STUDIES IN THE BIOLOGY OF THE LEECH. III

THE INFLUENCES OF CHANGE IN TEMPERATURE UPON LOCOMOTION

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FORWARD LOCOMOTION

Locomotion in the leech may be differentiated into the following types: First, movements of reptation, i.e., the elongation and shortening of different somites. This includes normal creeping or crawling movements, and looping. Second, movements of undulation as expressed in swimming.

A. MOVEMENTS OF REPTATION

True reptation is accomplished by the contraction of the circular muscles followed by a contraction of the longitudinal muscles. In forward locomotion, by reptation, a wave of contraction of the circular muscles originating in the anterior somites travels posteriorly. This results in the elongation of the animal and a subsequent head movement forward. At this point the anterior sucker usually becomes attached. Following this initial wave of contraction is a corresponding contraction of the longitudinal muscles. This later contraction results in the shortening of the animal. The posterior sucker remains attached throughout the period of extension while the anterior sucker becomes attached during the period of shortening. The suckers are primarily organs of fixation but function in normal crawling and looping.

Looping movements are a modification of the movements of true reptation. These movements consist of the normal elongation of the animal followed by a contraction during which the anterior and posterior suckers are brought close together. This movement resembles that of the measuring worm. In this movement the ventral longitudinal muscles play an important role.

It is axiomatic that the nervous system plays an essential part in the process of locomotion. The sequence of muscle
contraction in the earthworm during locomotion has previously been described, (Bovard, 1918).

The question which we desire to raise next is; what is the relationship in the leech between the neuro-muscular system and the stimuli that will produce a specific mode or rate of response?

**The Influence of Change in Temperature Upon Locomotion**

It is well known that the type of behavior expressed by certain animals may be conditioned by temperature. It is further evident that the rate of activity is, within limits, proportional to the temperature. D. F. Miller (1929), clearly demonstrated the relation of temperature to the activity of fly larvae. He found that the rate of locomotion varied directly with the temperature from 2°C, to 40°C, and inversely with the temperature above that point. Further that the rate of contraction increases directly with the temperature between 0°C, and 45°C.

Of the factors influencing locomotion in the leech temperature is the most obvious. With a constant light source and with the leeches partially immersed in water a series of tests were made to determine the influence of temperature changes upon locomotion. Temperatures ranging from 15°C, to 35°C, were used. Below 15°C, normal crawling could not be recorded accurately, while above 35°C, forward locomotion by crawling could not be induced. Beyond this temperature swimming movements replaced normal crawling. The accompanying tables will illustrate the results of these experiments.

The effects of temperature-change, upon the number of extensions is illustrated in Table I, column 2. It should be noted that, the number of extensions increases gradually as the temperature rises from 15°C, to 25°C, but that within the rise through the next 3°C, the number of extensions nearly doubles. In the last 7°C, increase in temperature there is a gradual increase in the number of extensions.

The average length of one extension through a temperature range of from 15°C, to 35°C, is shown in Table I, column 3. The average length of one extension increases as the temperature increases to 25°C. Further temperature increase results in a rapid decrease in the average length of extension.
The effect of temperature change upon the "rate" of locomotion in the leech is shown in Table I, column 4. The number of centimeters traveled per second increases as the temperature approaches 28° C., after which the speed of locomotion decreases.

Comparing these experiments on the leech with those on the earthworm I find that the two animals yield nearly the same results.

**TABLE I**

<table>
<thead>
<tr>
<th>Temperature °C.</th>
<th>Number of Extensions Per Second</th>
<th>Average Length of Extension in cm.</th>
<th>Centimeters Per Second</th>
</tr>
</thead>
<tbody>
<tr>
<td>15</td>
<td>.26</td>
<td>1.7</td>
<td>.442</td>
</tr>
<tr>
<td>18</td>
<td>.28</td>
<td>1.9</td>
<td>.532</td>
</tr>
<tr>
<td>20</td>
<td>.29</td>
<td>2.2</td>
<td>.638</td>
</tr>
<tr>
<td>22</td>
<td>.31</td>
<td>2.6</td>
<td>.806</td>
</tr>
<tr>
<td>25</td>
<td>.34</td>
<td>3.2</td>
<td>1.088</td>
</tr>
<tr>
<td>28</td>
<td>.51</td>
<td>2.4</td>
<td>1.224</td>
</tr>
<tr>
<td>30</td>
<td>.57</td>
<td>2.0</td>
<td>1.140</td>
</tr>
<tr>
<td>33</td>
<td>.60</td>
<td>1.8</td>
<td>1.080</td>
</tr>
<tr>
<td>35</td>
<td>.63</td>
<td>1.7</td>
<td>1.071</td>
</tr>
</tbody>
</table>

**B. UNDULATORY AND SWIMMING MOVEMENTS**

Undulatory movements are common to all leeches. In some these movements are more pronounced than in others. In Haemopis marmoratis (Say) this type of movement is frequently expressed. These movements have been variously described, as respiratory and excretory. So far as I have been able to determine no connection between these so-called "causal movements" and the movements themselves exists.

For convenience of reference I have differentiated between rhythmic movements which result in locomotion, designated, as swimming movements, and movements which occur while the leech is attached posteriorly, designated, as undulatory movements. These two expressions of behavior are fundamentally the same and differ in the rate of contraction depending on the type and intensity of the stimuli.
Either undulatory or swimming movements may be insti-
gated by any one of a variety or combination of stimuli. Those
environmental stimuli which proved most successful were:
changes in temperature; changes in dissolved oxygen and free
carbon-dioxide; mechanical, electrical and chemical changes.
Water currents (mechanical) also stimulated rhythmic move-
ments.

<table>
<thead>
<tr>
<th>Temperature °C</th>
<th>Number of Undulations in Swimming per min.</th>
<th>Number of Undulations while Attached per min.</th>
</tr>
</thead>
<tbody>
<tr>
<td>10</td>
<td>0</td>
<td>30</td>
</tr>
<tr>
<td>12.5</td>
<td>0</td>
<td>33</td>
</tr>
<tr>
<td>15</td>
<td>72</td>
<td>35</td>
</tr>
<tr>
<td>17.5</td>
<td>76</td>
<td>37</td>
</tr>
<tr>
<td>20</td>
<td>80</td>
<td>40</td>
</tr>
<tr>
<td>22.5</td>
<td>85</td>
<td>45</td>
</tr>
<tr>
<td>25</td>
<td>91</td>
<td>52</td>
</tr>
<tr>
<td>27.5</td>
<td>97</td>
<td>68</td>
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<td>30</td>
<td>104</td>
<td>86</td>
</tr>
<tr>
<td>32.5</td>
<td>115</td>
<td>0</td>
</tr>
<tr>
<td>35</td>
<td>130</td>
<td>0</td>
</tr>
<tr>
<td>37.5</td>
<td>175</td>
<td>0</td>
</tr>
</tbody>
</table>

Under experimental conditions it is possible to demonstrate
that the rate of undulation and swimming movements may be
controlled by regulating the temperature (see Table II). A
series of experiments in which the dissolved oxygen and free
carbon-dioxide content was varied (at a constant temperature
of 25° C.), clearly demonstrated that the rate of undulation is
not dependent upon the gaseous concentrations in the water
but that a change in concentration of dissolved oxygen or free
carbon-dioxide may initiate undulations. At low temperatures
(below 15° C.), undulatory movements predominate, while at
high temperatures (above 30° C.) swimming movements pre-
dominate. Temperature at these critical points is a direct
factor in determining the type of behavior expressed.
The leeches were placed in a large shallow container which was partly filled with water. This container was immersed in a water bath, the temperature being regulated from the outside. Leeches were first exposed to low temperatures and gradually to higher temperatures. Coordinated movements are replaced by spasmodic contractions as the temperature rises above 35° C.

Table II, gives a comparison of the undulatory and swimming rate at different temperatures. This series of tests employed a range in temperature of from 15° C., to the lethal temperature of 42° C.

CONCLUSIONS

A

1. As the temperature increases between 15° C., and 35° C., the number of forward extensions increases.
2. The average length of extension increases between 15° C., and 25° C., after which further increase in temperature results in a decrease in the length of extension.
3. The rate of crawl increases with a temperature increase to 28°C., beyond which the rate of crawl decreases.
4. Swimming movements replace crawling as the temperature is increased above 30° C.

B

1. The rate of undulation and contraction increases with the increase in temperature from 10° C., to 37.5° C.
2. Undulatory movements normally occur at lower temperatures than swimming movements.
3. Undulatory movements are replaced by swimming movements as the temperature is increased above 30° C.
4. Since either undulation or swimming may occur between 15° C., and 30° C., some, at present, unknown factor may determine which form of activity is expressed.

BIBLIOGRAPHY