

THE SPECIAL SENSES

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PART II. VISUAL RECEPTORS

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In two consecutive reviews in this journal Olmsted (61, 62) has reviewed the literature on the eye up to September 1939, therein discussing also such subjects as eye movements, pupil, lens, and ocular fluids. This being so, the present author feels that he is doing more justice to the intentions of the editors and to the present situation¹ as well as to his own special background if he concentrates on a more limited field.

Some recent summaries.—Many of those engaged in visual research have recently summarized our knowledge in different branches of this field. Very comprehensive, especially with regard to contributions from zoological quarters, is a book by von Studnitz (78) who also has published an article on the duplicity theory (79). A general review of some recent experimental work has been written by Wright (95), whereas summaries by Lythgoe (52) and Bartley (2) have the character of analytical discussions of the mechanism of dark adaptation (Lythgoe) and neurological aspects of visual reactions (Bartley). In the introduction to his work on the regeneration of visual purple Zewi (97) supplements the author's (28) review, "Processes of adaptation in the vertebrate retina in the light of recent photochemical and electrophysiological research," with regard to the photochemistry of visual purple. Wald (89) has given an account of his work on the chemical aspects of visual purple decomposition, and Stiles (75) summarizes the results of his own and Crawford's research regarding the curious "directional sensitivity of the retina" that they have discovered.

Photosensitivity of visual purple.—The newest contribution to

¹ Latest periodicals from the U. S. A., of those which have been accessible at all, are those published in July 1940; British periodicals since April 1940 have practically ceased to arrive.

this question (70) is one which provides the author with an opportunity of paying a tribute to the memory of a fellow worker, Dr. R. J. Lythgoe of University College, London, a leading expert among the devotees of the eye, who died in the spring of 1940. A thorough knowledge of the subject of vision, scrupulous criticism, accuracy, and experimental initiative guided his research, part of which was carried out in collaboration with the photochemist, Dr. Goodeve. Among Lythgoe's recent contributions should be mentioned the first accurate absorption curves at different pH levels for the yellow, relatively stable indicator substance (Kuehne's "visual yellow," Wald's "retinene" or a substance closely related to it) into which visual purple in solution decomposes upon illumination (51); the first accurate measurements of the extinction coefficient for visual purple (51), and of the quantum efficiency (about 1.0) of this photochemical reaction (23), which has been analysed in several papers; and the discovery of the interesting "transient orange" photoproduct (51, 53) which is the initial, very labile stage of visual purple decomposition. In the latest experimental work (70) the photosensitivity is measured directly in terms of the product of the extinction coefficient and the quantum efficiency for a number of wave lengths. It was found that the photosensitivity actually runs parallel with Lythgoe's earlier standard curve for the extinction coefficient alone, a fact which definitely proves that the large values for visual purple absorption in the blue end of the spectrum do not depend on admixture of impurities. In the meantime Ludvigh & McCarthy's (50) measurements of the light lost owing to selective absorption in the extra-retinal part of the eye have appeared, showing light from the blue end to suffer severe losses on its passage to the retina. Their work finally explains (49) why the sensory (44) and the electrophysiological data (26, 27), obtained with an intact eye, have fallen inside the absorption curve for visual purple in the blue end of the spectrum. Such comparisons nowadays presuppose correction of the data on the basis of equal quantum efficiency rather than on equal energy, as was first pointed out by Dartnall & Goodeve (22).

Actually, the frog's eye may at higher intensities give larger electrical responses to blue and violet than would be expected on the basis of its average visibility curve for low intensities, a fact noted by several observers. [See author's recent summary (28), p.

48]. We shall return below to the interesting question of "blue reception."

Two phases in visual purple regeneration.—Zewi (97) has published an extensive analysis of the regeneration of visual purple in live frogs, based on over one thousand five hundred eyes. Curves illustrating dark adaptation in terms of visual purple concentration plotted against time showed the effect of temperature on the regenerative processes to be large. Very interesting seems the observation that the slow course of regeneration in intact animals at low temperatures was duplicated by the equally slow course of regeneration in excised eyes. In the latter case regeneration was independent of temperature. In other words, that part of the regenerative process which is sensitive to temperature is lacking in excised eyes. It presupposes live frogs. Short times of preadaptation with strong light led to an initial period of delay in the regeneration of visual purple. None of Zewi's regeneration curves could be fitted into one of the well-known types of chemical reaction. Von Studnitz (80) has emphasized the significance of the oil globules for regeneration.

Illumination enhances regeneration of visual purple.—Another result of Zewi's work was the observation that illumination of the frogs speeds up regeneration of visual purple. A step further along this road is reported in a paper by Chase & Smith (12), continuing work begun by Chase (11) dealing with the old subject of regeneration in solution. Under these conditions there is relatively little visual purple formed but the process seems to take place without changes in the absorption spectrum of the substance. In view of the results mentioned above, one must presume that only one phase of the regenerative process, the one found in excised eyes, can be concerned. In accordance with this supposition stands the fact that regeneration in solution is independent of temperature. Now this phase of regeneration was found to be enhanced by previous illumination of the solution with blue light. The maximum of the effect was located somewhere between 0.490 and 0.440μ . The authors have not been aware of the fact that a similar favorable effect of previous illumination with blue light upon the regeneration of the retinal electrical response of the frog has also been demonstrated (34). Visual purple regeneration may be stimulated by decomposition products of its own breakdown or by some other blue-sensitive substance which may or may not have other

tasks to carry out in the sensory mechanism. To quote Lythgoe (52): "One cannot help wondering whether the photosensitive substances responsible for day vision are formed in this way: the bright light may be the essential agent in the preparation of the visual purple for the reception of high illuminations." The subject is further considered by Granit *et al.* (34). Actually the visual purple of the living animal is never completely bleached away (32, 52, 97).

Oxygen and visual purple regeneration.—Recent results with sensory methods have shown that dark adaptation was disturbed during oxygen deprivation in a low-pressure chamber (55) or during inhalation of gaseous mixtures with low oxygen content (54). The results were held (55) to be due to an effect on the central nervous system rather than on the photochemical substrate. Now neurons are known to be sensitive to lack of oxygen; Hartline (37) has shown that the eye is no exception. Similar results in experiments on visual acuity (56) in a low-pressure chamber also lend themselves to such an interpretation. In these experiments red light was used and hence stimulation of visual purple was insignificant. Nevertheless it should be emphasized that visual purple regeneration is exceedingly sensitive to oxygen lack (97). According to Lythgoe (52), "It seems possible that we have two methods for the regeneration of visual purple. Regeneration from its breakdown products almost certainly involves the addition of energy to the system, and this energy can be provided either by the absorption of light or by a chemical process needing oxygen."

The decomposition of porphyropsin.—In the rods of certain fresh-water fishes, the visual purple of amphibians and mammals, known as rhodopsin, is replaced by a purple pigment with a maximum in the region of 0.535 to 0.540 μ (difference spectrum). For this substance the name "porphyropsin" has been suggested (Wald). According to Wald, who has summarized his work on this subject (89), decomposition of rhodopsin in the retina leads to formation of vitamin A. One of the intermediate decomposition products is a yellow carotenoid substance, Wald's "retinene," closely related to Lythgoe's "indicator yellow." Now it seems that the decomposition of porphyropsin also leads to a similar intermediate product with vitamin A₂ as the end stage (87). Retinene and vitamin A seem to be replaced by these two new carotenoids, retinene₂ and vitamin A₂, with slightly different ab-

sorption spectra. Vitamin A₂ is a recent discovery by the biochemists. A study of the distribution of these two vitamins in fishes (88) is perhaps less directly concerned with vision.

Visual purple; sensitivity to light; vitamin A.—In a recent review in Swedish (29), the author has criticized the view that sensitivity to light is merely the equivalent of concentration of visual purple. The experimental work behind this criticism consisted of parallel measurements of the electrical response to light and the concentration of visual purple (31, 32). Thus, for instance, after bleaching with 3400 m.c. leaving some 40 per cent visual purple, the electrical response of the cat's eye is reduced to next to nothing. On the other hand nearly maximal responses of the frog's eye may be obtained without measurable reduction in the amount of visual purple present. Lythgoe (52) has added other arguments, among them a comparison referring to the human eye: "There are no figures for the concentration of visual purple in the human retina at different periods of dark adaptation, but we will assume that the figures of Granit *et al.* (32) for the cat are applicable to man. Between the tenth and thirtieth minutes the concentration of visual purple increases from 57 to 95 per cent of its final value. According to the simple theory, the visual threshold should be divided by about one half (57/95) during this period, whereas it is, in fact, divided by about one thousand. In other words, the increase in concentration is not nearly enough to account for the great increase in sensitivity."

Similar objections are raised by him in connection with the question of the night blindness and vitamin-A deficiency. To Olmsted's list of references (61, 62) from this steadily expanding, but theoretically uninteresting field, should be added the newest ones (46, 59, 60, 66, 68, 84, 85, 86, 94). One can only wish that the demonstration by Johnson (46), confirming Tansley (81), that lack of vitamin A may lead to degenerative changes in the retina at an early stage should not be forgotten. Their results could explain why some authors (41, 66) find experimental hemeralopia to affect the cone system too and to be relatively resistant to vitamin-A therapy. That the vitamin somehow is involved in the mechanism of regeneration of visual purple (see above) need not be the only explanation of experimental hemeralopia worth considering.

Colour reception analyzed with microelectrodes.—This technique which recently has been used with some success in other fields by

Buchthal (10), and by Forbes and his collaborators (67, 83) as well as by Lorente de Nó (48) in the central nervous system, is particularly well suited for the analysis of spectral properties of single or a limited group of elements in the eye. Granit & Svaetichin (33) describe it in detail and give illustrations of the activity of single elements responding to different parts of the spectrum. Using the light-adapted frog's eye they compare the average spectral distribution curve for a great number of elements acting together with the distribution curves obtained from a single or a restricted number of elements. The average curve has its maximum between 0.555 and 0.560 μ and is made up of contributions from elements with much narrower sensitivity bands and different maxima. A definitely isolated element has its maximum between 0.600 and 0.580 μ . There is also a "blue" receptor with a maximum somewhere around 0.460 to 0.480 μ . The "green" receptor with a maximum between 0.500 to 0.530 μ may or may not be identical with visual purple. Precautions were, however, taken to exclude visual purple. Somewhat surprising was the fact that the element with a maximum of 0.580 to 0.600 μ after dark adaptation changed into one with the maximum of visual purple (around .500 μ) and the high sensitivity of the rods. Whether this means that a cone changes into a rod or that rods and cones go to the same final common path, which after dark adaptation is taken over by the rods, is difficult to say. The fact, however, is in itself of primary importance. The presence of a "blue" receptor confirms earlier results with the electroretinogram (28, 34, 35). A significant observation also was the striking rotation of activity among the different elements, which is a serious source of error in experiments of this kind.

Photochemical model of the retina.—In two papers Weigert has continued description of his "artificial retinae," gelatine films containing visual purple dissolved in digitonin (90, 91). In view of some of the results referred to above (11, 12, 33, 34, 35, 52), it is indeed interesting to find that illumination of such films with certain monochromatic lights leads to changes in the absorption spectrum. There are rather striking analogies with the behavior of the vertebrate retina, particularly those effects which are produced by mixing two monochromatic lights. The one article (91) describes in detail and with great clarity both the results and the technique of measuring the selective effects in the gelatine films

with the aid of photodichroism. To their paper the reader must be referred for instruction in this matter.

General observations on excitation and inhibition.—A most interesting report by Hartline (38) deals with the off-effect in single fibers of the optic nerve. A third of the fibers respond only to cessation of illumination or to a sudden reduction of intensity. This discharge is completely inhibited by reillumination, as indeed was to be expected. Hartline's concept of the "receptive field" (37) of a fiber of the optic nerve again proves its usefulness. The sensitivity within the receptive field as well as the boundaries of it can be mapped by moving a very small spot of light over it. The receptive field is most sensitive in its center. In accordance with this stands the fact that an off-response is obtained only when the spot of light is shifted to a less sensitive part of the receptive field, as well as after a sudden decrease of the illuminated area. Further, the greater the area reilluminated the more effective is the suppression of the off-discharge. "Thus there are inhibitory effects due to illumination which converge upon the ganglion cell from all portions of its receptive field and are summed in the total inhibition produced" (Hartline, 38).

In a paper by Granit & Helme (30) the electroretinogram and the impulses in the optic nerve, recorded during polarization of the retina, were described. The responses in both retina and nerve were found to be greatly enhanced when the inside of the eye was the cathode, and depressed when it was the anode. The components of the retinogram are discussed in this paper as well as in a valuable summary by Bartley (2) who also emphasizes the significance of the rotation of activity mentioned above.

Bernhard (4) has shown that during illumination of the eye, a slow potential change derived from the ganglion cells spreads electrotonically along the optic nerve. Some records from the frog's optic tectum illustrate potential changes in this region. Bishop and O'Leary (7) have also described potentials from the optic pathway. Simultaneous records by Bernhard of the human electroretinogram and the α -rhythm demonstrate that the blocking of the α -rhythm, following illumination, always takes place after a constant interval from the onset of the electroretinogram.

Crescitelli & Jahn (14, 45) have found notable diurnal changes in the electrical response of the compound eye. Very interesting is their observation that at sufficiently high temperatures the elec-

trical response of the grasshopper eye to short flashes of light ends with a series of rhythmic waves which are suppressed by increased duration of stimulation. Cooling the eye was found not to leave a negative component corresponding to that of the vertebrate eye.

In two papers by Wilska (92, 93) microrecording from the retina as in the colour work, described above, has been reported. His most noteworthy result is the proof that the inhibition of the off-effect found by Granit and by Hartline in cold-blooded eyes also exists in the cat's eye. In other respects his results are covered by Hartline's earlier work (37).

Measurements of the latent period of the *a*- and *b*-wave of the electroretinogram have been published by Piéron & Segal (64). From the fact that the latency of the *a*-wave is far less sensitive to cold than that of the *b*-wave, they conclude that the *a*-wave represents part of a more distally located "primary response" to light.

Therman (82) has determined the size of the electrical responses to red and blue light in the frog's eye in relation to state of adaptation. The response to blue increases in the dark, and diminishes during light adaptation while the response to red increases. The retinal pigment can be made to take up the "light adapted," expanded position after an injection of epinephrine. This, however, does not lead to the changes in the electroretinogram accompanying "real" light adaptation. The expanded pigment cannot therefore have exerted any protective action on the rods.

Some effects of repetitive electrical stimulation of the eye have been reported by Bouman (8) and Schwartz (72). In two papers Miles (57, 58) adduces evidence in favour of the view that the so-called polarity potentials of the eye are due to the current of rest, which changes during eye movements owing to the displacement of the bulbar poles relative to the electrodes applied on the skin outside the eye bulbs. Similar arguments are advanced by Lindsley & Hunter (47). See also Baudouin *et al.* (3).

Directional sensitivity of the retina.—By this term is meant the now well-known fact that a pencil of light reaching the cones at an angle is less effective in creating a perception of brightness than one entering them along their own vertical axes. Directional sensitivity is not found in rods, according to Stiles (75). The newest contribution by Stiles (77) shows that the effect is absent

in the parafovea until the eye has been light adapted and supposedly become dominated by cone vision. An interesting effect of wave length had previously (76) been noted in the form of colour changes as the angle of incidence of the beam was altered. The new measurements of the effect of the angle of incidence upon the difference threshold of a small foveal monochromatic patch, placed in a field of larger dimensions, both of which are variable with respect to wave length and intensity, show changes in directional sensitivity at different levels of brightness. These mimic the changes obtained in the parafovea when rod vision, owing to increased brightness, is replaced by cone vision. Stiles concludes that the effects on a pure cone population in an analogous manner are due to one type of cone being replaced by another. He gives a preliminary calculation of the spectral properties of the three types of cones assumed in order to explain the data. Perhaps one should remark that the experimental conditions imposed favour effects of interaction in the retina which may complicate evaluation of the results.

As to the explanation of the directional sensitivity Wright & Nelson (96) may be right in suggesting that it depends on differences in the refractive index between the receptors and the surrounding medium. Neither can Best's (5) view be neglected, that the absence of a directional effect in rod vision may be due to the capacity of the rods to summate and thus to collect all the light of the less perfect image of the tilted beam till it matches the brightness created by the central beam.

Some work with sensations.—By "indirect adaptation" Schouten & Ornstein (71) mean the fact that illumination of an adjacent or distant area depresses the brightness of a test field. The use of Wright's binocular method has greatly facilitated the study of such processes, as can be seen in this paper as well as in one by Pitt (65). There is α -adaptation which spreads almost instantaneously and soon depresses the sensitivity of the whole retina to an almost stationary level. During this period of stationary low brightness, something else in addition takes place in the retina, as is shown by the circumstance that the recovery curves after adaptation are slowed down by longer exposures. This delayed recovery is an expression of β -adaptation. After short exposures the α -process alone rises very quickly. It is held to be electrical in nature. For details concerning these and related facts the

reader is referred to the two very instructive papers mentioned.

From the point of view of retinal and central mechanisms measurements of visual acuity and brightness discrimination as functions of log brightness cannot deal with very different mechanisms. Yet in Hecht's (39, 40) older attempts to apply his well-known "photochemical system" it struck one that, in the equations for the rod and cone systems, the constants came out as 0.0906 and 0.794 respectively for "visual acuity," and as 100 and 0.25 for brightness discrimination. The absolute values are of no significance but it did not seem very reasonable that the ratio of rod to cone constants should be so absurdly different in the two cases. Hecht & Mintz (42) have now studied visual acuity under simplified conditions of visual resolution and give an interesting mathematical treatment of this problem in which the distribution of light over the retinal image is also considered. They state that the visual resolution and intensity discrimination now are described by the same equation. In view of the older results a comparison of the constants would have been worth having.

Crozier & Holway (15) present measurements of brightness discrimination and deduce an equation without reference to specific theory. In a number of papers (16 to 21) Crozier & Wolf report continuance of their work on the reactions to flicker in different animals, determining the point of fusion with the aid of behavioristic reactions. They claim that the curve for flicker-fusion against log intensity is a probability integral in log I, and state, in opposition to Hecht, that the physicochemical nature of the excitatory process cannot be deduced from measurements of this type. The authors have been trying systematically to elaborate a descriptive quantitative system based on the probability integral.

Graham and his collaborators (24, 25) have contributed to the old question of summation at the threshold relative to size of stimulus. An interesting new feature of the quantitative treatment of the data is their utilization of Hartline's concept of the "receptive field" (see above). Bartlett & Gagné have tested binocular summation at the threshold with negative results (1). Visual thresholds have also been studied by Chevallier & Roux (13).

The blind spot is monographically treated by Bröns (9) who also adduces experimental evidence to the effect that the filling-in of this physiological scotoma is due to special connections of the

nerve fibers from the parapapillary zone. See also Saubermann (69). A thesis by Olsson (63) deals with the colour changes of a test field as it moves towards the periphery. His results lead him to dispute the existence of the so-called yellow macular pigment.

Interesting from the point of view of retinal physiology is the demonstration by Smith (73, 74) that in cats the reactions to apparent and real movement persist after all somatic cortex has been removed. Animal behavior is also used by Birukow (6) and by Grether (36) for the analysis of the colour sense of frogs and chimpanzees respectively. For the same purpose Hecht & Pirenne (43) have used the iris muscle contraction to establish that the visibility curve of the owl is consistent with the idea that its scotopic photochemical system is visual purple.

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