Behavioral Plasticity in the Sensitive Plant, *Mimosa*

PHILIP B. APPLEWHITE

*Biology Department, Yale University, New Haven, Connecticut 06520*

The leaves of the sensitive plant *Mimosa* can adapt their closing response to electrical and mechanical stimulation so that they reopen to repeated stimulation. The more intense the stimuli and the longer the intertrial interval, the longer it takes to adapt. Leaves adapted to the effects of mechanical stimulation can still respond by closing to electrical stimulation and vice versa. The physiology of this phenomenon is discussed and compared to animals.

**INTRODUCTION**

Normally when touched or otherwise stimulated, the leaflets of the "sensitive plant," *Mimosa*, will close and the stem (petiole) will fall rapidly. It is virtually common knowledge that such plants adapt to constant stimulation by reopening since they can be seen open in the rain. Adaptation of the leaflets to repeated stimulation under laboratory conditions was mentioned in the literature in 1873 (Pfeffer). With the leaflets fully open, the initial stimuli produced closure but under constant repeated stimuli the leaflets eventually opened fully again and did not then close. A study in 1906 (Bose) dealt primarily with the petiole-falling response, where it was demonstrated that under constant electrical or mechanical stimulation, the petiole would first fall and then rise. It would not fall again under this constant rate of stimulation unless a suitable rest period was interspersed.

More recently, Holmes *et al.* (1965, 1966) have demonstrated adaptation to drops of water falling or light brush strokes on *Mimosa* so that the leaflets eventually open to repeated presentations at regular intervals. Initial attempts to classically condition this plant met with failure (Holmes *et al*., 1965, 1966). A report claiming conditioning (Haney, 1969) was not substantiated in a replication by Levy *et al.* (in press). Furthermore, we have shown (Applewhite and Gardner, 1971) that certain periods of light with the appropriate action spectrum, used as the CS in some conditioning experiments, will produce rapid leaflet closure whether or not this is paired with touch, the UCS. Therefore, the combination of light and touch stimuli can be quite inappropriate for conditioning *Mimosa*. In any case, *Mimosa* is an intriguing object of
study in plant behavior, and interesting comparisons between it and animals can be made in the area of adaptation to stimuli.

MATERIALS AND METHODS

*Mimosa pudica* was grown in soil from seed, raised in a greenhouse with a 16-hr light : 8-hr dark cycle under natural and fluorescent lighting. When the plants were 3 months old, they were changed to a 14-hr light : 10-hr dark cycle under incandescent lighting. Experiments were run when the plants were 11 months old, and between 4 hr after the beginning of, and 3 hr before the end of, the light cycle. From each plant, leaves (of the same size with 12 pinnules or leaflet pairs per leaf) were excised and floated in water, a standard procedure (Fondeville *et al.*, 1966) that does not damage the leaves, in a plastic petri dish. This petri dish was attached to a solenoid (activated by a Grass stimulator) which could be raised a constant height and then dropped. This stimulus was of constant intensity and was sufficient to close the leaflets. To promote opening, the leaves were illuminated with an incandescent light source of intensity 45 mW/cm²/sec for the entire experiment. Two different stimulus intensities were run; the petri dish was raised and dropped 0.4 cm (low intensity) or 0.7 cm (high intensity), with an intertrial interval of 2 sec. Within the first two stimuli, the leaflets closed and the stimuli were repeated until the leaflets opened again as judged by their tips touching the water for 10 sec. This tip-touching indicated that the leaves were fully open. At this point they were considered adapted to the stimuli. After various rest periods of the order of minutes, two more stimuli at 2-sec intervals were given to all leaves each time to determine the time necessary for recovery, i.e., closure, to occur. If one of the stimuli produced closure, it was considered recovered. Then, after allowing the leaflets to reopen, further stimuli of the same intensity and interval were given to readapt the leaflets to determine if the previous adaptation procedure now had any effect. At the low-intensity level, an intertrial interval between stimuli of 15 sec was used in addition to the 2-sec one. Here, two stimuli were also used at 2-sec intervals to test for recovery. After reopening, the same low intensity and 15-sec intervals were used to test for readaptation. For each intensity and intertrial interval combination, two leaves from 14 different plants were used; therefore, 28 different leaves, but from the same plants, were used in each column in Table 1.

If platinum electrodes are placed in the water on either side of the leaves, a current (9 V/cm, 100 msec) will cause the leaflets to close. This was the minimum adequate current to cause closure as determined by pilot studies. The mechanical high-intensity stimulus (dropping the petri dish) is given at intervals of 2 sec until adaptation occurs. At this point, the above closure current was given at intervals of 2 sec to see if the leaflets could also
adapt to a stimulus of another mode. Two leaves each from 14 plants were used here. This procedure was reversed but with two new leaves each from the 14 plants in that adaptation was obtained to continuous electrical stimulation (9 V/cm, 100-msec duration every 2 sec), and then the high-intensity mechanical stimulus at 2-sec intervals was given—an intensity known to produce closure.

A "dishabituation" stimulus was inserted toward the end of a series of low-intensity mechanical shocks to determine if this extra stimulus would prolong the time to reach adaptation. A more intense dishabituation stimulus, either mechanical or electrical, only serves to produce leaflet closure and consequently it must take longer for the leaves to adapt, that is to open, than if a dishabituation stimulus were absent. A better test was to use a lower intensity mechanical (petri dish raised 0.2 cm) or electrical dishabituation stimulus (6 V/cm, 100 msec) that did not produce closure of the leaflets at two different times in the adaptation process. For each of these four possibilities 28 new leaves as before were used. The leaves were presented with the low-intensity mechanical stimulus used above with the same intertrial interval of 2 sec. From previous experiments it was known it would take a mean time of 13 min for them to adapt (Table 1). After 5 or 10 min, one dishabituation stimulus was given, either mechanical or electrical, and then the previously given stimuli were resumed.

RESULTS AND DISCUSSION

In Table 1 are presented the results of adaptation to mechanical stimulation at two intensities and intertrial intervals. The number of minutes

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**TABLE 1**

Mechanical Stimuli Habituation

<table>
<thead>
<tr>
<th></th>
<th>Intertrial interval 2 sec</th>
<th>Intertrial interval 15 sec</th>
<th>Low intensity</th>
<th>High intensity</th>
<th>Low intensity</th>
</tr>
</thead>
<tbody>
<tr>
<td>Min of stimulation before opening</td>
<td>Mean</td>
<td>13</td>
<td>24</td>
<td>29</td>
<td></td>
</tr>
<tr>
<td></td>
<td>SD</td>
<td>4</td>
<td>6</td>
<td>5</td>
<td></td>
</tr>
<tr>
<td>Percentage of leaves closing after rest</td>
<td>5</td>
<td>12</td>
<td>0</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>of (min)</td>
<td>15</td>
<td>33</td>
<td>0</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td></td>
<td>25</td>
<td>100</td>
<td>50</td>
<td>64</td>
<td></td>
</tr>
<tr>
<td></td>
<td>40</td>
<td>–</td>
<td>100</td>
<td>100</td>
<td></td>
</tr>
<tr>
<td>Min of stimulation before opening repeat</td>
<td>Mean</td>
<td>11</td>
<td>21</td>
<td>32</td>
<td></td>
</tr>
<tr>
<td></td>
<td>SD</td>
<td>5</td>
<td>6</td>
<td>5</td>
<td></td>
</tr>
</tbody>
</table>
of stimulation before the leaves reopen is listed. After opening they were
given 5 min of rest; then, two mechanical stimuli of the same intensity of an
interval of 2 or 15 sec were given, and the percentage of leaves closing was
calculated. This procedure was repeated for subsequent time intervals until all
leaves closed. At this point, they were given repeat stimuli of the same
parameters they received initially and were adapted again. The results demon-
strate that after recovery (25-40 min depending on the parameters used) the
leaves can adapt again to the stimulus and the times necessary for this are not
significantly different from what they were when first adapted (P > 0.05
two-tailed Wilcoxon test). For statistical purposes, the average value for the
two leaves from the same plant was obtained. This was done to give a better
estimate of an entire plant's behavior rather than of just one excised leaf. It
takes significantly longer (P < 0.01 two-tailed Wilcoxon) to become adapted at
stronger intensities than weaker ones, and the adaptation lasts longer (up to
15 min longer). At this intertrial interval of 2 sec, the low-intensity shocked
leaves have all recovered after 25 min but the high-intensity ones required 40
min. Experiments with a variety of animals are in agreement with these
intensity effects (Applewhite and Morowitz, 1967; Pinsker et al., 1970).
Furthermore, with *Mimosa*, as with animals (Pinsker et al., 1970) it takes
longer to habituate as the intertrial interval becomes longer (P < 0.05 two-
tailed Wilcoxon) since it takes longer to deliver the stimuli. Although, as Table
1 indicates, it does take fewer total stimuli (116) at the longer intertrial
interval than at the shorter one (390) to produce the same amount of
adaptation. This agrees with animal studies with the cat (Thompson and
Spencer, 1966), *Aplysia* (Pinsker et al., 1970) and a crayfish neuromuscular
junction (Bruner et al., 1970). Another study with *Aplysia* utilizing a different
preparation (Peretz, 1970) found, however, that an equal number of stimuli
were needed at both long and short intertrial intervals to produce equal
adaptation. The results with *Mimosa* also indicate the leaflets remain adapted
more at longer rather than shorter intertrial intervals (Table 1) and this is in
agreement with adaptation of startle responses in rats (Davis, 1970).

It was found that *Mimosa* would close and adapt to a mechanical shock
immediately after being habituated to an electrical shock, as Table 2 indicates.
The reverse was true in that adaptation to a mechanical shock first could be
followed by adaptation to an electrical shock given second. There was no
significant difference (P > 0.05 two-tailed Wilcoxon) in the length of time it
takes to adapt to mechanical stimuli whether given first or second, and the
same applies to the electrical ones. The response is, therefore, stimulus
specific, as it can be for animals (Applewhite, 1971). The work of Holmes
(1965, 1966) suggested stimulus specificity of adaptation to water drops and a
light brush stroke. However, since brush strokes are administered by hand,
they are not of constant intensity and exact comparisons are not possible. If
there is stimulus specificity, the number of trials or time to adaptation for a
particular mode should be statistically the same whether it precedes or follows
adaptation to another mode. After becoming adapted to any strength electrical or mechanical stimulus, a more intense stimulus produces closure and suggests the leaflets are not fatigued; and that the closing response is somehow turned off. Further proof of this could come from the dishabituation experiments, but these were not successful. The less intense mechanical and electrical dishabituation stimuli had no effect ($P > 0.05$, Wilcoxon) upon the time to adapt (15 min with the mechanical and 12 min with the electrical dishabituation stimulus added) compared to controls receiving no dishabituation stimulus (13 min, Table 1). The conclusion must be that, so far, dishabituation cannot be demonstrated.

An interesting question remains and that is, is this adaptation response habituation? Habituation usually refers to a diminution of a response repeatedly produced by repeating stimuli. But in our procedure, the behavior is a diminution of a response (leaflet closing) that is produced only once, although the stimuli are repeated. If the leaflets were stimulated as described previously to produce closure and not stimulated again until fully open (about 8 min later) and this were repeated, habituation could be claimed if they eventually failed to close. However, we could never obtain this behavior. Holmes et al. (1965) claimed to obtain it but it appears his stimulus presentations were not constant. Given a slight decrease in stimulus intensity during the training trials, the leaflets would not close giving a mistaken impression that habituation was obtained. *Mimosa* certainly exhibits behavioral plasticity and in this shares many similarities with the protozoan *Spirostomum* and the flatworm *Stenostomum* (Applewhite, 1971), such as intensity, intertrial interval, and stimulus-specificity effects.

Physiologically, there may also be some important similarities. It is well known that the leaflet-closing response in *Mimosa* is due to changes that take place in the pulvinus (Weintraub, 1951), an easily identifiable structure at the base of each leaflet. Within this structure are motor cells with contractile vacuoles that expel liquid and it is believed that a sudden change in turgor pressure of these cells results in rapid movements (Sibaoka, 1969). The exact nature of these changes is unknown, but a general picture is beginning to

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**TABLE 2**

**Mechanical and Electrical Stimulation Compared**

<table>
<thead>
<tr>
<th>Min of stimulation before opening</th>
<th>Electrical (1st)</th>
<th>Mechanical (2nd)</th>
<th>Mechanical (1st)</th>
<th>Electrical (2nd)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean</td>
<td>9</td>
<td>26</td>
<td>22</td>
<td>10</td>
</tr>
<tr>
<td>SD</td>
<td>2</td>
<td>6</td>
<td>6</td>
<td>3</td>
</tr>
</tbody>
</table>
emerge. Indirect evidence suggests contractile proteins are present in the vacuole membranes and may be activated by an ATP-ATPase system, which in turn may be ion activated by the initial stimulus (Sibaoka, 1969). Large changes in potassium flow have been detected during rapid movement (Allen, 1969) and may be the important ion. For adaptation to occur, there must be a block somewhere in this chain of events. Without further evidence, the nature of this block is unknown. However, what is intriguing is that this suggested chain of events in Mimosa movement is so similar to that proposed for protozoan movement. In Spirostomum it is thought that ions activate an ATPase which affects contractile proteins in the myonemes causing contraction. Habituation in this protozoan (the failure to contract to repeated stimuli) is thought to occur because of changes in ion distribution which inactivate the ATPase and prevent contraction (Applewhite and Gardner, 1971). It would be interesting if habituation in Mimosa also took place at the level of ion flow. If so, the failure to produce dishabituation in Mimosa would not alter the basic ionic nature of the process. It was proposed that one ionic species undergoes diffusion to produce habituation, and a dishabituation stimulus only causes diffusion of a second ion. This increases the total time for diffusion of both ions and hence increases the time necessary for habituation (Applewhite and Gardner, 1971). As we learn more about the underlying biochemical processes of adaptation, we should be able then to state just how related all these behaviors are.

REFERENCES


