

### Springing the trap

Charles Darwin is known the world over as the founder (along with A R Wallace) of modern evolutionary biology. But he wrote a great many books besides *The Origin of Species*, and all of them illuminate the astonishing ways in which evolution works. In one of those books, *Insectivorous Plants*, Darwin examined plants that ate animals – in contrast to the usual situation, which is the other way round. Carnivorous plants seem to violate another of nature's rules: some of them possess the property of thigmonasty or touch-induced movement. Because they display the behaviour without nerves or muscles (though they are not unique in this; see Bonner 1994), carnivorous and sensitive plants, like the familiar *Mimosa pudica* (touch-me-not), raise the question of where to draw the boundary between plants and animals.

Among the carnivorous plants that he was familiar with, Darwin (1875; see van Wyhe 2005) thought that “. . . Venus's fly-trap, from the rapidity and force of its movements, is one of the most wonderful . . .”. This plant, *Dionaea muscipula*, has been found in only one location in the world, namely marshy soil in the eastern part of North Carolina, USA. It has a pair of modified leaves attached as lobes to a single foliaceous stalk. Two to four filaments are present on the upper surface of each leaf. The leaf margins are extended in the form of spikes. At rest, the leaves are open and resemble a pair of open palms held side by side. When a fly or other small insect lands on one of the leaves, a hair-trigger response is elicited. In Darwin's words, “As soon as a filament is touched, both lobes close with astonishing quickness; and as they stand at less than a right angle to each other, they have a good chance of catching any intruder.” The pair of leaves snaps shut in a fraction of a second and entraps the insect, which is eventually digested. About the marginal spikes, Darwin says that they “. . . at first seemed to me in my ignorance useless appendages”; but later, he saw that the space left between the intercrossing spikes, after the leaves had closed, might allow tiny, and therefore uninteresting, insects to escape: “. . . and one of my sons actually saw a small insect thus escaping”.

The mechanism by which the leaves close so rapidly was a long puzzle. The time taken for closure, about 100 ms (compare this with an average eye blink of 250 ms), makes it one of the fastest intentional movements observed in plants. By painting the surface with dots, Darwin was able to prove that during the process of closing, the superficial layer of cells of the leaf contracted over the whole upper surface. In an elegant study published recently (Forterre *et al* 2005), a group of scientists led by L Mahadevan of Harvard University have combined an experimental and theoretical study of the post-stimulation aspects of leaf closure and come up with a plausible model for what makes the leaves close. The explanation is that the leaves actively control a buckling instability qualitatively similar to the way that a tin lid or contact lens buckles when pressed.

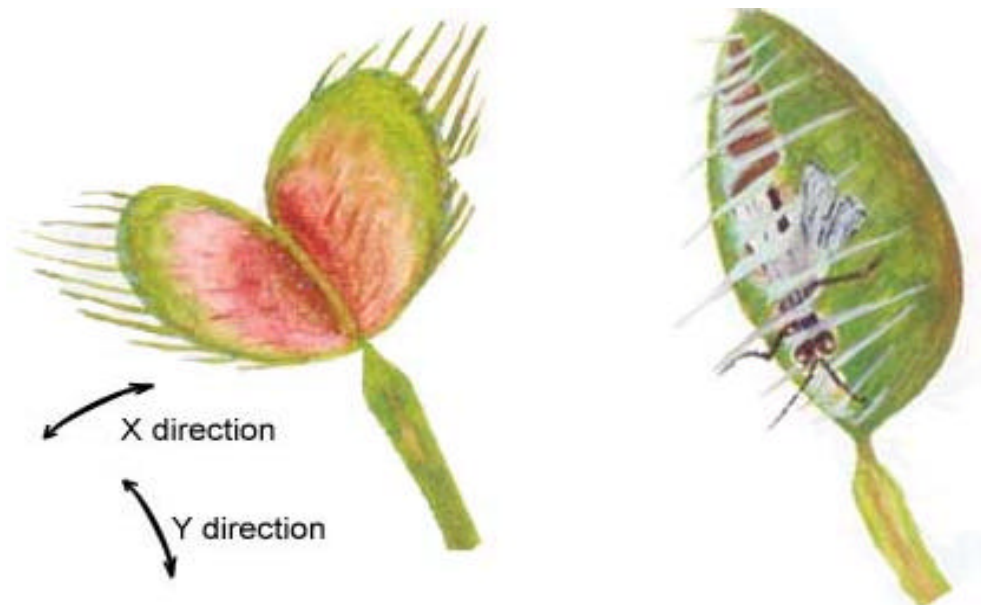
Translating microscopic motions into macroscopic displacement is a common task in mechanical design. This problem is faced in different contexts by nature and engineering design. Nature's solutions often follow from the addition of motions serially and by magnification through levers. For example, limb movement results from the microscopic relative movement of actin and myosin protein filaments that are arranged in series to increase the amount of motion, and in parallel to increase the force, along with the lever arrangement at the joints. In engineering practice, apart from levers, linkages and gears are used to amplify the motion. For example, in an automobile the motion of the piston in an engine is transformed and amplified about 100-fold through gears, thereby causing the wheels to rotate.

Another factor that affects the performance of any such displacement generating device is the speed with which the motion is achieved. This speed is decided by natural frequency and the effective

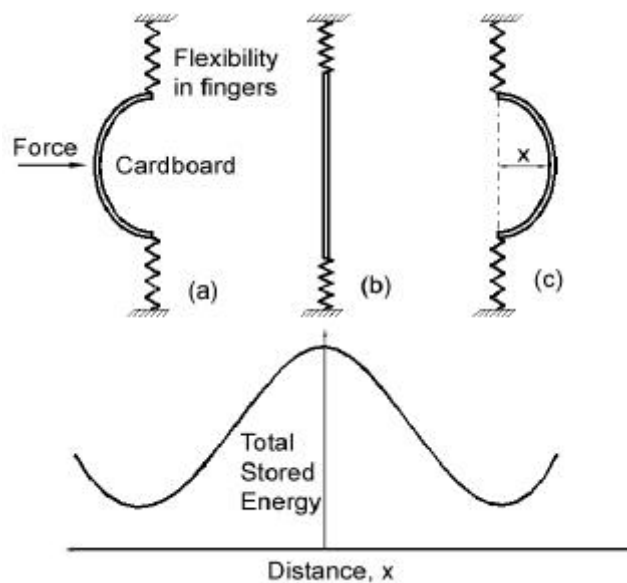
damping of the system. The natural frequency, given by the square root of the ratio of the effective stiffness to effective mass, can also be thought of as the ratio of an elastic factor to an inertia factor. So, to achieve rapid movement, the elastic factor has to be larger than the inertial factor. Enhanced amplification of motion usually means a more complicated mechanism. In general, this increases the effective mass of the system and hence the inertia, and brings down the speed of the actuation for a given energy release rate.

Forterre *et al* (2005) found that the leaf geometry of the Venus flytrap plays a crucial role in the rapid closure of the leaf. The underlying microscopic actuation could be acid-induced wall loosening or a rapid loss of turgor pressure. This alone does not explain the rapidity with which the trap closes. For example, in *M. pudica*, it takes about a second for the leaves to move through 40 degrees (Chua *et al* 2003), even though the same microscopic mechanism seems to be at work. By studying the geometry of snapping of the Venus flytrap, Forterre *et al* concluded that the doubly-curved nature of the leaf leads to the rapidity of the closure. The leaf in open condition is curved outward (convex) and its curvature inward (concave) in the closed condition. However the leaf is also slightly curved in the perpendicular mid-rib direction (y-direction) just like a horse saddle (figure 1). In the closed condition, it turns out that the leaf assumes an ellipsoidal shape. This means that the curvature in the x-direction changes from convex to concave while the other curvature remains constant.

This geometry enables the plant to utilize a bistable mechanism for a fast macro-displacement with minimal energy costs. Bistable mechanisms are used widely in engineering—from the ordinary electrical switch to the snap-shut caps of shampoo bottles. As the name indicates, a bistable device has two stable equilibrium states of low energy separated by an intermediate state of higher energy. A card held between two fingers as shown in the figure 2a is an example of a simple bistable mechanism. When a slight force is applied at the center of the card, it will flip as in figure 2b. Any intermediate position of the card will have higher energy since the springs will be in a compressed state. The leaf of the Venus fly trap exemplifies a compliant bistable mechanism.



**Figure 1.** Artistic impression of the leaf of the Venus fly trap. The leaf is normally convex along the 'x' direction. While snapping the trap this changes to concave. There is no change in curvature along the 'y' direction.



**Figure 2.** A cardboard held slightly curved like a 'C' between two fingers is a bi-stable mechanism (a). When a small force is applied in the direction shown by the arrow, it will flip into the other stable position (c). Any intermediate position (b) will have a higher energy and hence is unstable. The leaf of the Venus fly trap also changes shape in a similar way while springing the trap. The force is generated by the cells on the leaves due to acid-induced wall loosening or a rapid loss of turgor pressure.

From purely natural frequency considerations, the time-scale of switching is of the order of 0.001 s. Forterre *et al* found that the measured speed at which the leaves closed depended on a dimensionless geometric parameter

$$\mathbf{a} = \frac{L^4 K^2}{h^2},$$

where  $L$  is the size of the leaf,  $K$  its mean curvature and  $h$  the thickness of the leaf. Typically,  $L = 1$  cm,  $K = 0.1$  cm<sup>-1</sup> and  $h = 0.1$  cm giving  $\mathbf{a} = 1$ . The observed timescale of motion for the leaf is about 0.1 to 1 s. In fact, it is the internal damping provided by the flow of the interstitial water through the surrounding elastic tissues that dictates the actual speed.

Forterre *et al* measured the displacement of different points on the leaf as it closes with the help of high speed video cameras. To obtain three-dimensional information, they recorded stereoscopic images from different angles using a pair of mirrors. With these measurements, they identified two distinct pieces in the puzzle of trap snapping: an inferred active biochemical component and a passive elastic component. Upon stimulation, the plant 'actively' changes its curvature, the biochemical and microscopic mechanism for which remains poorly understood. Once this change occurs, the geometry of the doubly-curved leaf provides the mechanism by which elastic energy is both stored and released, and the hydrated nature of the leaf induces the rapid damping that is equally crucial for efficient prey capture.

**References**

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