



Figure 12. Venus flytrap captures insects through an electrical process. The plant's lobes are covered with trigger hairs. If an insect steps on two hairs or the same hair twice, a cellular action potential is generated. The action potential triggers a mechanical system that causes the lobes to close on the insect, which is then digested.

lower than normal, the current decreases. The channel apparently needs calcium to open, but too much calcium causes it to close. No one knows how a high calcium concentration inhibits the channel.

The reversal potential of the calcium-activated chloride current depends on the chloride concentration as predicted by the Nernst potential for this ion. Moreover, the channel is voltage-dependent. In other words, the channel will open only at specific plasma-membrane potentials. In a simple form, a voltage-dependent channel could be created from a membrane-bound molecule with a large dipole moment, one end positive and the other negative. The positive end would swing toward the negative side of the membrane, and this movement could place the molecule across an opening in the membrane, closing the channel. If the potential across the membrane were to switch,

the molecule would swing around, which might uncover or open the channel. The calcium-activated chloride channel opens when the membrane is depolarized to potentials less than -160 millivolts. This reveals that a membrane depolarization, such as a receptor potential, is necessary to open the calcium-activated chloride channel, but depolarization is not enough. Current will flow through the channel only if the membrane is sufficiently depolarized and if both calcium and chloride are present.

Inside Action

As I mentioned earlier, a characean cell has three compartments that bathe the two excitable membranes: the plasma membrane and the vacuolar membrane. An animal cell has only one membrane, and this makes an axon much simpler than a characean cell. An axon is geometrically similar to an electrical cable, and thus cable theory can be easily applied to such a

system. This is the reason that Cole and Curtis began studying the squid axon rather than continuing with characean cells. The vacuolar membrane of a characean cell adds a second component to the action potential.

At rest, the vacuolar membrane potential is about -10 millivolts. In this case, the membrane is negative outside the vacuole, which is the reverse of the plasma membrane. During an action potential, the vacuolar membrane hyperpolarizes (becomes more negative outside the vacuole) to about -50 millivolts. The average Nernst potentials at the vacuolar membrane are 121 millivolts for calcium, -51 millivolts for chloride, 49 millivolts for sodium and -2 millivolts for potassium. These numbers indicate that chloride is the only ion capable of carrying the vacuolar membrane potential to -50 millivolts. Chloride moves out of the vacuole to make the membrane potential more negative.

In a characean cell, the plasma membrane and the vacuolar membrane interact. The vacuolar membrane, however, can be studied separately by making the plasma membrane permeable to all ions—essentially, by making it disappear. This is done by placing a cell in a calcium-free solution that contains EGTA (ethyleneglycol-bis-tetraacetic acid)—a calcium chelator—and is at 4 degrees Celsius. This treatment stops protoplasmic streaming because ATP escapes from the cell. Streaming can be reactivated by adding ATP to the bathing solution.

In a so-called plasma-membrane-permeabilized cell, a vacuolar-membrane action potential can be initiated by increasing the calcium concentration of the bathing solution from zero to one micromolar. If the chloride concentration is increased in the protoplasm, the calcium-induced action potential decreases as predicted by the Nernst equation, if chloride is assumed to be the only current-carrying ion. Anthracene-9-carboxylic acid, a chloride-channel blocker, completely eliminates the potential. Minehiro Kikuyama of the University of the Air in Japan measured the movement of chloride from the vacuole to the protoplasm and found that an increase in protoplasmic calcium creates an increase in chloride moving out of the vacuole. If the fluid in the vacuole is replaced with a chloride-free solution, there is no increase in protoplasmic chloride, indicating that the chloride does come from the vacuole.

In intact cells, the vacuolar mem-

brane's action potential develops only after the plasma membrane has been excited. This indicates that some mechanism couples the plasma membrane's action potential to the vacuolar membrane's action potential. Calcium is assumed to be the coupling agent for several reasons. First, a characean action potential increases the concentration of calcium in the protoplasm. Second, removing calcium from a cell's external solution does not affect the plasma membrane's action potential (as long as the calcium is replaced with a similar ion, such as barium), but this does inhibit the vacuolar membrane's action potential. And finally, a microinjection of calcium into the protoplasm generates an action potential in the vacuolar membrane.

It is now possible to describe the fundamental steps in a characean action potential (*Figure 11*). An external stimulus causes a depolarization of the plasma membrane (a receptor potential). The receptor potential arises from the movement of calcium through the plasma membrane and into the protoplasm. If enough calcium moves into the proto-

plasm, it depolarizes the plasma membrane enough to open the calcium-activated chloride channels, generating additional depolarization as chloride passes out through the plasma membrane. The calcium diffuses across the five to 20 microns of protoplasm to the vacuolar membrane at a speed of about one micron per second. At the vacuolar membrane, the calcium activates chloride channels on the membrane, allowing chloride to move from the vacuole into the protoplasm, which hyperpolarizes the second membrane. The plasma membrane's action potential ends as potassium leaves the protoplasm, and the vacuolar membrane's action potential ends as potassium moves from the vacuole to the protoplasm.

Other Excitable Plants

Other plants employ electrical signals to elicit behaviors and physiological processes. Although the mechanistic explanations for many plant responses have only recently emerged, the responses themselves have been known for some time. Charles Darwin, among

others, noted that many plants respond to mechanical stimulation. Darwin became interested in carnivorous plants such as the Venus flytrap, which he called "one of the most wonderful in the world," and he was the first to show that the plant digests captured insects.

At rest, the lobes of a Venus flytrap sit passively open. Each lobe secretes a type of nectar that attracts insects, and so-called trigger hairs are embedded in the inner surface of each lobe. If an insect steps on a lobe and either hits two trigger hairs or hits the same hair twice, the mechanical stimulation generates an action potential, and the lobes close, capturing the insect.

The sundew gets its name from its appearance. This plant shines as if coated with dewdrops because it is covered with sticky hairs that can capture insects. Once an insect is captured, it begins to struggle, and the mechanical stimulation to the plant induces action potentials that cause the hair to wrap around the insect. Neighboring hair cells also produce action potentials, and they, too, wrap around the insect, thus



Figure 13. Sundew entangles insects in the plant's sticky hairs, which adhere to an insect's feet. When the insect tries to escape, the mechanical stimulus to the plant generates an action potential that causes the hair to wrap around the insect. Neighboring hairs also produce action potentials, and these hairs, too, wrap around the insect. Secretory cells then release enzymes that digest the insect.



Figure 14. *Mimosa pudica* plays possum when touched. Normally, this plant stands upright (top). But when the plant is touched, an action potential causes the touched leaves and stems to droop and appear dead. The first action potential triggers action potentials in other parts of the plant, and these stems and leaves also droop; soon the entire plant appears to be dead (bottom).

providing a secure trap. Then nearby secretory cells exude enzymes, forming a little stomach that digests the insect.

One of the best-known examples of plant behavior comes from *Mimosa pudica*, often called the sensitive plant. When the leaves of the plant are touched, they bend over and appear dead. The drooping arises from a mechanically driven action potential. Moreover, an action potential propagates from the stimulated region throughout the plant. This causes drooping in the rest of the plant, a defense mechanism apparently designed to make the whole plant look unappealing.

Not all plant action potentials, however, cause obvious responses. In *Luffa*—the plant whose gourd or fruit is used for “loofah” sponges—action potentials cause a transient inhibition of growth. And in a variety of flowers, pollen landing on the stigma generates an action potential, which may be involved in subsequent pollination or the maturation process. In tomato seedlings, a mechanical wound induces electrical activity that causes the accumulation of proteins that limit further damage to the plant.

Electrical phenomena control many responses in plants. In a characean alga, we understand many of the details of the mechanism that leads from a duck’s nip on the plant to the cessation of protoplasmic streaming. But we are just beginning to address the similarities between the electrical excitability in characean algae and higher plants, let alone animals. In any case, it is apparent that plants can perform long-distance communication through electrical signals, such as the passing of information from a mechanical stimulus from one *Mimosa* stem to another. Many biologists continue to describe electrical excitability as part of the animal world. In the future, we should think of plants as excitable too.

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