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The Spectral Properties of the Visual Receptors of the Cat.

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The micro-electrode technique, used in several previous contributions to the problem of colour reception (GRANIT *et al.*, 1939—42), is particularly well suited for mammals on account of the ease with which large isolated spikes are obtained from the inside of their retinae. Rats (1941 a) and guinea pigs (1942 a) have previously been used in these experiments. Such spikes are here shown in fig. 1 for the cat's eye.

The cats have been decerebrated, given some 5—10 cc urethane (20 %), cornea and lens have been removed from one eye — the eye of the side on which the carotid artery has been left untied before decerebration — and the micro-electrode finally been inserted under the microscope in the usual manner. This combination of urethane and decerebration proved to be better than heavier anaesthesia or decerebration alone.

The large spikes, seen in fig. 1, are either well synchronized discharges from the axones of several ganglion cells or else impulses in single fibres. The all-or-none law is no reliable criterion for the degree of isolation as with the micro-electrode several factors, among them the influence of adjacent elements, less well placed relative to the electrodes, may cause changes in the size of the spikes. Differentiation between single and synchronized fibres — though theoretically important — cannot either be obtained by the analysis of the spectral properties of a given discharge of spikes because of the known existence of convergence of several

receptors towards the same ganglion cell. This cell may be the final common path for several rods as well as for rods and cones together (POLYAK, 1936). For this reason we have to expect both rod- and cone-properties from the same isolated spike, even if it belongs to a single fibre rather than to a number of well synchronized fibres. Actually all experiments up to date have proved this postulate to be correct.

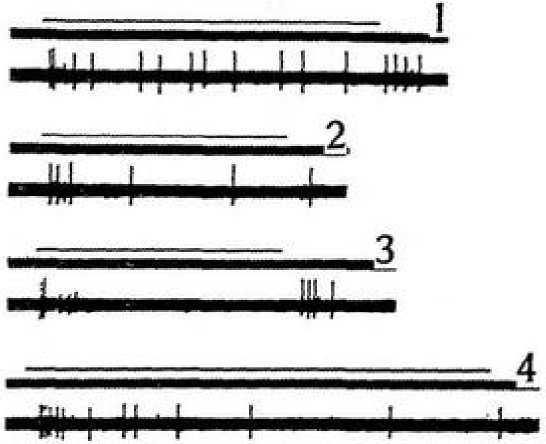

Fig. 1. In each record light signal, time in 50/sec. and spike activity.
1, stimulus of relative energy 6.3 at wave-length 0.620 μ;
2, same at relative energy 2.3;
3, relative energy 2.5 at 0.460 μ.
4, from another experiment to illustrate element reacting merely to onset of illumination; wave-length 0.500 μ.

Fig. 1 refers to a particularly interesting, though not a very common type of response, in which an originally light-adapted eye had become dark-adapted during the experiment. The spikes illustrated had first given the distribution of sensitivity characterizing the so-called photopic dominator of fig. 3 whereupon, during dark-adaption, the sensitivity had risen greatly in the short wave-lengths. At this moment the records were taken. 1 and 2 are responses to stimulation with red light at relative energies 2.3 and 6.3, record 3 to stimulation with blue light at relative energy 2.5. These records are selected from a number of pictures in which a much larger range of relative energies from the threshold upwards led to the same characteristic difference in the responses to red and blue stimuli. Thus this difference could not be an intensity effect. The blue stimuli gave discharges only at "on" and "off" and nothing *during* illumination, the red stimuli elicited a train of impulses *during* illumination in addition to increasing the frequency at "on" and "off". No difference could be seen between the spikes set up in the ganglions by the differently coloured stimuli and yet the red end of the spectrum must have activated the discharging fibre through another channel than the blue one.

Alternatively, as stated, the spikes, though they look as if coming from a single fibre, may have come from well synchronized elements, split up into separate fibres by the differently coloured stimuli. But n the latter case one would expect the spikes to decrease in size, when light from the ends of the spectrum are used as stimuli, because the rod and cone ranges only overlap in the middle of the spectrum. Visual purple, for instance, has a negligeable effect from $0.620\ \mu$ further out towards the red. But even though the size of the spikes somewhat varies, it does not vary with wave-length. True convergence of rods and cones towards the same ganglion cell is therefore the probable explanation of the experiment illustrated in fig. 1.

True convergence is also the most probable explanation of the fact that in the cat as well as in all other animals with mixed eyes the absorption curve for visual purple sooner or later will determine the distribution of sensitivity of almost any discharge of spikes after some time in the dark. With the light-adapted cat this is a particularly serious source of error on account of the rapidity with which dark-adaptation often takes place, and steps have to be taken to counteract the influence of dark-adaptation. The presence of the broad dominator band of sensitivity in the cat's eye in light-adaptation (see fig. 3) makes checking of dark-adaptation more important than in the mammals hitherto studied though in principle the procedure is the one already used in several previous contributions to this problem.

Procedure.

A large spike was located. With the electrode inserted the animal was then left in the illumination from the microscope-lamp, placed above the eye (2,400 m.c.), for 10 min., sometimes longer. It was then allowed to recover, and its eye was illuminated by brief flashes of light of different wave-lengths at intervals of 10 sec. in order to measure the energy necessary for the threshold in each wave-length. Recovery curves during dark-adaptation were plotted from these data in terms of energy reciprocals against time in the dark for a number of regularly recurring wave-lengths (cf. the eye of the rat, Granit, 1941 a). Between these curves stray observations on other wave-lengths were inserted

into the diagrams at their appropriate time moments. From these diagrams the distribution of sensitivity could be calculated.

A characteristic of such diagrams, of which some have been published in the work on the rat's eye (1941 a), is that sooner or later the sensitivity in the short wave-lengths, best represented by wave-length $0.500\ \mu$, which is at the top of the absorption curve for visual purple, begins to increase at a very much faster rate than the sensitivity to light of long wave-lengths. Different receptors register this change after different intervals in the dark. Generally there is a clear break in the curve, as shown already with the rat's eye (Granit, 1941 a) and also with the frog's eye (Granit, 1941 b), after which the rate of rise of sensitivity becomes particularly fast for wave-lengths around $0.500\ \mu$. The turning point in the cat's eye often comes after about 10—15 min. in the dark. Sometimes the break is less well marked, the rate of rise of sensitivity being fast from the beginning, sometimes the change in relative sensitivity to long and short wave-lengths is very much delayed. When this is so a relatively pure cone population may have been struck or else deficient circulation, caused by the decerebration, may have retarded the regeneration of visual purple (Zewi, 1939).

If the experiments are to reproduce the true photopic distribution of sensitivity, the result must either be obtained within the first 10—15 min. or else controls must have demonstrated that the experiment refers to a type of element with delayed dark-adaptation proper, defined as delayed rise of sensitivity for wave-length $0.500\ \mu$.

Applying these principles it is possible to obtain from each diagram a series of values illustrating the photopic distribution of sensitivity. This is the definition of the term *series* used in all this work. Sometimes the same spike could be kept under the electrode for repeated re-adaptation to light. This gave one or several new sets of values thereby increasing the accuracy with which a series could be determined. Behind a series can thus be a greater or smaller number of readings of which each series is a final average. Several series of similar distribution of sensitivity have generally been averaged in the presentation of the results.

The Photopic and Scotopic Spectra.

Lythgoe's (1937) absorption curve for visual purple is drawn in fig. 2. The circles around it represent 31 averaged values, based on 102 readings from 4 series in 4 dark-adapted cats. The scotopic values are relatively too high in $0.540—0.580\ \mu$. The maximum of this increase around $0.560\ \mu$ is perhaps due to influence from the photopic dominator, shown in fig. 3. But back reflexion from the *tapetum lucidum* provides another probable explanation of this hump in the scotopic curve.

The most striking fact about the light-adapted eye of the cat is that it possesses the broad photopic dominator band of sensitivity with maximum around 0.560 μ (fig. 3), previously seen in the eyes of frog (GRANIT, 1941 b), snake (GRANIT, 1942 c) and pigeon (GRANIT, 1942 b), but not in the rat (GRANIT, 1941 a) and the guinea pig (GRANIT, 1942 a). These two are the only mammals hitherto studied. The cat is thus the first mammal with photopic vision well enough developed to be represented by this very characteristic dominator band. The finding is important since it demonstrates that the principles discovered for lower vertebrates also are valid for mammals.

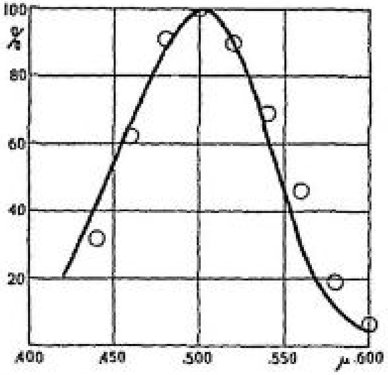

Fig. 2. LYTHGOE's (1937) absorption curve for visual purple. Circles from experiments on 4 scotopic cats (see text).

The large circles of fig. 3 and the curve drawn between them refer to 4 particularly good series, good in the sense that the dominator was little if at all influenced by incipient dark-adaptation and that the values in the short wave-lengths were recorded at a very early stage of the recovery in the dark after light-adaptation. The black dots refer to 87 averages collected from 188 readings representing all the twelve series in which the dominator with maximum in 0.560 μ was reasonably free from influence from the absorption curve for visual purple. A slight rise in the green is just noticeable. As there were 33 photopic series the dominator has been present in 36 % of the photopic elements analyzed. The great majority of them represented single spikes of the kind shown in fig. 1.

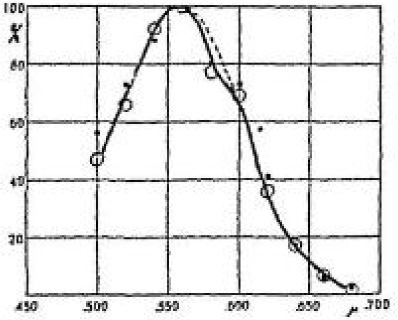

Fig. 3. Photopic dominator of cat, as described in text.

There is a regularly recurring asymmetry in the dominator which in fig. 3 has been filled out by a broken line. Completed in this manner the curve is identical with the dominator found in the frog's eye. What is the reason for the asymmetry?

In order to answer this question we must first consider the organisation of colour reception as revealed by these experiments on different animals. Perfect colour reception seems to necessitate a dominator band for the perception of luminosity and a number of narrow modulator bands in different regions of the spectrum to modulate the impression of luminosity (white) to colour (GRANIT, 1941 c). One of the most regularly recurring modulators, seen in rats, frogs and snakes, has its maximum in 0.600 μ. The asymmetry in the dominator curve of fig. 3 could be due to unsuccessful isolation or deficient development of this modulator which therefore only would be capable of pushing up a hump in 0.600 μ. Up till now it has always been possible to isolate this modulator in those animals where it has been present. But the narrow "red" modulator has not been found in the isolated state in the cat's eye. The hump in this region therefore suggests some defect in the development of the modulator. The dominator may also be somewhat modified by back reflexion from the *tapetum* leading to a relative increase of stimulus strength in the region of the spectrum that is reflected.

If the *tapetum* be removed from the eye for examination it is found to reflect a dominantly yellow-green light. To my eye pure yellow is in 0.580 μ. Yellow-green would therefore correspond fairly well to the maximum of the dominator in 0.560 μ which thus by back reflexion may have received an additional stimulus making it possible to diminish the energy used for the spectral stimulus in this region. This in turn would lead to an accentuated top of the dominator curve. The *tapetum* of the cat's eye is a very efficient reflector, especially by comparison with the black pigment which in most eyes absorbs stray light of all wave-lengths. It is therefore reasonable to expect it to modify the curves in the region where it reflects maximally. The rise in the scotopic curve of fig. 2 in the same region suggests that in both cases the same factor is at work. Therefore a common explanation seems probable.

Some of the experiments for which the early values after light-adaptation were plotted in fig. 3 were continued, despite incipient dark-adaptation, for some time afterwards in order to illustrate the expansion of the dominator towards the short wave-lengths. In fig. 4 the filled circles illustrate 63 averages from 7 series of this type (119 readings). The curve is drawn *between* the values for 0.520 μ and 0.540 μ but the indication of a hump in 0.520 μ is probably significant. The asymmetry to the right of 0.560 μ is still noticeable.

So far we have *only* been concerned with 36 % of the photopic series, those possessing their maximum in 0.560 μ. In the remaining 64 % light-adaptation did not succeed in pushing the maximum further to the right than to 0.520 μ: These curves have always had a secondary *maximum in 0.560 μ. As such* curves were obtained in the majority of our experiments the maximum for all 33 photopic series averaged together lies in 0.520 μ. The average photopic curve obtained in this manner is shown in fig. 4 (line between open circles). In this curve 425 readings from 13 cats have been collected into 200 averages which in their turn have been averaged for the values plotted (open circles). The result means that the dominators have been too few to effect a complete Purkinje shift but sufficiently many to create a relatively large secondary hump in 0.560 μ and give the eye a considerable sensitivity to red light.

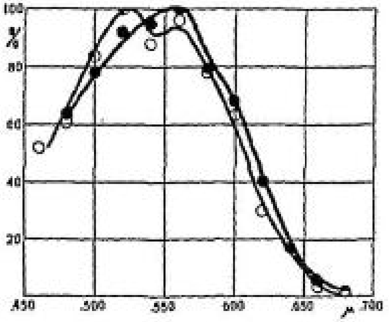

Fig. 4. Averages, as described in text.

As a matter of fact PIPER (1905) failed to find a Purkinje shift with the electroretinogram as index but the reason for this may also have been that he did not realize what precautions have to be taken to ensure light-adaptation in an animal of this type. To the absence of a Purkinje shift in PIPER's experiments may also have contributed the fact that the electroretinogram to a stimulus spreading diffusely over the retina is an average from the whole retina including the periphery where cones may be scarce or absent. Finally, in the author's experience (GRANIT, 1935, GRANIT, MUNSTERHJELM and ZEWI, 1939) really efficient light-adaptation in cats almost removes the b-wave or at any rate makes it so small that within the first 10 min. after light-adaptation quantitative work with the electroretinogram as index is very difficult.

With a method based on animal behaviour MURR (1932) succeeded in demonstrating *after light-adaptation* a shift of the luminosity curve of the order of 0.015 μ towards the long wave-lengths but his results for the completely *dark-adapted* eye, when corrected for equal quantum intensity and compared with visual purple absorption, are difficult to understand without assuming experimental errors of some kind. It is an exceedingly narrow curve with maximum around 0.525 μ, and in 0.480 μ at only about 30 % as compared with 88 % for visual purple. MURR only knew the energy of his stimuli *at* the light source and relied upon it being similarly distributed after passage through the spectroscope and reflexion from the grey paper covering the food which the animals had to locate. This fact must be responsible for considerable errors in the calculation of the energy of the spectral light reflected to the eye.

The average photopic curve of fig. 4 contains the dominator and at least one additional sensitivity curve combined with it. It is possible to show that this second curve in the green cannot be an unmodified curve for visual purple absorption. This can be done by adding to the dominator the absorption curve for visual purple in different proportions and plotting on a percentage basis the complex curves obtained. These do not show the sharp hump in 0.520 μ, seen in the average curve of fig. 4, though actually, with certain proportions between dominator and visual purple, the maximum is located in 0.520 μ.

From the experiments with rats and guinea pigs it is known that after light-adaptation a number of elements are found to be characterized by sensitivity curves which look like abnormally narrow curves for visual purple absorption. If similar elements are found in the cat's retina in sufficient numbers they would combine with the dominator to give just the kind of curve shown in fig. 4.

The curves of fig. 5, both referring to early values for single spikes in the light-adapted eye show that this explanation of the hump in 0.520 μ probably is correct. Influence of the dominator is very marked in the curve drawn in broken lines, less marked in the curve drawn in full which is the narrowest one ever obtained in the experiments with the cat. Both show that a narrow band of modulator type can be superimposed upon the dominator. The maximum of this modulator is between 0.500 and 0.530 μ in these curves. But con-

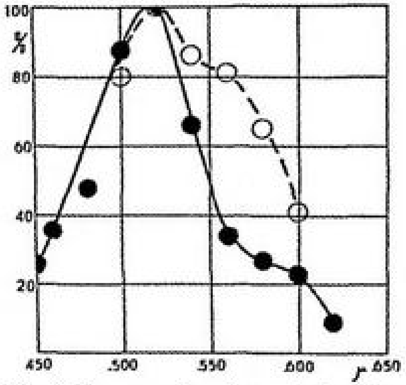

Fig. 5. Two experiments on single spikes showing combination of narrow "green" curve with dominator. See text.

sidering that on the right side of the maximum the dominator contributes to the total result, it is necessary to place the maximum of the modulator nearer to 0.500 μ. This means that it must be identical with the modulator seen previously in guinea pigs and rats and there described as an abnormally narrow absorption curve for visual purple.

Thus, in order to explain all our results with the light-adapted retina of the cat, it has only been necessary to supplement the demonstration of the existence of a dominator and a green modulator by the assumption that they combine so that the average photopic curve of fig. 4 is dominated by an abnormally narrow absorption curve for visual purple upon which is superimposed the dominator, slightly modified by back reflexion from the *tapetum lucidum*. On account of the dominator the maximum of the average curve is shifted to 0.520 μ instead of being in 0.500 μ where it is found in guinea pigs and rats which are lacking the dominator.

Colour Reception.

Schultze (1866) stated that the cat's retina contains 2 or 3 times more rods per cone than the human eye. Considering that in the eye of the guinea pig, which according to the same author is lacking cones, the dominator band and all red-sensitive elements are absent, and that, further, the dominator, where it is found, is responsible for the Purkinje shift in light-adaptation, it is clear that the dominator must be located to the cones. The narrow "green" band with the maximum of visual purple absorption has been seen in the guinea pig (Granit, 1942 a) and in the rat (Granit, 1941 a). It must therefore be located to the rods and probably is due to a slight modification of the visual purple molecule. That this band can be used by different animals in the state of light-adaptation seems clear. But whether it actually serves as a modulator for green, in every respect comparable with the "red" modulator in 0.600 μ and the "green" one in 0.530 μ, is perhaps less certain. If it does, the cat may be able to discriminate colours in the green region of the spectrum, though this discriminative mechanism must be primitive. The lack of a definite "red" modulator suggests relatively incomplete discrimination also in the red. However the experiments have not definitely excluded red-sensitive modulators. The hump in 0.600 μ suggests inadequate development of such elements.

The presence of the dominator in the animals, previously studied, has indicated good colour vision. By this criterion the cat's retina is an improvement upon the retinae of guinea pigs and rats. If the modulators are few they may be difficult to discover, and, yet, the animal be able to discriminate colours with sufficiently strong stimuli. But no doubt even the presence of the dominator *without* modulators must be regarded as an advantage as through this band a large range of the spectrum becomes available in daylight at a level of intensity diminishing the usefulness of visual purple.

Most mammals with cones have some kind of *area centralis* in which cones are present in larger quantities than elsewhere. The relative number of rods and cones in the area which the cat uses in day-light will determine whether the maximum of its photopic luminosity curve is around 0.560 μ or around 0.520 μ or occupies some place between these two points. Considered from the point of view of the human eye the cat would thus, if colour blind, either be a *deuteranope* or a *protanope*, both states being defined as red-green blindness, the former with the luminosity curve of normal subjects, the latter with the luminosity curve shifted towards the short wave-lengths. It is also possible that the cat, in case it possessed some red modulators, is better defined as merely being deuteranomalous or protanomalous. These states would be slightly modified by *tapetum* reflexion.

Cats are generally regarded to be colour-blind (Stagner, 1931). So is the human periphery. But if strong lights are used the human periphery becomes colour-sensitive suggesting that it merely is a question of the relative number of modulators in different regions of the retina. Similarly the cat, with a very limited number of modulators, may be sensitive to colour if it is well light-adapted and very strong stimuli are used. In testing this properly atropine would have to be used to keep the pupil well opened as otherwise the contraction of it to a small slit may prevent both light-adaptation and sufficiently strong stimulation.

Summary.

The micro-electrode technique has been used for the recording of spikes of activity from the retina of the cat in order to study the distribution of sensitivity to spectral light of the retinal elements.

In dark-adapted cats the distribution of sensitivity corresponds to the absorption curve for visual purple.

In light-adapted cats some elements give the broad so-called photopic dominator band with maximum in 0.560 μ, others a narrow curve with maximum in 0.520 μ combined with the dominator in different ratios.

The narrow curve is probably identical with the band seen in the eyes of rats and guinea pigs corresponding to an abnormally narrow absorption curve for visual purple, in the cat shifted somewhat to the right because of the added effect of the dominator.

Some results indicate that back reflexion from the *tapetum lucidum* plays a rôle in determining the shape of the curves in the yellow-green region of the spectrum.

The colour vision of the cat has been discussed in the light of the results arrived at.

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