GALVANIC STIMULATION OF LUMINESCENCE IN PELAGIA NOCTILUCA.

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The physiological evidences of excitation are muscle contraction, gland secretion, and luminescence. As a result of electrical stimulation Panceri[1] obtained luminescence in various light-producing cœlenterates. Recently E. B. Harvey[2] has studied galvanic stimulation of luminescence in *Noctiluca*, but was unable to discover any polar effects. I found, however, that the ctenophores *Mnemiopsis* and *Beroe* gave clear results with polar stimulation when a small current of a few milliamperes was passed through them.[3] On the make, a luminescent glow lasting several seconds occurs at the anode; and in *Mnemiopsis* a break flash can frequently be observed at the cathode. It should also be noted that in these two forms muscle contraction goes hand in hand with the luminescent response; *i.e.*, contraction of the musculature on the anodal side occurs at the make of the current. These facts serve to render it clear that the two ctenophores studied react to the electric current according to a reversal of the law of Pflüger. Now Pflüger's law has been assumed to be universal in its application, and an explanation has been sought in the field of ion effects.[4] Specifically, stimulation at the cathode on the make has been referred to the heightened irritability conferred by the excess of Na ions which collects at the cathode as a result

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[1] Panceri, P., *Ann. sc. nat. zool.*, 1872, xvi, series 5, September.

[2] Harvey, E. B., *Carnegie Institution of Washington, Pub. 251*, 1917, 245.

[3] Moore, A. R., *Proc. Soc. Exp. Biol. and Med.*, 1924-25, xxii, 80.

[4] Loeb, J., The dynamics of living matter, New York, 1906, 102.

of the flow of the current. This explanation can serve for the reversed Pflüger's law in either of two ways. First, the ionic conditions of stimulation may be reversed, in which case stimulation would be due to Ca and not to Na ions. In the second place, the locus of the action of the ions in stimulation may be on the side of the membrane opposite to that in the frog nerve. As to the first point, I have shown that *Mnemiopsis* is stimulated to luminescence by Ca, Sr, and Ba ions but not by Na and Mg ions.[5] I also found that the ion effect took place at the water-protoplasm boundary and not within the cells of the organism, because stimulation by the electric current occurred at the anodal face even when that was a cut surface.

With a view to obtaining further information on the galvanic stimulation of luminescence I worked with specimens of the medusa *Pelagia noctiluca*.[6] At the outset I found them less sensitive to the electric current than the ctenophores. For this reason I used platinum electrodes to carry the current into the trough. Non-polarizable electrodes were, however, tried and found to give concordant results, but the luminescence excited was faint because of the weakness of the current.

If a specimen of *Pelagia* is put into a rectangular glass dish containing sea water and a current of 200 ma. passed through, a glow occurs along the margin on the anodal side of the animal. In very sensitive specimens the luminescence spreads from this region like a blush over the whole bell. The glow continues during the flow of the current and ceases at the break. Under certain conditions there is a secondary glow on the cathodal side on the make and during the flow of the current.

It was first attempted to answer the question: Does the electric current produce its effect directly by acting on the luminescent

[5] Moore, A. R., *Am. J. Physiol.*, 1925, lxxii, 230.

[6] 2 years ago Heymans and I[7] recorded the inhibiting effect of light on the luminescence of *Pelagia* and a day-night rhythm in luminescence. This year I failed to find either of these effects. Even exposure to strong sunlight for half an hour did not appreciably reduce the luminescence which appeared upon stimulating the animal in the dark. I have no idea how to account for such an extraordinary difference in behavior during the two seasons.

material contained in the cells, or indirectly by producing excitation in non-luminous tissue such as nerves and ganglion cells which in turn convey the impulse to the luminescent organs?

As a first step in the analysis, it was necessary to determine what effect, if any, the electric current exerted upon the luminescent material apart from the animal. Some of the luminescent slime was collected in sea water, put into a watch-glass, and the current passed through. On the make and during the flow of the current there was a bright glow at the cathode. Now there are two effects of the current either of which causes the photogenic granules to glow. One of these is the movement of the gas bubbles at the pole, which is sufficient mechanical stimulation to cause a very faint light. In the second place, the alkali which collects at the cathode is an important factor since hydroxyl ions are effective in causing the luminescent material of *Pelagia* to glow.[7] The phenomenon is therefore fundamentally different from the one described by Harvey.[8] He found that if the current were passed through a solution containing oxyluciferin and luciferase, the oxyluciferin is reduced in contact with the cathode and reoxidized in the vicinity of the cathode but that hydroxyl ions inhibit this reaction.

Since, in *Pelagia*, the luminescent material in solution glows only at the cathode, while the animal glows at the anode during the passage of the electric current, it is necessary to conclude that in the latter case the stimulation to luminescence by the current is indirect, in that the current acts on non-luminescent structures which transfer the impulse to the luminescent cells. It was also found in the cases where cathodal stimulation of the animal occurred that the animal lay very close to the cathode, so close as to be acted upon by the alkali formed by the current. That alkali will cause luminescence of the animal was shown by letting fall a drop of N/10 NaOH in sea water near the rim of a specimen of *Pelagia* swimming in sea water. The result was a luminescent glow in the region involved. N/10 acetic acid applied similarly did not have any effect. These facts suggest that the cathodal glow is caused by hydroxyl ions formed at the cathode.

[7] Heymans, C., and Moore, A. R., *J. Gen. Physiol.*, 1923–24, vi, 273.

[8] Harvey, E. N., *J. Gen. Physiol.*, 1922–23, v, 275.

The question has often been raised as to whether luminescence is not a by-product of muscular contraction. The two phenomena occur together in $CaCl_2$ poisoning. In pure $CaCl_2$ solution *Pelagia* is hypersensitive, the musculature becomes systolic and spontaneous luminescence spreads over the whole bell.[7] But in a solution of KCl these effects are separate, for the reason that while potassium causes relaxation of the musculature, luminescence is excited throughout the bell and tentacles. Furthermore, the galvanic current causes swimming pulsations of the bell (rhythmical contraction and relaxation of the musculature) but a continuous glow. For these reasons it must be concluded that luminescence is not dependent upon the contraction of muscles but is an independent phenomenon which occurs as the result of primary stimulation.

Last year I found, in *Mnemiopsis*,[5] that a transverse incision in the animal resulted in the formation of an additional anode at the cut surface. In *Pelagia*, however, no such result was obtainable. Even when the animal was cut in two completely, there was no glow from the cut surface of the bell when this faced the anode. In fact it could be shown that galvanic stimulation occurred only along the margin of the umbrella, for if the margin were cut off, the bell gave no response to the current. The isolated margin, however, gave the usual galvanic reaction, namely, luminescence at the anode. This result serves to indicate that the current acts upon nervous elements in the margin of the bell.[9] In this respect the experiment recalls the earlier one of Loeb and of Loeb and Budgett on *Amblystoma*,[10] in which they found that the skin secretion took place at the anode during the passage of the galvanic current. They also proved the dependence of the phenomenon on the nervous system, since section of the cord alone caused the formation of an additional anode. They found that NaOH when applied to the skin caused secretion, and concluded that the current acted by means of the positive ions in the medium surrounding the animal. These ions migrate toward the cathode. They would therefore impinge upon the anodal side

[9] Loeb, J., *Am. J. Physiol.*, 1899–1900, iii, 383. Romanes, G. J., Jellyfish, starfish and sea urchins, New York, 1885, 65.

[10] Loeb, J., *Arch. ges. Physiol.*, 1897, lxv, 308. Loeb, J., and Budgett, S. P., *Arch. ges. Physiol.*, 1897, lxv, 518.

of the animal and stimulate secretion there. This is identical with the mechanism which I have suggested to explain anodal stimulation of luminescence in *Mnemiopsis* and *Beroe*.[5] But stimulation at the cathode in *Pelagia* is due to hydroxyl ions. There are, therefore, two kinds of ionic stimulation, namely (1) anodal, which is referable to the blocking of positive ions by the tissue on that side, and (2) cathodal stimulation, when the animal is near the cathode, is due to the diffusion of alkali (hydroxyl ions) outward from a region of high concentration.

CONCLUSIONS.

1. *Pelagia noctiluca* responds to galvanic stimulation by a luminescent glow at the anode. If placed near the cathode a secondary glow occurs also on the cathodal side.

2. The luminescent slime of *Pelagia* when subjected to the galvanic current glows around the cathode. This is referred partly to the movement of hydrogen bubbles, but in the main to the alkali formed at the cathode.

3. The cause of galvanic stimulation in *Pelagia* is ionic. (1) Anodal stimulation is referred to the blocking of positive ions by the tissue on that side. (2) Cathodal stimulation, when the animal lies near the cathode, is due to the diffusion of alkali outward from a region of high concentration (the cathode).

4. Only the margin of the bell is excited to luminescence by the galvanic current. It is therefore concluded that nervous elements are the seat of excitation.

5. Luminescence is not a result of muscular contraction, since K ion causes relaxation of musculature but a continuous luminescent glow in *Pelagia*. The galvanic current causes pulsations of the bell (contraction and relaxation of the musculature) but a continuous glow.