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THE CAUSE OF PULSATION

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THE following is an account of a research which was pursued at the Marine Laboratory of the Carnegie Institution at Tortugas, Florida.

An interesting jellyfish, *Cassiopea xamachana,* lives upon the muddy bottoms of the lagoons of coral islands in the Florida and West Indian regions. Here the stilted roots of dense green mangroves fringe many a lagoon whose half stagnant waters have never felt the surge of ocean waves. Looking down through the clear depths one sees the bottom almost carpeted with the *Cassiopea* medusæ. Over wide areas they lie with their disks nearly touching and their bell-rims languidly pulsating. At a glance one might mistake them for sea-weeds, deceived as one would be by their delicate blue-green and gray-blue color, and by the tree-like shape of the branching appendages which bear the mouths of the medusa, and which project upward and outward hiding the pulsating disk below them.

At regular intervals around the rim of the jellyfish we find about sixteen minute club-shaped organs, each set within a deep niche. The microscope serves to show us that each of these little clubs contains at its outer end a mass of crystals, and upon one side a simple cup-like eye. Even in medusæ six inches in diameter these sense-clubs are smaller than the heads of the smallest pins; mere specks barely discernible to the eye, yet if they be cut off we find that the medusa ceases to pulsate, while the cut-off portion of the rim still contracts rhythmically. It is thus evident that the stimulus which produces each and every pulsation arises in the sense-clubs.

The question is, why is it that the central disk of the medusa does not pulsate in sea-water when its sense-clubs are removed? Curiously enough, if we stimulate the disk in any manner, such as by a mechanical or electrical shock, or by touching it with a crystal of common salt, it gives a few vigorous pulsations and then lapses into quiescence.

But if we cut out the center of the medusa and also remove the rim, thus forming a ring tissue without sense-organs (Fig. 2), this

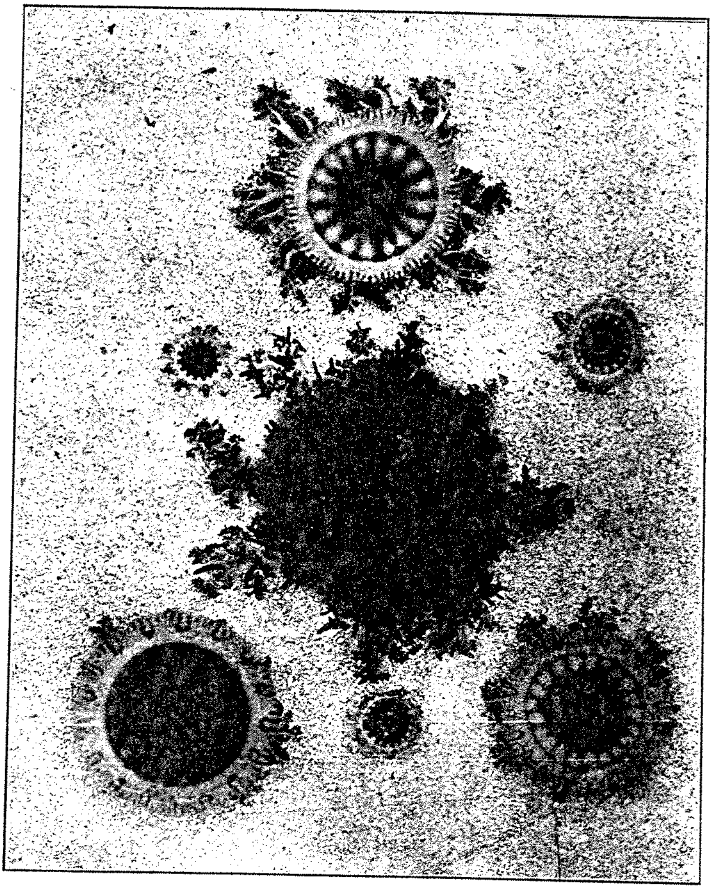


FIG. 1. LIVING MEDUSÆ OF *Cassiopea xamachana* ON A SANDY BOTTOM. The large medusa in the middle is in the natural attitude with its mouth-arms uppermost. The smaller medusæ have been turned over in order to show their pulsating disks.

ring remains quiescent in sea-water unless we stimulate it at any point such as at *S* with a single momentary touch of a crystal of potassium, or in some other manner, when a contraction-wave starts out from the point touched. In a narrow ring, however, the waves can go only in opposite directions from the stimulated point. Now one of these waves is apt to be strong and the other weak; for the nervous network which

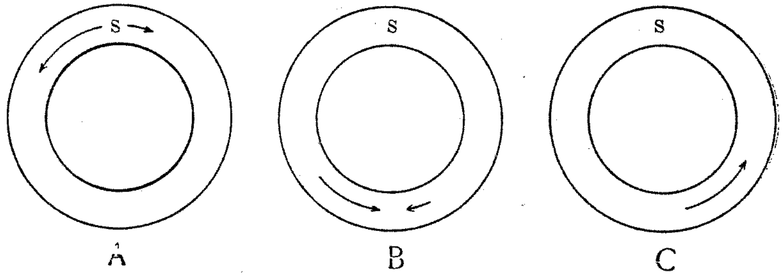


FIG. 2. SHOWING HOW A PULSATION-WAVE MAY BE "ENTRAPPED" IN A CIRCUIT OF TISSUE.

transmits them is almost certain to be more complete on one side than on the other of any stimulated point. Of course the waves meet as in Fig. 2, *B,* and then the strong wave destroys the weak one and continues around the ring. There is then only one wave left in the circuit and this travels constantly around (Fig. 2, *C*) for hours or days until something stops it, such as the cutting of the circuit or a fresh stimulus which produces a wave that meets and destroys it.

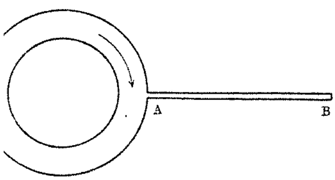
The weak wave was destroyed by the strong one in the above experiment because a weak stimulus can not set tissue into pulsation, which has been caused to pulsate through a strong stimulus, until after an appreciable interval of rest. Thus a weak stimulus following *immediately* after a strong one will produce no contraction, whereas a strong stimulus may cause tissue to pulsate even immediately after it has responded to a weak one.

It is now evident that the disk without its sense-organs *can* pulsate in sea-water if only a wave be once started in it, but that under normal conditions there is nothing to *start* a wave, and thus the disk remains quiescent. In other words, the sea-water is indifferent, and neither stimulates nor inhibits pulsation.

It is now time for us to determine why it is that the sea-water does not stimulate the disk when its sense-organs are removed. In the first place we must know the composition of sea-water, and chemical analysis shows that it consists of a mixture of sodium chloride (common salt), magnesium chloride and sulphate, potassium chloride, and calcium chloride and sulphate.

Numerous experiments show us that the common salt is a strong stimulant to both nerves and muscles. On the other hand, magnesium, calcium and potassium, all inhibit and do not stimulate the disk. Indeed, the stimulating effect of the common salt in the sea-water is exactly offset by the subduing tendency of the magnesium, calcium and potassium; and thus it is that the sea-water as a whole neither stimulates nor inhibits the pulsation of the jellyfish. The sea-water mainains the medusa in a delicately balanced fluid for it contains poisons ınd antidotes as does our blood, which exactly counteract one the other. For example, the jellyfish dies in less than two hours if placed in a olution having the amounts and proportions of the common salt and he potassium of the sea-water, but if we simply add the calcium it ulsates very rapidly for more than twenty-four hours. Finally, howver, the calcium produces so strong a muscular tetanus that the ulsating tissue is torn literally to shreds; but all of these injurious ffects disappear when we add the magnesium, which causes the pulsaon to become much slower and more regular, and wholly prevents ıe calcium from producting tetanus. Another curious fact is that ere it not for the presence of the calcium the magnesium would so upefy the nervous and muscular tissue that no pulsation could arise. his is the more remarkable because magnesium and calcium are both ıhibitors of pulsation, yet when both are present they tend in a easure to offset each other, magnesium mainly inhibits the muscles, hile calcium stupefies the nerves.

But to return to our subject, let us carry out some experiments to scover the nature of the stimulus which produces each pulsation of e jellyfish. If we cut a ring from the medusa's disk such as is shown in Fig. 3 and leaves a long narrow strip *AB* attached to it, and then start a contraction-wave traveling around the ring; every time the wave passes the point *A* a side-tracked portion of the wave will pass along the strip from *A* to *B*. When each side-tracked wave comes to the end *B* it es out, for it can not return over the recently stimulated tissue ong which it has just passed. Thus we see that the index strip 3 simply serves to catch a portion of each wave which passes its se.



3. 3. A PULSATING RING WITH AN "INDEX-STRIP."

Now suppose we place the ring in a pure solution of magnesium oride, and allow the index strip *AB* to remain in natural sea-water. en the contraction-wave gradually dies out in the pulsating ring, for magnesium paralyzes the muscles; and at the end of about a arter of an hour all movement will have ceased in the ring, but long er this we find that the strip *AB* still continues to transmit conctions at regular intervals of time. We see then that whenever the nething which produced the contraction in the ring comes around the point *A* it is still capable of setting up a contraction in the ip *AB*, although it can not now cause the muscles of the ring itself pulsate.

The explanation is that the stimulus which produces pulsation is nervous in nature, and travels through the nervous tissue quite independent of the presence or absence of the muscles. When therefore the magnesium paralyzes the muscles the nervous stimulus still travels around the ring even though the muscles can not now respond to it by contraction.

We now are in a position to state that each pulsation is due to a nervous stimulus which originates somehow in the sense-organs. The question is, how does it originate?

In all of the large jellyfishes called Scyphomedusæ, the marginal sense-organs are little clubs, the axial cores of which *always* contain a terminal mass of crystals. These crystals consist of calcium oxalate with a slight addition of uric acid and urea. The uric elements are relatively inert and need not be further considered. The presence of calcium oxalate, however, acquires some meaning when we find that the sense-organs can not continue to give rise to pulsations unless they be constantly supplied with soluble calcium, and all movement ceases in a few moments if the jellyfish be placed in sea-water deprived of calcium. We see at once that there must be some oxalate which is constantly forming in the sense-organs, and which is precipitating the soluble calcium chloride and sulphate of the sea-water to form the insoluble calcic oxalate crystals of the sense-club.

The question before us is, what oxalate is being formed in the sense-organs? We know that in certain tissues in the bodies of animals oxalic acid, and other oxalates, are formed apparently through the incomplete oxidation of carbohydrates. Now we find that even so small a quantity as one part by weight of oxalic acid in one thousand parts of sea-water paralyzes the sense-organs and permanently *prevents* their giving rise to pulsation, although so weak a solution is not sensibly poisonous to the general tissues of the medusa. Also the oxalates of potassium and magnesium finally inhibit pulsation, and it can not be that any of these is the cause of pulsation in the sense-organs.

The key to the mystery seems to be found, however, when we immerse the sense-organs in a solution of from 1 to 5 parts of *sodium oxalate* in 1,000 parts of sea-water; for this immediately stimulates them into great activity, whereas it has no effect if applied to any part of the medusa other than the sense-organs.

Now *sodium oxalate* precipitates the calcium which enters the sense-organ from the sea-water to form calcium oxalate, and sets free common salt and sodium sulphate: both of which are powerful nervous and muscular stimulants. The chemical formula for this reaction is as follows:

$$Na_2C_2O_4 + CaCl_2 = 2NaCl + CaC_2O_4,$$
$$Na_2C_2O_4 + CaSO_4 = Na_2SO_4 + CaC_2O_4.$$

FIG. 4. WHERE *Cassiopea* LIVES. Lagoon of Bahia Honda Cay, Florida Coral Reef.

Thus the sodium oxalate which forms in the sense-organs is simply changed into ordinary table salt, which acts as a stimulus to produce pulsation.

We can prove experimentally that this suffices to explain the phenomenon of pulsation, for if we simply add from 1 to 5 parts of common salt to 1,000 parts of sea-water, we find that this slight excess of salt acts as a powerful stimulant to the sense-organs, but produces no pulsation if placed upon other parts of the jellyfish.

It thus appears that each sense-organ normally maintains a certain excess of common salt which acts as a stimulus, and which is prevented from becoming too concentrated by the fact that being soluble it is constantly dissolving out into the surrounding sea-water.

It may trouble us for a moment to see why a recurrent pulsation should arise from a constantly present stimulus, but long ago Romanes discovered that a weak constantly present stimulus, such as a faradaic current of electricity, will cause rhythmical pulsation, the jellyfish responding to it periodically and regularly.

We see then that the natural stimulant which produces the pulsation of the jellyfish is only that most familiar substance common salt!

The hearts of higher animals behave in a manner so similar to that of the pulsating jellyfish that we need not be surprised if it be demonstrated that here also a slight excess of *sodium chloride* gives rise to each and every pulsation.