BIOPHYSICS

Antennae as Gyroscopes

Moths use their antennae as part of a motion sensing system that ensures stable flight.

R. McNeill Alexander

Flying insects need to detect unwanted movements of their own bodies, so that they can make any necessary corrections to restore the status quo. They need to know, for example, when their flight is disturbed by an eddy in turbulent air or by an imperfectly executed wing beat. Dragonflies depend on sight for this information. That works well in bright daylight but would not be satisfactory in near-darkness because eyes cannot provide precise information quickly in dim light. Moths active at night need information about unwanted movements to maintain flight stability, especially when hovering to collect nectar from flowers. On page 863 of this issue, Sane and colleagues (*1*) explain how a hawk moth senses its own rotations.

These researchers found that the moth's movement-detection system depends largely on the Coriolis effect, which keeps spinning gyroscopes stable. This effect is an apparent deflection of an object viewed in a rotating frame of reference, seemingly attributable to an apparent force. We already knew of the importance of Coriolis forces for dipteran flies (house flies, mosquitoes, etc.). Instead of having four wings like other insects, dipterans have only two. Their hind wings have been reduced to tiny club-shaped halteres (see the figure) that beat at the same frequency as the fore wings. If their halteres are cut off, these flies become unstable in flight and soon crash to the ground. Pringle (*2*) explained how Coriolis forces on the halteres inform flies of rotations of their bodies, enabling them to fly stably. Sane *et al.* now find that hawk moths can do this with their antennae, although detection of aerodynamic as well as Coriolis forces may have a role.

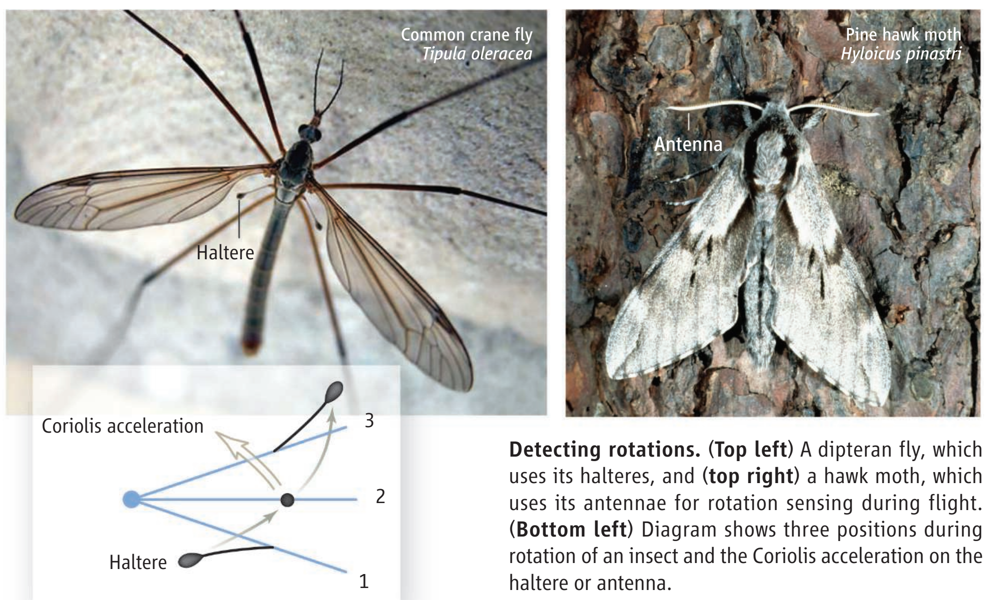
In the diagram, a rod representing a fly's body is rotating with constant angular velocity in the plane of the page. At the same time, a haltere hinged to the rod moves in a plane perpendicular to the paper. As the rod rotates from position 1 to position 3, the haltere swings from one side of it to the other, with constant angular velocity relative to the rod. Although both angular velocities are constant, the haltere has Coriolis acceleration, perpendicular to its plane of movement. Two effects contribute to this. First, the speed of the haltere is increasing as it moves further from the rod's axis of rotation. Second, the haltere's path curves to one side, as shown by the arrows. Coriolis forces must act on the haltere to give it these components of acceleration.

When a rotating-mass gyroscope is disturbed, the heavy wheel rotating at high speed strongly counteracts the disturbance. In contrast, the Coriolis forces on halteres are tiny, far too small to stabilize the fly directly. Instead, they cause slight bending of the stalk of the haltere, which is detected by sense organs, which in turn stimulate the fly to make the necessary adjustments to its wing beat.

Strepsiptera (tiny parasitic insects) have reduced fore wings that seem to work like halteres (*3*), but we did not know until now whether other insects use Coriolis forces to sense rotations. In their report, Sane and colleagues describe rotation detectors that work on the same principle in hawk moths. Like most other insects, moths have four wings and no halteres. They use their antennae in the way that flies use halteres. High-speed films of moths hovering in front of an artificial flower showed that the antennae vibrate at the wing beat frequency (about 27 Hz). When the flower was made to sway, the moth tracked its movements, and small deflections of the antennae, attributable to Coriolis forces, could be seen in the films. Separate electrophysiological experiments showed that sense organs at the bases of the antennae were sensitive enough to detect these deflections.

A simple experiment confirmed the importance of the antennae for stable flight. Intact moths hovered well in the flight chamber, but if their antennae were amputated near their bases, the moths were far more likely to crash to the ground or collide with the wall. When the antennae were glued back on, the moths' hovering ability was largely restored. Axons crossing the cuts had been severed, so the sensory information must have been provided by the organs at the bases of the antennae.

Animals need three-dimensional information about rotations. Vertebrates get this from three semicircular canals in each ear. One might expect each canal to be sensitive only to rotation in its own plane, but the situation is not quite so simple (*4*). Nevertheless, a set of three canals is sufficient to sense any



Detecting rotations. (**Top left**) A dipteran fly, which uses its halteres, and (**top right**) a hawk moth, which uses its antennae for rotation sensing during flight. (**Bottom left**) Diagram shows three positions during rotation of an insect and the Coriolis acceleration on the haltere or antenna.

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rotation. One might not expect two halteres, or two antennae, to be capable of distinguishing three components of rotation, but they can, for a rather subtle reason.

The spectrum of Coriolis forces has peaks at the frequency of the haltere beat and at twice that frequency, and the relative magnitude of the peaks depends on the plane of rotation of the body. Thus, the sense organs in the stalk of the haltere experience a mix of two frequencies of mechanical stimulation, which changes as the plane of rotation changes, enabling each haltere to distinguish two components of rotation. The third possible component (in the plane of the haltere's beat) generates no out-of-plane force, but flies can still fly after one haltere has been amputated, suggesting that each haltere may be capable of distinguishing all three components. They could conceivably get the third one by sensing tension as well as bending in their stalks, but this would require the ability to measure tiny fluctuations in a much larger centripetal force (*5*). In any case, two halteres or antennae set at different angles, each capable of distinguishing two components of rotation, can together provide full information about rotations in three-dimensional space.

Now we would like to know whether other insects, as well as hawk moths, use their antennae to sense rotations. That capability seems potentially useful to any flying animal.

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ATMOSPHERIC SCIENCE

Pumping Up Surface Air

Towering cumulus clouds associated with thunderstorms enable the spread of pollution on intercontinental scales.

Lyatt Jaeglé

Many nitrogen, hydrocarbon, and sulfur pollutants involved in acid rain and photochemical smog are usually removed within hours or days near Earth's surface, but have much longer lifetimes if they reach the cold and dry upper troposphere at altitudes from 8 to 12 km. Towering cumulus clouds associated with thunderstorms (see the figure) can rapidly transport these pollutants to the upper troposphere. This process, combined with fast winds at high altitudes, allows the spread of pollution over intercontinental scales (*1*). Subsequent chemical transformation of these species in the upper troposphere leads to the production of ozone (*2*) and of aerosol particles (*3*), which affect global climate. In addition, convection moistens the upper troposphere, where water vapor has a large effect on climate and its response to increasing concentrations of greenhouse gases (*4*).

However, the rate at which the upper troposphere is flushed out and resupplied with fresh surface air cannot be measured directly. It is therefore difficult to evaluate the influence of deep convection on climate and air quality. On page 816 of this issue, Bertram *et al.* (*5*) use extensive observations obtained during a recent aircraft campaign to infer the turnover rate of the upper troposphere over the eastern United States and Canada during summer. These data will allow quantitative tests of models to assess how deep convection affects the composition of the upper troposphere.

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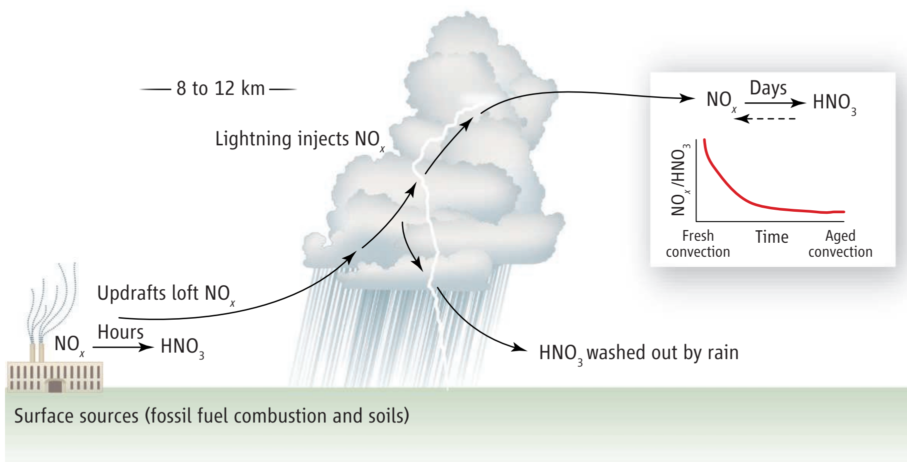

Tracking deep convection. A thunderstorm causes convective transport of NO_x from surface sources to the upper troposphere; lightning injects additional NO_x. Rain washes out the water-soluble HNO_3. High NO_x and low HNO_3 thus indicate fresh convection. As the cloud-processed air is transported downwind over the following days, NO_x is converted to HNO_3, at a rate determined by local chemistry. The NO_x/HNO_3 ratio thus provides a clock that allows the time since convection to be inferred.

Bertram *et al.* use measurements of nitrogen oxides (NO_x, which is the sum of NO and NO_2) and nitric acid (HNO_3) to quantify the influence of convection on the upper troposphere. The data were obtained by the NASA DC-8 research airplane, which sampled the atmosphere over eastern North America in July and August 2004 (*6*). Upper tropospheric air recently affected by upward motions in clouds usually contains high levels of NO_x but low levels of HNO_3, compared to the surrounding air (*7*). The NO_x originates from ground-level sources, such as electric utilities and cars, and from the lightning that accompanies convective clouds. NO_x is not very water-soluble and is thus efficiently transported through these clouds. In contrast, the very water-soluble HNO_3 is quickly removed by rain during convection. Once in the upper troposphere, NO_x is slowly oxidized to HNO_3 and HNO_3 regenerates NO_x until steady-state levels are reached 1 to 2 weeks later (see the figure).

Bertram *et al.* observed NO_x/HNO_3 ratios that were often 5 to 20 times as high as expected from steady-state equilibrium. They use this imbalance to calculate the time since convection occurred. Simultaneous measurements of hydrogen oxide radicals and other chemical parameters constrain the rate at which NO_x is oxidized to HNO_3. The authors use a photochemical box