

# CHANGES IN THE ROD-VISUAL CELLS OF THE FROG DUE TO THE ACTION OF LIGHT

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TWO FIGURES

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## PRELIMINARY

Whenever the results of experimentation upon any particular animal, or group of animals, are at variance with a well established canon, it is desirable that such results be subjected to the closest scrutiny possible before the existence of a deviation from the generally accepted norm is admitted. The present paper, which attempts to answer the following query, is concerned chiefly with the reëxamination of a case of this kind—Query: *Are the photomechanical responses of the visual rods of the frog similar to those occurring in the retinas of other investigated vertebrates?*

Both the rods and the cones of many vertebrates undergo positional changes when subjected to photic or thermal stimulation (Arey '15, '16).

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Wherever movements of the cones have been detected, light causes a shortening, and darkness an elongation, of the contractile portion of the inner member known as the myoid (figs. 1 and 2, *my.con.*).

Stort ('86), working on the crow, first showed that the rod myoid of birds exhibits photomechanical changes which are the exact reverse of those found in the cone—that is, elongation in the light and retraction in the dark. The following year ('87) he extended his observations upon certain fishes. Although this striking response in fishes can be demonstrated with comparative ease (especially in fishes possessing large rods; Arey, '15, '16), it was not until long after that these forgotten observations were corroborated and their correctness admitted.

With respect to the frog's rod,<sup>2</sup> however, Angelucci ('84, '90) and Gradenigro ('85) came to a different conclusion. These workers recorded that the myoid of the inner member (figs. 1 and 2, *my.bac.rb.*) of the frog's rod shortens when exposed to light and elongates in darkness. Gradenigro (p. 343) states this conviction most emphatically: "Zuerst habe ich mit positiver Bestimmtheit ersehen dass an der Froschretina unter der Einwirkung des Lichtes die Stäbcheninnenglieder kürzer und dicker werden, in ähnlicher, wenn auch nicht so ausgedehnter und rascher Weise, wie Englemann bei den Zapfennengliedern die Beobachtung gemacht hat."

Angelucci ('90, p. 245) makes a similar straightforward assertion, which applies to both the red and green visual rod:

<sup>2</sup> There are two kinds of visual rods in the frog's retina. The more numerous form (figs. 1 and 2) has a short inner member (*my.bac.rb.* + *ell.bac.rb.*) and a long outer member (*prs.dst.bac.rb.*). Since the first imperfect observation by Müller ('51), it has been shown repeatedly that, in the fresh retina of an animal which has previously been retained in darkness, the outer member of the rod appears reddish due to the presence of unbleached visual purple (rhodopsin). Schwalbe ('74) saw a second type of rod (figs. 1 and 2) characterized by an elongated inner member (*my.bac.vr.* + *ell.bac.vr.*) and an abbreviated outer member (*prs.dst.bac.vr.*); Boll ('77) also described this element and interpreted correctly its green appearance, in fresh dark-adapted retinas, as due to a specific photo-sensitive material, which, from its color has been called visual green (chloanopsin). Hence red and green rods differ both anatomically and as to the nature of their photo-sensitive contents. Unless otherwise stated reference to the red visual rod is usually understood.

“Die Stäbchen sind dick und sowohl in ihrem äusseren Glied als in ihrem myoïden Theil zusammengezogen. . . . Auch die grünen *Schwalbe*'schen Stäbchen sind sowohl in ihrem äusseren als in ihrem inneren Gliede zusammengezogen.”

Arcoleo ('90), using pithed toads, likewise reported similar responses.

More recently, Lederer ('08), in a brief communication, has challenged the results of the previously named workers on the frog's rod. From the study of fixed material, which had been subjected to teasing, he concludes (p. 764): “Die Hellstäbchen waren im allgemeinen länger, schlanker und hatten gleich breites Innen- und Aussenglied, während bei den Dunkelstäbchen, die kürzer und plumper erschienen, das Innenglied dort, wo es an das Aussenglied grenzt dicker wird.” It should be remarked in passing that Lederer's two schematic figures of isolated frog's rods have presumably been interchanged—at least, it is obvious that they illustrate conditions exactly the reverse of those which his text descriptions maintain. His experience with stained celloidin sections is summarized in the following statement (p. 764):

man nach den Zupfpräparaten am gefärbten Schnitte ebenfalls ähnliche Verhältnisse hätte erwarten sollen. Indessen waren hier die Veränderungen der Stäbchenschicht sehr wenig markant. In ungefähr der Hälfte der geschnittenen Licht-Bulbi zeigten die Stäbchen längere, gestrecktere Form, grösseren Abstand ihres Aussengliedes von der Membrana limitans externa, die Dunkelstäbchen gedrungenere gestalt, kleinere Distanz von der äusseren Grenzmembran. In der anderen Hälfte der Schnitte aber war eine Veränderung der Stellung der Stäbchen sehr wenig ausgesprochen, und die Hell- und Dunkelstäbchen das Aussenglied ungefähr gleich weit von der Membrana limitans externa entfernt.

The rods of certain amphibians exhibit photomechanical movements which should be clearly distinguished from those produced by the contractility of the myoid. Thus Stort ('87) first asserted, that, in the dark, the nuclei of the rods in Triton (figs. 1 and 2, *st.nl.ex.*) migrate partially through the external limiting membrane, thereby causing the whole rod to become extended, whereas, in the light, these nuclei lie wholly within the outer nuclear layer. The contractility of that portion of the

rod-visual cell between the rod nucleus and the external reticular layer was believed to cause these changes. Angelucci ('90) made similar observations on the salamander, as did Garten ('07) on Triton.

Changes in the cylindrical outer member (figs. 1 and 2, *prs.dst. bac.rb.*) have also been reported. Ewald und Kühne ('78) first observed a swelling of the outer member of the frog's rod as the result of strong illumination. That Lederer ('08) obtained

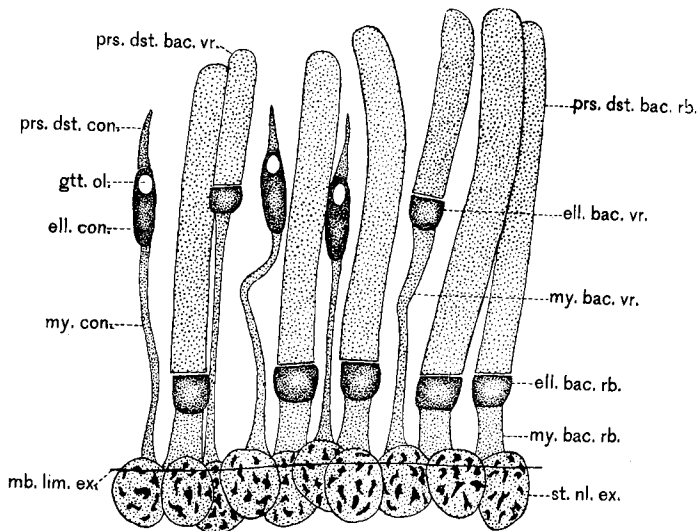


Fig. 1 From a dark-adapted retina of the frog, *Rana pipiens*, showing the positions assumed by the rods and cones.  $\times 1130$ . *ell.bac.rb.*, ellipsoid of red rod; *ell.bac.vr.*, ellipsoid of green rod; *ell.con.*, cone ellipsoid; *gtt.ol.*, oil globule; *mb.lim.ex.*, externa limiting membrane; *my.bac.rb.*, myoid of red rod; *my.bac.vr.*, myoid of green rod; *my.con.*, cone myoid; *prs.dst.bac.rb.*, outer member of red rod; *prs.dst.bac.vr.*, outer member of green rod; *prs.dst.con.*, outer member of cone; *st.nl.ex.* external nuclear layer.

results, the exact opposite of those reported by Ewald and Kühne, is assumed from the context of the previously cited quotation (p. 431), and from his illustrations.

Angelucci ('84) measured the length of the outer member of the frog's rod and found it shortens in the light; later ('90) he confirmed this result by measurements of the large rods of the

salamander where the differences in length were more striking. Arcoleo ('90) and Garten ('07) reported similar conditions for the toad and frog respectively.

In most accounts of the changes occurring in the anuran rod, due to the action of light, reference is not made to the number of individuals experimented upon, and in no case are definite measurements of length given, judgment of the eye apparently being the only criterion adopted.

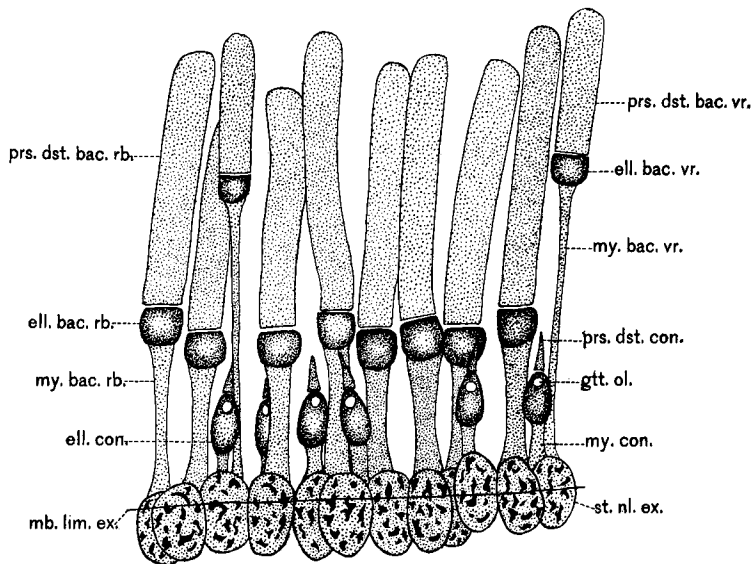


Fig. 2 From a light-adapted retina of the frog, *Rana pipiens*, showing the positions assumed by the rods and cones.  $\times 1130$ .

In the experimentation which forms the basis of this paper, an attempt has been made to correlate an influence of light with the following possible changes in the frog's visual rod: 1) changes in the position of the red rod nucleus with respect to the external limiting membrane; 2) changes in the length of the red and green rod myoids; 3) relative changes in the length of the red rod myoid at the center and at the periphery of the retina; 4) changes in the diameter of the various component parts of the red rod.

## EXPERIMENTATION

Individuals of *Rana pipiens*, approximately uniform in size, were exposed to bright diffuse daylight for eight hours, or to total darkness for a minimum length of twenty-eight hours. At the expiration of these periods of light and dark-adaption, the cranium of each animal was first split sagittally, and then cut transversely just caudad to the eyes. The resulting moieties of the cranium, with the contained eyes, were dropped into Perenyi's chromo-nitric fixative; in this solution they underwent fixation, the condition of illumination being identical with that to which they had been experimentally subjected. The operation on dark-adapted animals was accomplished by the light from a photographic red lamp and demanded but a few seconds time.

After dehydration and the removal of the lens, the eyes were imbedded in paraffine, sectioned  $8\mu$  thick, and stained with Ehrlich-Biondi's acid fuchsin-orange G-methyl green mixture. In light-adapted retinas the expanded pigment masked the visual cells to a greater or less degree, hence, nascent oxygen was used as a bleaching agent in these preparations. The results obtained with the Ehrlich-Biondi stain were very satisfactory, yet it is of interest to note that the staining reaction of several definite structures was often variable. For example, the outer member of the red rod in most cases stained red with the acid fuchsin, yet in some retinas from the same series they were colored an intense orange from the orange G, although the treatment in both cases had been, so far as is known, identical, the series having been carried along simultaneously step by step. Moreover, in one preparation, at least, it was observed that the outer members in one half of the retina were stained orange, whereas in the other half they were stained red. This selective stainability is doubtless indicative of a variable physiological cytoplasmic state. Preparations in which the outer members of red rods selected the orange G, showed the green rods stained red with the acid fuchsin. In retinas that had been bleached (potassium chlorate and hydrochloric acid being the reagents

used), the rod outer member varied in color from blue-violet to red-violet. Cases involving a somewhat similar variability might be cited with respect to several other structures in the retina.

Experimentation was made upon sixty retinas, from which twenty-three light-adapted and twenty-three dark-adapted preparations were selected for measurement. Preparations, in which the external limiting membrane was not apparent, or in which wrinkles caused oblique sections, were rejected. All measurements were made with a Leitz 1/12 homogeneous immersion objective and a Zeiss No. 2 micrometer eyepiece.

#### *A. Influence of light on the position of the red rod nucleus*

The object of this series of measurements was to determine the effect of light and darkness upon the position of the nuclei of the red rods with respect to the external limiting membrane.

The nuclei of the rod- and cone-visual cells comprise the external nuclear layer (figs. 1 and 2, *st.nl.ex.*) of the retina. According to Greeff ('00, p. 133), these two kinds of nuclei in amphibians can be distinguished, morphologically, only with great difficulty; hence it is essential to inquire whether any criterion exists whereby the rod nuclei can be identified with a tolerable degree of certainty. The illustrations of the frog's retina given by Greeff ('00, pp. 96, 102) represent the nuclei of the red rod-visual cells as lying considerably nearer the external limiting membrane than the nuclei of either the green rod-visual cells or of the cone-visual cells. If, therefore, in any preparation attention be directed to the nuclei which protrude farthest beyond the external limiting membrane, one may be reasonably sure that the nuclei of the red rods only are under consideration. Ten light-adapted and ten dark-adapted retinas were selected at random for measurement. Not only was considerable regional variability in the position of nuclei found in individual retinas, but also the variability in any limited area was extensive—ranging from nuclei whose edges were at the same level as the external limiting membrane to nuclei which were  $3.0 \mu$  above that membrane. Partly for this reason, and partly to be certain that only the

nuclei of red rods were under observation, attention was directed solely to the mean distance to which the maximally extended nuclei protruded beyond the external limiting membrane.

The following values (grand means) were obtained: in light (10 retinas),  $2.9\mu$ ; in darkness (10 retinas),  $2.2\mu$ .

On account of the degree of variability observed, I do not regard this slight difference, which, incidentally, is not in agreement with the results of Stort ('87) and Garten ('07) on Triton, or of Angelucci ('90) on the salamander, as indicative of a photic influence. Since the condition recorded in Triton and the salamander is not clearly demonstrable in my preparations of the frog, it follows that whatever changes are found in the rod myoid will be due chiefly to the activity of the myoid itself.

*B. Influence of light on the length of the rod myoid. Relative changes at center and periphery of retina*

*a. Red Rods.* In every retina, at least ten measurements were made, on each side of, and not far from, the optic nerve. The averages of these twenty or more values are given in tables 1 and 2 as central measurements. Similarly the means of at least twenty measurements (ten on each side), made well toward the periphery of the retina, are recorded as peripheral measurements. In order to avoid unconscious selection all measurements were made on consecutively-placed rods. The myoid length in the tables constitutes the distance from the external limiting membrane to the nearer edge of the rod ellipsoid (figs. 1 and 2, *my. bac.rb.*).

The tables show that there is considerable variation in individual retinas, yet the rod myoid unmistakably elongates in the light and shortens in darkness (figs. 1 and 2). Although the mean values, at the center and periphery of individual retinas, may also vary greatly in either set, the grand means are practically identical.

The measurements of individual light- and dark-adapted rods overlap in many instances; furthermore, the mean for certain groups of ten deviates considerably from the average for both groups of ten, which constitutes the central or peripheral values



of the tables, as the case may be. In such instances the process of averaging two groups of ten serves to mask this condition, hence the tables, for the sake of compactness, are faulty in this respect.

The conclusion follows, therefore, that the photomechanical responses of the frog's red visual-rod myoid are in agreement with those of other vertebrates in which changes have been demonstrated.

The older workers (Angelucci '84; '90; Gradenigro, '85; and Arcoleo '90) perhaps erred, either in not making actual measure-

TABLE 1

*Measurements from twenty-three dark-adapted retinas of Rana pipiens. The values are in micra and represent measurements taken along axes coinciding with radii of the eyeball. Each value for the length of the red rod myoid is the mean obtained from twenty consecutively-placed elements*

NUMBER OF ANIMAL	NERVE FIBER LAYER TO EXTERNAL LIMITING MEMBRANE	CHORIOID TO EXTERNAL LIMITING MEMBRANE	LENGTH OF RED ROD MYOID AT CENTER OF RETINA	LENGTH OF RED ROD MYOID AT PERIPHERY OF RETINA
1	107	64	5.0	4.9
2	136	70	4.0	5.7
3	114	72	4.6	3.3
4	114	64	4.4	4.9
5	122	69	6.6	7.0
6	110	69	5.3	6.7
7	100	64	4.0	6.4
8	106	64	6.7	6.6
9	129	67	6.4	6.4
10	100	69	9.3	7.6
11	114	69	6.9	6.9
12	129	69	5.9	5.7
13	114	73	6.2	5.7
14	97	62	3.6	4.3
15	97	63	4.7	5.0
16	111	69	4.6	5.1
17	107	63	5.4	6.0
18	107	64	6.4	6.2
19	114	63	6.6	6.4
20	103	60	7.2	6.9
21	89	57	7.2	6.3
22	93	62	5.7	7.2
23	93	60	6.4	6.2
Mean.....	109	66	5.8	6.0

ments, or were influenced by their observations on the more strikingly mobile cone (figs. 1 and 2; *my.con.*), the movements of which are the reverse of those exhibited (such is my belief) by mobile rods in general.

In recent papers ('15; '16) the writer favored the anomalous photomechanical responses of the frog's rod, reported by the several older workers, as being more trustworthy than the somewhat confusing account of Lederer<sup>3</sup> ('08). The writer ('15),

TABLE 2

*Measurements from twenty-three light-adapted retinas of Rana pipiens. The values are in micra and represent measurements taken along axes coinciding with radii of the eyeball. Each value for the length of the rod rod myoid is the mean obtained from twenty consecutively-placed elements*

NUMBER OF ANIMAL	NERVE FIBER LAYER TO EXTERNAL LIMITING MEMBRANE	CHORIOID TO EXTERNAL LIMITING MEMBRANE	LENGTH OF RED ROD MYOID AT CENTER OF RETINA	LENGTH OF RED ROD MYOID AT PERIPHERY OF RETINA
1	100	67	9.9	10.2
2	111	73	13.6	14.9
3	93	74	11.9	12.0
4	129	62	11.7	12.6
5	117	72	11.9	12.6
6	114	72	12.6	11.9
7	114	64	13.3	12.2
8	127	64	9.2	12.2
9	127	69	8.6	10.3
10	119	72	16.9	16.2
11	114	72	13.9	14.7
12	120	72	14.3	14.7
13	92	62	9.9	9.2
14	102	69	13.4	13.0
15	107	60	13.0	11.9
16	125	63	9.6	9.2
17	100	62	11.4	12.4
18	106	62	9.9	9.6
19	93	61	8.6	7.9
20	96	69	12.7	9.6
21	107	64	7.9	7.2
22	97	64	8.6	9.7
23	129	69	11.9	12.9
Mean.....	100	67	11.5	11.6

<sup>3</sup> Lederer's figures of isolated rods do not necessarily show how long the rod myoid really was, either in darkness or in light. Presumably, the myoid, as the result of teasing, broke approximately at the level of the external limiting

furthermore, made use of these data in an argument against the feasibility of attempting to advance (in the light of our present knowledge) a single rational explanation for the diverse photo-mechanical movements of the visual rods. It is evident, however, that the conclusion reached in the present investigation renders this particular objection invalid.

It is reasonable to expect, although material is not available at present to put the matter to an experimental test, that the photomechanical behavior of the toad's visual rod will be found to vary in no essential detail from that herein described for the frog.

*b. Green rods.* From the sixty retinas experimented upon, the ten light-adapted and ten dark-adapted preparations which showed the most perfect histological preservation were selected for measurement. In each retina, measurements were made of the myoid length (figs. 1 and 2, *my.bac.vr.*) of ten consecutively-placed green rods; the results are recorded in tables 3 and 4.

TABLE 3

*Measurements from ten dark-adapted retinas of Rana pipiens. The values are in micra and represent measurements taken along axes coinciding with radii of the eyeball. Each value for the length of the green rod myoid is the mean obtained from ten consecutively-placed elements*

NUMBER OF ANIMAL	NERVE FIBER LAYER TO EXTERNAL LIMITING MEMBRANE	CHORIOID TO EXTERNAL LIMITING MEMBRANE	LENGTH OF GREEN ROD MYOID
1	95	66	21.4
2	94	65	23.0
3	98	75	28.6
4	90	69	26.2
5	112	68	22.5
6	135	82	27.7
7	102	63	24.4
8	109	70	24.0
9	105	70	24.1
10	115	72	22.5
Mean.....	106	70	24.4

membrane, although nothing to this effect is stated. Furthermore, the varicose and atypical appearing rods naturally increases one's caution in accepting his conclusions. Although Lederer gave but little emphasis to his observations on sectioned material (p. 431), I believe that those observations constitute the strongest evidence in support of his thesis.

TABLE 4

Measurements from ten light-adapted retinas of *Rana pipiens*. The values are in micra and represent measurements taken along axes coinciding with radii of the eyeball. Each value for the length of the green rod myoid is the mean obtained from ten consecutively-placed elements

NUMBER OF ANIMAL	NERVE FIBER LAYER TO EXTERNAL LIMITING MEMBRANE	CHORIOID TO EXTERNAL LIMITING MEMBRANE	LENGTH OF GREEN ROD MYOID
1	105	68	25.0
2	102	72	26.1
3	127	75	28.2
4	120	69	28.2
5	97	68	31.0
6	112	63	28.2
7	127	87	25.5
8	120	75	27.7
9	127	72	32.4
10	123	66	24.9
Mean.....	116	72	27.7

The tables show that although the difference in the length of the rod myoid, in darkness and in light, is small, the length of the light-adapted element is quite consistently the greater (figs. 1 and 2); hence it seems probable that this difference is significant and the photomechanical responses of the red and green rods are analogous.

This conclusion is not in accord with the results of Angelucci ('94). Angelucci believed that the red and green rod myoids responded similarly to photic stimulation, yet in both cases a shortening was said to take place.

### C. Influence of light on the diameter of the red rod

From my preparations many rods were measured, yet no constant or significant differences were found in the diameters of the outer members (figs. 1 and 2, *prs.dst.bac.rb.*), or of the ellipsoids (figs. 1 and 2, *ell.bac.rb.*) of the inner members, which could be attributed to the influence of light and darkness. The myoid of the inner member (figs. 1 and 2, *my.bac.rb.*) naturally becomes tenuous when elongated by the action of light (p. 436).

One is inclined to question the morphological normality of the teased rods figured by Lederer ('08), especially since the appear-

ance of these elements in his own sectioned material was dissimilar. In the figures corresponding to the text descriptions of dark-adapted rods (the figures and their appended descriptions are apparently interchanged in his paper), the varicose outer members are twice, and the ellipsoids three to four times, as broad as the corresponding parts of the light-adapted rods.

My observations, therefore, are opposed both to those of Lederer ('08) who believed that darkness causes the rod to swell, and to those of Ewald and Kühne ('78), who recorded that light acts in this manner.

#### SUMMARY

1. Distinct movements of the nuclei of the red rod-visual cells, due to photic stimulation, are not demonstrable. Hence movements of the rods are not produced indirectly in this way.

2. The myoid of the rod-visual cell elongates in light and shortens in darkness. *Therefore, contrary to the conclusions of the older workers, the photomechanical response of the frog's rod myoid is found to be similar to that occurring in the retinas of all other investigated vertebrates.*

The mean length of approximately 1000 myoids from 23 light-adapted retinas is 11.6  $\mu$ .

The mean length of approximately 1000 myoids from 23 dark-adapted retinas is 5.9  $\mu$ .

3. A significant regional difference in the length of the red-visual rod myoid is not apparent from comparisons of approximately 2000 measurements made at the center and the periphery of light- and dark-adapted retinas.

4. The myoid of the green visual rod probably elongates slightly in the light and shortens in darkness.

The mean length of 100 myoids from 10 light-adapted retinas is 27.7  $\mu$ .

The mean length of 100 myoids from 10 dark-adapted retinas is 24.4  $\mu$ .

5. Definite changes in the diameter of the outer member, or of the ellipsoid, of the red visual-rod can not be correlated with photic influences. The rod myoid, however, does become tenuous in the light.

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