**Article Addendum**

**Plant electrical memory**

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Electrical signaling, short-term memory and rapid closure of the carnivorous plant *Dionaea muscipula* Ellis (Venus flytrap) have been attracting the attention of researchers since the XIX century. We found that the electrical stimulus between a midrib and a lobe closes the Venus flytrap upper leaf without mechanical stimulation of trigger hairs. The closing time of Venus flytrap by electrical stimulation is the same as mechanically induced closing. Transmission of a single electrical charge between a lobe and the midrib causes closure of the trap and induces an electrical signal propagating between both lobes and midrib. The Venus flytrap can accumulate small subthreshold charges, and when the threshold value is reached, the trap closes. Repeated application of smaller charges demonstrates the summation of stimuli. The cumulative character of electrical stimuli points to the existence of short-term electrical memory in the Venus flytrap.

Plants are capable of intelligent responses to complex environmental signals.1-27 Signaling and memory play fundamental roles in plant responses. The existence of different forms of plant memory is well known.1-22 Depending on the duration of memory retention, there are three types of memory in plants: sensory memory, short term memory and long term memory. A few examples of studies involving plant memory are: transgenic memory of stress,1,6,10 immunological memory of tobacco plants and moun-...
plant. Applying impulses in the same voltage range with different polarities for pulses of up to 100 s did not open the plant. It was found that energy for trap closure is generated by ATP hydrolysis. ATP is used by the motor cells for a fast transport of protons. The amount of ATP drops from 950 μM per midrib before mechanical stimulation to 650 μM per midrib after stimulation and closure. However, it is not clear if electrical stimulation triggers closing process in the motor cells, or contributes energy to the closing action.

The action potential delivers sufficient electrical charge to the midrib, which can activate the osmotic motor. To check this hypothesis, we measured effects of transmitted charge from the charged capacitors between the lobe and the midrib of Venus flytrap. Transmission of a single electrical charge (mean 13.63 μC, median 14.00 μC, std. dev. 1.51 μC, n = 41) causes trap closure and induces an electrical signal propagating between the lobes and the midrib. The electrical signal in the lobes was not an action potential, because its amplitude depended on the applied voltage from the charged capacitor. Charge induced closing of a trap plant can be repeated 2–3 times on the same Venus flytrap plant after reopening. Transmission of a single electrical charge (mean 13.63 μC, median 14.00 μC, std. dev. 1.51 μC, n = 41) causes the trap to close and induces an electrical signal that propagates between the lobe and the midrib. Figure 1 illustrates that the Venus flytrap can accumulate small charges, and when the threshold value is reached, the trap closes. A summation of stimuli is demonstrated through the repetitive application of smaller charges. If we apply two or more consecutive injections of electrical charge within a period of less than 50 s, the trap will close when a total of 14 μC charge is reached.

Repeated application of smaller charges demonstrates a summation of stimuli. If we apply two or more injections of electrical charges within a period of less than 20 s, the Venus flytrap upper leaf closes as soon as the total of 14 μC charge is transmitted. Similar phenomenon was reported by Czaja, who determined the intensity of threshold stimuli to be 2.4 μC for a closing electrostimulation of another carnivorous plant Aldrovanda vesiculosa, and 0.91 μC for an opening electrostimulation. Our attempts to open the Venus flytrap upper leaf by changing polarity of injected charge and increasing the charge from 14 μC to 100 μC were not successful. Usually, the trap opens a few days after closing in the same way as after mechanically stimulated closing.

Previous work by Brown and Sharp indicated that electrical shock between lower and upper leaves can cause the Venus flytrap to close, but in their article, the amplitude and polarity of applied voltage, charge and electrical current were not reported. The trap did not close when we applied the same electrostimulation between the upper and lower leaves as we applied between a midrib and a lobe, even when the injected charge was increased from 14 μC to 750 μC. It is probable that the electroshock induced by Brown and Sharp had a very high voltage or electrical current.

It is common knowledge that the leaves of the Venus flytrap actively employ turgor pressure and hydrodynamic flow for fast movement and catching insects. In these processes the upper and lower surfaces of the leaf behave quite differently. During the trap closing, the loss of turgor by parenchyma lying beneath the upper epidermis, accompanied by the active expansion of the tissues of the lower layers of parenchyma near the under epidermis, closes the trap. The cells on the inner face of the trap jettison their cargo of water, shrink and allow the trap lobe to fold over. The cells of the lower epidermis expand rapidly, folding the trap lobe over. These anatomical features constitute the basis of the new hydroelastic curvature model.

In terms of electrophysiology, Venus flytrap responses can be considered in three stages: (i) stimulus perception, (ii) signal transmission and (iii) induction of response (Fig. 1).

**References**


**Figure 1.** Mechanism of the Dionaea trap closure.
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