LEAST RETINAL ILLUMINATION BY SPECTRAL LIGHT REQUIRED TO EVOKE THE "BLUE ARCS OF THE RETINA"¹

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ABSTRACT

Interest in the "blue arcs of the retina," first described by Purkinje, has recently been renewed by Ladd-Franklin, who establishes (in a series of papers) to a high degree of probability the theoretical views of Druault. Druault suggested (and later, independently, Ladd-Franklin also) that the blue arcs are due to the emission of light by the fibers of the optic nerve that pass over the surface of the retina. It has been repeatedly mentioned by Ladd-Franklin and others (Druault, Troland, Amberson, Ellis) that the blue arcs are obtained more easily with red light than with a stimulus of any other color. This suggests that the origin of the nerve activity causing the blue arcs lies in the retinal cones rather than in the rods, since the rods are relatively insensitive to red light.

The blue-arc phenomenon has been tentatively linked by the author with a certain phase (called the Purkinje phase, or Bidwell's "ghost") of the periodic afterimage following brief stimulation by light of the extrafoveal retina. The Purkinje phase undoubtedly depends on the action of the rods; hence, the two phenomena which are quite similar in some respects would differ in origin if the blue arcs were really initiated by cone action.

As a check, then, on the origin of the nerve activity producing them, the blue arcs were aroused by pure spectral light (2° circular field), the retinal illumination being subsequently reduced until the blue arcs no longer appeared. In this way the retinal illumination required to evoke the blue arcs has been determined as a function of wave length for the author's right eye.

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I. INTRODUCTION

The "blue arcs of the retina," known since Purkinje's account of them in 1825, have attracted considerable recent attention.² When the macular³ region of the retina is stimulated by a patch of light (observers have usually used a circle or vertical band), the subject reports not only the image of this stimulus, but usually also two "blue arcs."⁴ These arcs correspond quite exactly to the position of the nerve fibers which extend across the inner surface of the retina from the stimulated area to the exit point of the optic nerve ("blind spot").⁵ It is universally agreed⁶ that activity of these nerve fibers in some way causes them to become visible as the "blue arcs of the retina." H. Gertz proposed to account for the arcs by secondary stimulation of neighboring retinal structures through (1) an external circuit of, or (2) induction by, the action currents set up by the primary stimulus. This sort of explanation (by secondary electric stimulation) has been accepted by Troland, Amberson, Ellis, and Davis. There is some uncertainty as to which structure is to be thought of as being affected by the secondary electric stimulus, whether it be the nerve fibers parallel to those primarily excited (Amberson),⁷ the ganglion cells of those fibers (Amberson),⁸ the nerve fibers (bipolar cells) perpendicular to them (Troland),⁹ or the rods and cones themselves (H. Gertz; Davis).

² Zeeman, *Zs. f. Psych. u. Physiol. d. Sinnesorgane*, **6**, p. 233; 1894. Siethoff, *Zs. f. Psych. u. Physiol. d. Sinnesorgane*, **14**, p. 375; 1897. Tscherning, *Klin. Monatsbl. f. Augenheilk.*, **36**, p. 223; 1898; *Ann. de la Policlin. de Paris*, 1898; *Encyclopédie française d'ophtalmologie*, III, p. 228; 1904. Charpentier, *Compt. Rend. d. l. Soc. d. Biol. (ser. 2)*, **8**, p. 765; 1885. Thomsen, *Skand. Arch. f. Physiol.*, **37**, p. 1; 1918. O. Gertz, *Hosp.-Tid., Københ. (R)*, **5**, pp. 7, 1197; 1914. H. Gertz, *Ueber autoptische Wahrnehmung der Sehtätigkeit der Netzhaut*, *Skand. Archiv. f. Physiol.*, **19**, pp. 381-408; 1907; *ibid*, **21**, pp. 315-350; 1909. Also *Ueber entoptische Wahrnehmung des Actionsstroms der Netzhautfasern*, *Zentralbl. f. Physiol.*, **19**, pp. 229-233; 1905. J. C. Hubbard, *A Curious Secondary Visual Phenomenon Resulting from a Stimulation of the Macular Region*, *Psych. Bull.*, **7**, pp. 196-199; 1910. A. Druault, *Sur un Phénomène Entoptique en Rapport avec le trajet des fibres optiques dans la rétine (phénomène des arcs)*, *J. de Physiologie et de Pathologie générale*, **16**, p. 649; 1914. L. T. Troland, *The "All or None" Law in Visual Response*, *J. Opt. Soc. Am.*, **4**, pp. 160-185; 1920. *An Entoptic Phenomenon Demonstrating the Optic Impulse*, *Psych. Bull.*, **17**, p. 55; 1920. W. R. Amberson, *Secondary Excitation in the Retina*, *Amer. J. Physiol.*, **69**, pp. 354-370; 1924. Christine Ladd-Franklin, *J. Opt. Soc. Am. and Rev. Sci. Inst.*, **12**, p. 494; 1926; *ibid*, **14**, p. 474; 1927; *Proc. Nat. Acad. of Sci.*, **12**, p. 413; 1926; *Science*, **66**, p. 239; 1927; *ibid*, **67**, p. 162; 1928; *Comptes Rendus*, **185**, p. 584; 1927; *J. Opt. Soc. Am. and Rev. Sci. Inst.*, **16**, p. 333; 1928. F. W. Ellis, *Secondary Excitation of the Retina and the Variation of the Intensity of the Resulting Sensation*, *Am. J. Physiol.*, **82**, p. 290; 1927. *The Nature of the Stimulus which Excites the Blue Arcs of the Retina and Related Phenomena*, *Am. J. Physiol.*, **84**, p. 485; 1928. H. Davis, *Theory of "Visible Radiation" from an Excited Nerve Fiber*, *Science*, **67**, p. 69; 1928.

³ If Amberson's results are correct (*loc. cit.*, p. 359), only those portions of the macular region which contain rods are effective in producing the blue arcs. Stimulation of the central rod-free area does not do it.

⁴ Often called "blue" inaccurately as an abbreviation; the color is a slightly reddish blue.

⁵ Amberson (*loc. cit.*, p. 361), confirming this conclusion previously based on shape and approximate size only, has shown for 10 observers that the length of the arcs corresponds to the papillo-foveal distance.

⁶ Except Siethoff (*loc. cit.*), whose views are shown to be untenable by Druault (*loc. cit.*, p. 650) and, later, by Amberson (*loc. cit.*, p. 357) also.

⁷ Amberson, *loc. cit.*, p. 367.

⁸ Amberson, *loc. cit.*, p. 368.

⁹ Troland, *loc. cit.*, p. 167.

In 1914 there appeared a paper by Druault, apparently until now unknown in this country,¹⁰ which opposes grave objections to the secondary electric stimulation theory and which proposes another explanation, namely, that the fibers are visible because they emit physical light. Ladd-Franklin (1920-1926) independently formulated similar objections and also independently proposed the same alternative explanation. She added, however, the conclusive argument that the blue arcs must result from action upon the light-sensitive substance in the rods and cones by physical light, because (for many subjects) the blue arcs are followed by a chromatic residual image (dark greenish yellow).¹¹ Only stimulation of the light-sensitive substance in the cones by physical light yields a chromatic residual image; electric stimulation does not do it nor stimulation by pressure.¹²

Though, to be sure, acceptance of the theory of visible radiation proposed by Druault, even following Ladd-Franklin's definitive argument in its favor, has been far from universal; nevertheless, the writer has been inclined to accept it, persuaded partly by confirmation obtained in connection with the Purkinje phase of the periodic afterimage following momentary stimulation of the extra-foveal retina by light.¹³ It was found that a number of the properties of the Purkinje phase, which have hitherto remained unaccounted for, yielded perfectly to the same explanation that had been proposed (by Druault and Ladd-Franklin) for the blue arcs, namely, that active nerve fiber gives off physical light. In the case of the Purkinje phase we assume that light is emitted by the nerve structures (bipolar cells, etc.), leading from the outer surface of the retina (rod-cone layer) to the inner surface.

But there are two outstanding differences between the two phenomena. If we are to ascribe the Purkinje phase entirely or partly to the same sort of bioluminescence, or production of visible radiation to which we ascribe the blue arcs, it would be well to examine these differences.

First, the blue arcs are, at best, very faint, as would befit phenomena of secondary retinal stimulation. The Purkinje phase by the right choice of experimental conditions can be made very vivid and striking. Detailed images nearly as distinct and brilliant as the primary image often appear.¹⁴ The explanation of the brilliance of the Purkinje phase may lie in the fact that the nerve structure to which bioluminescence is attributed lies perhaps one-third to one-fifth as far from the rod-cone layer as the fibers on the inner surface of the retina;

¹⁰ Sent to Mr. Priest in response to a request for reprints of papers on the subject of color vision.

¹¹ Ladd-Franklin, *Sci.*, **66**, p. 240; 1927. H. Gertz, *Skand. Archiv.*, **19**, p. 404; 1907.

¹² Ladd-Franklin, *Sci.*, **66**, p. 240; 1927.

¹³ D. B. Judd, *A Quantitative Investigation of the Purkinje Afterimage.*, *Am. J. Psych.*, **38**, pp. 507-533; 1927.

¹⁴ Judd, *loc. cit.*, p. 519.

hence, for the same *brightness* of radiating surface (active nerve fiber) the rod-cone illumination would be much higher than that causing the blue arcs, the Purkinje phase appearing, on that account, much more *brilliant*.¹⁵ Another alternative explanation (perhaps less satisfying) is to say that the observed Purkinje phase is the sum of two components: (1) The contribution of physical light from contiguous active nerve fiber and (2) the contribution of a nature similar to that of the other phases (Hering phase, third positive phase, negative phases, etc.).¹⁶ This explanation is favored by the fact that the properties of the Purkinje phase which are particularly suggestive of emission of physical light are observed under conditions which do not give a brilliant image but which give an image of brilliance comparable to that of the blue arcs.

Second, the Purkinje phase seems to arise from initial activity of the rods. It does not appear in the fovea, and it does not appear following a primary stimulus of pure spectral red light (say, of 650 m μ). On the other hand, the blue arcs, according to Ellis,¹⁷ though contrary to Amberson,¹⁸ appear "best defined and most intense when the stimulating image falls within the fovea." Furthermore, a red primary stimulus not only evokes the blue arcs successfully, but a red light is the best for demonstration of the blue arcs.¹⁹ From these facts the conclusion is suggested that the blue arcs are due to nerve activity initiated by the retinal cones.²⁰

It is the purpose of the present paper to give the results of an experiment designed to show whether cone activity initiates the nerve activity responsible for the blue arcs (as the facts just presented suggest) or whether rod activity initiates it (as Amberson has concluded and as the connection of the blue arcs with the Purkinje phase in other respects suggest).

¹⁵ The use of the terms "brightness" and "brilliance" is as given in the report of the colorimetry committee. See J. Opt. Soc. Am. and Rev. Sci. Inst., 6, p. 534; 1922.

¹⁶ Consult in this connection: Hartline (Am. J. of Physiol., 73, p. 600; 1925) who has succeeded in demonstrating that one of the positive afterimage phases (probably the third positive phase) is correlated with a rise in electric potential in the retina.

¹⁷ Ellis, loc. cit., p. 290; 1927.

¹⁸ Amberson, loc. cit., p. 359.

¹⁹ Thus, Druault (loc. cit., p. 649) says, "Le phénomène peut s'observer avec n'importe quelle lumière, mais plus facilement avec la lumière rouge." Ellis says (loc. cit., p. 293; 1927) "Red light is ordinarily employed to excite the blue arcs, and it is especially well adapted for this purpose * * *." Ladd-Franklin (loc. cit. Nat. Acad. Sci.) recommends for demonstration of the blue arcs "A simple band of bright red light thrown upon a screen in a dark room." Hubbard (loc. cit., p. 196) suggests diffuse light from a "ruby lamp" for demonstration of the blue arcs, and further says, "The brushes (arcs) appear very faint at the extreme red. They increase in brightness as the eye travels up the spectrum and are brightest in the orange red * * *."

²⁰ In spite of this evidence, Amberson (loc. cit., p. 359), from regional considerations alone, concludes that, "* * * the effects under discussion are rod, rather than cone, phenomena, in the sense that the primarily excited and conducting fibers must arise from ganglion cells on the rod pathways in the region of primary stimulation."

As the title of this paper indicates, the experiment consisted of determining the least retinal illumination by spectral light required to evoke the blue arcs. It is apparent that if the rods initiate the nerve activity responsible for the blue arcs a pure spectral stimulus of wave length say, $640\text{ m}\mu$, would have to be at a much higher illumination (measured in photons—a unit embodying “cone” visibility by reason of the method of measurement) than a stimulus of wave length less than, say $550\text{ m}\mu$, because the rods are relatively insensitive to light of wave length $640\text{ m}\mu$. On the other hand, if the cones initiate the nerve activity, a stimulus of a given number of photons would yield a certain definite degree of nerve activity regardless of the wave length of that stimulus (retinal region stimulated remaining constant). If this definite degree of nerve activity were just enough to evoke the blue arcs, it is evident that the retinal illumination required would be a constant independent of wave length. We can determine, then, from the shape of the curve of least retinal illumination against wave length (whether it be a constant illumination or higher for long wave lengths) whether, at the lowest illumination evoking them, the cones or the rods initiate the nerve activity responsible for the blue arcs.

II. APPARATUS

The apparatus used was that designed by Priest²¹ for another purpose but which is perfectly adapted without change to the present purpose. It provides (1) a 2° circular field which may be more or less strongly illuminated by light of any wave length from $400\text{ m}\mu$ to $660\text{ m}\mu$, and (2) an auxiliary photometer by which the brightness of the field may be measured using the flicker method. It should be noted here that the slits (both collimator and ocular) were opened to a width corresponding to $10\text{ m}\mu$, and that filters reducing stray light were used for wave lengths less than $460\text{ m}\mu$ and greater than $630\text{ m}\mu$. Also, the diaphragm and ocular slit were so arranged as to constitute an artificial pupil, roughly rectangular, of about 1.5 by 2.0 mm. The auxiliary photometer was calibrated by comparison with a Holophane light meter,²² but great care was not taken to insure absolute accuracy, since relative accuracy rather than absolute accuracy is important in this experiment. The absolute values reported (fig. 1) may be in error by as much as 20 per cent, but the relative photometric errors are in the neighborhood of 5 per cent.

²¹ I. G. Priest, Apparatus for the Determination of Color in Terms of Dominant Wave Length, Purity and Brightness, *J. Opt. Soc. Am. and Rev. Sci. Inst.*, 8, pp. 174-198; 1924.

²² Adjusted and checked by R. P. Teele, photometric section, Bureau of Standards.

The surrounding field illumination for the right (observing) eye was nearly zero, but for the left eye it was somewhat higher, being due to the blackened surface of the eye shield illuminated by the artificial light of the room. The field on which the arcs appeared was therefore not black, but (since no retinal rivalry appeared) a fairly dark gray. No attempt was made to choose conditions highly

FIG. 1.—Retinal illumination (photons) required to elicit the blue arc phenomenon as a function of the wave length of the primary light stimulus

This function agrees well with the ratio of cone visibility to rod visibility from data by Abney

favorable to the production of the blue arcs. They might have been evoked at considerably lower illuminations than those reported if a long narrow vertical slit had been used instead of the circular field, or if they had been projected onto the dark field of the thoroughly dark adapted eyes. The attempt was rather made to approach a uniform and stable state of adaptation.

III. METHOD OF PROCEDURE

The readings were taken on four mornings from 8 to 9 o'clock. The room containing the apparatus was lighted throughout the hour by incandescent lamps. Adaptation was further affected by frequent reading of the illuminated dial of the ammeter attached to the lamp of the auxiliary photometer and by the use of the photometer.

At the start of a determination the wave-length drum was set to the desired reading, a 1 per cent (or 3 per cent or 10 per cent) sector disk was inserted before the collimator slit, and the right eye applied to the eyepiece. The blue arcs were produced by moving the fixation point horizontally away from the stimulus (2° circular field) and were seen to develop from a horizontal band into ever-widening arcs as the distance between the stimulus and fixation point increased. Then, the retinal illumination was decreased (by decreasing the current through the lamp whose ribbon filament was imaged on the collimator slit) to perhaps one-half its value, and the blue arcs again produced by sweeping the fixation point across the right-hand surrounding field. This process was repeated until the blue arcs appeared in only about half the attempts to produce them. The brightness of the field resulting in this condition was then photometered by the flicker method, the 1 per cent sector disk being removed, and the surrounding field illuminated so that its brightness was about 0.5 ml. Since the adjustment of the illumination to the point which just evokes the arcs (that is, a liminal setting) can not be made at all precisely (perhaps a 100 per cent error is not uncommon), only one flicker setting was made. The setting of the wave-length drum was noted on the record sheet. This constituted a single determination.

These determinations were continued without pause until 9 o'clock. No certain evidence of fatigue with respect to the blue arcs, nor of significant change in level of adaptation was found.

The retinal illuminations (I) were calculated from the brightnesses (B) of the surface being viewed according to the formula:

$$I_{\text{(photons)}} = 3.18 B_{\text{(millilamberts)}} A_{\text{(sq. mm)}}$$

or, since the artificial pupil had an area (A) of 3.0 sq. mm:

$$I = 9.54 B$$

On January 14 the hour was spent in making liminal settings for the sake of practice. Regular observation was commenced on January 16, and all the readings taken thereafter appear plotted in Figure 1, a separate symbol being used for each of the four days.

IV. RESULTS AND DISCUSSION

It is immediately apparent on glancing at Figure 1 that, notwithstanding the low precision (which gives a range of readings at each wave length of about 3 to 1), there is a definite rise²³ with increasing wave length in retinal illumination required to evoke the blue arcs in the author's right eye. Thus, although red light serves best to demonstrate the arcs, still it is true that at the lowest illuminations producing them spectral light of long wave length is definitely less effective than light of short wave length. This situation strongly suggests that the retinal rods initiate the nerve activity responsible for the blue arcs when the retinal illumination is quite low (less than one photon). We shall now proceed to inquire whether the rise in illumination for a stimulus of long wave length is in quantitative agreement with the assumption that the retinal rods initiate the nerve activity responsible for the blue arcs. The derivation of the shape of the curve expected on this assumption may be accomplished in this way:

The liminal setting in each case corresponds to a constant number of impulses per second over the fibers of the optic nerve. The constant number of impulses corresponds to a constant state of activity of the rods (we assume rods, not cones) affected by the primary stimulus. With constant state of adaptation (which has been approximated by the experimental procedure) this constant retinal activity

²³ The points representing the work of each day taken separately all show a very similar rise, but there seems to be a tendency for all points of one day (for example, 1/20/28) to fall above the corresponding points for another day (for example, 1/19/28). This may be due either to (1) a different adaptation level, or (2) a different criterion of appearance or nonappearance of the blue arcs. With respect to (2) it may be remarked that some difficulty was found in adopting a definite and describable criterion for appearance of the arcs. On this account the criterion, although easily remembered throughout a given hour, may not have been the same on the next or any other day. At a liminal illumination a sweep of the fixation point along the horizontal sometimes brought out the moving arcs faintly but with clarity, at other times the suggestion of movement was present without the form of the arcs, and sometimes nothing at all could be detected. There were many gradations between these describable appearances.

It is appropriate at this time to remark that with higher retinal illuminations the arcs are unmistakably more brilliant than at any of these doubtful stages and take on the pale reddish-blue color that has suggested the name "blue arcs" (at the doubtful stages the arcs appear gray, a fact which is consistent with the "visible radiation" theory). In respect to brilliance variation, my observations substantiate those of Hubbard, who says, "The intensity of the brushes increases with the intensity of the exciting light, * * * " and also those of Ellis (*loc. cit.*, p. 293; 1927) who criticizes Troland's (*loc. cit.* J. Opt. Soc. Am.) view that the arcs constitute an example of the "all or none law in visual response." While it is true that the observations of Ellis agree with my own, still I do not agree with his criticism of Troland's view because that view is consistent with some variation in brilliance of the arcs even though their brightness (visible radiation theory) or the action current (secondary electric stimulation theory) may be constant. The brilliance should depend, according to that view, somewhat on state of adaptation (and does depend on it, see Amberson, *loc. cit.*, p. 356) and number of nerve fibers activated by the primary stimulus Troland, *loc. cit.*, J. Opt. Soc. Am., p. 168). It seems, on the other hand, reasonable to suppose that Troland himself did not see nearly the variation in brilliance of the arcs that Ellis, Hubbard, or myself have seen, since from measurements he gives (*loc. cit.*, J. Opt. Soc. Am., p. 179) the brilliance of the arcs is only slightly above the threshold. Perhaps Troland might never have been led to cite the blue arcs as an example of the "all or none" law in visual response, if their maximum brilliance for him had been greater. It is my opinion, however, that they should still be thought of as a legitimate example of the "all or none" law even when the observations of Hubbard, Ellis, and myself be taken into account. If Troland's view is to be rejected, evidence must be found by Troland's own technique showing that the brilliance of the blue arcs for other observers is actually as variable as the qualitative observations (just cited) indicate.

is due to the constancy of the product, $E_\lambda(V_r)_\lambda$, where E_λ is the energy (that is, ergs per second per unit visual angle) of the light stimulus of wave length λ , and $(V_r)_\lambda$ is the rod visibility for that wave length. We have the relation, then, that the shape of the curve of retinal illumination (I_λ) must be such that

$$E_\lambda(V_r)_\lambda = \text{a constant}$$

But we measure E_λ by measuring the illumination corresponding to a large multiple (most often here, 100) of it, thus:

$$E_\lambda = KI_\lambda/(V_c)_\lambda$$

where $(V_c)_\lambda$ is the cone visibility of light of wave length λ . (K is the constant which determines the units in which E_λ is expressed.) We believe that only the cones are effective in this photometric measurement by reason of the experimental conditions adopted (2° field of high brightness, bright surrounding field). Solving for I_λ from these two relations, we obtain

$$I_\lambda = (V_c)_\lambda/(V_r)_\lambda \text{ times a constant}$$

On Figure 1 is also shown, therefore, this ratio, $(V_c)/(V_r)_\lambda$ evaluated from data by Abney.²⁴ It is seen that this ratio (multiplied by a constant arbitrarily selected to secure the best agreement) varies with wave length in such a way as to agree substantially with the measurements taken of the least retinal illumination (I_λ) required to evoke the blue arcs.²⁵ There are two outstanding departures

²⁴ Abney, *Researches in Colour Vision*, pp. 94, 98; London: Longmans-Green; 1913. Column IV, Table IV, p. 94; Table VI, p. 98. This data of Abney is taken because none of the more recent observers apparently used quite the field size which would make their results applicable to this case. It seems clear from Amberson's results (*loc. cit.*, p. 359) that the blue arcs result from a stimulation of the outer zone of the macular region (that is, the macula lutea minus the central rod-free area). Abney's data refer specifically to the macula lutea (yellow spot). To my knowledge, no other investigator gives this specification. There are apparently large individual variations in the size of the yellow spot; Parsons (*Introduction to the Study of Colour Vision*, Cambridge: University Press, p. 13; 1924) says that the macula may vary from 4° to 12° in different individuals. In Amberson's case, a 6° circular field includes all retinal elements capable of giving rise to the blue arcs. Visibility data taken with a 6° field would, however, be as reliable as that taken (as Abney's data was) specifically for the observer's yellow spot only if the yellow spot of the observer covered the entire 6° field. Otherwise errors would be introduced by absence of information concerning macular pigmentation. Laurens (*Am. J. of Physiol.*, **67**, p. 354; 1924) gives data referring to a 2° field, which is probably too small. This data checks Abney closely, however, giving, as expected, a ratio curve (V_c/V_r) which does not rise quite so steeply as that shown in Figure 1.

²⁵ It is convenient to note at this point that the results of Troland (*loc. cit.*, *Psych. Bull.*) on the least retinal illumination required to evoke the blue arcs are not in complete agreement with those referring to the present author's right eye. Just how serious the discrepancies are can not be determined because the account of Troland's results is purely qualitative and is contained in a brief abstract. He says "Measurements of the threshold of the phenomenon with respect to intensity indicate that this is in the neighborhood of one photon, and that there is a distinct minimum in the middle of the spectrum, the curve for the effect corresponding roughly with a reciprocal of the visibility curve." The present results indicate that the threshold is in the neighborhood of one one-hundredth photon (for some wave lengths). There is a minimum (though not distinct) in the middle of the spectrum, and the curve does not (see fig. 1) resemble, even roughly, a reciprocal of the visibility curve (it scarcely rises at all toward short wave lengths). It is possible that these differences are to be expected from the relatively low brilliance (see footnote 23, p. 348) of the blue arcs in Troland's case. Such a brilliance might reasonably necessitate the intensity threshold of one photon which Troland found. This high threshold should account for the rise of the curve toward short wave lengths. (See footnote 26, p. 350.)

from perfect agreement: (1) The rise of the ratio between 550 $m\mu$ and 600 $m\mu$ is steeper than that of the average I_λ ; and (2) the ratio is smaller between 400 $m\mu$ and 500 $m\mu$ than the average I_λ . Although the agreement is as good as, perhaps better than, can be expected in view of the fact that two different observers are involved, perhaps a part of the failure of the I_λ curve to rise as steeply as the ratio curve may be ascribed to the fact that the slit widths of the spectrometer were quite large (10 $m\mu$). The failure of the I_λ curve to fall to the low values between 400 and 500 $m\mu$ reached by the ratio curve may be ascribed to the fact that the primary stimulus, though quite weak (about 0.04 photons), introduced enough scattered light into the field on which the arcs were projected to interfere seriously with their observation.²⁶ This scattering became more and more troublesome as the wave length of the primary stimulus was decreased. Similar difficulties have been noted by Hubbard,²⁷ Troland,²⁸ and Ellis.²⁹

It may be concluded, in my opinion, from the work just described, that at low retinal illuminations the blue arcs are evoked from nerve activity initiated by the retinal rods. This conclusion is in agreement with Amberson's results on retinal regions giving rise to the blue arcs. Although other work (summarized in the introduction)³⁰ suggests that the cones may also initiate the nerve activity responsible for the blue arcs, it is my opinion that this has not yet been established as a fact.³¹

²⁶ We should expect Troland's curve resulting from a much higher illumination (about 1 photon) to depart considerably more from the ratio curve on this account. Such a departure is in agreement with the actual curve he found. (See footnote 25, p. 349.)

²⁷ Hubbard, loc. cit., p. 198.

²⁸ Troland, loc. cit., J. Opt. Soc. Am., p. 176.

²⁹ Ellis, loc. cit., p. 292; 1927.

³⁰ In agreement with this work, I find that a red (630 to 640 $m\mu$) primary stimulus is best in my case also for demonstration of the blue arcs, but it is only slightly better than a green or yellow stimulus. This I ascribe, not to participation of the cones, but to the resulting comparative freedom from scattered light of the field on which the arcs must be projected. This explanation is also given by Ellis (loc. cit., p. 293; 1927).

³¹ My view is that probably all nerve fiber, forming rod pathways or cone pathways, retinal or central, active or inactive, is emitting physical light. It seems likely that the rate of emission increases as the degree of activity of the fiber increases (though it is possible that this view conflicts with Troland's undisputed contention of essentially constant brilliance of the blue arcs). It seems significant in this connection to note that the only two cases (blue arcs and Purkinje phase of the periodic afterimage), which demand the postulation of "visible radiation," arise in association with, and only in association with, intense activity of the rod pathways. My view is that the radiation emitted under other conditions (for example, from cone pathways activated by primary stimuli usual for demonstration of the blue arcs—note Amberson's failure to obtain the arcs from purely foveal stimulation—or from rod pathways after a few seconds duration of the stimulus—note transitory character of the blue arcs which has troubled the proponents of the secondary electric stimulation theory since its inception) is too weak to be detected even by the wonderfully sensitive retinal layer only a fraction of a millimeter away. We should not expect the retinal cones to initiate the nerve impulse which causes visible blue arcs because the light scattered from the primary image strong enough to stimulate the cones suitably would be many times as intense as the light emitted by the active fibers of the cone pathways. Furthermore, we should not expect the rods to retain a sufficiently high sensitivity to initiate for more than a few seconds the nerve activity which results in vivid blue arcs. The sensitive substance bleaches out rapidly; and during this rapid bleaching out, and only during this rapid bleaching out, do vivid blue arcs (or vivid Purkinje phases) appear.

It is also true, in my opinion, that the hypothesis of visible radiation from active nerve fiber proposed by Druault and Ladd-Franklin and used by me ³² to account for certain properties of the Purkinje phase of the periodic afterimage is somewhat strengthened by this work, because this work indicates that the nerve activity responsible for the blue arcs sometimes (perhaps always) arises from the same origin (retinal rods) as that responsible for the Purkinje phase of the periodic afterimage following brief stimulation of the retina ³³ by light. The two phenomena are linked, therefore, by one more common property. Since cogent arguments (Ladd-Franklin) indicate that the blue arcs are due to visible radiation from active nerve fiber, it is, in my opinion, reasonable to suppose that the Purkinje phase is due, at least in part, to the same cause.

WASHINGTON, November, 1928.

³² Judd, loc. cit., p. 527. The term used here as a substitute for "visible radiation" is "bioluminescence."

³³ In further confirmation of this linkage of the Purkinje phase with the blue arcs, may be mentioned the fact that W. T. M. Forbes obtains them both only with abnormally high retinal illuminations. (See for the Purkinje phase: Judd, loc. cit., p. 521, fig. 2, observer W. T. M. F. requires 56 photons, which is about one hundred times that required by some other observers.) He requires about 10 photons (compare Judd, present work, 0.01 photon) for evoking the blue arcs. This evidence was pointed out by Doctor Forbes himself, who says (letter of November 14, 1928), "You have, as confirmatory, the fact that in my case the blue arcs did not appear with weak stimuli, * * *" and (as just cited) neither did the Purkinje phase.