Planaria dorotocephala, and although M/1000 KNC is lethal within a few hours, there still remains an oxygen consumption of about ten per cent. of the normal to be accounted for.[6] In Planaria agilis and in certain molluscan tissues the remaining oxygen consumption after maximum depression by cyanide is twenty per cent. of the normal.[7] Suitably diluted solutions of the cyanides appear to accelerate metabolism and in one case at least relatively strong solutions are required to depress cellular respiration.[8] It is also true that an oxidative enzyme has been isolated, the activity of which is not appreciably affected by cyanide.[9] The wide discrepancy between the theory and the observed facts is obvious. Cyanide is therefore not a "specific negative catalyst" in the strict sense that Warburg's theory requires.

A slight recovery of oxidative metabolism in the presence of cyanide has sometimes been noted. This, Warburg says, is due to the oxidation of the cyanide itself by the catalytic action of the iron-containing substance. Since the cyanide is said to render the catalyst incapable of transferring oxygen, a reasonable doubt arises that a catalyst can be instrumental in oxidizing a substance that has rendered it incapable of catalyzing an oxidative reaction.

The writer has recently studied the recovery period after depression by KNC more intimately than has been done heretofore.[10] When Planaria are removed from a solution of KNC in which their oxygen consumption has been depressed fifty per cent., the oxygen consumption rises above the normal during the first hour after removal from the cyanide. The extent of rise above normal is considerable, is independent of the duration of depression of KNC and persists, with gradual decrement, for at least six hours. To bring Warburg's theory into alignment with these facts it is necessary to assume that the quantity of active iron or of oxidizable materials in the cell increases during the period of depression. However, the fact that the extent of rise in rate of oxygen consumption above the normal is independent of the duration of depression renders these assumptions exceedingly improbable. A third assumption is possible, namely, that the catalyst, after being freed from the cyanide, becomes excessively active. Concerning this possibility there is no information available.

Why anhydrous conditions are necessary for the action of the iron catalyst in commercial nitrogen-fixing processes or why the reaction is strongly inhibited by minute quantities of carbon monoxide and other impurities is unknown, despite the vast amount of research that has been expended. The oxidative reactions in the living organism go on in a much more complicated system. Warburg's emphatic postulation regarding the action of cyanide on the system may be considered premature.

From the effects of cyanides on oxidation in living systems it is perfectly clear that the resemblance between Warburg's models and the oxidative mechanisms in the cell is distinctly limited. As Warburg states, the idea that iron is of importance in oxidative metabolism is not new. Warburg's results have yielded suggestions as to the possible nature of the rôle of iron. However, the universality of iron in biological oxidative mechanisms is not proven, and his theory as at present formulated is quite inadequate to explain many of the facts that are associated with changes in rate of oxidations in the living organism.

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6 Hyman, L. H., 1919, *Amer. Jour. Physiol.*, xlviii, 340.

7 Allen, G. D., 1919, *Amer. Jour. Physiol.*, xlviii, 93; Gray, J., 1924, Proc. Roy. Soc., Ser. B, xcv, 95.

8 Hyman, L. H., 1919, *Amer. Jour. Physiol.*, xlviii, 340; Townsend, 1901, Md. Agri. Exper. Sta. Bull., No. 75, 183; Lund, E. J., 1918, *Amer. Jour. Physiol.*, xiv, 365; 1921, *ibid.*, lvii, 336.

9 Dixon and Thurlow, 1925, *Biochem. Jour.*, xix, 672.

10 Buchanan, J. W., 1926, *Jour. Exper. Zool.*, xliv, 285.

SPECIAL ARTICLES

VISIBLE RADIATION FROM EXCITED NERVE FIBER: THE REDDISH BLUE ARCS AND THE REDDISH BLUE GLOW OF THE RETINA

THERE is a singular phenomenon—one of the countless interesting entoptic phenomena discovered by Purkinje[1]—which has remarkable consequences. In a perfectly dark room you give yourself a band of red light—any light of the spectrum, and white light as well, will give the phenomenon but it is rather more easy to obtain with red light. What you will see is not only the band of red light, but also stretching out from it on both sides big slightly reddish blue arcs—the bigger the further away you stand. They are not of the color of the rod pigment (visual purple), which is of a slightly bluish red. The angular size and the shape of these reddish blue arcs make

1 Purkinje: "Beobachtungen und Versuche zur Physiologie der Sinne," 1825, ii. 74. This rare work of Purkinje—so rare that Gertz reproduces the whole discussion which Purkinje gives of this phenomenon because so few of his readers will be able to see his book—has now been reproduced in Czecho-Slovakia: Purkinje, Johann Evangelista, *Opera Omnia.* Praze: C. Calve, 1919. My name for this phenomenon, "the reddish blue arcs" and "the reddish blue glow of the retina," has been very generally accepted.

it absolutely certain that what you are seeing is the fibers of the optic nerve which lie on the surface of the retina. Since the beautiful work of Vogt with blue-green (red-free) light[2] these fibers can be plainly seen in any one's eye with the aid of the ophthalmoscope; until now they had only been seen by the anatomist and by means of the entoptic phenomenon here described.

But why are these fibers visible? The explanation hitherto given, by Gertz and by others, is that the action current of the optic nerve fibers which carry the red light excitation causes a "secondary excitation" in adjoining fibers. Such a nerve current as this, however, if it occurred, would not be provided with the right "place-coefficients";[3] no adjoining fibers, though stimulated, would enable you to actually "see" the nerve fiber in question, for they would have the place-coefficients of those rods or cones from which they comé. It is with nothing but rods or cones, or bipolar cells, or ganglia, that the "seeing" of these reddish blue fibers could be done.

But there is an additional feature of this phenomenon which throws great light upon its nature: it is followed by an after-image. It has been shown by Lazareff[4] directly (what was perfectly well-known before) that any production of a light sensation (whether chromatic or achromatic) due to the passage through the head of an electric current is followed by no exhaustion; the nerve is like the heart and the organs of respiration—the refractory period suffices for complete restoration. When, however, exactly the same sensation is brought about by the action of physical light upon the retina there is extreme exhaustion, as measured by the Nagel adaptometer. But what is exhaustion in the light-sensitive substance in the rods and cones? It is merely another name for the after-image.[5] The specific residual image that follows, a whitish reddish blue sensation, would be in color a less bright yellowish green. A person who gets this after-image says at once "It is a dark olive," which is correct both as regards brightness and chromatic quality. This fact excludes the possibility of any nervous structure whatever being the thing which is directly acted upon by the "blue arcs." Of this the experiment of Lazareff (*loc. cit.*) is absolute proof. His experiment is this: it is found that exactly the same visual sensation (say a slightly reddish blue) can be produced (1) by physical light and (2) by an electric current, but that in case (1) there is extreme exhaustion (and a residual image), and that in case (2) there is no exhaustion (and no residual image). What can be the cause of this extraordinary difference? The sensation (and therefore the cortical process) is the same in both cases. All the conducting nerve-fibers are certainly stimulated in both cases. But there is the possibility of a difference in what takes place in the retina:

(1) There is no question that in the case of the physical light stimulus it is the light-sensitive substance in the cones (and the rods) that is acted on, and that it is the photochemical products of the dissociation produced by light that act then on the nerve-ends in the cones and rods. If the electric current acted on the light-sensitive substance (as it is hard to think that it could—it has not got the excessive specificity of the visible radiations) then there would be no possible difference between the two situations, and there could not be (1) the existence of the residual image in the one case, and (2) its non-existence in the other. Hence we must conclude that (1) with the existence of the residual image goes the stimulation by physical light and (2) with the non-existence of the residual image goes direct stimulation of nerve by the electric current. The "blue arcs" and the "blue glow" which belong in the case of the after-images make themselves seen therefore by physical light and not by any sort of a "secondary excitation."

But this is not so strange a situation as it appears to be at first sight. There is another case in which visual sensations of all kinds are produced, but without any residual images—that in which the optic nerve is directly stimulated by pressure. There are several (no less than six) different forms in which pressure can be applied to the optic nerve:

(a) The "pressure phosphenes"—rings produced by pressure with the finger on the corner of the eye.

(b) Light-sensations (all the colors of the rainbow) produced by pressure with the hand on the whole eyeball. (This is dangerous.)

(c) What I have called the pull-phosphenes (got by moving the eyeballs vigorously to one side and the other). One sees the exit point of the optic nerve.

(d) The so-called "self-light of the retina." This is now believed to be due to permanent pressure on the retina by the fluids of the eyeball.

(e) After a fall on the ice, if one hits the back of the head, one "sees stars."

(f) In case of enucleation of the eyeball, at the

[2] Handb. der biol. Arbeitsment., 1922, Abt. V, Lief. 55, 376.

[3] It has been necessary to introduce this new term; without it we have nothing but the wholly erroneous "local sign."

[4] Lazareff, *Comptes rendues de l'Académie des Sciences*, 178, 1100, 1924.

[5] I have introduced the terms "persistent image" and "residual image" for positive after-image and negative after-image, respectively. They save the tired brain, in each case, one unnecessary syllogism.

moment when the optic nerve is cut there is a visual sensation. (J. J. Abel.)

In the last two cases, no residual image has ever been observed; in the other four cases it is perfectly well known that there is no residual image. Stimulation by the electric current then falls into the same category with stimulation by pressure—the optic nerve (or *some* part of the nervous structure—the cortex itself is sufficient—see Fedor Krause[6]) is acted on directly, while in the case of chromatic stimulation by light it is the highly specific light-sensitive substance in the cones that is acted upon photochemically.

In fact, it is any way plain that this light-sensitive substance in the cones (the *Sehstoff*[7]) has been made highly specific in order to respond *specifically* to the 160 energy-radiations in the spectrum which we can distinguish as different sensations. There is no such specificity as this in an electric current—hence one could have predicted that it could not attack the light-sensitive substance directly.

There are additional considerations:

(1) The optic nerve-fibers are non-myelenated, but occasionally there occurs a congenital defect of myelenated fibers in this region of the retina. I have had such a case and this individual did not see the blue arcs.

(2) In a case of traumatic blue-blindness, the blue arcs were seen, while there was no blue sensation from external objects. But blue blindness, even when congenital, is nearly always a retinal defect and traumatic blue-blindness is known to be due to yellowish exudations on the surface of the retina. This would prevent blue light coming through from external objects, but would not prevent the reddish blue fibers underneath it from being seen by the cones.

(3) Since it is known (a) that nerve, when excited, gives off CO_2 (Shiro Tashiro, G. H. Parker); (b) that it gives off heat which, though excessively small in amount, can be measured (A. V. Hill, *Proc. Roy. Soc.*, 1927) and (c) (more important still) that every organic substance (if of high vitality) gives off radiations which enable it to take its own photograph (A. Nodon, *Comptes rendus*, 1924, 178, 1101) it is no far cry to suppose that nerve (especially when stimulated, but perhaps also when not stimulated) can give off radiations which are *visible* by means of the human rods and cones close by.

(4) But if this is the case, why has it not been discovered before, since physiologists are always working with stimulated nerve-fibers? The answer is: They do not so often work with non-myelenated fiber.[8] Moreover, they do not work in an absolutely dark room, that is necessary to seeing this phenomenon.

(5) The blue glow (seen by hardly any of the (twelve) observers who have written on this subject since Purkinje) is due to the visibility of the point-like (when seen in cross-section) bipolar cells which surround the red band.

The argument then stands thus: Nothing but the light-sensitive substance in the rods and cones can furnish an after-image, and this can be affected by nothing but physical light; consequently, when the observer sees the reddish blue arcs (and the reddish blue glow) of the retina he is actually "seeing" his own optic nerve-fibers (and bipolar cells).

I have set out my argument very fully here because, though it is really quite irrefragable, some of my readers[9] have seemed to find it difficult to follow. I have defended this view of the blue arcs and the blue glow (at Woods Hole and elsewhere) for some six or seven years. The recent work of Lazareff and Nodon, while it is delightfully to the point, is not at all essential to my proof: it has been well known since 1899 (S. I. Franz, *Psychol. Monographs;* Fedor Krause, *loc. cit.*) that visual sensations due to the electric current are not followed by an after-image[10] and so belong to a very different category from visual sensations due to physical light.[11]

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[6] *Klin. Wochenschr.*, Jg. 3, p. 1269, 1924.

[7] This is apparently not the rod-pigment, the visual purple (as some suppose it to be), for the (white) brightness-distribution in the extreme periphery (where there are rods only) is, in photopic vision, the same as in the centre of the retina (v. Kries).

[8] Hallowell Davis, *Physiological Reviews*, 1927, p. 583. —I tried to see objectively if any light was given off by the splanchnic nerve of a dog when stimulated in a dark room by an electric current. But one would not expect a light so faint as this must be (A. V. Hill) to be seen at any distance, although it is visible to the rods and cones close by. Besides, the dog I tried was not of high vitality—it had, for several hours, been the subject of vivisections.

[9] *Proc. Nat. Acad. of Sciences, 12,* 413, 1926.

[10] Any more than sensations due to pressure.

[11] It is a singular fact—hitherto unexplained as far as I have been able to find out (but one which ought to throw great light upon the nature of the nerve impulse) —that the light-sensation produced by the electric current (galvanic) is of opposite (''complement'') colors according to the direction in which the current flows, and also with the make and the break of the current [circuit?]. The colors are reddish-blue and greenish-yellow. This has led ardent followers of Hering (G. E. Müller and others) to think that our after-image is in some way involved in this—but without sufficient reason.