction. However, the curves in which such a secondary hump was seen (six elements) have been averaged in Fig. 8 with respect to the region 5800–7000 Å. From 5960 Å towards the short wave-lengths the curve rises strongly. On the assumption that the curve in Fig. 8 represents a separate modulator unit from that in Fig. 7 the broken line has been drawn to show the probable further course of the curve. Granit (1941*b*, 1945) was able to demonstrate both in the retina of the frog and of the cat two modulator units in the red and yellow region of the spectrum with spectral maxima at 5800 and 6000 Å respectively as shown in Figs. 7 and 8 (broken line). Secondly, when Figs. 5–8 are compared, it is seen that the pigeon's modulators are all displaced towards the red end of the spectrum, approximately 100–200 Å as compared with the corresponding frog modulators. This is also the case in Fig. 8. It is thus probable that the curves averaged in Fig. 8 demonstrate the presence of a modulator unit different from that shown in Fig. 7, although for some reason it has not been obtained in the isolated state as the other ones.

DISCUSSION

The experiments described above establish the existence in the pigeon retina of modulator units similar to those found in the retinae of other vertebrates (Granit, 1947), but displaced towards the red end of the spectrum by about 100–200 Å and often somewhat asymmetrical in shape with a steeper slope towards the short wave-lengths. It was stated above that the general shift of photopic sensitivity towards the long wave-lengths is probably due to the absorption of light in the coloured globules of the cones and not caused by any differences in the photochemical system involved. Assuming then that in threshold measurements as used here, nervous interaction is insignificant and that accordingly the modulator curves depict the properties of the receptors, it is possible to calculate what kind of an absorbing filter would be needed in order to change the modulator curves of the frog into those of the pigeon as recorded in the present work. This calculation has been performed using the averaged curves shown in Figs. 5–8. For this purpose the pigeon's modulators have first been reduced so that the ordinates in all parts of the spectrum are lower than or equal to the corresponding values of the frog modulators. Those wave-lengths where the ordinates of both curves are equal have been assumed to be unaffected by absorption. For other wave-lengths absorption has been calculated as the difference between the corresponding ordinates of both curves in percentages of the ordinates of the frog curves considering that the sensitivity curves give relative values for the reciprocal of light intensity used at threshold. Such a procedure gives the least absorption that must be postulated in order to account for the differences observed.

The results have been plotted in Fig. 9. Curve *A* corresponds to the 5960 and 6130 Å modulators (Figs. 7 and 8) the results for these two units being approximately the same. Curve *B* is calculated for the 5430 Å modulator (Fig. 6), and curve *C* for the 4790 Å modulator (Fig. 5). The absorption curves obtained from extracts of chicken retinae, as given by Wald & Zussman (1938) have been plotted for comparison. Kühne considered that these three substances were identical with the coloured components of the main types of oil globules present in avian retinae: red, yellow and green. There is a clear resemblance between curves *A* and *a*, and *B* and *b*. This is not, however, quite so clear in case of the *C* curves, although the maxima of both curves coincide.

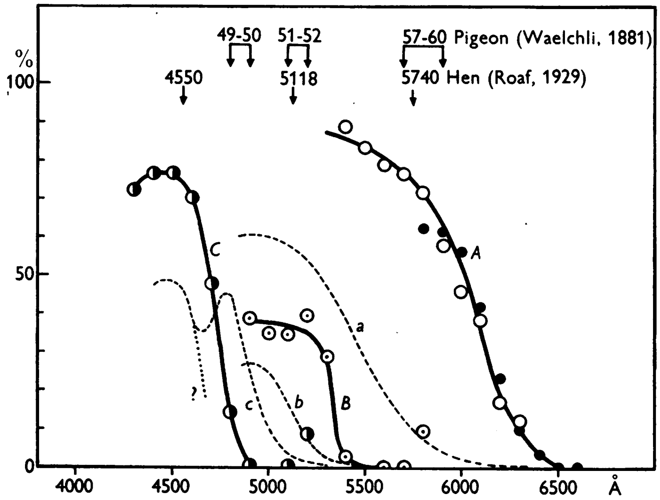

Fig. 9. Calculated absorption curves for the oil globules (full line) compared with Wald & Zussman's (1938) absorption curves (broken line) for the coloured substances extracted from chicken retinae. Above the curves results from measurements on oil globules by Roaf (1929) and Waelchli (1881). Full explanation in text.

At the top of Fig. 9 some results on microspectrophotometric measurements on coloured globules are given for the three main types corresponding to the three substances that can be extracted from the retina. The results of Waelchli (1881) refer to the pigeon and are based on a method of visual estimation. The wave-length region indicated refers to the region of steepest rise of absorption. Roaf (1929) used retinae of the domestic hen and determined by a microspectrophotographic method the shorter wave-margin of light transmitted. Blässer (1926) also made some determinations on the globules of the hen, and gives 6060 Å as the absorption margin for the red and 5270 Å for the yellow globules. All measurements on the globules agree in that the onset of absorption is restricted to a very narrow region of the spectrum. According to Waelchli (1881) the absorption rises very steeply within 100–200 Å. This agrees well with the absorption curves calculated and also with the fact that the modulator curves often seemed to be sharply cut off towards the short wave-lengths (cf. Fig. 4). Waelchli (1883) also points out that the colours of the globules are very constant, only the green type showing some variation.

The data presented above suggest that the assumption on which the calculation was based is essentially correct. This means that the present experiments lend further support to the view that the photochemical substances involved in vision are the same in the avian eye as in other visual purple vertebrate eyes. If this is true it is likely that the modulator curves recorded represent in a relatively pure state the sensitivity curves of the individual receptors, because if nervous interaction mainly determined the modulator curves the agreement between the calculated absorption curves and what is known from work on the coloured globules would probably have been obscured. The stability of the modulator maxima in different states of adaptation also supports this conclusion. Nervous interaction as the cause of the narrowness of the curves cannot, however, be excluded. Such interaction is known to occur (Granit, 1948, 1949) at least at higher levels of stimulation. It can also be supposed to have about the same effect on the modulator curves of the frog as on those of the pigeon, thus making it possible to calculate the absorption curves of the globules in spite of the fact that the modulator curves do not fully agree with the underlying photosensitivities of the receptors. However, this possibility does not rule out the interpretation that each modulator unit primarily is caused by the activity of cones provided with either green, yellow or red globules: green for the 4790 Å modulator, yellow for the 5430 Å modulator and red for the 5960 and 6130 Å modulators. This accounts for all three main types of globules and thus for the majority of the cones. There are, according to Waelchli (1883), in addition some very pale green and nearly colourless globules; possibly these are related to the 4410 Å modulator that was observed in some cases.

Granit (1947, 1950) has suggested that the photopic dominator curve is produced by summation of the various modulator units. This interpretation is supported by the present results when explained as above because all oil globules and thus all cones are accounted for by the modulators. In addition, the characteristic steepness of the absorption curves of the oil globules (Waelchli, 1881; Roaf, 1929) does not allow us to explain the shift of the broad dominator curve from 5600 to 5800 Å if it were caused by a special dominator substance and a special type of cone.

SUMMARY

1. The spectral sensitivity curves of isolated retinal elements in the eye of the pigeon have been recorded with the micro-electrode technique both in the photopic and scotopic state. As a check of the reliability of the experimental procedure, the scotopic sensitivity curve for the massed discharge of a great number of units was recorded, showing a good agreement with the visual purple absorption curve.

2. The sensitivity curves of single elements have been observed to fall in two categories: (*a*) broad scotopic or photopic dominator curves, the latter ones similar to the curve recorded by Granit (1942); and (*b*) modulator curves with maxima at 4800, 5400 and 5900–6100 Å. The modulator curves have been averaged in Figs. 5–8.

3. It is shown that the narrowness and somewhat asymmetrical shape of the modulator curves and the shift towards the red end in the spectrum as compared with those of other vertebrates (Granit, 1947) can be explained by the absorption of the coloured globules in the avian retina. It is thus probable that the modulator sensitivity bands are primarily caused by cones with either green, yellow or red globules. This implies that the photopic dominator curve is produced by the summed activity of the different modulators.

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