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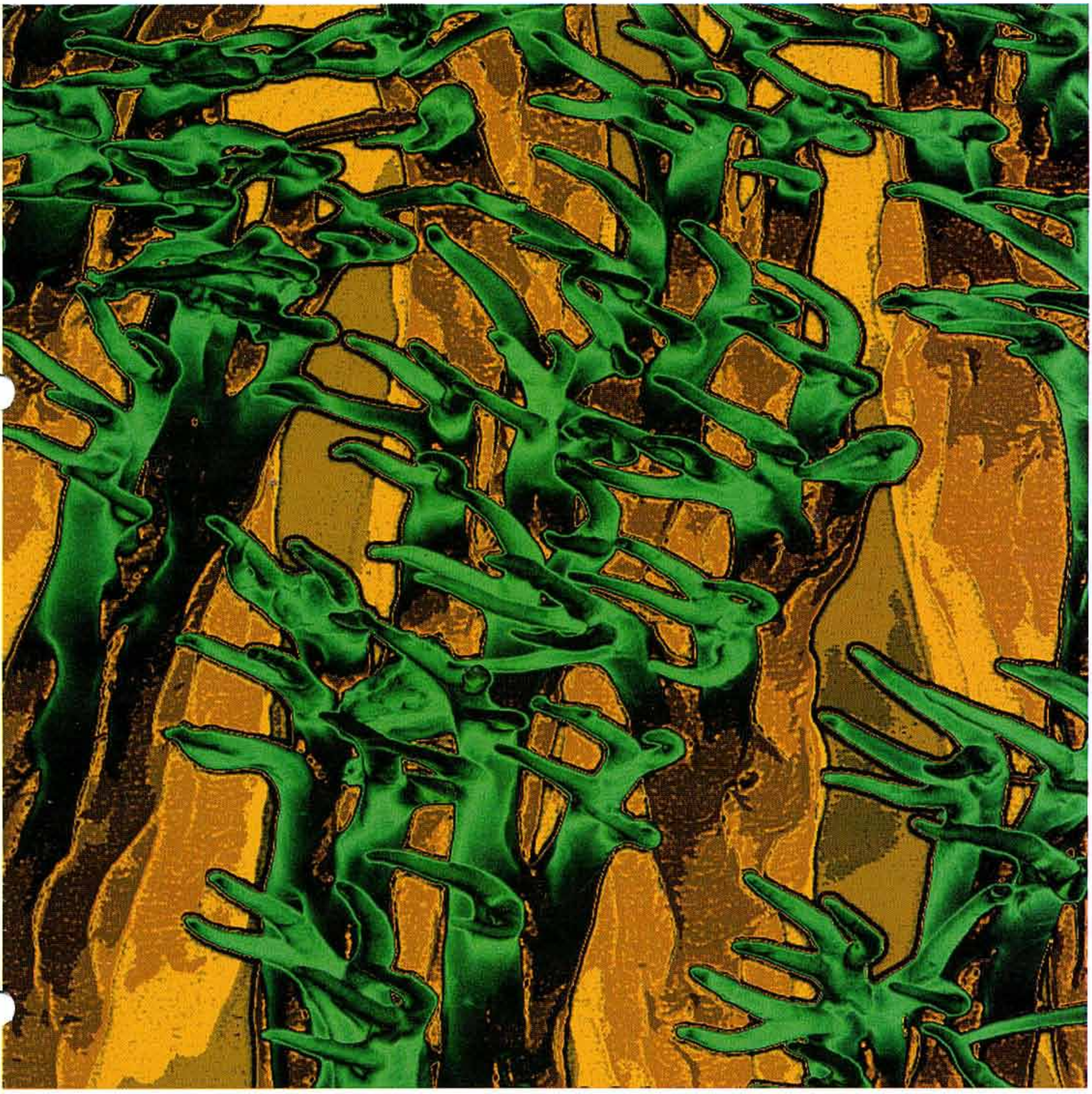

How Ants Walk Upside Down

Stephen W. Carmichael and Kai-Nan An[1], Mayo Clinic
carmichael.stephen@mayo.edu

Have you ever observed an ant crawling on the underside of a leaf and wonder how it does that? Furthermore, consider that this insect can stay attached to its substrate even when a massive (relative to the ant) raindrop suddenly threatens to dislodge it. This requires an impressive adhesive force, and it must still allow the ant to detach and run swiftly. These insects must have fast and effective control over adhesive forces between their foot pad and the substrate, but almost nothing is known about the mechanisms of how insects control surface attachment and detachment. In Hymenoptera (insects with membranous wings), there is a smooth pad called the arolium on the feet. As in many other insects, a thin liquid film between the arolium and the surface mediates adhesion to smooth surfaces. In an intriguing study, Walter Federle, Elizabeth Brainerd, the late Thomas McMahon, and Bert Hölldobler[2] used several different microscopes and other experimental procedures to determine how the arolium is deployed and retracted during movement.

Asian weaver ants (*Oecophylla smamgdina*) and honeybees (*Apis mellifera*) were the experimental animals. Techniques used included serial thin sectioning of epoxy-embedded specimens examined with the light microscope, scanning electron microscopy of intact or dissected feet (including specimens that were obtained by rapidly freezing ants running on strips of smooth plastic), and high speed video observations made through a dissecting microscope. In an ingenious series of experiments, amputated ant legs were sealed onto the point of an injection needle and controlled~pressuresw ere applied to determine the role of hydraulic mechanisms in the deployment of the arolium. The needle was fixed on the stage of a light microscope so that the arolium could be observed while pressure was being applied. In another experiment, ant and bee legs were amputated and fixed in a position were the claw-flexor tendon could be grasped with a pair of fine forceps attached to a micromanipulator. The tendon could be pulled in steps of 10 microns.

The arolium is a soft cuticular sac located between the claws. Its adhesive contact zone has a highly specialized fibrillar cuticle texture as is seen in other insects. It is supported by two hard structures that we will refer to as the arc and the handle. The movement of the arolium is complex and was described as a rotation around a horizontal axis located near the end of the handle and as a lateral expansion of the arolium when the limb is extended and an invagination when the limb is retracted. In the retracted position, the distal edges of the arolium are folded up near the base of the handle so that the handle is partially hidden. When the arolium unfolds, these edges move down to the surface and the handle becomes exposed.

In the experiments where pressure was applied to the inside of the amputated limb, the arolium was seen to inflate completely with pressures between 10 and 16 kPa. When the claw-flexor tendon was pulled, not only did the claws retract, but the arolium also moved and unfolded. In the honeybee, pulling on the claw-flexor tendon caused a rotation of the arolium but almost no lateral extension. When the arolium is folded down to the surface, vertical pressure on the ventral base of the arc elastically expands it in the lateral direction. Federle et al. purposed that the observed inflation of the arolium can be explained by hydraulic compression of a reservoir associated with a gland connected to the arolium that is caused by movement within the limb. By the action of the claw flexor tendon, the volume within the limb is compressed and liquid is forced down into the arolium, causing it to inflate.

These and other studies suggested two interrelated mechanisms for walking on rough and smooth surfaces. The underlying control of these two mechanisms apparently resides in the mechanical system itself. When the limb comes into contact with a rough surface, flexion of the claws is stopped when the claws interlock with a protrusion on the surface. On a smooth surface, the claws slip and find no resistance, and deployment of the arolium occurs at this later stage. Apart from being actively extended, arolia partly in contact with a surface can also be passively unfolded when the leg is pulled toward the body. This reaction can be activated even in dead insects or severed leg. The ants' impressive capacity to withstand strong and sudden impacts (raindrops) is probably due to this passive extension mechanism, which works without a neural feedback loop and may thus be faster than a reflex.

1. The authors gratefully acknowledges Dr. Walter Federle for reviewing this article.
2. Federle, W., E.L. Brainerd, T.A. McMahon, and B. Hölldobler, Biomechanics of the movable pretarsal adhesive organ in ants and bees. PNAS 98(11):6215-6220,2001.