

The Dark-Adaptation of Mammalian Visual Receptors.

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The experiments on colour reception in mammals, published in preceding volumes of this Journal, consisted in following after light adaptation the recovery of sensitivity in the dark by threshold measurements in different wave-lengths. Consequently a large material of observations on dark adaptation was accumulated in this work. I have now inspected this material from the specific points of view of dark adaptation and added to it some systematic series of observations completing it in certain respects. A brief report of these results follows.

Of particular interest is that the guinea pig's eye (GRANIT, 1942) is a pure rod eye which in the experiments on the cat's retina (GRANIT, 1943) was compared with an eye having a number of cones sufficient to cause a Purkinje shift in a large percentage of the elements under the electrode. There is no Purkinje shift in the guinea pig's eye. This difference is due to the fact that the cat possesses a "carrier" of the Purkinje shift in the broad dominator band of sensitivity with maximum in 0.560μ , an element lacking in the guinea pig.

Method.

A single spike or a place giving a highly restricted discharge having been located by the microelectrode (inserted into the opened eye) the animal was light-adapted to 2,400 m. c. for 10 min. and then allowed

to dark-adapt. In the colour work the course of dark adaptation was followed by measuring the threshold for the wave-length used as standard calibration wave-length, generally 0.500μ , which is at the top of the visual purple absorption curve. From the point of view of dark adaptation the experiments on colour were often incomplete because of their relatively short duration. Many of them were interrupted, when dark adaptation proper set in, for the simple reason that this process always involved dominance of the photosensitive properties of visual purple and thus a source of error when regarded from the point of view of the experimental problems which at that time were in the centre of interest.

In the new experiments that now were added white light instead of spectral light was used for following the decrease in the threshold during dark adaptation of long duration.

Results.

For quantitative work cats are better preparations than guinea pigs because they can be used as decerebrated animals with no more anaesthesia than is necessary for suppressing spontaneous eye movements (5—10 cc 20 % urethane). The guinea pigs received 4—6 cc urethane and, as the final threshold is very much influenced by the degree of anaesthesia, this must be the explanation of the fact that the thresholds are pushed upwards and during dark adaptation decrease far less in guinea pigs than in cats.

Some typical curves from the cat's eye are shown in fig. 1. The most striking fact is that dark adaptation runs a very different course in the three lowermost curves (2—4) referring to three different experiments with white light. The uppermost curve (1), redrawn as a dashed line at the initial level of the others, was obtained by inserting an Ilford spectral red filter and making alternative threshold measurements for red light in the experiment in which curve 2 for white light in the same figure was measured. The red light (curve 1) excludes significant participation of visual purple in the process of dark adaptation. Hence, just as first shown by KOHLRAUSCH (1922) for the human eye, only the first phase of dark adaptation, the one commonly ascribed to cones, is present with this light. Curve 2 for white light, taken at the same occasion is seen not only to participate in this initial phase but also to possess a second delayed phase, dark-adaptation proper, bringing the threshold down to a level of sensitivity that only can be reached by elements activated by the highly photosensitive visual purple. The spectra of the discharge were not

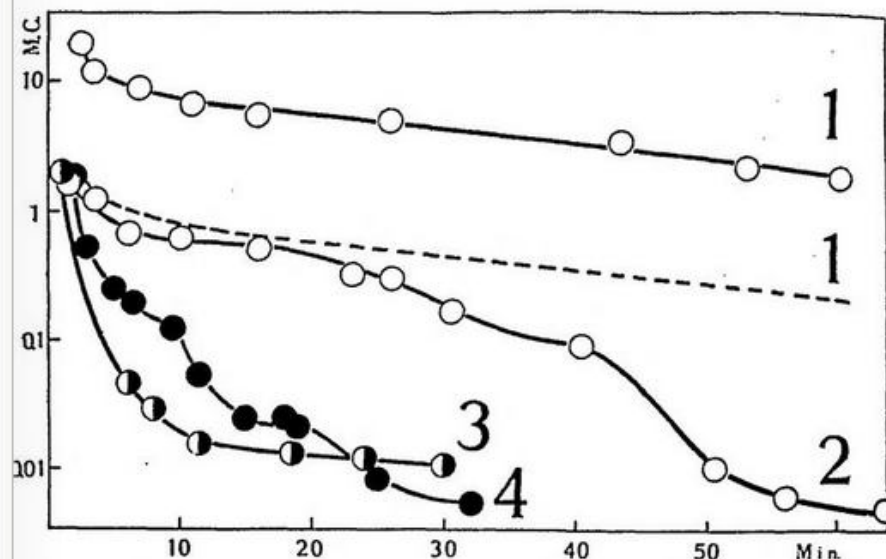


Fig. 1. Ordinates, absolute threshold in log meter candles, against time in the dark in minutes on the abscissa.

1 and 2, from the same experiment with highly restricted discharge, 1 with red filter inserted in the light beam.

3 and 4, two different experiments on dark-adaptation of single spike.

measured in this particular case, neither before nor after dark-adaptation but the colour work has shown very definitely that the delayed phase of dark adaptation always signifies that the spectral properties of visual purple become dominant.

The small initial drop of the threshold that is followed by a period of delay before dark adaptation proper sets in is not seen in all elements. Some of them, sample curve 3, show an immediate and continuous drop of threshold ending in the asymptote common for all curves. The remaining curve 4 illustrates a not uncommon step-like drop of the threshold. In this case it lasts about 10 min. before dark adaptation proper sets in.

Inspection of the material obtained in the colour work with the guinea pig shows that in this pure rod eye curves of different type also were obtained. From the point of view of a strict duplicity theory it would have seemed reasonable to expect only smoothly and rapidly dark-adapting elements such as 3 of fig. 1 in this eye and, above all, no period of delay. However, this is not the case. A period of delay before dark adaptation proper is seen every now and then in this eye too despite the absence of dominator

and Purkinje shift. Elements of this type can hardly in the cone-free guinea pig eye have been cones but must be some kind of cone-like rods. The curves from the eye of the guinea pig were just as complicated as those from the cat's eye, even though perhaps the majority could be said to be of the simple type illustrated by 3 in fig. 1.

Comment.

It is out of the question to explain all the different curves for dark adaptation of individual elements by equally many differences in the adaptive process. Pressure by the micro-electrode might be considered, but the curves 2—4 of fig. 1 all reach much the same final level of sensitivity and 2 illustrates an element still active at maximal sensitivity after more than an hour. Without excluding pressure by the micro-electrode as a source of error in some experiments it is permissible in view of such results as those presented in fig. 1 to exclude an artefact of this nature in many if not in most experiments.

All results can be very simply explained by assuming two kinds of receptors: (i) Real rods and (ii) Cones and cone-like rods. (i) The real rods dark-adapt along a smooth curve beginning without any period of delay as exemplified by 3 in fig. 1. (ii) The cones and the cone-like rods adapt quickly to a semi-stationary level representing a relatively high threshold in the dark, as shown by curve 1 for red light in fig. 1.

In fig. 2 cone-like rods are illustrated as schematic cones, real rods as rods without thereby hypothecating anything regarding differences in form between them.

The difference is probably wholly on the photochemical plane. It can be seen in fig. 2 that owing to the convergence of several receptors towards the same fibre in the optic nerve (the one from which the micro-electrode records) real rods may be combined with cones and cone-like rods in different proportion. In a combination of type 3 real rods alone contribute to the element recorded from and consequently a smooth curve of type 3 in fig. 1 is obtained. In a combination of type 1 the cone-like rod (or cone) will first display its own adaptive

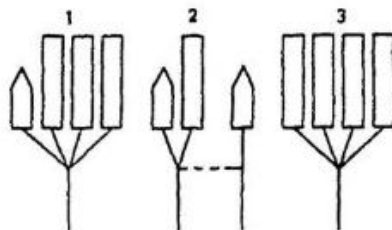


Fig. 2. See text.

properties. But after regeneration of a sufficient amount of visual purple in the real rods, *i. e.*, after a period of delay, they have recovered enough to determine the thresholds during the later phase of dark-adaptation, above called dark-adaptation proper. Again, with a great number of cones or cone-like rods and few real rods coupled to the fibre recorded from it may last very long before the latter can make their influence felt in threshold measurements.

A combination of type 2 has been drawn to illustrate that convergence also may be brought about by horizontal connexions such as horizontal cells and amacrine cells.

These are not the only experiments which make it necessary to assume the existence of intermediate forms between rods and cones. The work on colour reception in the same animals (GRANT, 1942, 1943) has necessitated the same assumption.

Explanation of the different curves on the idea of convergence of a variable number of receptors of two different types presupposes that it can be shown that there is summation of individual converging receptors upon the same fibre in the optic nerve. This has been shown directly by HARTLINE (1940) with the frog's eye.

Summary.

Dark-adaptation has been followed in cats and guinea pigs by measuring the absolute threshold of single or highly restricted discharges, isolated with micro-electrodes.

The curves obtained are of different types, as illustrated in fig. 1.

The different adaptation curves can be explained by the assumption that there are two kinds of rods converging in different proportion towards the same fibre in the optic nerve, (i) real rods and (ii) cone-like rods with adaptive properties similar to those of cones.

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