Learning to move in the real world

Leaping squirrels show that locomotion entails perceiving and innovating possibilities for action from moment to moment

By **Karen E. Adolph**[1] *and* **Jesse W. Young**[2]

Comparative research reveals extraordinary animal athleticism—mites lift >1000 times their body weight, mantis shrimp strike their prey with the force of a bullet, and peregrine falcons dive toward prey at 335 mph (539.13 km/hour) (*1*). Even human babies travel the distance of eight football fields per hour during free play (*2*). However, movement in the real world is not about being the strongest, fastest, or most active. Rather, effective action is a moment-to-moment process of matching the current status of the body to features of the environment (*3*). Locomotion—like other actions—must be tailored to local conditions. On page 697 of this issue, Hunt *et al.* (*4*) provide an elegant demonstration of the creativity of functional movement, showing that wild squirrels tune their leaps to branch bendiness and target distance, even inventing ingenious maneuvers when required.

Matching behavior to local conditions—that is, perceiving "affordances" for action—involves perception-action coupling (*5*). Animals must generate perceptual information about which actions are possible and then select appropriate actions from this set of possibilities (*2*, *3*). The arboreal canopy is an ideal natural laboratory for studies of perception-action coupling because support diameters vary from tiny twigs to massive boughs, with more than three orders of magnitude of variation in branch compliance (*6*). Moreover, mistakes can have serious consequences—falling injuries account for most limb-bone fractures in free-ranging primates (*7*). Arboreal animals must avoid errors or quickly correct them.

Hunt *et al.* created an outdoor obstacle course and trained wild squirrels to jump from cantilevered perches to cross gaps of varying distances. Launch perches varied in compliance, requiring squirrels to negotiate a critical trade-off: Moving toward the end of the perch would shorten leaping distance but compromise stability and force production; staying closer to the base would ensure a secure launching platform but at the cost of increased gap distance. Squirrels launched closer to the base of the perch, which suggests that support compliance is a critical factor in arboreal locomotion (*8*). Notably, squirrels also demonstrated the creativity of functional movement. After learning the leaping task, squirrels encountered new adjustments to launch-perch compliance and gap distance, necessitating moment-to-moment modifications in behavior to ensure gap-crossing success. Squirrels innovated new strategies—parkour-like jumping maneuvers off the back wall of the apparatus when launching impulse was insufficient to cross the gap, and front and back flips to grasp the landing perch when their leaps over- or undershot the target.

Squirrels are not alone in the precision and creativity of their locomotion. Every animal must perceive and exploit affordances for locomotion under variable conditions (*3*, *5*). Bats and iguanas alter locomotor forces to compensate for increased body mass associated with feeding and pregnancy (*9*, *10*). Running guinea fowl adjust limb postures within a single step to maintain stability after an unexpected drop (*11*). Likewise, human infants gauge affordances with exquisite precision and invent new locomotor strategies on the fly (e.g., sliding down steep slopes or high drop-offs on their bottoms, backward feetfirst, or headfirst like Superman) (*2*, *3*).

So how do animals learn to gauge and adjust their movements? Hunt *et al.* suggest that trial-and-error learning governs affor-

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[1]Department of Psychology, New York University, New York, NY, USA. [2]Department of Anatomy and Neurobiology, Northeast Ohio Medical University, Rootstown, OH, USA. Email: karen.adolph@nyu.edu; jwyoung@neomed.edu

PHOTO: LAWRENCE WANG, DOMINIC PANG, SEBASTIAN LEE, JEREMY SNOWDEN, TINA KUANG, FRANK ALIAGA AUQUI

Wild squirrels adjust their leaps in real-time to the mechanical properties of the environment, elegantly demonstrating the creativity of functional movement in the real world.

dance perception in the course of a single session. However, adult squirrels have had a lifetime of learning, so development must be a critical factor. During development, new affordances emerge as animals' bodies, skills, and effective environments change (*2*). Human infants can grow up to 2 cm in a single day (*12*). One week, babies are crawlers; the next, they are walkers (*13*)—yesterday, objects on the coffee table were out of sight and beyond reach; today, they are accessible (*2*). Thus, learning occurs in the context of development, and the flux of body growth and motor-skill acquisition ensures that infants do not learn fixed solutions. Indeed, static solutions would be maladaptive in a continually changing ecosystem. Instead, infants "learn to learn." They learn to detect information for affordances at each moment to determine which actions are possible with their current body and skills in a given environment. Learning amid development results in perception-action coupling that is sufficiently flexible to scale up to the novelty and variability of action in the real world (*2*, *3*).

Human perceptual-motor development is an iterative process, where experience moving in a variable environment generates perception of new affordances that, in turn, facilitates new experiences (*2*). Human infants move to learn while they are learning to move. Likely, infant squirrels and other arboreal animals show similar calibration and creativity as they learn to navigate the canopy, particularly because misperceptions can prove fatal. Future work should consider the ontogeny of perception-action coupling in natural habitats.

Just as movement in the real world requires flexibility and creativity, researchers studying natural locomotion must be as ingenious as their animal subjects. The trick is to capture movement in all its complexity while retaining sufficient experimental control and measurement fidelity (*2*). The study of Hunt *et al.* is a beautiful example. Their unexpected results elucidate what every homeowner knows: Squirrels are clever acrobats when navigating complex environments. ■

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STRUCTURAL BIOLOGY

Maturation of HIV-1

Structural transformation of HIV-1 matrix during virus maturation promotes infection

By **Yuta Hikichi** *and* **Eric O. Freed**

HIV-1 particle assembly is driven by the Gag polyprotein precursor, which contains several structural and functional domains that engage in protein-protein, protein-lipid, and protein-RNA interactions during virion assembly. Concomitant with virus release from an infected cell, the viral protease cleaves the Gag precursor to liberate the mature Gag proteins, triggering a morphological transformation of the virus particle, called maturation. The matrix (MA) domain plays key roles in directing Gag to the plasma membrane of the host cell and in the incorporation of the viral envelope glycoprotein (Env) complex into the assembling particle. On page 700 of this issue, Qu *et al.* (*1*) report the cryo–electron tomography (cryo-ET) structure of MA in both immature and mature particles. The results provide important insights into HIV-1 assembly and maturation and the role that MA plays in these processes. These findings may suggest new antiviral strategies that target MA.

The Gag polyprotein precursor contains MA, capsid (CA), nucleocapsid (NC), and p6 domains (*2*, *3*). The NC domain is flanked by two spacer peptides, SP1 and SP2. The structure of the intact HIV-1 Gag precursor has been challenging to determine because of its large size and flexibility. However, structures are available for individual mature Gag proteins and for some domains of the Gag precursor—notably, CA. As an isolated protein, MA folds into a highly globular structure (*4*, *5*). A myristic acid moiety covalently linked to the amino terminus of MA anchors Gag in the lipid bilayer of the virion, and a highly basic region of MA interacts electrostatically with the acidic headgroup of the host cell plasma mem-

Virus-Cell Interaction Section, HIV Dynamics and Replication Program, Center for Cancer Research, National Cancer Institute, National Institutes of Health, Frederick, MD, USA. Email: efreed@nih.gov

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