striction and virtual separation from the thorax. Normal periodic reversal was observed several times throughout this period. It is clear that head and thorax are not necessary to initiate backward beating of the dorsal vessel.

Since Japanese lacquers are different from the American, it may be possible that the enamel paint used by Yokoyama would have a different effect from that produced by our Brunswick black and so induce backward beating in the less mature larva. It should be noted, however, that local paralysis in the less mature larva brought on by the use of Brunswick black often did not check forward beating. The insect apparently had not reached the stage of development at which backward beating was possible; so that, upon partial recovery from the operation, only forward pulsation occurred. In the more mature larva ready to spin, narcotization of the posterior segments, if not intense, still inhibits very imperfectly the strong tendency to beat forward.

That minute quantities of acid added to Ringer's solution quickly paralyze the dorsal vessel of the larva was shown by Pigorini,[4] 1917, who found that acetic acid at a dilution of $\frac{1}{1000}$ and formic acid at even greater dilution ($\frac{1}{5000}$) were instantly lethal.

To solve the problem of backward beating one should first answer the fundamental question, why it beats forward. Evidently there is a pronounced metabolic gradient from the posterior end of the larva which is never lost and only intermittently neutralized. To it, as development proceeds, is added the condition in which the middle region (young pupa) or the aorta (adult) are intermittently more active. These gradients are adaptations to the great influx of hemolymph (1) into the posterior end of the heart, (2) into the region of the node of double-action or central beating in the young pupa (usually between abdominal segments 3–4), and (3) from the thorax, with its pulsating mesothoracic vesicle, in the older pupa and adult.

SUMMARY

(1) Premature reversal of direction of heart-beat in *Bombyx* was induced in spinning larvae and those about to spin by blocking the 3 most posterior pairs of spiracles with Brunswick black, in accordance with the experiments of Yokoyama.

(2) This method and the injection of lactic and other acids paralyze the muscles of the body wall and heart in that region, thus preventing forward and permitting backward beating.

(3) Attempts to produce periodic reversal in the larva in the early days of the 5th stage by Yokoyama's methods failed.

(4) The application of ether, alcohol, or xylol to the 3 posterior pairs of spiracles, or immersion of these segments in alcohol, was effective in inducing premature reversal at the close of the 5th stage, exclusively forward beating being resumed as soon as narcosis disappeared.

(5) Amputation of the posterior end of the body of the larva, including the end of the dorsal vessel in abdominal segments 7 and 8, did not prevent forward peristalsis.

(6) Amputation of head and thorax from the abdomen of a pupa did not interfere with normal periodic reversal in the abdomen.

(7) Thus periodic reversal in the dorsal vessel takes place without the intervention of any terminal ganglia.

(8) The suggestion of Yokoyama and earlier writers (Bataillon, Fischer) that general acidosis initiates normal backward beating is not corroborated.

(9) The metabolic gradient of the larval dorsal vessel is never lost, but intermittently neutralized in the prepupa, pupa and adult by increased metabolic action at two other points: the central node (in the young pupa) and the aorta with its mesothoracic pulsating vesicle (in the adult).

(10) These gradients are adaptations to the large influx of hemolymph into the dorsal vessel at three principal regions.

The writer gratefully acknowledges assistance rendered by a grant from the Joseph Henry Fund. Useful suggestions by Dr. C. C. Stewart were incorporated in this article during its revision.

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[4] Atti. R. Acc. Lincei, Anno 314, Ser. 5, Vol. 26, 2° Semest., p. 15–19, 1917.

AMOEBOID MOTION AS THE PRODUCT OF PROTEIN SWELLING

THE nature of protoplasmic movement, as seen in its simplest form in the extrusion of pseudopodia by the amoeba, is still a matter of debate. Whether we deal with the apparently haphazard actions of the free-swimming amoeba or the directional movement of a leucocyte, the fundamental nature of and the reason for the movement remain obscure. The most popularly accepted belief is that the amoeba suffers a surface tension change, but the material in which such surface tension change occurs has never been touched upon to my knowledge. It occurred to me that the extrusion of a pseudopodium by an amoeba might depend upon a localized swelling with consequent softening of a surface area in a properly "stim-

ulated" animal; this giving rise to inequalities in tension within the total organism and resulting in an extrusion of protoplasm at the point of stimulation and a movement in the direction of its source.

Since proteins constitute the essential hydrophilic colloid which makes up the living cell and since we are familiar with a series of chemically well-defined substances which make such proteins swell, the effects of these substances in evoking protoplasmic movement were studied. *Those materials which are known to be hydrators of proteins will, when properly employed, lead to the extrusion of pseudopodia by amoeba and a movement of the organism in the direction of the "stimulus."*

I found that a stock amoeba, grown in an aquarium, would come to rest in approximately spherical form after two washings and a rest period of thirty minutes in a .3 per cent. sodium chloride solution. Transfer was made by means of a capillary pipette in order that as little as possible of the aquarium water might be transferred.

In each of the following experiments a single amoeba was placed in a hollow-ground slide carrying 0.25 cc of the salt solution. The exact position of the amoeba was followed by the insertion of a double-ruled glass disk in the eyepiece of the microscope. This ruling yielded a square, approximately the size of an amoeba, with eight lines radiating from it, each pair of which bounded a lane along which the chemical solutions employed might be introduced and the swelling observed. The solutions were introduced from a capillary pipette fitted with a rubber bulb.

When .005 cc of 5/N HCl is introduced close to an amoeba which has reached a state of inactivity in a sodium chloride solution, the animal responds by sending out a process toward the acid. The whole amoeba may be observed to move toward the acid. After such initial and directional movement and after the acid has had time to diffuse, pseudopodia may be sent out in haphazard fashion over larger areas of the stimulated surface. If, after such treatment, the amoeba is returned to its normal habitat, it moves about normally.

Lactic, acetic and sulphuric acids act similarly when employed in the same amount and strength.

While all acids increase the hydration capacity of protein colloids, they show a large quantitative difference and this difference does not follow their dissociation in aqueous solution or the concentration of the hydrogen ions they yield, but is specific—hydrochloric, lactic, acetic and sulphuric acids, for instance, are effective in the order named when compared. *The same is true of their effects in eliciting amoeboid motion.*

In the same amount hydrochloric acid is effective at a concentration of N/4, lactic acid at N/2, acetic acid at 1/N. Sulphuric acid is not effective until a concentration of 5/N is reached. In the case of each acid the speed and amount of reaction of the amoeba is increased as the concentration of the acid is increased.

Urea, the amines and the alkalies are among the substances which act as hydrators of proteins. *These all have the property of inducing amoeboid movement.*

A crystal of urea (weight – 0.001 gm.) acts in the same manner as the acids.

Paraphenylenediamine proved to be the most satisfactory of all the agents which I studied. This substance dissolves so slowly that the amoeba may be observed to migrate in the direction of the crystal. The movement is slow and flowing in character and differs in no respect from "normal" amoeboid movement. The amount used was the same as in the case of urea. If, after such treatment, the animal is returned to its normal habitat, it moves in a "normal" manner.

When 5/N NaOH is used in the same manner as the acids, the amoeba responds in the same way.

All inorganic salts antagonize—even without chemical neutralization—the swelling effects of acids upon protein colloids. They do this in a definite order, univalent radicals being less effective than divalent at the same molar concentration, and these than trivalent. *The same is true of amoeboid movement.*

In this group of experiments the amoeba was permitted to come to rest in .3 per cent. sodium chloride solution and then placed in .25 cc of a solution of the salt to be tested; .005 cc of 5/N HCl was used as a "stimulus" in each case. Ferric chloride produces complete inhibition of movement at a concentration of .05/M; calcium chloride and magnesium chloride between .1/M and .2/M; while sodium chloride does not produce this effect until a concentration of .6/M is reached. For any given salt the response of the amoeba to the "stimulus" decreases as the concentration of the salt solution increases.

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