THE RELATION BETWEEN RATE OF LOCOMOTION AND FORM IN AMŒBA PROTEUS[1]

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Mast and Prosser (1932, p. 336) maintain that the rate of locomotion in *Amœba proteus* is highest in monopodal specimens, lowest in multipodal specimens, and intermediate in bipodal specimens, and that ". . . selection of monopodal specimens greatly reduces the variability in rate," but they present no evidence in support of their conclusions. The experimental results presented in the following pages concern these conclusions. They were obtained as follows:

About 50 specimens of *Amœba proteus* were taken at random from a culture, washed[2] three times in redistilled water, and transferred to a Pyrex glass dish containing .001N sodium chloride solution.[3] The dish was then put into a constant temperature apparatus (Pitts, 1932) on the stage of the microscope and left for one hour for adjustment. A single specimen was now selected and projected with a camera lucida on black paper; then the position of the posterior end of the projected image was marked at intervals of one minute, and the outline of the image of the animal sketched at the intervening half minute. This was continued for seven minutes after which it was repeated with each of four other specimens differing in form, and with each of five similar specimens in a number of other dishes. This was continued until records were in hand for 60 specimens, 20 monopodal,[4] 20 irregular monopodal, and 20 multipodal specimens. All of these observations were made on specimens which had been in the sodium chloride solution from one hour to one hour and 45 minutes. The temperature during the observations

[1] This investigation was carried on under the direction of Professor S. O. Mast.

[2] The washing was performed by putting the amœbæ into watch glasses containing redistilled water, allowing them to settle and attach, then removing the water with a pipette, and finally pouring on more redistilled water.

[3] Kahlbaum's purest sodium chloride, accurately weighed and dissolved in water redistilled from a tandem Pyrex glass still (Mast, 1928).

[4] A monopodal amœba is defined as an elongated cylindrical animal, smooth in outline, which moves continually by the projection of a single pseudopod. Marine limax amœbæ of the type used by Pantin (1923) are regularly monopodal in form. *Amœba proteus* readily assumes the monopodal form if it is allowed to become stellate in redistilled water and then transferred to a dilute salt solution (Mast, 1928).

was 23 ± 0.5°. The results obtained are presented in Tables I and II and Fig. 1.

The results in Table I indicate that the rate is highest in monopodal forms and lowest in multipodal forms, and that the variation in rate of the different specimens is least in monopodal forms and greatest in a random sample, the coefficient of variation being 11.4 for the monopodal forms, 17.8 for the irregular monopodal forms, 27.9 for the multipodal forms, and 34.4 for the random sample. Thus it is evident that the variability of any given selected group is considerably less than that of a random sample, and that selection of strictly monopodal forms leads to least variation. The results obtained consequently support the conclusions of Mast and Prosser.

Schwitalla (1924) claims that locomotion in *Amœba proteus* is rhythmical, and he describes a two-fold rhythm—a rhythm of short duration consisting of rapid accelerations and retardations and a rhythm

TABLE I

Summary of statistics concerning the rate of locomotion of monopodal and multipodal amœbæ.

Form	Number of Specimens	Mean Apparent Rate	Probable Error	Standard Deviation	Coefficient of Variation
		mm. per minute	*per cent of mean*		
Monopodal	20	21.05±.35	1.65	2.30±.25	11.40±1.26
Irregular monopodal	20	19.72±.53	2.69	3.52±.37	17.85±1.96
Multipodal	20	9.44±.40	4.20	2.63±.28	27.86±3.20
Totals and averages	60	15.99±.48	2.99	3.49±.34	34.36±2.35

of long duration superimposed upon the short periods. He says (p. 490): " Only rarely will the same rate of locomotion be found to have been sustained for two successive minutes. Sometimes such an uniform rate may be maintained for two or three minutes, and in exceptional cases for five and seven minutes." And (p. 492): " In two successive minutes, a doubled rate, or a rate reduced by one-half occurs with comparative frequency."

Hahnert (1932) made a study of locomotion of monopodal specimens of *Amœba proteus* over a period of some twenty minutes and found the rate of locomotion to be surprisingly constant. He found in one specimen, for example, an average rate of 252.6 micra per minute with a standard deviation of only 13.6 micra per minute or 5.4 per cent. Similar results were obtained with nine other specimens tested. He found no indication of rhythmic variation in rate of locomotion like that observed by Schwitalla, and consequently concludes that "the process of ascertaining the rate of locomotion is greatly simplified by using monopodal specimens."

TABLE II

Data Concerning the Rate of Locomotion of Monopodal and Multipodal Amœbæ

Designation of Individuals	1	2	3	4	5	6	7	8	
				Monopodal Specimens					
1st minute	20.0	20.5	22.5	22.5	20.0	21.0	23.0	19.5	
2d minute	20.0	18.0	21.0	23.5	21.0	22.0	25.0	21.0	
3d minute	22.0	20.5	21.0	23.0	20.0	21.0	24.0	20.0	
4th minute	21.0	20.5	21.5	22.0	22.0	22.0	23.5	20.0	
5th minute	20.5	20.0	21.5	22.0	22.0	22.0	23.0	19.0	Total
6th minute	20.0	21.0	21.5	20.5	23.0	23.0	22.5	20.0	average
7th minute	20.5	20.5		22.5	23.0	23.0	24.5	21.0	rate
Average rate	20.57	20.14	21.50	22.79	21.43	22.00	23.64	20.71	21.35
				Irregular Monopodal Specimens					
1st minute	21.0	10.5	19.5	25.0	24.0	18.5	19.0	23.5	
2d minute	20.0	19.5	18.5	25.0	19.5	15.0	19.0	18.0	
3d minute	16.5	15.0	19.0	18.5	21.5	18.0	16.5	22.0	
4th minute	10.5	9.0	14.5	21.0	21.5	15.0	18.5	23.0	
5th minute	12.5	18.5	16.0	23.5	24.0	16.5	16.0	22.5	
6th minute	18.0	27.5	17.5	25.5	20.0	21.5	21.0	19.0	
7th minute	20.0	12.0	18.0			23.5	22.0	20.0	
Average rate	16.93	16.00	17.57	23.08	21.75	18.29	18.86	21.14	19.20
				Multipodal Specimens					
1st minute	12.0	10.0	11.0	6.5	6.5	10.0	9.5	10.5	
2d minute	14.0	11.5	14.0	10.5	7.5	9.0	9.0	16.0	
3d minute	11.0	10.5	7.5	7.0	8.5	13.0	10.5	4.0	
4th minute	8.5	9.0	7.5	8.0	8.5	13.0	16.0	10.5	
5th minute	6.5	5.0	10.0	9.5	8.5	9.5	17.5	11.5	
6th minute	3.5	5.5	9.0	9.5	7.0	8.0	16.5	14.5	
7th minute	3.0	8.0	14.0	7.5	4.0	10.0	17.5	12.0	
Average rate	8.36	8.50	10.43	8.36	7.21	10.36	13.79	11.21	9.77

By examining the rate of locomotion obtained during each of the seven-minute periods of observation of the individual specimens studied in this investigation, some insight is obtained as to the nature and reason for the rhythmical variation in rate which Schwitalla observed and which

Hahnert maintains is not evident in monopodal specimens. By referring to Fig. 3 of Schwitalla's paper it will be seen that there was great variation in the form of the amœbæ used, *i.e.* that some were nearly monopodal, some bipodal, and others multipodal.

It is evident from Table II of the present paper, in which the rates for successive minutes for eight specimens were taken at random from each of the three groups of forms studied, that the variation from minute to minute is much less for monopodal than for irregular monopodal

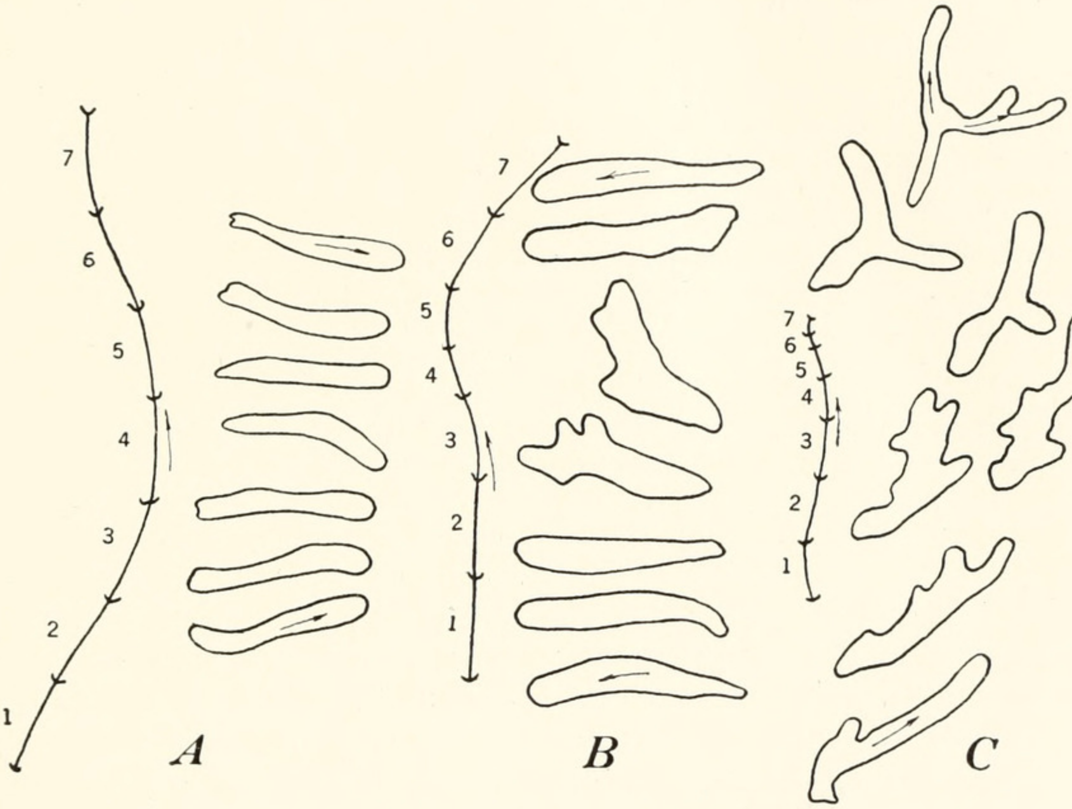

FIG. 1. Camera sketches illustrating the relation between form and rate of locomotion in *Amœba proteus;* curves, projected paths made by these specimens; arrows, direction of locomotion; cross lines on curves, position of the posterior end at minute intervals; outlines, form of the specimens at minute intervals during the time the paths were made.

Note the constant rate of locomotion attending the constant monopodal form (*A*); the decrease in rate as the form becomes irregular (*B*), fourth minute); the increase in rate as the monopodal form is assumed (*B*, seventh minute); and the decrease in rate as irregularity in form increases (*C*).

or multipodal specimens. For instance, by comparing specimen 1 of each of the three forms (Table II), it will be seen that the maximum variation within the seven-minute period for the monopodal specimen is 2 mm., or 9.7 per cent of the mean; for the irregular monopodal specimen 10.5 mm., or 62 per cent of the mean; and for the multipodal specimen 11.0 mm., or 131.6 per cent of the mean. This shows that the greater the irregularity of the form of the amœba, the greater the irregularity of locomotion.

Figure 1 gives the records obtained concerning the rate of locomotion of these three specimens, and likewise the outline sketch of them at the intervening half minute. Figure 1*A* indicates clearly that as long as the amœba retains a strictly monopodal form it moves with a fairly uniform velocity. Figures 1*B* and 1*C* demonstrate that in variable specimens of irregular monopodal and multipodal form the marked increases in rate are for the most part due to the assumption of a monopodal or semi-monopodal form (Fig. 1*B*, seventh minute) ; and that the more irregular the form of the animal the slower the rate (Fig. 1*B*, fourth minute, and Fig. 1*C*). It consequently seems probable that the long rhythms which Schwitalla observed were due to change in form of the amœbæ. The short rhythms which he observed were probably due to periodic breaks in the plasmagel sheet, for with each break of this sheet (Mast, 1926) there is a forward spurt of locomotion (Mast and Prosser, 1932). It has, however, been demonstrated that selection of monopodal specimens reduces the variation between rates taken at different times on a single individual. Consequently, in experiments dealing with the effect of environmental factors on rate of amœboid movement, monopodal specimens should be used.

Summary

The rate of locomotion in *Amœba proteus* is highest in monopodal and lowest in multipodal specimens. The average rates obtained for 20 specimens in .001N sodium chloride was 278 micra per minute for monopodal forms, 260 micra per minute for irregular monopodal forms, 125 micra per minute for multipodal forms, and 211 micra per minute for an average of all forms.

The variation in rate is least for monopodal amœbæ and greatest for multipodal amœbæ.

The rate of locomotion of any single individual over a seven-minute period is least variable for monopodal specimens and most variable for multipodal specimens.

The rhythmicity of locomotion in *Amœba proteus* observed by Schwitalla (1924) is largely due to change in form, the rate increasing as the amœba becomes more nearly monopodal and decreasing as it becomes more irregular in form.

LITERATURE CITED

Hahnert, W., 1932. A Quantitative Study of Reactions to Electricity in Amœba proteus. *Physiol. Zool.*, **5**: 491.

Mast, S. O., 1926. Structure, Movement, Locomotion, and Stimulation in Amœba. *Jour. Morph. and Physiol.*, **41**: 347.

Mast, S. O., 1928. Factors Involved in Changes in Form in Amœba. *Jour. Exper. Zool.*, **51**: 97.

Mast, S. O., and C. L. Prosser, 1932. Effect of Temperature, Salts and Hydrogen Ion Concentration on Rupture of the Plasmagel Sheet, Rate of Locomotion, and Gel/Sol Ratio in Amœba Proteus. *Jour. Compar. and Cell. Physiol.*, **1**: 333.

Pantin, C., 1923. On the Physiology of Amœboid Movement. I. *Jour. Mar. Biol. Assn.*, **13**: 24.

Pitts, R., 1932. Constant Temperature Apparatus Adapted for Use on the Microscope Stage. *Science, N. S.*, **76**: 626.

Schwitalla, A. M., 1924. The Influence of Temperature on the Rate of Locomotion in Amœba. I. Locomotion at Diverse Constant Temperatures. *Jour. Morph. and Physiol.*, **39**: 465.