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Falling Aphids
Land on Their Feet

widely utilized to examine ROS levels. However, measurements based on redox-sensitive dyes such as DCFH can be problematic because they depend on dye uptake and lack any specificity towards a particular type of ROS. The advent of protein-based redox sensors like redox-sensitive GFP (roGFP) have improved specificity to particular ROS and can be targeted to different compartments within the cells to gather spatial resolution of ROS levels.

What remains to be explored? Four big challenges face ROS biology: (1) The intracellular targets of ROS are not well defined; these targets are likely to be context dependent. (2) The measurement of ROS continues to be challenging especially *in vivo*. (3) The use of rigorous genetics in mammalian model organisms is essential to further elucidate the physiological role of ROS. (4) The development of selective pharmacological scavengers against different types of ROS is needed to test whether ROS are a cause or consequence of pathological conditions. Understanding ROS biology is paramount especially from a public health point of view. Antioxidants are the most widely used or abused drugs worldwide. However, a large number of clinical trials have uniformly failed to demonstrate beneficial effects of antioxidants on a variety of pathologies. We must understand the importance of ROS in normal physiological processes and rationally design antioxidants that do not undermine normal physiology but might be effective under pathological conditions.

Where can I find out more?

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Adaptive aerial righting during the escape dropping of wingless pea aphids

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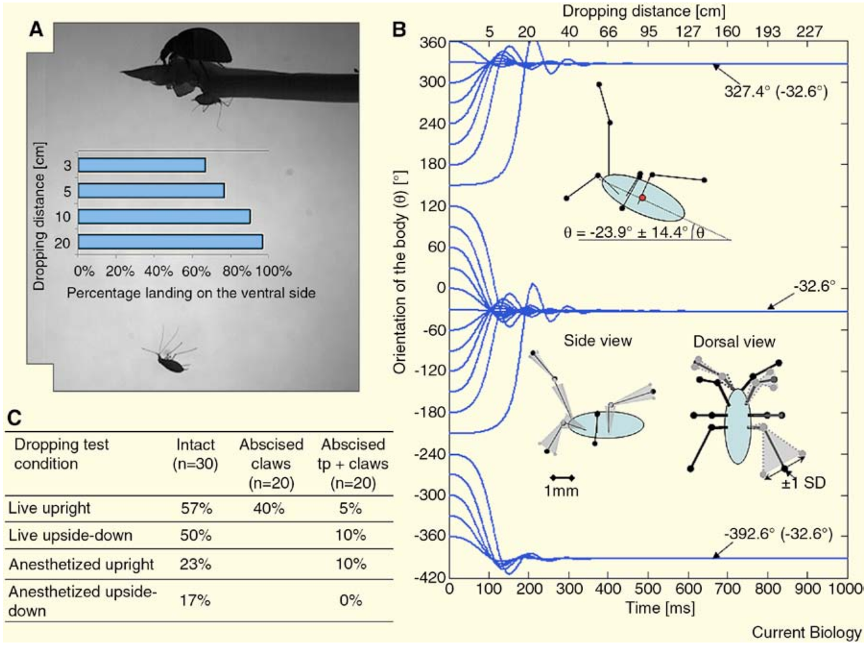
Pea aphids (*Acyrthosiphon pisum*) are small sap-sucking insects that live on plants in colonies containing mostly wingless individuals. They often escape predators, parasitoids and grazing mammalian herbivores by dropping off the plant [1,2], avoiding immediate danger but exposing themselves to ground predators, starvation and desiccation [3]. We show here that dropping pea aphids land on their legs, regardless of their initial orientation on the plant (like a defenestrated cat), by rotating their body during the fall. This righting ability is intriguing, as wingless aphids have no specialized structures for maneuvering in mid-air. Instead, they assume a stereotypic posture which is aerodynamically stable only when the aphids fall right-side up. Consequently, the body passively rotates to the stable upright orientation, improving the chance of clinging to leaves encountered on the way down and lowering the danger of reaching the ground.

We evoked dropping behavior in aphids situated on a fava bean (*Vicia faba*) stem by introducing a predator (ladybug, *Coccinella septempunctata*). The stem was positioned at different heights above a viscous substrate (petroleum jelly) that captured the landing posture. We found that up to 95% of the aphids landed upright after dropping 20 cm (Figure 1A). The aphid's body appendages play an important role in aerial righting: when dropped upside-down from delicate tweezers, live aphids (n = 20), dead aphids (random appendage posture, n = 23) and aphids with amputated appendages (n = 25) landed on their ventral side in 95%, 52% and 28% of the trials, respectively (Fisher Exact, $p < 0.001$). High-speed video visualization of the fall revealed that aphids do not jump off the plant, but rather release their hold, allowing gravity to accelerate them downwards. The aphids start rotating after falling a few body lengths (Supplemental movies S1 and S2) reaching a final right-side up orientation within the first 13.7 cm of the fall (~170 ms) in 90% of the trials (n = 45). Early during the fall aphids assumed a stereotypic posture and maintained it throughout. The aphids moved their antennae forward and up and the hind tibiae backward above the body. In that posture, the aphids reached the ground with the long axis of the body tilted upward so that their ventral-caudal end touched the ground first (Figure 1A,B).

The stereotypic posture was used to construct a mathematical-physical 'model aphid' using mean mass, volume and mass-moment of inertia, measured from five aphids (Supplemental information). Using the model, we simulated body rotations due to air resistance acting on the appendages during the free fall. The simulations show that the stereotypic posture provides static longitudinal stability; i.e., at any starting orientation, the air resistance on the appendages works to return the body to a balanced (zero net aerodynamic torque) orientation, such that the ventral side faces downwards and the longitudinal axis of the body is tilted at 32.6° upwards (Figure 1B). This aerodynamic mechanism is based on the anisotropic drag of a slender (length/diameter >10) cylinder, where the drag of a cylinder aligned normal to the flow is greater than the drag of the same cylinder in axial flow [4]. By orienting the different segments of the appendages at specific angles at a distance from the center of mass, the falling aphids create a pitching torque imbalance that works to rotate the body to the stable orientation. The stable orientation obtained in the model is only 0.6 standard deviations higher than the mean orientation angle (23.9 ± 14.4°) observed in falling aphids.

Controlled descent and gliding are not uncommon in wingless arboreal arthropods [5–7] and aerial righting has been demonstrated in larval stick insects [8]. Controlled descent and righting reflexes may have been primordial precursors for the development of insect flight [6,7] as they improve the fitness of arboreal species trying to avoid reaching the ground [6]. We therefore hypothesized that aphids falling upright would be more successful in stopping the fall on a lower part of their host plant by clinging



Dropping test condition	Intact (n=30)	Abscised claws (n=20)	Abscised tp + claws (n=20)
Live upright	57%	40%	5%
Live upside-down	50%		10%
Anesthetized upright	23%		10%
Anesthetized upside-down	17%		0%

Figure 1. Aerial righting in pea aphids.
(A) An aphid evading a ladybug by dropping off a horizontal stem. The aphid is in the typical stable orientation after falling ~7 body lengths (i.e. less than 3 cm, see Supplemental Movies S1 and S2). The chart shows the proportion of aphids landing on their ventral side as a function of dropping distance (*n* = 30 per group). (B) Computer model simulations of the rotation of the body during free fall in the stable posture. Blue lines denote multiple model simulations differing in the initial orientation (intersection with the vertical axis) of the aphid (-360° to 360°). The upper insert shows an illustration of the mean (±SD) stable orientation angle measured from videos. The model aphid stabilizes on the same angle (-32.6°, i.e the long axis is tilted above the horizontal axis) regardless of the starting orientation, although the time to reach the steady orientation varies. The sign of the angles refers to the sense of rotation. Model aphids starting their fall upside-down and head first rotate to the stable orientation clockwise (negative values) when viewed from the aphids' left side, and aphids falling upside down with the caudal side leading, rotate counterclockwise (positive values; see Supplemental information). The bottom inserts show the mean stereotypic descent posture of falling pea aphids (side and dorsal views in body frame of reference) as measured from the movies and used in the model (compare with the falling aphid in (A)). The shaded grey areas denote ±1 SD of the mean orientation measured (n = 7). The red dot denotes the center of mass (Supplemental information). (C) The percentages of aphids that stayed on a tilted leaflet after being dropped from 15 cm using tweezers. Half of the aphids were anesthetized with CO_2 and in two groups the claws and claws as well as tibial pulvilli (tp) were abscised (see Supplemental Movies S3–S5).

to leaves they hit during the fall. When aphids (*n* = 56) were released over a tilted broad bean leaflet (Supplemental movie S3), 54% of the 35 aphids that landed in a ventral posture stayed on the leaflet. All 21 aphids that landed in a non-ventral posture bounced or rolled off the leaflet (Supplemental movie S4). Apparently, upright aphids use their tibial pulvilli (adhesive pads [9]) to cling to leaves at landing, since abscising the tips of the aphids' legs reduced their ability to stay on the leaf (Figure 1C; Supplemental movie S5).

Small body size provides a scaling advantage for falling aphids. First, small creatures reach lower terminal falling velocities [10], meaning that aphids take a longer time to fall the same distance than larger creatures. This also eliminates the risk of physical damage at impact. Second, in the flow regime typical of tiny aphids, the aerodynamic force coefficients of cylindrical appendages increase steeply with the decrease in size and speed (Reynolds number < 20; Supplemental information). Finally, the aerodynamic torques that rotate the body depend on area and length (scale with body length to the power of 3), while the mass-moment of inertia that these torques need to overcome scales with body length to the power of 5. Consequently, smaller size entails an increase in the aerodynamic-torque: rotational-inertia ratio, thus resulting in faster (more agile) righting. Combining these general predictions explains how slender cylindrical appendages, normally used for walking and sensing, suffice to right aphids in less than 0.2 seconds while falling at low speeds.

The righting mechanism described here requires no dynamic control or constant feedback from the nervous system during the righting itself. It works by simply assuming a specific posture. Dead aphids landed ventrally less frequently than live aphids, suggesting that this posture is not a simple consequence of air resistance aligning the appendages with the direction of the fall. Rather, the aphids actively assume the descent posture (a tarsal or other reflex) and then allow gravity to do the rest.

Supplemental information

Supplemental information including experimental procedures, one figure and one table can be found with this article online at http://dx.doi.org/10.1016/j.cub.2012.12.010.

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