Dispatches

Biomechanics: An Army Marching with Its Stomach

A novel X-ray technique shows that the internal organs of crawling caterpillars slide past the body walls like pistons in a new kind of legged locomotion.

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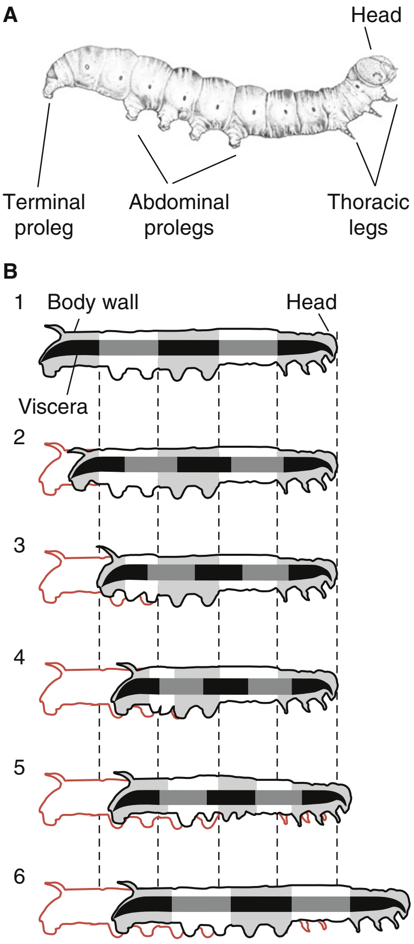
The question of how animals move almost effortlessly from place to place has long been of great interest to researchers [1–3]. This has applied to the locomotion of both animals with rigid articulated skeletons and soft-bodied animals that move with soft hydrostatic skeletons. Animals with rigid articulated skeletons move around by manipulating a series of linked lever-arm systems that can be represented by a series of joint angles [4]. While soft-bodied animals have bodies that can twist, turn, and squeeze in ways that are too intricate to be represented by a series of fixed joint angles [5], this does not stop them from swimming, crawling, digging or even rolling [6] toward a destination. How is it that soft-bodied animals move in such a variety of ways?

One of the most successful body designs for soft-bodied animals is a cylindrical body wall surrounding a body cavity with muscle, viscera and internal organs; a body design exemplified by worms, slugs, leeches and caterpillars. Understanding the specifics of how these animals move is very difficult because any given position of the external body can be generated by any number of positions of the internal musculature. Consequently, it requires analysis of both the motions of the external body wall and the motions of the internal structures. While magnetic resonance imaging and ultrasound both can allow analysis of moving internal structures, these two techniques currently have insufficient spatial resolution to measure the motion of tissues within smaller animals [7]. This leaves the question "what are the internal body motions that allow soft bodied animals to locomote?" mostly unanswered. In this issue, Michael Simon and colleagues [8] answer this question by using a new technique called real-time phase-contrast X-ray imaging to simultaneously film the internal and external movements of a crawling soft-bodied animal, the caterpillar.

Real-time phase-contrast X-ray imaging generates images by exploiting the differential diffraction properties of X-rays through tissues of different densities [7]. A beam of X-rays is emitted, diffracted by the tissues of the animal, and then collected by a detector which then uses this information to re-construct a picture of the animal's internal structures. There is a conflict between using higher beam intensities, which generate clearer images, and lower intensities, which inflict less damage to the target. The conflict can be avoided if the anatomical landmarks are tissues with sufficiently different densities that lower beam intensities can be used while still providing clear images.



Current Biology

Figure 1. Body wall and visceral motion during caterpillar locomotion.

(A) Anatomical sketch of a caterpillar, from [10]. The head, thoracic legs, abdominal prolegs, and terminal proleg are marked. (B) Example schematic of the motion of the body wall and the viscera of a caterpillar during a step, adapted from [8]. The body wall is represented in light grey and white and viscera are represented as dark grey and black boxes internal to the animal. The body wall and viscera have been schematically divided into fifths so that the movement of the body wall can be clearly differentiated from visceral movement. In sections 2–6, the initial position of the caterpillar is shown in red, and the initial position of each fifth is marked with a vertical dashed line. From rest (1), the posterior-most portion of the body wall compresses and moves forward, compressing and moving the viscera forward (2). Note that the viscera of the middle section have moved forward while the body wall of the middle section has not moved. The posterior of the animal continues to compress and move forward (3), until the terminal proleg is placed on the ground (4). This motion has compressed and moved the viscera forward. Then the middle and anterior portions of the body wall are moved forward sliding along the viscera (5), until the viscera and body wall are back in alignment (6).

This is where the internal anatomy of the caterpillar makes it an ideal subject for using this imaging technique. Caterpillars are little more than digestive systems on legs, with legged body walls surrounding viscera that contain a very metabolically active digestive tract. In order to provide the large amounts of oxygen needed for digestion, the viscera are also populated by large numbers of air-filled trachea [9]. The low density of the air filled trachea combined with the higher density of the other structures within the viscera provide landmarks which allow lower X-ray beam intensities to generate clear pictures. On the outside of the animal, there are clear landmarks to track the movements of the body wall, and on the inside, the trachea provide clear landmarks to track movements of the viscera. This allowed Simon *et al.* [8] to combine X-ray images with conventional cameras to examine the internal and external motions of crawling caterpillars.

Unlike worms, caterpillars crawl by using a series of stubby, non-articulated structures attached to each body-wall segment. Each stubby structure is called a 'proleg' (Figure 1A). In a wave of activity that starts at the tail and moves to the head, each proleg is first swung forward until it contacts the ground, and then the ground contact is used to propel the animal forward. You might assume that each section of viscera would move synchronously with the body wall that surrounds it. Surprisingly, however, this is not the case, as X-ray images showed that near the abdominal prolegs, the viscera move out of phase with the body wall. While the abdominal prolegs are in stance, the viscera move through the body wall like a piston, and then, after stance, the abdominal prolegs swing forward and slide back along the viscera (Figure 1B) [8].

Motions of the viscera are ubiquitous in many animals, but are generally associated with digestion, not locomotion. In caterpillars, however, visceral motion is a critical part of the step cycle. Thus, analysis of the internal and external body motions of the caterpillar has demonstrated a new kind of legged locomotion, one in which the body wall and viscera are acting as two separate components, a container and the contained. With each step, the contained first slides like a piston within the container, and then the container slides forward along the contained. The consequence of this type of locomotion is that the mechanical properties of the viscera are as important to locomotion as the mechanical properties of the body wall.

It is still not known, however, exactly what advantage this new form of locomotory pistoning locomotion gives the caterpillar. Simon *et al.* [8] suggest that it may minimize impacts to the viscera, facilitate different kinds of locomotion, add stability, aid respiration, or allow better digestion. Even though the advantages of visceral-body wall pistoning are unclear, this work used a novel imaging technique to show a new kind of legged locomotion, i.e. locomotion that both involves pistoning movements of the legs and the viscera. Napoleon famously said "An army marches on its stomach"; Simon *et al.* [8] have shown that an army of caterpillars marches (partially) with their stomachs.

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Cell–Matrix Adhesion: Slip and Immobilization under Force

When force is applied to cell–matrix adhesion complexes, they respond by growing larger and stronger. It emerges that strengthening involves transient motion of the transmembrane integrin receptors and their eventual immobilization to the extracellular matrix.

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Focal adhesions are discrete sites at the cell periphery where the actin cytoskeleton connects to the extracellular matrix (ECM) through transmembrane integrin receptors and numerous specialized proteins that link actin filaments to the intracellular domains of integrins [1,2]. Focal adhesions transmit forces from the actin cytoskeleton to the substrate, allowing the cell to migrate and remodel the ECM. At the same time, focal adhesions are the sites where the cell probes the environment and generates signals that control important aspects of its behavior, such as migration and proliferation. The composition, assembly and regulation of focal adhesions have been studied intensely for several decades, but the biophysical properties of the mechanism of force transmission have only recently become accessible for experimental quantitative studies. This is thanks largely to the development of high-resolution traction-force microscopy — a method capable of resolving forces applied to the ECM at the level of a single focal adhesion [3]. The study of Aratyn-Schaus and Gardel [4], published in a recent issue of *Current Biology*, combines traction force and fluorescence confocal imaging to provide an informative and esthetic visual account of how focal adhesions grow and remodel under applied force. The authors discover a previously unidentified phase in the life history of focal adhesions: a frictional slip of the integrin molecules before they become affixed to the ECM.

Focal adhesions have unusual physical properties. The most curious and counter-intuitive feature is probably their ability to grow and strengthen in response to a force. Focal adhesions appear at the cell periphery as small isotropic clusters