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Fast Motion of Plants: from Biomechanics to Biomimetics

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Abstract

The Venus flytrap (*Dionaea*) can capture insects by perceiving more than one consecutive touches, with closure motion occurring within a fraction of a second, a speed that is among the fastest in the plant kingdom. The fast motion of plants such as *Dionaea*, *Aldrovanda* (waterwheel plants) and *Utricularia* (bladderworts) represent fascinating examples in nature where physics, biochemistry, and engineering principles work together to fulfill biological functions. A more comprehensive understanding of these carnivorous behaviors in plants can be achieved with the joint efforts by researchers from biology, physics, chemistry, mathematics and engineering. Moreover, the principles learnt from these natural systems can be employed to develop bio-inspired structures and devices with a variety of engineering applications.

Introduction

Plants are traditionally perceived as immobile species, or at most, slow movers, and in the meantime, being harmless, or at best, protective. This may well explain the long-lasting fascination with carnivorous plants (i.e., plants that eat insects), and particularly those plants that feature fast movements to trap the preys. A typical, or perhaps the most exotic example, is the Venus flytrap (*Dionaea*), which can close its trap in less than 0.1s to capture insects for nutrients. The Venus flytrap was first discovered by Arthur Dobbs, Governor of North Carolina (1754-1765), who considered it the great wonder of the vegetable kingdom. Almost a century later, Darwin (1875) enthusiastically investigated the mechanisms involved in the Venus flytrap's fast motions, and called it "one of the most wonderful plants in the world".

The mechano-sensation, actuation and movements in plants have since become rich sources from which biomimetic design principles can be learned. In this article, we summarize a selected number of recent studies on mechanics of plants' fast movements, and then discuss the development of biomimetic design principles. A vast literature exists in these relevant problems. To gain a more comprehensive understanding on mechanics without muscles, readers are encouraged to refer to some excellent review articles (Ueda and Nakamura, 2006; Fratl and Barth, 2009; Ellison and Gotelli, 2009; Martone, 2010; Joyeux, 2011; Scorza and Dornelas, 2011; Dumais and Forterre, 2012). Here we choose to focus on a selected set of interesting phenomena, and hope to stimulate further studies of plant movements in these and other systems which will promote the development of bio-inspired technology with a wide spectrum of applications in engineering. Specifically, we first focus on the fast motion of *Dionaea* by discussing the biological structures, mechanics, electrophysiology and dynamics involved, and then compare the similarity and differences between different snapping species, *Dionaea*, *Aldrovanda* and *Utricularia*. Afterwards, we review the recent development in designing biomimetic structures using the design principles leant from these natural systems. Finally, we give perspectives and concluding remarks, and hope that a more comprehensive understanding of these interesting phenomena can continue to attract the attention from the scientific community, hopefully with joint efforts from researchers in different disciplines such as biology, physics, mathematics and engineering.

Fast Motion of Plants

The biological structures of Venus flytrap

When the Venus flytrap is cultivated successfully, its most spectacular feature is the modified leaves, each of which are comprised of two lobes, like a clam shell in a way (especially so when the trap is closed). The leaves of *Dionaea muscipula* are the protagonists of the hunting process because the special structural features: the “shell-like” appearance (Figure 1) of pairs of symmetrical leaves, three (or more) trigger hairs on the inner surface of each lobe, and a number of interlocking teeth (Figure 1) along the margin of leaves. The maximum length of *Dionaea muscipula* leaves is typically a few centimeters to ensure the traps are capable of catching various types of insects. It can be inferred that this size results from adaptation to the living environments, because the force of smaller traps will be too weak to catch most types of insects, and that preys can easily escape from the trap if the size of leaves are too big to keep them in captivity. The interlocking teeth play a role of letting go small, unworthy preys, suggesting that the Venus flytrap is not an unmerciful plant (Darwin, 1875).

In the structures of *Dionaea muscipula*, the most sensitive part is located in the two or three hairs on the inner surface of the leaf. If one of those hairs are touched by a certain external force, for example touches from insects or fingers, the plant does not move, but a consecutive touch on the same hair or a different hair within a window of 30 seconds, the trap will quick close by changing the shapes of the lobes from convex to concave. This shows that *Dionaea* has a short term “memory”, the mechanism of which will be discussed later. This mechanism also ensures that the Venus flytrap will not waste energy in capturing unworthy food, like a randomly fallen thing that touches the sensitive hair only once. In addition, there are also touch receptors (DiPalma, 1966) that can result in the closure of the Venus flytrap, and the sources of stimuli can include heat, electricity, toxic air, and so on. Nevertheless, these situations have been usually treated as damages. Interestingly, experiments have shown that there are effective touch receptors that stay on the outer surface of the leaf in *Dionaea muscipula*. Action potentials can be generated when these receptors are triggered, and less number of touches on the sensitive hairs (less

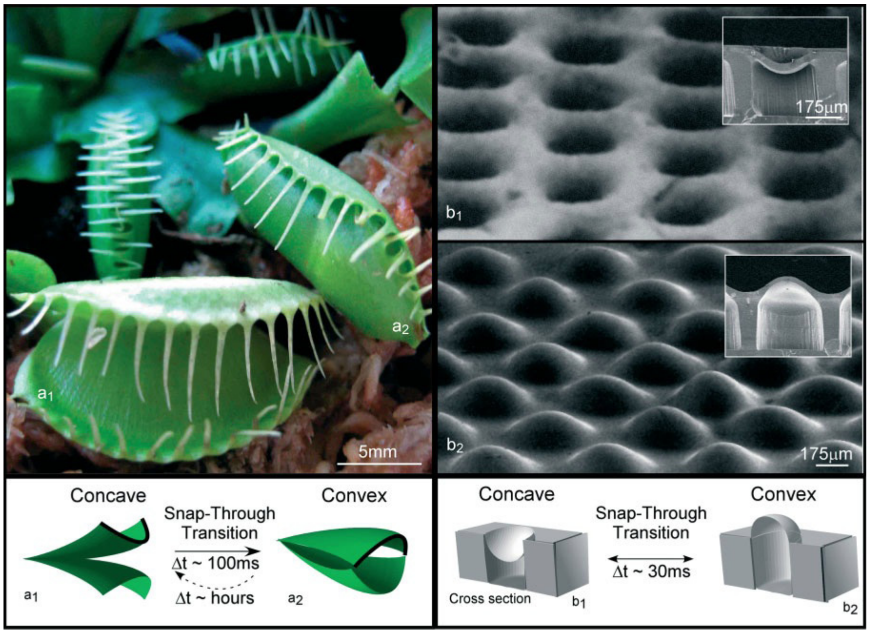


Figure 1. The Venus flytrap leaves can snap through from a concave (a1) to convex (a2) shape with mechanical instability. The responsive surface of concave microlenses (b1) uses the same process to snap to a convex shape (b2) in about 30 ms (Holmes and Crosby, 2007).

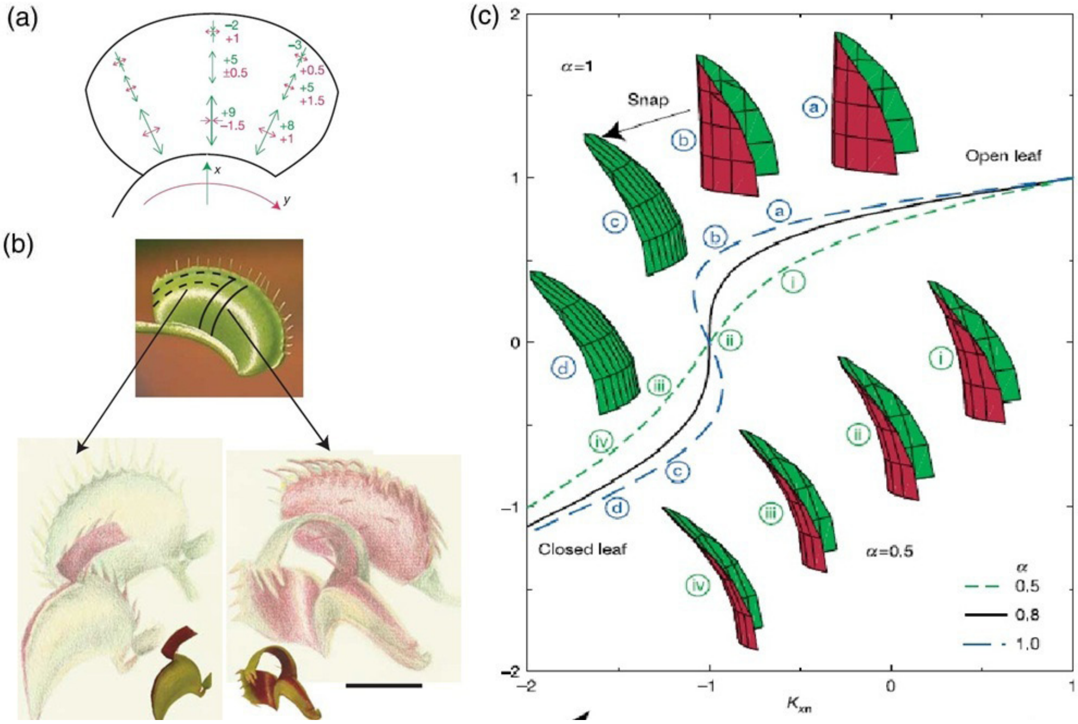


Figure 2. Strain field and natural curvature (Forterre, 2005). (a) Strain field measurement; (b) cutting of the closed leaf along the dotted lines to identify the natural principal curvatures along x and y directions; (c) smooth transition between different phase spaces: the dimensionless mean curvature as Km a function of the control parameter Kxn (see Methods in Forterre, 2005).

than two) are required to stimulate trap closure. In fact, these small structures have played a most important role for the closure of flytrap. Since the touch receptors bulge out of the outer surface of the leaf in *Dionaea muscipula*, the physical shape and position have increased the probability of capturing preys efficiently (DiPalma, 1966).

Biomechanics of fast movements in Venus flytrap

Plants do no have any muscles or nerves, so what enables the Venus flytrap to close it’s trap within a fraction of a second to capture the prey? The rapid closure of the Venus flytrap is an important topic for researching the nastic movements of plants. It is valuable to look for answers of the questions: why is the Venus flytrap capable to move their leaves to catch insects without any muscular engines? What are the underlying microscopic and macroscopic mechanisms? We know that most other plants are usually lack of this ability.

Darwin (1875) did the first systematic observations of the geometric shape changes during the closure of the Venus flytrap, i.e., from a convex to a concave configuration, and found through experiments that the inner layers of the lobes contract during this process. Subsequently, Brown (1916) proposed that this motion is due to the expansion of the outside of the lobes, and the reopening is due to expansion of the inner surfaces by contrast. Williams and Bennett (1982) proposed, based on their neutral buffer infiltration experiments (i.e., acidifying the cell walls to a pH value of 4.50 to 4.75) on the Venus flytraps’ leaves, that trap closure results from a H+ transport from the motor cells, immediately followed by acid-stimulated wall loosening, and subsequently, irreversible cell enlargement.

Reviving the spirit of Darwin using modern experimental technology and elasticity theory, Forterre and coworkers used mechanical instability

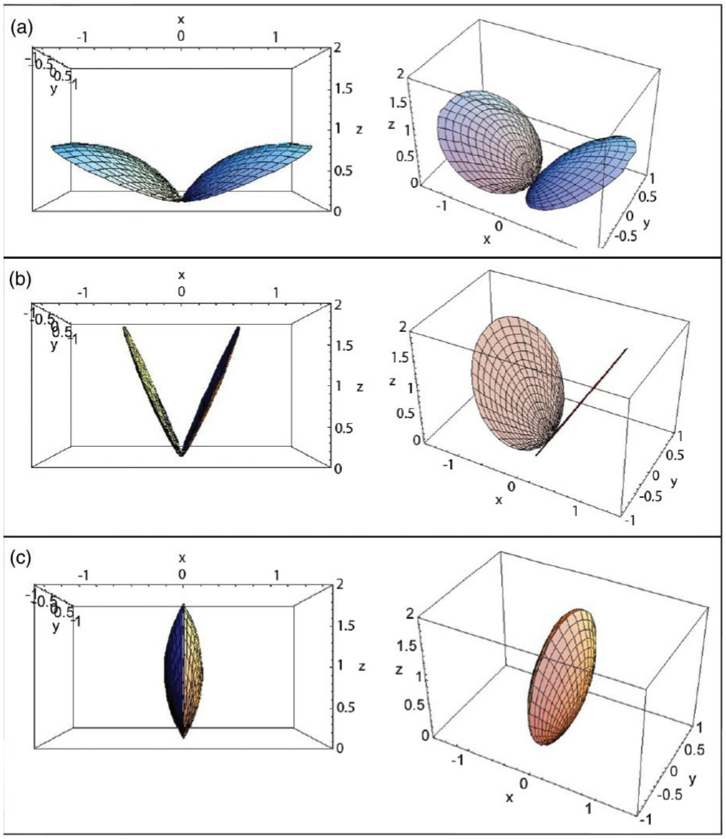


Figure 3. Modeling of the trap closure (front view on the left panel and side view on the right panel): (a)an open state with a convex shape; (b) an intermediate state with curvature equal to zero; (c) a closed state with a concave shape (Markin, 2008).

to interpret the process of the leaf closure in Venus flytrap. To gather the accurate data which could be used in calculating the geometrical values, the researchers drew arrays of ultra-violet-fluorescent dots on the surface of the leaves. During the process of the experiment, the Venus flytrap was irradiated by ultraviolet light, and the whole experiment was recorded by high speed camera. From their experiments, the researchers simplified the analysis by adopting the spatially averaged gaussian curvature and mean curvature of leaf. To analyze the source of these curvature, the researchers measured the strain field through marking the ultra-violet-fluorescent dots on the outer face of the leaf (Forterre, 2005), see Figure 2(a). Cutting experiments were also performed to obtain the decoupled natural curvatures in the closed state along the principal directions, as shown in Figure 2(b). Using a simply model with elasticity theory to account for the coupling between bending and stretching of a plate, it was shown that a dimensionless parameter that relates to the width, thickness and curvature of the leave is responsible for the bistability of the Venus flytrap (Figure 2(c)).

In a related work, a hydroelastic curvature model has been developed in addressing the mechanism of trapping behind the active movements of Venus flytrap (Markin, 2008). In the mechanical model of Markin et al. (2008), a thin, weakly curved, convex shell is employed to model the leaf of the Venus flytrap in the open state, whereby the natural principal curvatures are prescribed by the hydraulic state of the two sub-layers with different hydrostatic pressures (see Figure 3). This so-called bilayer couple hypothesis (Markin, 2008) is analogous to a bimetallic couple that can change shape in response to the temperature variation. The hydrostatic pressure is changed suddenly when the sensitive hairs are properly triggered, presumably through the water transportation via the pores that connect the two layers, although the cellular details of this process and the relevant anatomy remain poorly understood.

Electrophysiology and Biochemistry

The rapid motion of the Venus flytrap is typically triggered by mechanically stimulating the sensitive hairs consecutively within a window of 25-30 seconds, where an action potential is generated following a receptor potential upon mechanical stimulation, which may be responsible for the opening of pores between different hydraulic layers. Without any further stimulation, however, the lobes in this semi-closed state will gradually re-open in 10-12 hours (Yang, 2009). Upon further stimulation (for example, if the prey keeps struggling and touching the sensitive hairs), the flytrap will go to a fully-closed state.

Alternatively, the closure can be stimulated by an electrical pulse between the upper layer of one lobe and the midrib that exceeds a certain threshold. It is worth noting that the polarity is important in that a pulse with inverted polarity cannot trigger the trap to close (Markin, 2008). Interestingly, the plant exhibits short electrical memory, i.e., repeated pulses, each less than the threshold and within a period of around 50 seconds, can trigger the rapid closure when the accumulated electrical stimulus exceeds the threshold. In both the cases of mechanical and electrical triggering, there are three periods in terms of the dynamics: a mechanically silent period (no apparent movement), an accelerating movement period and a fast motion period where the lobes equilibrate to the new stable configuration (Markin, 2008).

In a closely related study, Volkov et al. (2007) also used ion channel uncouplers and blockers to investigate the mechanisms of different closure phases. It was found that both uncouplers and ion channel blockers can significantly increase the time delay of trap closure, and in the meantime, decrease the closing speed. Physiologically, uncouplers inhibit transport of H+ ions, while the ion channel blockers inhibit the flow of water (Volkov, 2008). The electrical stimulus can have a cumulative nature, i.e., small charges that add up to a threshold within a short period of time can stimulate the plant to close. Here the trap closure obeys the "all-or-non" rule, namely, either there is no motion for cumulated stimuli below the threshold, or the trap closes with a speed unaffected by the way the stimuli are applied– with an exception that the speed can be slowed by applying uncouplers and blockers.

On the other hand, the biochemistry of the "memory" in the Venus flytrap has been hypothesized to be due to a bioactive substance engaged in this process. Ueda and co-workers (2007) demonstrated that there exists a threshold of accumulated bio-metabolite for stimulating trap closure. Using bioassays to separate *Dionaea* extracts, a bioactive polysaccharide was identified that is capable of triggering trap closure in absence of any external mechanical or electrical stimuli. Putting the results from these studies together, it is promising that a more comprehensive understanding of the "memory" and actuation mechanisms in plants such as *Dionaea* can be achieved.

Mathematical models on the dynamics of the Venus flytrap

The Venus flytrap is smart for it excludes the distraction from rain drops or blasts of air, and catches insects of appropriate sizes while releasing small, unworthy ones. All of these speaks of the fact that it is well adapted to the natural environments. Emphasizing the decision-making capability and environmental adaptability of *Dionaea*, Yang et al. (2009, 2010) divided its phases into three distinct ones: open, semi-closed and closed, and constructed mathematically its nonlinear dynamics and control model based on water kinetic, including trigger, capture, release, seal and reopen processes. The fluid volume in the upper and lower layers are controlled, in a mutual inhibitory manner, by coupled differential equations where the evaporation and flux rates due to osmotic pressure are taken into account. The chemical "memory" of the flytrap is modeled by a linear system that describes the bio-active metabolite, whereby the action

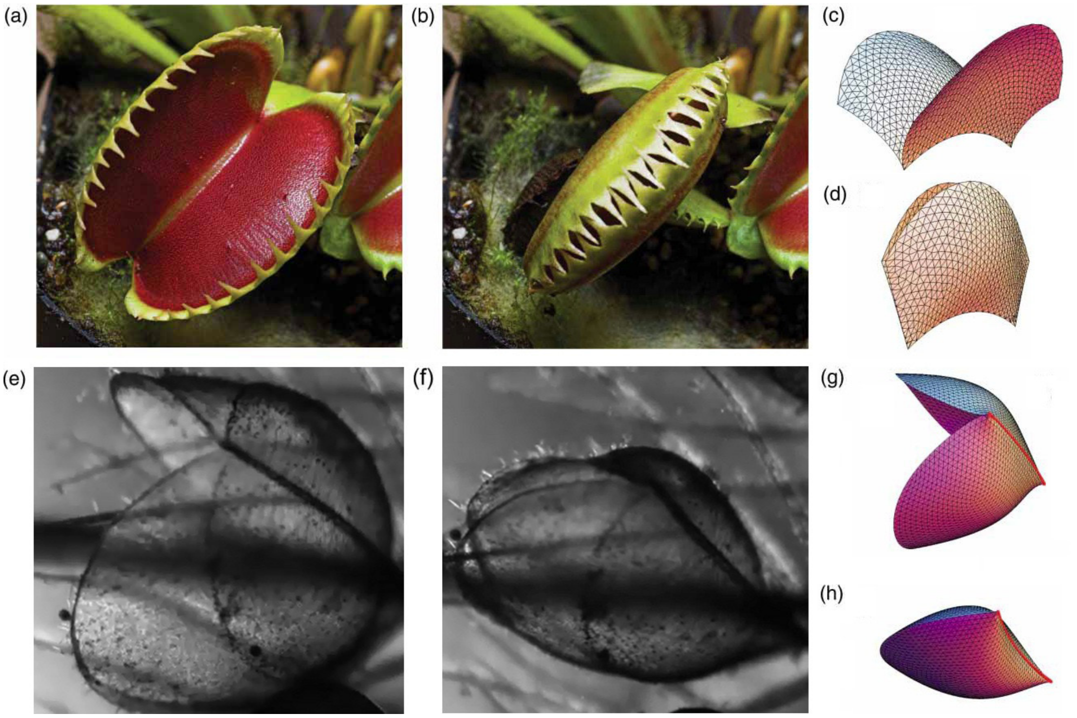


Figure 4. (a, b) Top views of the *Dionaea muscipula* lobes in open and closed configurations, respectively (photographs by Dr Barry Rice, Sierra College, Rocklin, CA, USA, adapted from Joyeux (2011)); the lobes are approximately 4cm wide. (c, d) Models of the trap in open and closed configurations, respectively (adapted from Poppinga and Joyeux (2011)). (e, f) Microphotographs of a *Aldrovanda vesiculosa* trap in open and closed configurations, respectively, approximately 5 mm long. (g, h) Models of the trap in open and closed configurations, respectively. (e) to (h) are adapted from Poppinga and Joyeux (2011).

potential triggered by touching the sensitive hairs is described by an exponential function. Li et al. (2011) further developed this mathematical model to demonstrate the nonlinear dynamics of this process. This model captures a few key features in the Venus flytrap's hunting cycle, including the "memory" in touch stimuli, fast closure motion, the decision-making intelligence, and the reopening process. It was emphasized that the semi-closed state is actually the most important one, because the flytrap needs to make a decision for next state when it was in semi-closed state. If it is teased and no further stimulation occurs, it will reopen in 10-12 hours, while if more simulations happen (e.g., the prey keeps struggling and touching the sensitive hairs), the plant will go to a fully closed state. It is of interest to apply this model as a control component in a number of engineering applications and to develop biomimetic robotics based on the design principles learnt from the movements of the flytrap.

Comparative biomechanics– *Dionaea*, *Aldrovanda* and *Utricularia*

The mechanics and dynamics in the rapid closure of *Dionaea muscipula* are different from other carnivorous snap-traps, *Aldrovanda vesiculosa* and *Utricularia*. In comparing the biomechanics of *Aldrovanda* and *Dionaea*, Poppinga and Joyeux (2011) modeled Aldrovandas trap as a pair of thin elastic shells with leaf-like shape connected to a midrib. The midrib that connects the lobes can be bent inward in the closed configuration (Figure 4(e),(f)). This model suggests that trap closure in *Aldrovanda* is more of a result from swelling and shrinking (Skotheim and Mahadevan, 2005) of tissues around the midrib, than mechanical buckling as in *Dionaea muscipula*. While in

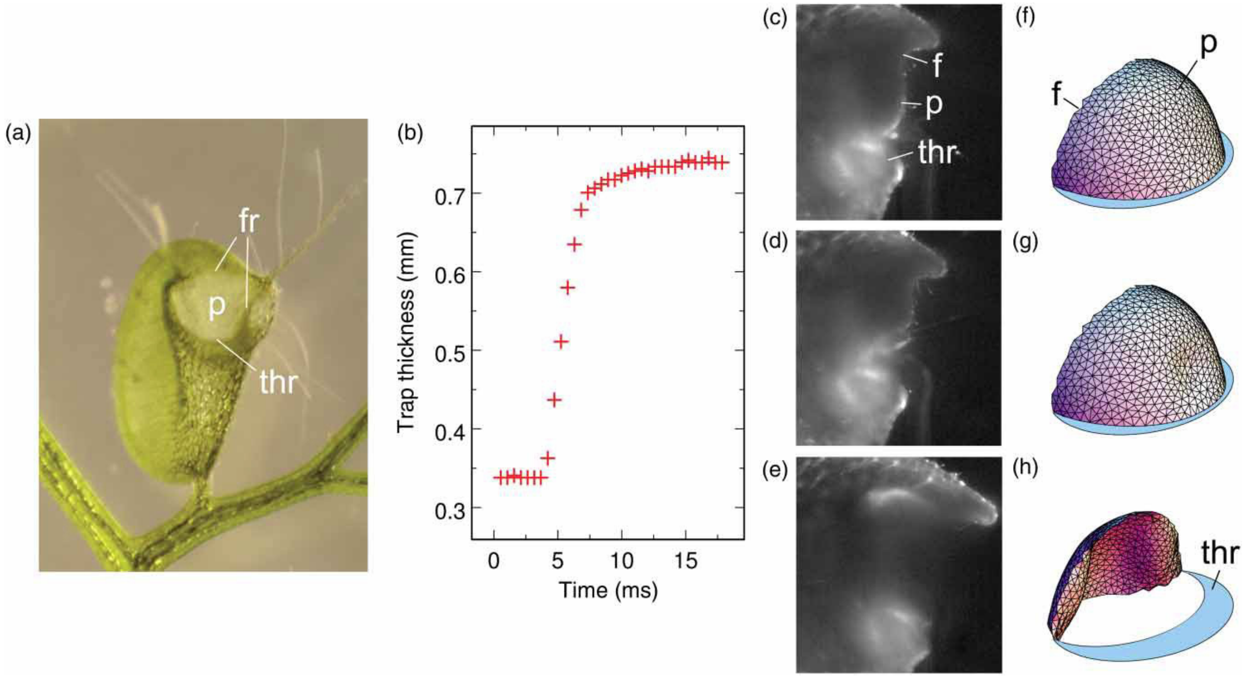
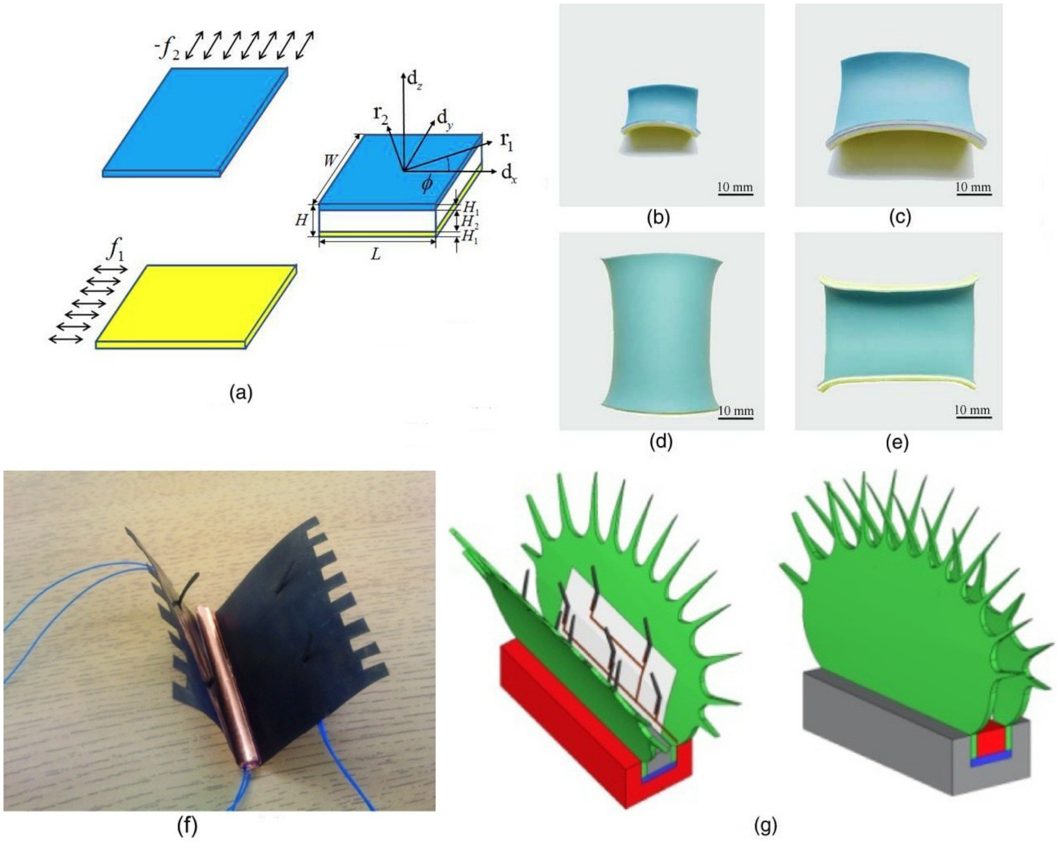


Figure 5. (a) Photograph of an *Utricularia inflata* trap (around 3mm wide), adapted from Vincent (2011). (b) Observed time evolution of the trap thickness right after manually triggering of one sensitive hair. (c,d,e) High-speed images of the firing of an *Utricularia australis* trap after manual triggering one sensitive hair. (d, e) Images acquired 7.6 and 8.6 ms after (c), respectively. The door is approximately 300μm wide. (f,g,h) Models of the trap door in set condition, at the onset of firing, and while swinging open, respectively. Figures 5(b) to 5(h) are adapted from Joyeux et al. (2011). thr, p and f denote the threshold, panel of the door and frame of the door, respectively.

the case of *Dionaea muscipula*, all the motor cells work together, in comparison to the case of *Mimosa pulvini* where the motor cells are divided into two opposing groups. Furthermore, the model implies that the rapid trap closure of *Aldrovanda* is greatly facilitated by the unique mechanical feature, i.e., a small bending of the midrib is sufficient to induce a large opening or closing of the trap. In comparison, the *Dionaea*'s traps do not exhibit as dramatic changes in midrib curvature during closure, rather, the lobes change the principal curvatures from a convex to concave shape using mechanical buckling, as has been discussed previously. *Utricularia*'s traps are of a suction type, perhaps the most complex of all the active trapping structures in plants (Joyeux, 2012). The thin walls of *Utricularia* become concave (modeled as spherical), with stored elastic energy in the doubly-curved shell during the trap-setting phase, meanwhile, the active cells transport water from inside out (Figure 5(a)). It is hypothesized that the pressure difference in the set-up trap is only slightly smaller than the critical pressure needed for buckling (Joyeux, 2011). So when the trigger hairs are touched, local deformation of the shell is enough to overcome the energy barrier, leading to the sudden deformation to release the elastic energy in the shell and enable suction of water into the trap (and hence the prey). Figure 4(d) further suggests that the swinging of the panel starts with local curvature inversion, and that the door acts more like a flexible valve that flips under external pressure (and change curvature from concave to convex) than as a panel that articulates on a hinge (Joyeux, 2012).

The different snapping behaviors and mechanisms in these carnivorous species are also of interest from an evolutionary point of view. Study has shown (Cameron, 2002) that *Dionaea* and *Aldrovanda* share a common ancestor of sticky "flypaper" traps with *Drosera* (sundews), despite the fact that the trapping mechanisms are different (snapping surfaces versus sticky



(a) (b) (c) (d) (e) (f) (g)

Figure 6. (a) Schematics of the table-top experiments: two thin latex rubber sheets (blue and yellow) were pre-stretched along perpendicular directions and bonded to a thicker elastic strip. When released, the bonded multi-layer sheet will deform into one of the following shapes in (b) to (e): (b) A saddle shape for a small, thin square. (c) A saddle shape for a thick square sheet. (d) A stable, nearly cylindrical shape (curving downwards) for a thin, wide strip. (e) The other stable, nearly cylindrical configuration (bending upwards) for the same sheet as in (d). Figures 6(a) to 6(e) are adapted from (Chen, 2012b). (f) The robotic Venus flytrap (VFT) with a pair of lobes (traps), embedded spine (copper roll), IPMC trigger fingers, and lead wires for sensing and actuation. (g) Schematics of a robotic VFT in an open and closed configuration (adapted from Shahinpoor (2011)).

surfaces). Meanwhile, the worldwide distribution of *Aldrovanda* is similar to that of *Utricularia*, although they are much less genetically associated, demonstrating parallel adaptations to similar living environments and available preys of similar sizes. *Dionaea*, in contrast, has been narrowed to the south and north Carolina in the United States in terms of the natural habitat. Although their natural habitats are dramatically different, *Dionaea* and *Aldrovanda* are genetically much closer (like siblings), while *Drosera* is more like a cousin. The question remains open where the snap-traps started and how they evolve, spread and eventually settle in their current habitats (Pennisi, 2002).

Biomimetics

The fast motion of the Venus flytrap has inspired a number of engineering designs of snapping structures (Doug and Crosby, 2007; Lee, 2010; Shahinpoor, 2011; Chen, 2012a) with potential applications in on-demand releasing coatings, adhesive surfaces, sensors, drug delivery devices and robotics (Lee, 2010).

Doug and Crosby (2007) exploited mechanical buckling of plates (two-dimensional analog of Euler buckling) to manufacture an array of lens-like shells using bi-axial compressive loads. A thin film of PDMS is bonded , through cross-linking, to another layer of biaxially Pre-stretched PDMS with patterned periodic arrays of holes. Upon releasing of the biaxial tension, an equibiaxial compressive load is applied to the edge of each circular plate, resulting in either a convex or concave shape that can be used as responsive, functional microlens arrays. The focal point of each individual lens can be either above the structure surface (when the microlens is convex), or below the structure surface (when it is concave), the transition between which can occur either locally (in a single lens) or globally, depending on the geometric spacing between adjacent lenses, the mechanical properties of the material and the way of triggering the transition (Doug and Crosby, 2007). Besides tuning the optical properties, this transition can also be employed to control a variety of properties such as wetting and frictional properties.

The Venus flytrap represents a typical example of multistable structure in nature, structures featuring more than one stable shapes, each having in its own functioning regime. Chen et al. (2012b) investigated, through both theoretical modeling and table-top experiments, the geometric and mechanical conditions of a bistable strip. A theoretical model for large deformation of shell structures is proposed, by modeling the deformation of a strip onto the surface of a torus with two tunable parameters. Meanwhile, a bistable strip is manufactured by uniaxially pre-stretching two elastic sheets in perpendicular directions, and then sandwiching between them another layer of adhesive (schematics shown in Figure 6(a). Figure 6(d) and 6(e) are bistable shapes of the same strip). Applying the theoretical model to interpret the experiments, two dimensionless parameters (one related to both the mechanical forces and geometry, and the other associated with forces) are identified that control bistability (when below the threshold, the strip remains monostable, as shown in Figures 6(b) and 6(c)). Moreover, the aspect ratio also plays a key role (i.e., via edge effects) in determining the energetic preferences between the two locally stable states. This work classifies the conditions for bistability, thus defining the design space for bistable morphing structures, and meanwhile, it extends the theory of plates and shells with large deformation. These results provide a mechanical framework for studying morphogenesis associated with growth and instability, and facilitate the design of multi-stable functional structures, from artificial muscles and bio-inspired robots to deployable, morphing structures in aerospace applications.

Also inspired by the Venus flytrap, Lee and coworkers (2010) created jumping robots using snap-buckling mechanism. Swelling-induced buckling of the hydrogel induces a doubly-curved structure that can be effectively controlled by swelling and de-swelling, and can thus by employed as three-dimensional microgel actuators. By exploiting mechanical instability, the power density of the as-manufactured device can approach that of the human muscle, demonstrating the efficiency of this device in storing and releasing the energy through controlled use of mechanical instability. Associating this strategy with other method of actuation, such as through change of temperature, pH value, swelling and de-swelling (Armon, 2011), surface stress (Chen, 2011; Chen, 2012a), etc., can lead to design of a wide variety of sensing and actuating systems.

The whole hunting process of Venus flytrap is very effective and efficient, which provides a perfect source of inspiration for engineering designs of robotics. Shahinpoor (2011) designed and fabricated a novel robotic Venus flytrap by employing IPMC artificial muscles as distributed sensors and actuators (see Figure 6). In this work, the lobes were integrated into a connected pair of lobes where a conductive copper spine is used as a “midrib”, which allowed the signals sensed by the IPMC trigger hair to be transmitted to the solid-state relay system and to activate a small dynamic voltage generator that can actuate the robotic trap. The experimental testing of the assembled flytrap robot revealed that it worked well: stimulated by the solid-state relay system, the flytrap robot closed under the functioning of the voltage generator once some stimuli were applied to the IPMC trigger hairs. Such biomimetic smart material systems and structures, integrated with appropriate sensors and actuators, can potentially be useful for biomedical applications and a number of engineering applications.

Perspectives and concluding remarks

Although plants do not have any nerves or muscles, some plants can move swiftly, through various snapping mechanisms, when triggered by certain stimuli. Here we review the most dramatic movements in the plant kingdom including those of *Dionaea*, *Aldrovanda* and *Utricularia*. While the collaborations between biologists, physicists, mathematicians and engineers have been successful in some of the studies reviewed here, many questions remain open that need further collaborations from researchers from various disciplines. For example, how action potentials are generated, especially through the touch receptors other than the sensitive hairs in the Venus flytrap, is not completely understood yet. It also remains elusive how the generation of action potentials is coupled to molecular-level activities that trigger the macroscopic snap-through behavior in *Dionaea*. In addition, the time scale involved in these fast motions is worth of further investigation. For instance, Skotheim and Mahadevan (2005) proposed that the time scale for water transport is set through a diffusion event, and a scaling law prediction was given about the poroelastic time, which, however, seems to be inconsistent with recent experimental study (Colombani and Forterre, 2011). This inconsistency warrants further investigation about the hidden mechanisms in these non-muscular engines built by nature. Although a lot of studies discussed here are related to *Dionaea*, the comparisons between the behaviors and mechanisms in *Dionaea*, *Aldrovanda* and *Utricularia* also raise interesting questions in evolutionary biology that remain to be elucidated. Furthermore, the biomechanics and design principles learnt from these carnivorous plants can inspire biomimetics research in designing artificial muscles and bio-inspired robotics with smart sensing/actuation capability and broad applications in engineering.

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