Touch Receptor of Venus Flytrap, Dionaea muscipula

Abstract. *Numerous small structures (stellate trichomes) protrude from the surface of marginal hairs, outer leaf surface, and stem of* Dionaea muscipula Ellis. *None are present inside the trap. Mechanical stimulation causes small action potentials and eventual closure of the trap, independently of the sensitive trigger hairs. Subthreshold stimulation of these structures appears to sensitize the trigger hairs and facilitate closure of the trap. This suggests that these structures act as touch sensors or receptors.*

Triggering of the leaf trap of *Dionaea muscipula* Ellis is apparently caused by displacement of sensitive large hairs on the inner surface of the leaf (*1*). There are three such hairs (sometimes double) on each leaf blade, and movement of any one of them causes a characteristic action potential (*2*). Continuous repetitive electrical activity and leaf closure, resembling spontaneous rhythm in the heart, may also be elicited by instillation of hypertonic solution (3 percent saline, for example) into the trap (*3*). Rough handling of the leaf without touching trigger hairs, heat, electricity, or other noxious stimuli also cause closure, but this has been ascribed simply to injury. Recently, however, we have observed that numerous small structures, described as stellate trichomes by Lloyd (*1*), which might serve as touch receptors, are present on the marginal hairs and the outer surface of the leaf; they are less numerous on the petiole or stem. None of these structures are present on the inner surface of the trap. Insects are attracted to them, and they are undoubtedly touched frequently, as they protrude above the surface of the leaf. This report describes these structures in some detail and attempts to establish their receptor function.

When these structures are examined at a magnification of 100, they resemble small rosettes. There are generally eight hair-like petals of noncellular, translucent material radiating from a central spindle; the overall diameter is about 80 microns. The central spindle is roughly egg-shaped and consists of eight cells which are radially arranged like staves in a barrel and whose longitudinal axis is horizontal to the flat plane of the rosette. Petals of the rosette can curl upward and close over the central spindle, resembling a flower bud. Drying in a resected leaf is particularly apt to cause this upfolding. However, the rosette always appears open in the natural state, and the function of this curling movement is unknown. The microscopic appearance is shown in Fig. 1. Spindle cells have small nuclei which stain deep purple, and the cytoplasm is packed with brown-stained refractile granules.

Action potentials which presumably arise from these peculiar structures were demonstrated by the following procedure. The leaf trap was arranged for the recording of its surface potentials as previously described (*2*), and a small loop of steel wire (diameter, 5 mil) was stroked gently across the outer surface of the trap. Generally eight to ten such stimuli were required to elicit the first potential, after which a small nonpropagated potential arose after each stroke (Fig. 2). These potentials are considered to be nonpropagated because of their small amplitude and characteristic contour. They have been described recently, and apparently they can also arise by subthreshold stimulation of the trigger hair (*4*). One or two of the potentials were larger; these were probably propagated, and after five or six such potentials the leaf trap contracted. Stroking the inner surface of the leaf trap in a similar manner, provided trigger hairs were avoided, neither elicited the potentials nor closed the trap.

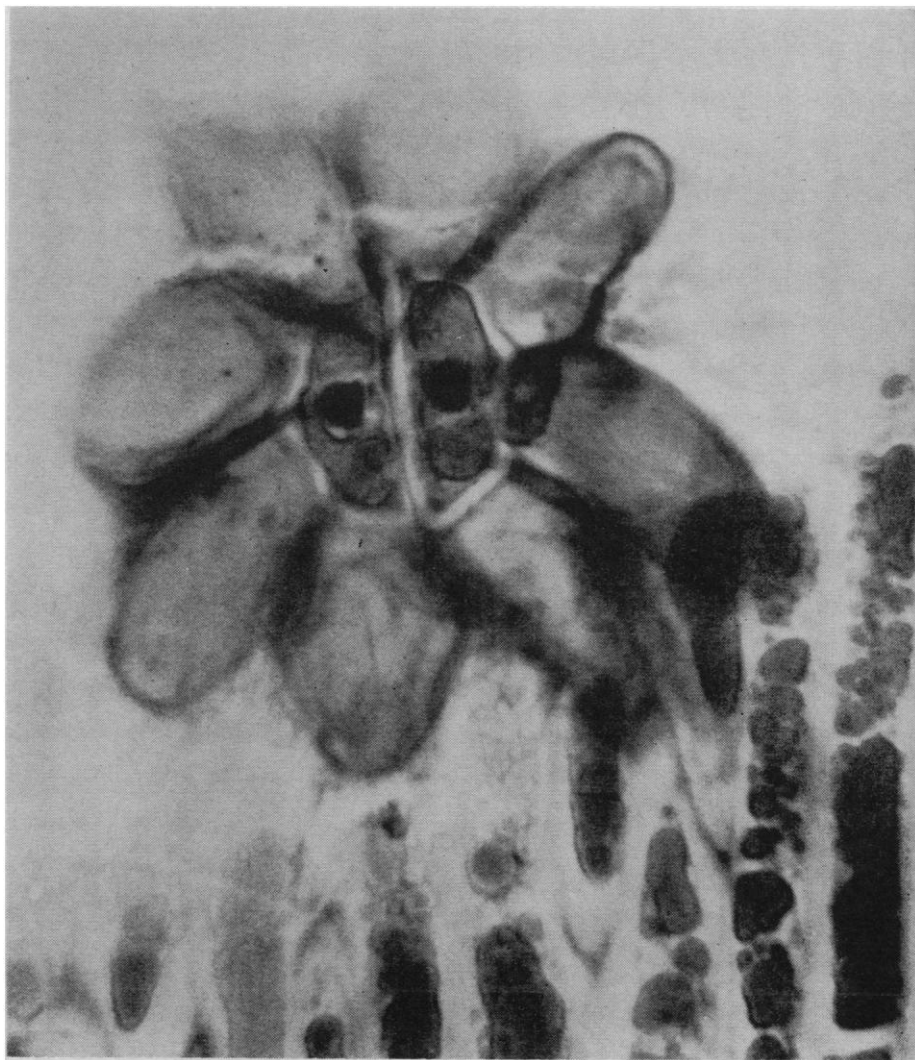The following experiment was performed to establish some functional purpose for the presumed receptors.

Fig. 1. Microscopic cross section of a touch receptor (stellate trichome) of *Dionaea muscipula*. Hematoxylin and eosin stain; × 400. The receptor has been displaced from its normal attachment by the microtome knife. Cells at the bottom are representative of the inner surface of the leaf trap.

Table 1. Results of 720 observations of the number of deflections of the trigger hair of *Dionaea muscipula* in order to cause closure, dependent upon locations and prior conditioning. Results are averages ± standard error.

Location of stimulus	Number of stimuli causing closure of trap		P
	Conditioned	Unconditioned	
Marginal hair	1.4 ± 0.14	2.0 ± 0.10	<.001
Outside trap	1.6 ± .11	2.1 ± .10	<.001
Stem	1.8 ± .08	2.2 ± .10	<.05
Inside trap	1.9 ± .15	1.8 ± .10	>.7

Twenty-five pods of adult *D. muscipula* were maintained in a greenhouse near Philadelphia from May to September. The plants were grown in sphagnum moss, in about 50 percent shade and with a relative humidity of at least 50 percent. The temperature in the greenhouse was the same as that outside. Fertilizer or other feeding was not given. Plants maintained in this way grew rapidly; they were vigorous and very sensitive. Daily, in the morning, each leaf trap was stroked either on the marginal hair, the outside surface of the trap, the stem, or the inside surface of the trap with a moderately stiff-bristle brush 4 mm in diameter. An attempt was made to apply approximately the same pressure and motion in each instance. Traps that were treated by this method were termed conditioned. A similar number of traps in which no stroking was applied served as unconditioned controls. Within 1 minute after stroking with the brush, the sensitive trigger hair of the inner leaf was deflected as many times as was necessary to cause trap closure. On the average, it required two deflections of the sensitive trigger hair to

cause closure (2). Results shown in Table 1 indicate that conditioning causes the trigger hair to become more sensitive because of the fewer deflections required to effect closure. This was especially true for conditioning of the marginal hair and the outer leaf trap, where numerous receptors exist. A questionable effect was obtained for the stem, where there are few receptors, while stroking the inner trap, where none are present, had no effect. Because the stellate trichomes protrude prominently from the surface of the leaf, they would naturally be the structures most disturbed by the brush stroke. No other specialized structures are present on the leaf except the stomata cells, and these are flush with the surface (5). It is possible that the brush stroke actually stimulated the surface epidermal cells, but this is unlikely because the inner surface of the trap, which does not contain the stellate trichomes, is not sensitive to this stimulus. Although the function of these structures is definitely secretory in some plants, their actual purpose in others has been a matter of conjecture (5). Our results suggest that they may serve as touch sensors and that in some manner they are capable of causing a change in the internal environment of the leaf trap, which renders it more susceptible to closure by deflection of the trigger hair. Pathways of nervous conduction have not been described in leaves, but it has been suggested that the veins and tracheids might subserve this purpose (5). Proof of the stellate trichome's function might be secured by individual stimulation with a microelectrode. This has been attempted but thus far has been inconclusive because of technical difficulties. A mechanism of touch interpretation would have obvious utility for the plant. Certainly it would increase the probability of insect cap-

ture and might also serve as a protective device against the mechanical trauma of other predators.

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References and Notes

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Arterial Constrictor Response in a Diving Mammal

Abstract. Angiograms were obtained in the harbor seal, Phoca vitulina, *in air and during diving. During diving there is arterial constriction of the vascular beds of muscle, skin, kidney, liver, spleen, and presumably of all vascular beds except those perfusing the brain and heart. There is sudden constriction and narrowing of muscular arteries close to their origin from the aorta. Constriction of small arterial branches is so intense that blood flow is essentially lost in all involved organs.*

The ability of certain aquatic mammals to dive for extended periods in the absence of external oxygen supply is of great interest to biologists. A number of adaptations have been described which presumably permit prolonged diving. Of these, diving bradycardia is historically the first to be described (1) and has received the greatest attention. This emphasis on bradycardia may in large measure be based on the relative ease of its demonstration in the laboratory or field. A priori, it is difficult to visualize the functional basis by which bradycardia operates to permit prolonged diving. Recent work has shown that diving bradycardia is accompanied by a fall in cardiac output (2). However, the precise role that this decreased cardiac output plays in permitting prolonged diving is obscure.

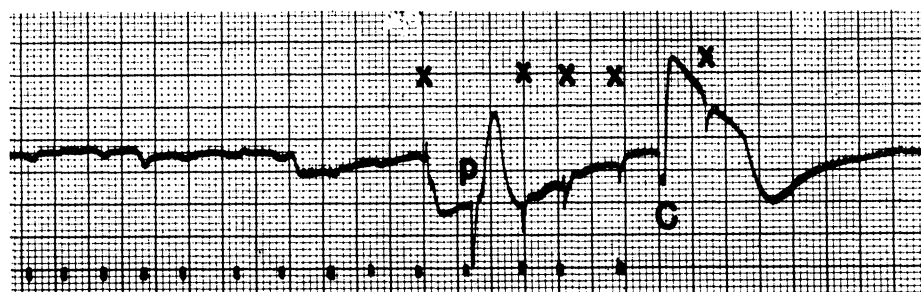Another adaptation which has been described is the development of arterial

Fig. 2. Action potentials from the leaf trap of *Dionaea muscipula*. Ordinate, dark lines equal 5 millivolts; abscissa, dark lines, 0.2 second. At each dot the outer leaf blade was stroked with a fine wire; at the crosses, a small potential was presumed to arise from the touch receptors. *P* represents a propagated potential, and at *C* the leaf closed. Oscillations prior to the first small potential are movement artifacts.