this we agree save that such a formulation of the facts, like that of WOERDEMAN, fails to distinguish clearly between competence and individuation. WEISS's objections, in fact, were not directed against the theoretical considerations actually advanced by those who are studying "chemical induction" but against considerations which he was afraid might be advanced, or which are sometimes advanced by those who are not so intimately concerned with the subject.

We wish to express the hope that uniformity may soon be established with regard to the concepts and nomenclature used by workers on these phenomena, and we believe that for the present the three terms Competence, Evocation and Individuation, as we have defined them above, form a vocabulary adequately congruent with the facts at present known.

# Comparative Physiology. — Shape and slope of rest curves of the stretched foot of the snail (Helix pomatia L.) in relation to its water content. (From the Laboratory of comparative Physiology of the University of Utrecht.) By N. POSTMA. (Communicated by Prof. H. J. JORDAN.)

(Communicated at the meeting of June 27, 1936).

JORDAN observed in his lengthening experiments that the foot muscle of hibernating snails is very dry and inclines to develop "contracture". He got the impression that this phenomenon could be prevented if the snail was allowed to take up water, creeping in a thin layer of water on the bottom of a vessel. This effect was to be expected, since JORDAN ascribed the resistance against extension to the viscosity of the foot muscle. The absorption<sup>1</sup>) of more or less water by the muscle will affect its viscosity. So it seemed useful to get more exact data concerning the relation between the water content of the foot muscle and its viscosoid tone (the slope of the length-time-curves).

Three series of extension experiments (HA 7—10 Febr., HB 10—13 Febr. and HC 11—14 Febr. '36) gave corresponding results, which confirm JORDAN'S suggestion and support some points of view concerning the mechanism of the tonus phenomena, suggested in my thesis (1935a). The results will be described in this paper.

## Experimental conditions.

After the epiphragma had been removed from about 14 hibernating

<sup>&</sup>lt;sup>1</sup>) That is what JORDAN (1927) called "Hydratation" (German); in this paper the synonymous term "Hydration" is used for the adsorption of water by the colloidal particles of the muscle: the change of free into bound water. Consult, for the technical terms, my paper 1935b.

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snails of the same weight, one half of them were kept on cabbagelettuce, which was saturated with water, in a vessel covered with a glass plate; thus there was no loss of water by evaporation. In 64 hours the average weight of these snails increased with 27 %. The remnant of the group of animals was kept on lettuce in an aquarium, covered with wire netting; on an average the weight was unaltered. On the fourth day the viscosoid tonus of the foot muscles was measured by recording the rest curves during 10 minutes; then the foot was unloaded and the angles between an horizontal line and the tangent in the lowest point of the lengthening curves were measured, as well as the increase of length. After its extension the foot muscle was removed from the lengthening apparatus and weighed. Next the foot was cut in slices which were dried in a drying oven at 110° C. till the weight was constant. The decrease in weight is the loss of water.

### Results.

Some curves are given in figure 1. If the statistical method is employed for the interpretation of the results obtained, the data must be selected

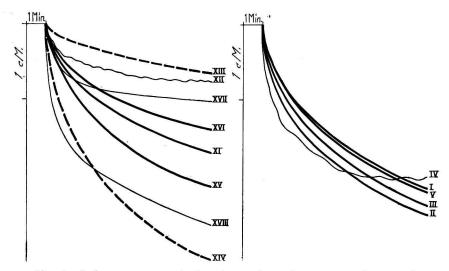


Fig. 1. Left part, composed after the results with respect to dry animals (of the three series), to demonstrate the different types of lengthening reaction. Right part gives the curves, obtained of the sodden snails of series HC.

critically. Therefore all myograms with spontaneous shortenings and contractions are left out of account (Series HA N<sup>0</sup>. IV and XII, HB N<sup>0</sup>. V, XV and XVII, HC N<sup>0</sup>. IV and XV). We only speak of a normal lengthening reaction if a greater lengthening-traject (ordinate) is regularly accompanied with a greater angle, measured at the end of the curves, these curves diverging fanshaped. A disturbance of  $3^{\circ}$  or more with respect to

the regular increase of the angle is taken as too strong a deviation (the angle has been estimated with an accuracy of  $\pm \frac{1}{2}^{\circ}$ ). Such curves are not of the normal type, no more than those that have a very steep beginning and change their slope by a sudden bend (curves XVII and XVIII fig 1), even when the angle does not derange the tabulated increase. In this way I selected out of 20 wetted snails 12 lengthening reactions which could be used and 7 out of 20 dry animals. The data are:

	Body w in g		Water cor	ntent²)	Length in c	•	Ang	le
Series HA								
Watery snails	28		78. <b>9</b> 6º/ <sub>0</sub>		1.81		18²/₃°	
Dry animals	21		77.50		1.08		13	
Ratio		133		102		167		144
Series HB								
Watery snails	25		80.38		1.70		16 <sup>1</sup> /2	
Dry animals	20 <sup>1</sup> /3		75.85		1.40		13	
Ratio		123		106		121		127
Series HC								
Watery snails	22 <sup>1</sup> /2		80.24		2.24		21 <sup>1</sup> / <sub>2</sub>	
Dry animals	18		77.15		1.60		16	
Ratio		125		104		140		134
Average ratio		127		10 <b>4</b>		143		138

TABLE I.

#### Discussion.

The water content found in the foot muscle of Helix agrees with the data of BELLION (1909) — 76.9—82.6 % —, like the alteration in weight by taking up water with that found by WEINLAND (1931): loss of water 2.01 gr, absorption 2.74 gr, average change in water content 4.75 gr.

If we compare the ratio of the data for sodden snails to that of dry animals — on the basis = 100 for the latter — the weight increases to  $127^{3}$ ), the lengthening traject to 143, the angle of the extension curve to 138 and the water content of the foot to 104. Consequently the contrast between the slope of the curves and the increase of length is very great in proportion to the difference of the water content.

With respect to the body fluid in the foot of the snail, we have to distinguish:

<sup>&</sup>lt;sup>2</sup>) Percentage of the weight of the lengthened foot muscle.

 $<sup>^{3}</sup>$ ) After correction for the shell, which does not participate in the absorption of water, the ratio increases to 137.

- I. the blood in the pedal part of the intestinal cavity;
- II. the blood in the slits of the schizocoelic system;
- III. the intracellular water, which is composed of the free water and that bound in the water-layer of the colloidal particles of the cells (hydration).

The viscosity of the foot will directly be determined by the ratio of the bound to the free water. Hydration is accompanied by increase of the water-layer at the cost of the free water. This change in the distribution of water will cause more resistance against lengthening: both the free water diminishing and the growth of the colloidal particles by the adsorbed water result in higher viscosity.

In control-observations the loss of blood was estimated. Foot and visceral mass were separated from each other over a watch-glass. Foot and the blood, escaping from the pedal part of the intestinal cavity, were collected on the glass. The foot muscle was transported to the lengthening apparatus and the glass with blood was weighed. The wetted snails gave  $2-2\frac{1}{2} \times$  as much as the dry ones. (Portion I).

During lengthening and the treatment after extension the foot squeezes out blood and therefore loses water. The loss was estimated at  $1\frac{3}{4}$  % of the weight of the fresh foot muscle (a part of portion II). The remaining part of the schizocoelic blood and the water content of the cells (portion III) together gave an average ratio of 104. The data obtained do not allow to know the ratio of free/bound water, decisive for the viscosity. But the fact that a difference of less than 4 % in water content is accompanied by a tenfold difference concerning the ordinate and the slope of the extension curves shows that the intake of water is of great importance for the viscosoid tone. This is in accordance with JORDAN's view. Obviously the water is chiefly absorbed in free state. The influence of the water content is accentuated if we restrict our attention to the sodden animals. Table II shows that a deviation in water content (the latter being relatively low) is accompanied by a small angle at the end of the lengthening curve.

5	Series HA			Series HB			Series HC	
	Water content	Angle		Water content	Angle		Water content	Angle
No. I	78 º/o	9 <sup>1</sup> /2°	No. V	79.8º/0	<b>4</b> 1/2°	No. II	78.55º/0	17 <sup>1</sup> /2°
IV	78.3	11 <sup>1</sup> /2	VI	80	7 <sup>1</sup> /2	III	78.9	17 <sup>1</sup> /2
Middle types	79	1 <b>8</b> ²/ <sub>3</sub>		80. <del>4</del>	16 <sup>1</sup> /2		80.2	21 <sup>1</sup> /2

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The blood in the intestinal cavity and that in the schizocoelic slits may also be of importance for the tonus level of the foot muscle. In the extension myograms obtained of watery snails the ordinate of the normal types varies from 2.36 to 2.70 cm, the angle from 20 to  $24^{\circ}$ ; this mutual agreement is in contrast with the diverging myograms got of dry snails: the ordinates range from 0.72 to 3.37 cm, the angles from 10 to  $28^{\circ}$ .

Three types of curves are to be distinguished in the normal myograms: curves VI, XV and XVI middle group; curves XIII and XIV extreme contrast, curve XIII hypertone, curve XIV hypotone. These types show different frequency in dry and wetted animals:

		Dry snails	Sodden animals
	Spontaneous	20º/0	150/0
reaction	Middle type	35	60
	Hypertone	15	5
Normal	Hypotone	30	20

TABLE III.

Recordingly the internal condition of the muscle is altered by the absorption of water, increasing the internal pressure: a well determined tonus level is better assured, which is lacking in the foot of snails in hibernation. This regulating principle is also evident from the fact, that in dry animals there is no correlation between a deviation of the angle from the middle type and a difference in water content, as it is in wetted snails (table II): a small angle is capriciously combined with different percentages concerning the water content. The responsible factor of this alteration must perhaps be sought in the extension exerted by the internal pressure, an effect to which the snail is exposed during every increase of contents (taking in food and absorbing water after rain showers). This suggestion is supported by the experience that the tonic condition of the foot of the snail may be altered by lengthening (POSTMA 1934 and 1935a): a foot that is poor in tonus becomes more tonic by applying it with a small load during a sufficiently long time-interval. So an extension exerted before a certain lengthening experiment unmistakably affects the result of this experiment. In this way the question arose if, during lengthening, the foot muscle reacts actively and therefore alters its properties. The increase of resistance in the rest curves during lengthening can simply be explained by mechanical effects, which occur also in plasticated rubber and other inanimate materials (JORDAN 1935b). Therefore it is impossible to prove here the alteration of the muscle's internal condition being of more than physical origin. Yet there are some phenomena, which support my suggestion that the muscle is reactive during lengthening :

1°. the activity of the dynamic component as soon as the equilibrium between static and dynamic tone is disturbed (my paper 1935b);

2<sup>o</sup>. the undulating slope of many extension curves (cf. POSTMA 1933, fig. 1 curve II);

 $3^{0}$ . the fact that in the foot of the seahare the loss of tone, caused by cooling, is prevented by extension, when a load is applied (JORDAN 1935a).

The differences, occurring in spite of the same water content (XIII as well as XVI 78.2 %) have to be ascribed to a dynamic factor which we are not able to control (Similarly HC XVIII and XV with 79 and 78.8 % water, ordinates 1.16 and 2.40 cm; HA XII and XV with 78.7 % water, ordinates 0.84 and 1.74 cm).

I wish to thank Prof. H. J. JORDAN for his interest in this investigation and Mr. R. R. DE JONG for the correction of the text.

## SUMMARY :

Absorption of water by the foot muscle of the snail results in lowering the tonus level (lower viscosity). Besides this it causes an equalization of the slope of the extension curves.

The increase of the slope and that of the ordinate of the length-timecurves are in perfect agreement with the intake of water, but are ten times as large as the increase of water content of the muscle itself.

The uniformity of the tonus level of watery snails is possibly related to the extension, exerted by the increase of the internal pressure, caused by the intake of water.

#### LITERATURE CITED :

- 1909 BELLION, M., Recherches expérimentales sur l'hibernation de l'escargot (Helix pomatia L.) Ann. Un. Lyon (N. S.) 27.
- 1927 JORDAN, H. J., (in collaboration with HIRSCH, C. G.) Ulebungen aus der vergleichenden Physiologie. Springer, Berlin.
- 1931 BRAND, TH. V., Der Jahreszyklus im Stoffbestand der Weinbergschnecke. Zs. f. vergl. Physiol. 14, 200–265.
- 1933 POSTMA, N., Recherches sur l'allongement du pied de l'escargot, etc. Proc. Royal Acad. Amsterdam, 36, 360-371.
- 1934 Ueber mehr oder weniger tonische Stimmung im Schneckenfuss. Acta Brev. Neerl. 4, 106—108.
- 1935a JORDAN, H. J., Tonische Verkürzung und tonisches Festhalten der Verkürzung bei den Muskeln von Aplysia limacina u.s.w. Proc. Royal Acad., Amsterdam, 38, 358–365.
  - b Viscosity effects in the living protoplasm and in muscles. First report on Viscosity etc. Chapter VI. Verhand. Kon. Akad. v. Wetensch. Amsterdam afd. Natuurk. 1e sectie, 15, 214—255.
  - a POSTMA, N., Onderzoekingen betreffende het herstel van de tonus bij de slakkevoet (Helix pomatia L.) enz. Thesis at Utrecht.
  - b Tonus phenomena in the foot of the snail (Helix pomatia). Proc. Royal Acad., Amsterdam, 38, 1036—1040.