

From The Neurophysiological Laboratory, The Caroline Institute,
Stockholm.

Colour Receptors of the Frog's Retina.

By

RAGNAR GRANIT.

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A preliminary account, dealing chiefly with the technique of micro-recording from the retina and of controlling the energy of the spectrum, but also presenting a number of typical curves for the spectral distribution of sensitivity of single or a restricted number of elements in the frog's retina was published in 1939 by GRANIT and SVAETICHIN. In their work it was proved that THOMAS YOUNG was right in his main idea that different elements had different colour sensitivity. Since that time work on the frog's retina has been regularly continued in parallel with work on other eyes in order to collect a very large material of observations permitting us to describe colour reception of the frog's eye with some pretense to completeness. A large number of observations has been necessary because the better the isolation with micro-electrode the more likely that common types of colour sensitive elements have been selected at the expense of rare ones.

Clearly it is impossible to explore every type of eye with the same degree of completeness, except in the course of years of research. I have therefore chosen to give an account of the typical sensitivity-bands for some types of retinae (GRANIT, 1941 a—d) and selected the frog's eye for a more exhaustive study of the problem. For this choice it has been of some significance that the retina of the frog has properties strongly reminiscent of the human periphery, Thus, the Purkinje-shift, first described for this eye by HIMSTEDT and NAGEL (1901), corresponds to that of the human eye, as demonstrated quantitatively by GRANIT and WREDE (1937) with the aid of the electroretinogram;

the visual purples seem to be identical in these two types of eye as are also their scotopic spectra (CHAFFEE and HAMPSON, 1924, GRANIT and MUNSTERHJELM, 1937, GRANIT, 1937). A difference seems to be the greater sensitivity of the frog's eye to blue light, discussed in the papers mentioned by the author and his collaborators.

An experimental material describing colour receptors can, of course, never be complete. But, having now analyzed well over 100 retinae, I have come to the stage when the experiments never bring anything new or unexpected. This is the reason for my attempt to summarize the observations.

Methods.

The necessary equipment has consisted of a spectrum, controlled with respect to energy, a graded and calibrated wedge for varying the intensity of the stimulus, micro-electrode, amplifier, cathode ray, and loudspeaker (see GRANIT and SVAETICHIN, 1939). The same unit has been used in a number of experiments with other types of eyes (GRANIT, 1941 a—d). An improvement of the technique since 1939 has been the use of an amplifier for the loudspeaker stage which is worked at the bend of the characteristic of the valve so that only spikes above a certain height become audible and base-line noise is removed. The whole retina has been illuminated with light from the monochromator. Before the experiment the frogs have been light-adapted in our standard light-adapting apparatus (ZEWI, 1939).

The principle of the experiments has been to listen to the discharge, which at the same time is seen on the screen of the cathode ray, and thus to determine the amount of energy necessary for the threshold or for another constant index such as cessation of "flicker". The results are given in terms of the inverse value of this amount of energy in the different wave-lengths, generally in per cent of the maximum.

Results.

1. Some General Observations.

Sometimes the micro-electrode isolates an element with the same degree of precision, as in HARTLINE's (1938) work on single fibres in the optic nerve, as seen for instance in fig. 1. Sometimes the discharge consists of a number of elements. When to all appearance a single element is active it is impossible to exclude the possibility that the unitary character of the response is due to synchronization. On the other hand, it is likely that

the better the isolation, the greater the probability that the type of element isolated belongs to the most common ones. For this reason it is necessary not to rely merely on experiments with isolated elements. Strict adherence to this criterion may, for instance, lead to the conclusion that blue elements are exceedingly rare whereas often the influence of the blue-sensitive substance can be traced in a less restricted type of response.

Most interesting is to follow how a discharge disappears below and rises above the threshold when the intensity of the stimulus is altered. Relatively rarely one finds, with decreasing intensity, the frequency of the spikes to diminish in such a fashion as to end with one or two spikes just above the threshold. A case of this type is shown in fig. 1. Common, however, is the grouped type of discharge, shown in figs. 2 and 6, which in response to variations in the intensity of the stimulus falls below and rises above the threshold as a grouped unit. Often the spikes of such a group are of different type. It

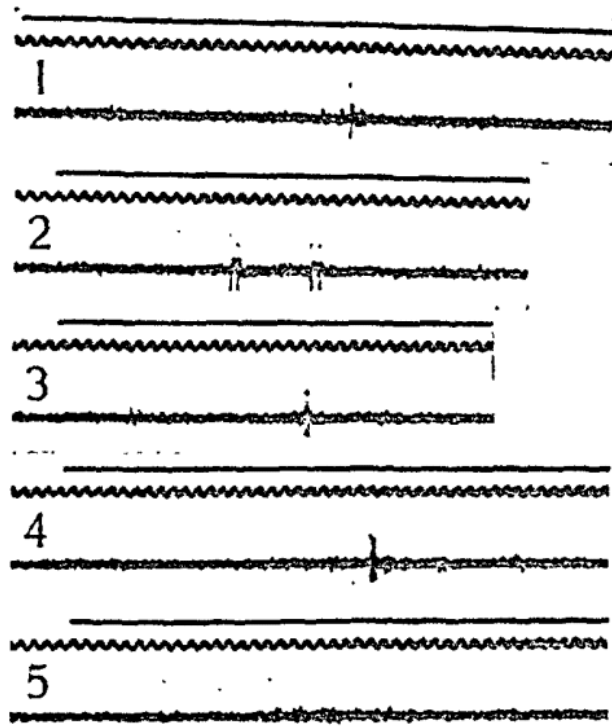


Fig. 1. Isolated spikes from frog's eye in response to different wave-lengths. Light signal and time in $1/50$ sec. above each record. From above downwards: 1, threshold at 0.600μ ; 2, well above threshold at 0.540μ ; 3, near threshold at same wave-length; 4, near threshold at 0.520μ ; 5, just below threshold at same wave-length, differing by 5 mm. on wedge from record 4. In this and most experiments the size of the spikes gradually diminishes in course of experiment. Note the long latent period at threshold.

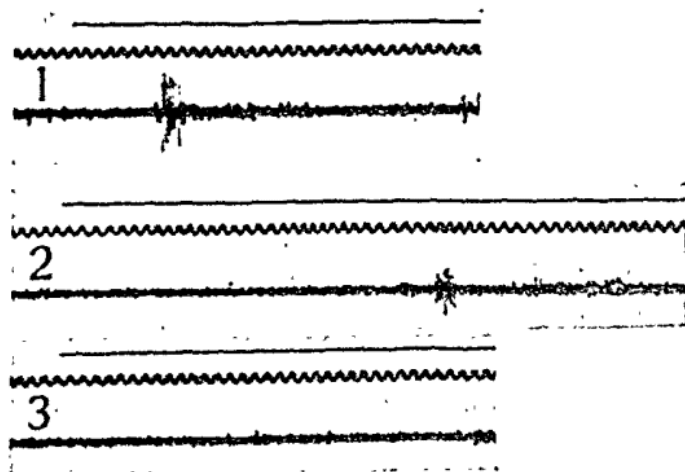


Fig. 2. Grouped discharge. Light and time signal as in fig. 1; 1, typical group near threshold at 0.540μ ; 2 and 3 from another experiment. Same wave-length and successive records at respectively 68 and 70 mm. on wedge, the former just above, the latter just below threshold.

is difficult to say whether this is a physiological variation in the discharge of a single unit or whether the group consists of several units with some rotation of activity (GRANIT, 1941 a). Nevertheless this group acts as a physiological unit to variations of colour around the threshold. Such "grouped discharges" have also been described by *e. g.* FORBES and his collaborators (RENSHAW, FORBES, and MORISON, 1940) in the hippocampus area and by ADRIAN and MORUZZI (1940) in the spinal cord.

2. Dark-Adaptation.

After light-adaptation the frog's spectrum generally has its maximum around 0.560μ with individual elements possessing maxima still further out in the long wave-lengths. Immediately afterwards the sensitivity begins to increase. A typical case is shown in fig. 3, where the relative energies at the threshold (E), the inverse value ($1/E$), and $\log E$ have been plotted against time of recovery in the dark for a diffuse discharge and wave-length 0.500μ . The two-step rise of sensitivity can be seen in all curves. The logarithmic plot is commonly used in sensory

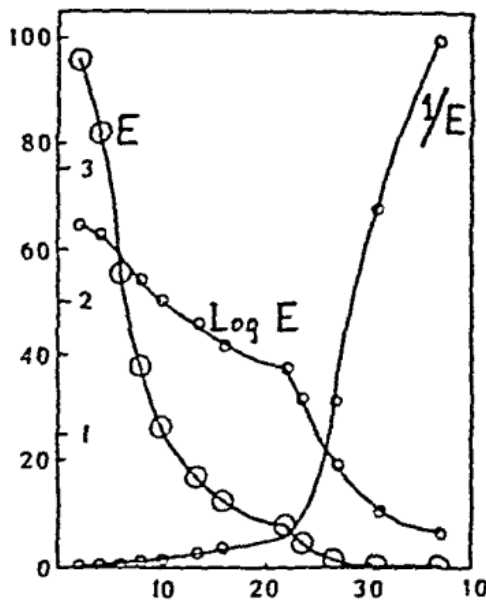


Fig. 3. Hungarian frog. Dark-adaptation of restricted discharge followed by measurements of absolute threshold for wave-length 0.500μ . Abscissae: time in the dark in min. Ordinates: E , relative energy necessary for threshold, in addition $1/E$ and $\log E$ have been plotted. To be compared with curves showing regeneration of visual purple in excised, opened eyes by ZEWI (1939).

work and has obvious advantages. The theoretically best plot is perhaps $1/E$ illustrating sensitivity — originally used also in psychophysical sensory work — since with the rat's eye, having very few cones, as well as with dark-adapted frogs a plot of $1/E$ against the wave-lengths of the spectrum has been shown to follow the absorption curve for visual purple (cf. CHAFFEE and HAMPSON, 1924, GRAHAM and RIGGS, 1935, GRANIT, 1941 c). The two phases of dark-adaptation, seen in fig. 3, are known since the work of KOHLRAUSCH (1922) for the human eye, and have been demonstrated electrophysiologically by a number of authors (GRANIT and WREDE, 1937, WREDE, 1937, RIGGS, 1937 for frogs; GRANIT, 1941 c for rats). It can be shown that the red

end of the spectrum does not take part in the second phase of the rise of sensitivity. This is illustrated by the uppermost curve of fig. 4. The same holds good for man.

Independently of the degree of isolation reached with the micro-electrode the second phase of dark-adaptation nearly always sets in. This phase goes with a shift in the absorptive properties tending to place the maximum of sensitivity around 0.500μ . With some justification it may thus be called dark-adaptation proper, meaning that the elements under the micro-electrode begin to react as they would do if their sensitivity were determined by visual purple. As we have pointed out elsewhere, the increasing sensitivity of rod vision is not proportional to the increase in the concentration of visual purple, as studied by ZEWI (1939) on frogs. This statement holds good both when size of the electroretinogram is used as index (GRANIT, HOLMBERG, and ZEWI, 1938, GRANIT, MUNSTERHJELM, and ZEWI, 1939), as well as when the index is sensitivity ($1/E$ in fig. 3). There is a period of delay in the rise of sensitivity of the rods but none whatever in the general rise of sensitivity nor in the regeneration of visual purple unless light-adaptation be very brief and intense (ZEWI, 1939). During this early period of increasing sensitivity the eye reacts as a cone-eye with a broadening photopic maximum around 0.560μ .

The work in which size of the electroretinogram to a constant stimulus was used as index of sensitivity in parallel with measurements of visual purple concentration (GRANIT *et al.*, 1938, 1939) cannot be directly compared with these experiments where the index has been energy necessary for the threshold, even though both sets of results are presented in a common unit such as $1/E$. The experimental conditions are too different. Thus it is important to realize that the intensity level of the constant stimulus, used for eliciting an electroretinogram, indicates incipient dark-adaptation at an earlier stage if the stimulus is of very low intensity than when it is of high intensity (GRANIT and WREDE, 1937, RIGGS, 1937), and that it is difficult to use so low intensities in work with the electroretinogram as to approach the condition that a few spikes just are allowed to pass through the micro-electrode. The latter also selects the most sensitive elements at their threshold while the great majority of elements, summing up to a measurable retinogram, still may be uninfluenced by dark-adaptation. Further, the size of the electroretinogram is proportional to \sqrt{E} (BOVIE, CHAFFEE, and HAMPSON, 1924) and therefore must increase very slowly in the early critical period of dark-adaptation, if not replotted in terms of some other unit. For these reasons the micro-

electrode technique should show up dark-adaptation before it is clearly visible in the deflection of the retinal response to a constant stimulus. The time and strength of light-adaptation also is of importance. In the work of RIGGS (1937) a short duration of light-adaptation and a weak adapting light were used.

The micro-electrode experiments on dark-adaptation were carried out after not less than 1 hour of light-adaptation to 20,000 m. c. in the same apparatus that was used by ZEVI (1939) in his quantitative measurements of visual purple regeneration under various conditions. His values for excised eyes can be directly compared with my curves. Visual purple regeneration is very much slowed down in excised eyes which lack the rapid regeneration component sensitive to temperature (ZEVI, 1939, 1940). In the intact animals a fast rise of the electroretinogram sets in when, during regeneration, the visual purple concentration has reached 50 % of its final value in frogs or cats. (GRANIT *et al.*, 1939). The fast rise, "dark-adaptation proper", of fig. 3, plotted from micro-electrode work in terms of $1/E$, sets in when 20 % of visual purple has regenerated in the excised eye. This difference between intact animals and excised opened eyes should be considered in the light of the remarks made in the previous paragraph.

Both methods demonstrate, the micro-electrode technique in addition with isolated elements, that cone-properties dominate until at a certain stage some "intermediate process" makes the visual purple an active rod-substance, and the maximum in the spectrum gradually shifts over to the region around 0.500μ . (For a discussion of this intermediate process see GRANIT *et al.*, 1939, LYTHGOE, 1940, and GRANIT, 1941 c.)

Though most isolated elements dark-adapt and sooner or later become dominated by the photochemical properties of visual purple, there are some exceptions. One such case is shown in fig. 8 where the element with maximum in 0.600μ did not change its absorption spectrum in the course of 40 min.

3. Dark-Adaptation and the "Blue" Receptor.

There can be no doubt but that the frog's retina possesses a "blue" substance. But for some reason or other the "blue" receptor is exceedingly difficult to isolate. However, by utilizing its adaptive properties significant results are obtained.

A most interesting case is the one shown in fig. 4 in which dark-adaptation was followed with a moderately restricted discharge for the wave-lengths 0.500, 0.650, 0.450 μ and plotted in terms of log intensity for a threshold response. The blue element (0.450 μ) dark-adapts at a faster rate than the others so that between the 12th and 25th min. of dark-adaptation the maximum of the sensitivity is in the blue region. Later, during the second phase of dark-adaptation visual purple takes the lead and the maximum shifts towards 0.500 μ . As pointed out above, the

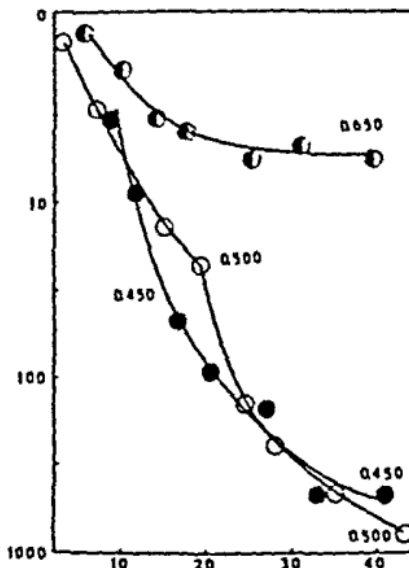


Fig. 4. The thresholds for three wave-lengths 0.650, 0.500, and 0.450 μ has been followed during dark-adaptation and plotted in terms of log energy necessary for discharge. Note fast recovery of "blue" (0.450 μ). Time in minutes.

extreme red (0.650 μ) does not take part in the second phase of dark-adaptation probably owing to the negligible absorption which characterizes visual purple outside 0.620 μ . It is a characteristic of the "blue" substance that after light-adaptation it recovers even faster than the region influenced by visual purple. This circumstance enabled GRANIT and WREDE (1937) for the first time to place its existence beyond doubt, though at that time only the spectra and not the recovery curves were measured.

What is the absorption spectrum of the blue substance? Fig. 5 shows the distribution of sensitivity for an off-discharge of a highly restricted character for which the index was cessation of flicker. It is plotted in terms of $1/E$: immediately after a light-adaptation of 2 hours (lowest curve), somewhat later (middle curve), and still later (uppermost curve). There the blue sensitive maximum is between 0.450—0.460 μ . An isolated grouped dis-

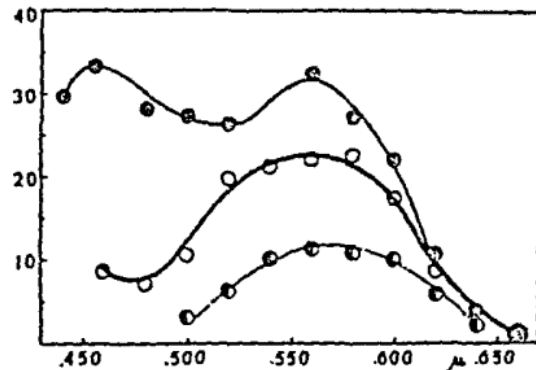


Fig. 5. Spectra for three stages of "recovery" after light-adaptation of restricted discharge. Ordinates: inverse value of energy necessary for threshold but not, as usual, in per cent of the maximum. Therefore the three curves also show three levels of increasing sensitivity. See text.

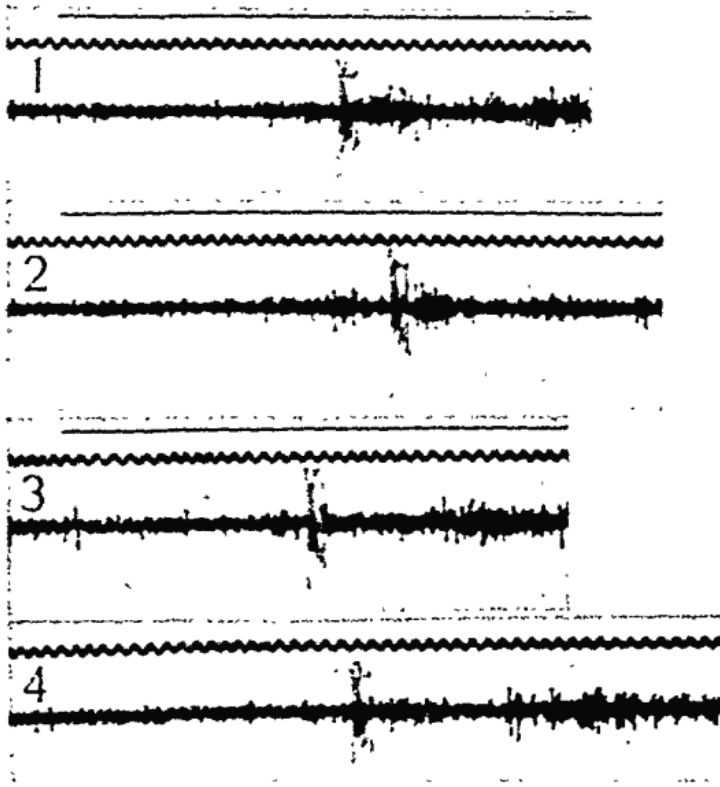


Fig. 6. Blue-sensitive grouped discharge giving sensitivity distribution shown in fig. 7. All values near threshold; only the grouped discharge audible in loud-speaker as sharp rattle. 1, wave-length 0.670μ ; 2, 0.530μ ; 3, 0.500μ ; 4, 0.450μ . Note, that the small inaudible discharge of spikes is less sensitive to short wave-lengths to judge by the fact that its latent period increases downwards in the records as wave-length shortens.

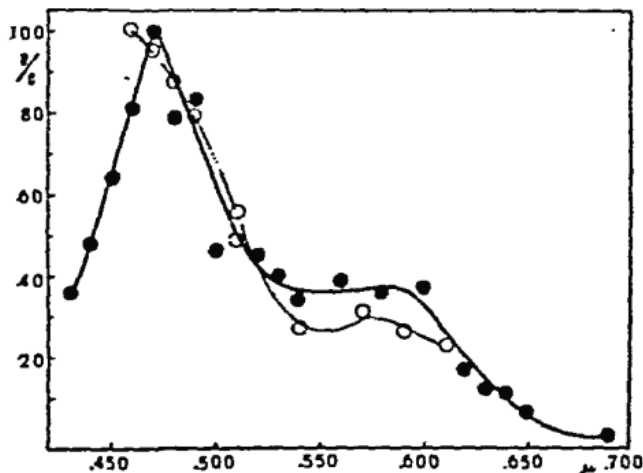


Fig. 7. Filled circles: distribution of sensitivity of the "grouped" discharge shown in fig. 6. Open circles: another "blue" receptor, less completely analyzed. Here, as in all curves to follow, the inverse value of energy necessary for the threshold has been plotted in per-cent of the maximum.

charge of a blue-sensitive element for which a complete curve was obtained is shown in fig. 6; its sensitivity distribution illustrate the filled circles of fig. 7. The open circles in the same fig. belong to another case in which the maximum sensitivity also was in the blue region but placed somewhat further out in the short wave-lengths. In other experiments the "blue" substance has merely made itself felt as an expansion of the curves in the short wave-lengths outside the absorption curve for visual purple.

The "blue" elements are so rare in the isolated stage that it is not possible to state whether they consist of a number of somewhat different narrow sensitivity bands, or whether the variations obtained merely are due to the limited number of observations available. The most striking property of "blue" elements apart from their distribution of sensitivity, is their fast recovery after light-adaptation, when compared with the rise of sensitivity directly due to

regeneration of visual purple. Also in the human eye sensory "blue" recovers faster than other colours (WRIGHT, 1937).

4. The Red-Sensitive and Green-Sensitive Elements.

As pointed out already by GRANIT and SVAETICHIN (1939) one often obtains relatively narrow sensitivity bands outside the average maximum of light-adapted eyes (in 0.560μ). I have confirmed this observation and come to the conclusion that the maxima of such elements are located between 0.580 — 0.600μ . Specimens of such elements are given in fig. 8. I have never seen a maximum beyond 0.600μ . When, however, the maximum shifts to 0.560μ or has been there from the beginning, the curves tend to become broad.

An example of broad curves with maximum in 0.560μ is shown in fig. 9 which is an average of several such elements. The curve practically coincides with the average curve for light-adapted frogs published by GRANIT and SVAETICHIN. The latter has only a still more marked expansion in the blue region. For some time I suspected this curve to indicate that several units took part in the response. But then I succeeded in establishing that similar curves also could be obtained when to all appearance a single unit was active. The broad curve with maximum around 0.560μ is the most common curve of all.

Maxima of sensitivity are also found in the region of

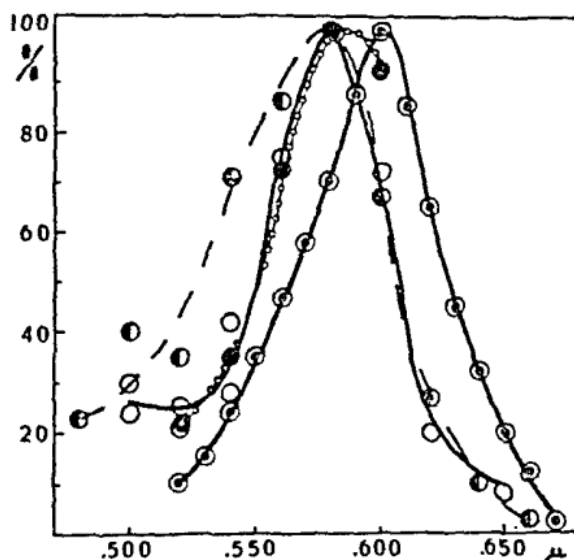


Fig. 8. Types of isolated photopic receptors with narrow bands sensitive to the red and yellow regions of the spectrum (0.580 — 0.600μ). Some show indication of beginning rise of sensitivity in the region of the maximum for visual purple (0.500μ).

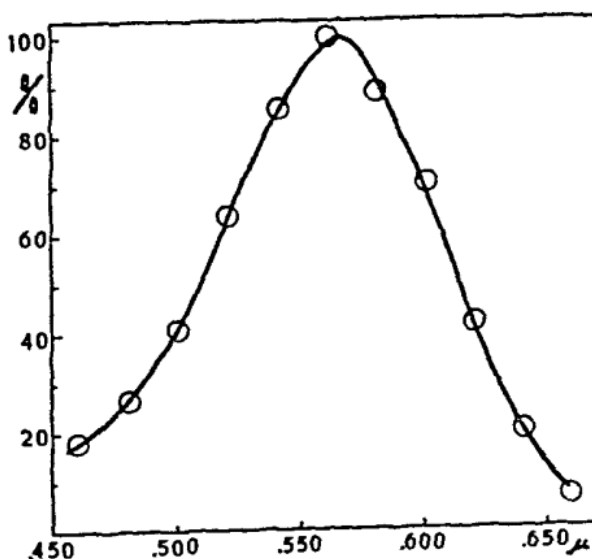


Fig. 9. Photopic elements with broad band of sensitivity with maximum around 0.560μ . Average curve (see text).

0.520—0.540 μ . Such curves are shown in fig. 10 and they also belong to the narrow type. GRANIT and SVAETICHIN (1939) discussed the possibility that these curves represented a certain amount

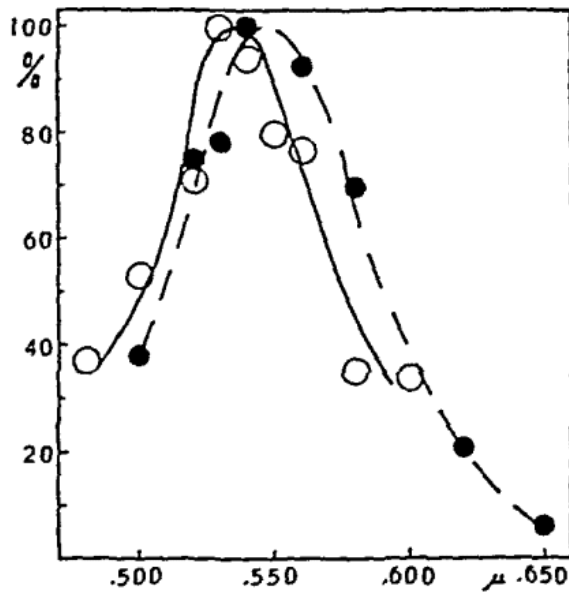


Fig. 10. Types of isolated photopic receptors with narrow bands sensitive to green, 0.560—0.540 μ .

of dark-adaptation of elements with maxima in 0.560 μ . I have since come to the conclusion that elements of this type are genuine. Isolated units have been seen to have this type of distribution of sensitivity so soon after light-adaptation that participation of active visual purple should be excluded. I have also seen them in the photopic eyes of guinea-pigs in which so far I have not found any maxima outside 0.540 μ .

It would be a mistake to believe that all curves have been as simple as those shown above. In order to illustrate how complex the results can be I have added fig. 11, without being able to

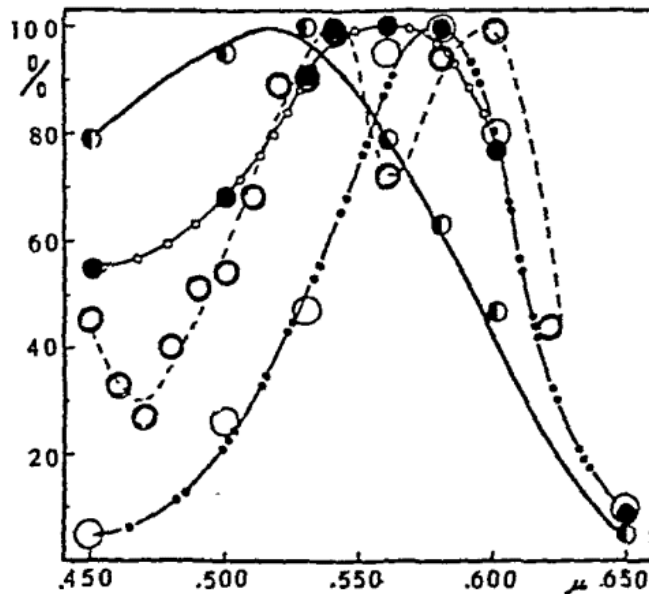


Fig. 11. Types of curves showing variations in the distribution of spectral sensitivity. See text.

state that such curves refer to single units of activity. But they do represent a high degree of isolation. On the other hand it should be realized that units may be coupled physiologically in the synaptic layer, that "double cones" have been described by the histologists, and that even the micro-electrode by causing irritation due to pressure may force elements to act in unison. There is also "rotation of activity"

(GRANIT, 1941 b) and formation of visual purple to be considered as factors antagonizing isolation. Briefly, it can be stated that, even when neglecting a source of error such as the dimensions of the micro-electrode itself, there is a great

number of complicating factors left, all of which conspire to antagonize isolation. For this reason the narrow curves that have been obtained have the great value of positive evidence.

Discussion.

BIRUKOW (1939) has recently studied colour discrimination in frogs and finds that they are capable of distinguishing colours. Very precise information can hardly be obtained on the basis of an analysis of animal behaviour, but it seems as if frogs had a type of colour system reminiscent of that in man, only with less developed sensitivity to green.

Assuming now that we have discovered all the important types of elements in frogs, what conclusions would offer the most reasonable description of colour vision in this animal? Would it be necessary to suggest a "polychromatic" theory of vision? What would, in the first instance, be the equivalent of brightness? There is every reason to suppose that the average photopic curve with its maximum around 0.560μ (GRANIT and SVAETICHIN, 1939) determines brightness in frogs just as in man. Perhaps brightness or "whiteness" in the frog has a slightly more blueish tinge. On this view brightness would be determined by the total number of impulses from the dominant receptors. The size of the electroretinogram in different regions of the spectrum would also give a good idea of the brightness distribution (GRANIT and WREDE, 1937, for photopic eyes).

It must have some significance that the majority of the curves obtained from photopic frogs tend to coincide with the average curve (see fig. 9). Brightness, after all, must be the fundamental quality of visual reception. It is hardly likely that the broad curves initiate impressions of any particular colour. They do differ to some extent from each other but it is not possible to state definitely that these differences exceed the limits of variations set by the difficulties of the experiment.

Colour must be the result of the amount of discrimination caused by sensitivity bands serving as "modulators" of the average curve and of the dominant type of distribution of sensitivity. Such "modulators" have also been found in a sufficient number and sufficiently far apart to serve, as it were, as landmarks for colour discrimination. We have seen that maxima of individual sensitivity bands may turn up within as large a range as from

0.450—0.600 μ . They have also tended to be grouped around certain regions of the spectrum. One such region of "modulators" has been 0.580—0.600 μ , less commonly maxima have been seen between 0.520—0.540 μ , and relatively rarely between 0.450—0.470 μ . Statistical averages of the "modulator" groups actually have three preferential regions, and on this basis it is possible to suggest a trichromatic theory instead of a polychromatic one. The sensitivity bands of these regions have also tended to be narrower than the average curve and that of dominating elements possessing the maximum of the latter. Therefore it is reasonable to assume that maxima of discrimination are to be found precisely in these regions. Discrimination would thus be a function of the number, steepness and density of these "modulators".

In the photopic rat's eye (GRANIT, 1941 c) there were only two narrow "modulator" bands with maxima in respectively 0.600 and 0.500 μ coupled together. The "dominating" element with maximum in 0.560 μ was lacking. The former band showed the characteristic two-step rise of recovery after light adaptation and during the later phase became transformed into a visual purple absorption curve. This led to the assumption that the perception of green of the photopic eye in this case was mediated by slightly modified visual purple. It is possible that visual purple behaves similarly in the frog's eye which implies that the maximum of discrimination in the green would shift towards 0.500 μ . If this were so, all the maxima of discrimination in the frog's eye would coincide with the maxima of hue discrimination of man, as determined, for instance, by WRIGHT and PITT (1934). Otherwise the "green" maximum would be slightly shifted to the right in comparison with man.

The broad curve of the dominating element of fig. 9 could be due to a coupling of the narrow curves which have maxima to either side of it, as indicated by fig. 12 in which some typical responses for the sake of comparison have been plotted to the same abscissa. The coupling might be "photochemical" in the sense that the substances are mixed already in the receptors, or physiological, meaning that different receptors are interconnected either as "double cones" or else in the synapses. As is well known there is in the retina convergence of receptors and bipolars towards the final common path taking its origin from the ganglion cell from which the micro-electrode picks up the

discharge (GRANIT, 1941 a). Thus, for instance, when a cone during dark-adaptation changes into a rod the reason for this probably is convergence.

Elsewhere (GRANIT, 1941 c, d) I have given experimental reasons for assuming the cone substances to be chemically related to the visual purple. So far only yellow substances have been found in solutions of bleached visual purple, substances such as the relatively light-resistant "indicator yellow" (LYTHGOE, 1937) or "retinine" (WALD, 1936, 1939) and the labile "transient orange" (LYTHGOE and QUILLIAM, 1938) which may account for the reception of blue. The work of HANSTRÖM (1940) indi-

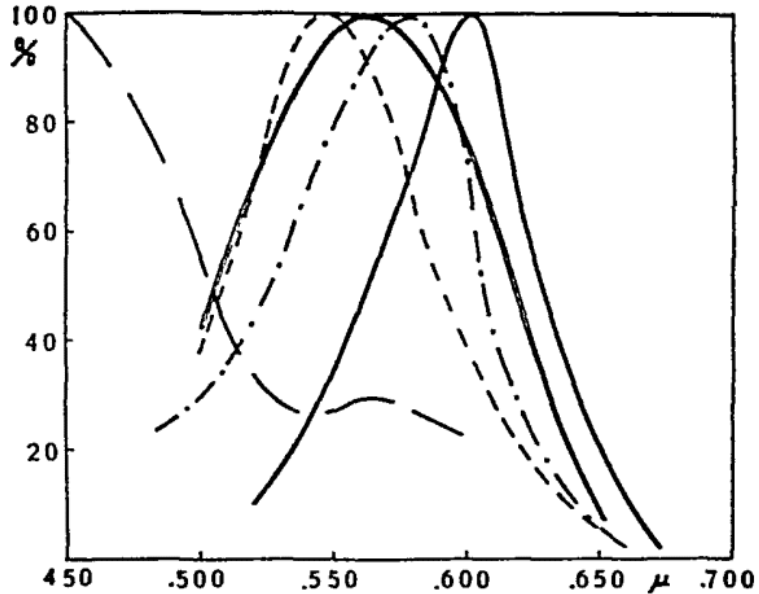


Fig. 12. Some of the previous curves plotted for comparison to the same abscissa.

icates the presence of a red substance in extracts from eyes of monkeys. v. STUDNITZ (see his book, 1940) claims to have found a substance in the frog's eye with maximum in 0.560μ and fitting our average photopic curve of this animal, but, on the other hand, he finds the same substance in the eye of the tortoise where the physiologically determined maximum is located between 0.600 — 0.620μ (GRANIT, 1941 a, d). It is therefore doubtful whether his methods are adequate enough to support his claims.

Summary.

Spikes have been recorded with micro-electrodes, amplifier and cathode ray oscillograph from the retinae of light-adapted frogs and during dark-adaptation.

The chief aim of this work has been to collect a large number of curves showing the distribution of sensitivity to spectral light of single or a restricted number of elements.

Most elements have a distribution of sensitivity which coincides with the average curve with its maximum in 0.560μ and

legs extending over a relatively large part of the spectrum (see fig. 9).

But there are also narrow bands of sensitivity with maxima ranging between 0.450—0.600 μ . The maxima of these bands are chiefly gathered around 0.580—0.600 μ , 0.520—0.540 μ , and 0.450—0.470 μ . Curves from the last mentioned group are rare.

Curves illustrating dark-adaptation (or recovery of sensitivity) for different wave-lengths are given in the paper and compared with visual purple regeneration.

The blue-sensitive elements recover at a faster rate than others after light-adaptation and in this way can also be isolated from the region around 0.500 μ occupied by the absorption band of visual purple.

The kind of mechanism of colour reception that might be expected from such a system is briefly discussed, and it is suggested that in many respects it may be very like that of man.

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References.

- ADRIAN, E. D., and G. MORUZZI, *J. Physiol.* 1940. *97*. 153.
 BIRUKOW, G., *Z. vergl. Physiol.* 1939. *27*. 41.
 CHAFFEE, E. L., W. T. BOVIE and A. HAMPSON, *J. opt. Soc. Amer.* 1923. *7*. 1.
 CHAFFEE, E. L. and A. HAMPSON, *Ibidem.* 1924. *9*. 1.
 GRAHAM, C. H., and L. A. RIGGS, *J. gen. Psychol.* 1935. *12*. 279.
 GRANIT, R., *Acta Physiol. Scand.* 1941 a. *1*. 370.
 —, *Ibidem.* 1941 b. *1*. 386.
 —, *Ibidem.* 1941 c. *2*. 93.
 —, *Ibidem.* 1941 d. *2*. 334.
 GRANIT, R., and A. MUNSTERHJELM, *J. Physiol.* 1937. *88*. 436.
 GRANIT, R., and G. SVAETICHIN, *Upsala Läkaref. Förhandl. N.F.* 1939. *45*. 161.
 GRANIT, R., and C. M. WREDE, *J. Physiol.* 1937. *89*. 239.
 HARTLINE, H. K., *Amer. J. Physiol.* 1938. *121*. 400.
 HIMSTEDT, F., and W. A. NAGEL, *Ber. naturf. Ges. Freiburg i. B.* 1901. *9*. 153.
 HANSTRÖM, E., *Acta Opthhal. Kbh.* 1940. *18*. 21.
 KOHLRAUSCH, A., *Pflüg. Arch. ges. Physiol.* 1922. *196*. 113.
 LYTHGOE, R. J., *J. Physiol.* 1937. *89*. 331.
 —, *Brit. J. Opthal.* 1940. *24*. 21.
 LYTHGOE, R. J., and J. P. QUILLIAM, *J. Physiol.* 1938. *94*. 397.
 RENSHAW, B., A. FORBES and B. R. MORISON, *J. Neurophysiol.* 1940. *3*. 74.

WALD, G., *J. gen. Physiol.* 1935—36. *19*. 351.

—, *Ibidem.* 1939. *22*. 775.

WREDE, C. M., *Skand. Arch. Physiol.* 1937. *77*. *Proc. Physiol. Soc.*

WRIGHT, W. D., *Proc. Roy. Soc. B.* 1934. *115*. 49.

WRIGHT, W. D., and F. H. G. PITT, *Proc. Physiol. Soc.* 1934. *46*. 459.

ZEWI, M., *Acta Soc. Sci. Fenn. N. S.* 1939. *2*. 4.

—, *Acta Physiol. Scand.* 1940. *1*. 271.