

binding. Furthermore, as acetylation occurs only after microtubule polymerization, the enzyme responsible for this modification should probably localize to the microtubule lumen.

The preference of ER sliding for acetylated microtubules may indicate a functional difference between this type of ER motility and that mediated by the tip attachment complex. Intermembrane contacts are important for many functions of the ER and other membranous compartments [9]. The authors' results led them to hypothesize that the sliding mechanism may be used as a way for ER tubules to find and contact other organelles along a subpopulation of microtubules.

To explore this possibility, Friedman *et al.* [8] tracked the movements of two other organelles, mitochondria and endosomes, with respect to both ER and acetylated microtubules. A majority of both organelles remained in persistent contact with the ER. However, only mitochondria appeared to also localize preferentially to acetylated microtubules, suggesting that ER contacts with mitochondria, but not endosomes, are enriched along acetylated microtubules. Consistent with this finding is the fact that both ER and mitochondria are cargoes of kinesin-1, while endosomes are moved by KIF16B, a member of the kinesin-3 family [15]. Further, work by Cai *et al.* [6] showed that another kinesin-3 family member, KIF1A, displayed no preference for acetylated microtubules in COS-7 cells.

By biasing protein association with a particular subset of microtubules, acetylation allows for subpopulations of microtubules to act as compartments along which specific cargoes can find each other, and be found in return. In a sense, these microtubule compartments can be thought of as cellular pubs that attract a specific cargo crowd for mingling. Microtubule acetylation is also probably involved in the regulation of cell migration both in fibroblasts [16] and neurons [17]. It is attractive to speculate that polarization of moving cells requires kinesin-dependent recruitment of selective cargoes to the leading edge of migrating cells.

Additional investigation is necessary to determine whether this selective motor recruitment applies to other microtubule modifications and other

motor proteins. It is possible that at least some other microtubule motors have a higher affinity for either a specific tubulin isoform or a particular post-translational modification, similar to the preferential recruitment of kinesin-1 to acetylated microtubules. Such selectivity could create multiple microtubule compartments to recruit particular cargoes — different pubs for different crowds (Figure 1). Once bound to microtubules, the cargo can undergo bidirectional transport to facilitate its movement through the crowded cytoplasm. Cargoes recruited to the same subset of microtubules will interact with much higher efficiency, thus promoting exchange of molecules between particular cell compartments. If this simple model is correct, it indicates that, in addition to their role as tracks for long-distance transport, microtubules serve an important role as scaffolds for the organization and compartmentalization of the otherwise randomly distributed cellular components.

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## Insect Vision: A Few Tricks to Regulate Flight Altitude

A recent study sheds new light on the visual cues used by *Drosophila* to regulate flight altitude. The striking similarity with previously identified steering mechanisms provides a coherent basis for novel models of vision-based flight control in insects and robots.

Dario Floreano  
and Jean-Christophe Zufferey

Insects predominantly use vision to steer, to regulate their flight speed

and height, to avoid impending obstacles, to chase moving targets, and to land on objects. Their evolutionary success, ability to fly in complex environments, and the

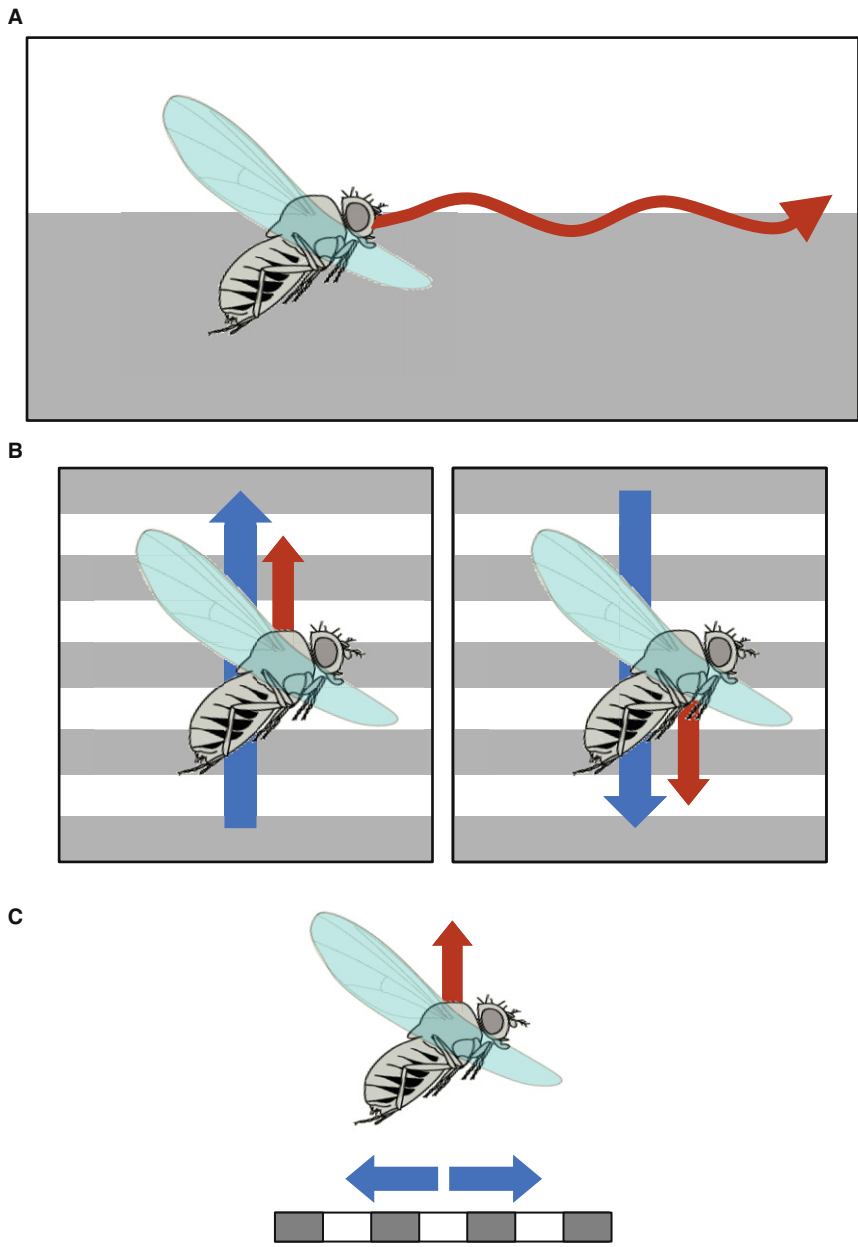


Figure 1. Visual regulation of altitude in *Drosophila*.

Novel findings suggest that *Drosophila* regulate altitude (A) by aligning with static horizontal edges, (B) by increasing or decreasing lift in accordance with the vertical displacement of horizontal structure, and (C) by increasing lift in the presence of optic flow expansion in the ventral field when flying at low altitude.

relatively compact size of their brains and bodies make flying insects not only an appealing subject of research for biologists, but also a compelling source of inspiration for computer scientists and engineers aiming at creating vision-based flying machines [1].

Many experimental studies performed so far on flying insects

have concentrated on visual cues for horizontal steering behaviors. Decades of observations of insects in arenas with controlled visual stimulation have shown that they selectively respond to specific patterns of retinal image motion (optic flow) to stabilize flight [2], regulate speed [3], and avoid collisions [4]. However, little is known

about the visual cues used to control flight altitude. A recent computational model [5], which was validated in experiments with a miniature helicopter, predicts that insects may regulate flight altitude by maintaining a constant angular speed of the ventral optic flow — lower flight altitude generates higher image speed in the ventral area of the compound eyes.

In contrast to this prediction, the novel experiments performed by Straw *et al.* [6], recently published in *Current Biology*, suggest that *Drosophila* does not regulate altitude by monitoring image speed in the ventral area. The authors used an advanced flight arena with computer-controlled speed and direction of images projected on the ground and walls. In a first series of experiments, they cancelled the natural motion of the ground image caused by the insect flight and imposed a controlled set of ventral optic-flow speeds and directions. Because insects did not react to this optical stimulation by changing altitude, the authors ruled out the hypothesis that ventral optic flow is used to maintain altitude and searched for alternative ways in which *Drosophila* could regulate altitude.

In the first set of experiments, Straw *et al.* [6] showed that insects roughly align their flight altitude with the height of horizontal edges that appear near the eye equator, independently of the presence, speed, or direction of a ventral image. They also showed that insects change flight altitude in order to maintain alignment with vertically moving horizontal edges (Figure 1A). This behavior is remarkably similar to previously identified behaviors of horizontal stabilization [7] and tracking of vertical edges [8], suggesting the duplication or use of the same neuronal circuitry for horizontal steering and altitude regulation.

In a second set of experiments, the authors showed that insects increased altitude when presented with lateral, upward moving horizontal gratings and decreased altitude when presented with downward moving gratings (Figure 1B). This behavior, which cannot be explained by edge

alignment, could be mediated by a separate mechanism to compensate for unintended altitude changes — dropping altitude would generate coherent upward motion of the image and thus trigger increased lift. Once again, this behavior is reminiscent of the fly's optomotor response to wide-field horizontal shifts of the visual scene in order to compensate for unintended deviations from straight flight [9,10].

In a third set of experiments, they showed that insects are also sensitive to optic flow on the ventral area, but only when the optic flow corresponded to a pattern of radial expansion centered under the insect at a height of less than 15 cm (Figure 1C). This behavior, which could serve as emergency collision avoidance, is analogous to the well-documented behavior of steering away from areas of expanding fields when flying on a horizontal plane [2].

These results not only provide a novel explanation for flight altitude regulation, but also suggest that insects may use the same few sensory-motor reflexes to control flight in the three dimensions. This hypothesis is very appealing because it provides the basis for the formulation of a novel, coherent theory of vision-based flight regulation that abstracts from the division between flight in the horizontal and vertical dimensions. Such a theory could also generate new predictions about the function and architecture of the neural circuitries mapping optical stimulation of the compound eyes into motor control and drive novel experiments to elucidate the behavioral, neuronal, and genetic basis of vision-based flight control.

Nonetheless, this study raises a few questions. For example, it is not clear to what extent the findings apply also to other insect species. Experimental evidence indicates that honeybees do regulate their ventral optic flow, which makes them react to varying ground speeds by changing their altitude [11], as predicted by the computational model of Franceschini *et al.* [5]. Furthermore, there seems to be a precise correlation between the magnitude of the ventral optic flow

and the altitude of honeybees during landing [12]. Finally, it is not clear to what extent horizontal edges are present in the natural habitat of these insects, at what distance they must be to be used by the animal, and what happens to altitude regulation when no such edges are present.

The work of Straw *et al.* [6] also shows the increasing relevance of computational models developed and tested on robots in order to understand biological principles of behavioral systems. Although the model of ventral optic flow regulation [5] was not confirmed by experimental observations of this study (notwithstanding the caveats mentioned above), it did provide a precise working hypothesis that motivated this novel study. In the future, robotics computational models could also be useful for precisely formulating, refining, and validating in an artificial behavioral system the new mechanisms suggested by Straw *et al.* [6].

Finally, these novel findings can also guide the development of novel control strategies and optoelectronic devices for miniature robots autonomously flying in urban environments, in buildings, or in forests. Although engineers and computer scientists have successfully used ventral optic flow to regulate altitude both in simulated [13] and real flying robots [14–17], those solutions assume the presence of detectable texture in the ventral area of the robot, which in reality is not always the case. Horizontal contrast, which is often prominent in built environments and forests, could replace or complement other strategies for altitude control. The capability and need of detecting horizontal contrasts near the equator line of the eyes may also affect the design of artificial compound eyes, which are attracting growing interest in the engineering community [18–20] because they could offer a field of view, size, and response speed that is better than conventional single-aperture cameras for motion-related tasks.

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