sufficient number of atoms in the trap, and if the cross-section for absorption of a scattered photon is greater than that for absorption of a laser photon, which was possible because the frequency distribution of scattered light was not the same as that of the laser light.

The observation of collective behaviour in neutral-atom traps at moderate densities is another unexpected and rather beautiful result in this new field. The authors have pointed the way towards a theoretical understanding of the collective effects and have shown that atom traps are important not only for the study of single-atom phenomena and atomic collisions, but also for the understanding of radiation hydrodynamics. □

Christopher Foot and Andrew Steane are in the Clarendon Laboratory, University of Oxford, Parks Road, Oxford OX1 3PU, UK.

INSECT FLIGHT

Unconventional aerodynamics

Roland Ennos

MORE evidence has appeared showing that insects fly by mechanisms quite unlike those used by aeroplanes and helicopters. Zanker and Gotz[1-3] have measured the instantaneous forces produced by tethered *Drosophila melanogaster* flies and find that they cannot be explained by conventional aerodynamic theory. The forces are also evidence that these flies have unusual methods for producing lift.

During the steady flight of an aircraft, air travels faster over the top of the wings than over the bottom and so there is a net circulation of air around the wings. It is the movement of the wing through the air with its attached circulation that results in lift. But if an aerofoil is accelerated from rest it must move a distance equal to several times its own width before the circulation around it and the lift it produces can build up to the steady-state values, a phenomenon known as the Wagner effect.

Conventional analyses of animal flight treat the wings like those of fixed-wing aircraft; they assume that, at each instant, each wing section will produce the same lift as a wing section moving at the same steady velocity and with the same attitude. Total lift is then calculated by integrating these forces over space and time. This is certainly valid for gliding, but wing velocity and attitude are both continually changing in flapping flight. In the extreme case of hovering flight (Fig. 1), the wings travel a distance only a few times their own width during each beat before reversing their direction of travel and rotating by over 90°. Considering the problem of the Wagner effect, it is unlikely that this 'quasi-steady' assumption would be valid for hovering insects. Studies over the past twenty years of the aerodynamics of insects in free flight[4-7] have usually concluded that the forces resulting from a conventional lift mechanism would not be adequate to support or propel the insect, and this has been verified by the results of Zanker and Gotz.

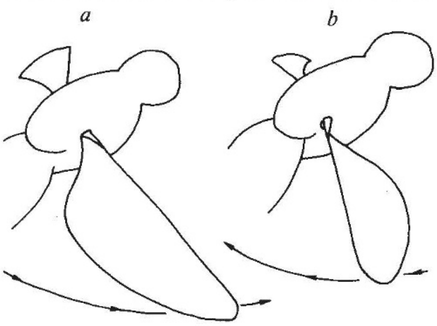

FIG. 1 The wingbeat of a hovering insect. The wings move back and forth, rotating by over 90° between the end of the downstroke (*a*) and the upstroke (*b*), and again at the end of the upstroke.

In addition, Zanker[3] investigated the compensatory reactions of tethered flies in response to changes in visual stimuli (which would make the flies believe they were yawing, pitching or rolling) and changes in the speed of the air blown past them. Flies responded with changes in their wingbeat movements that in free-flight would have stabilized them, but conventional aerodynamic analysis of the altered wingbeat suggested that in some cases these responses would have made the flight more unstable. These insects must have been using different mechanisms both to produce lift and to manoeuvre.

The first unconventional lift mechanism to be discovered was the 'clap-and-fling' described by Torquel Weis-Fogh[4]. He noticed that in the flight of the tiny chalcid wasp, *Encarsia formosa*, the wings were always clapped together at the top of the upbeat of the wings before being rotated and so moved apart, leading-edge first (Fig. 2). He proposed that air rushing into the partial vacuum created as the wings separated would form attached circulations which would create large amounts of lift during the coming wing stroke. This effect has been experimentally verified, and in fact is widely used by flying animals. For instance, the noisy take-off by pigeons is caused by the dorsal clapping of their wings to produce the large amounts of lift they need.

Large values of lift also seem to be produced by animals after they rotate their wings at the start of a wingbeat, even when the wings are well separated. This occurs particularly when this rotation is rapid and is delayed until after the wing has reversed its direction of motion. In hoverflies, for instance, the delay of wing rotation until after the start of the downstroke seems to enable them to produce large amounts of lift and allows them to hover when the wings are flapped through an angle of only about 50°, compared with 120° in most insects[5]. On the other hand, in higher flies such as *Drosophila*, the wings often bend downwards at the end of the downstroke at a line of weakness across the wing[1-3,6,8,9] before flicking back up, leading-edge first. This causes fast, late rotation, which could enable them to generate large amounts of lift during the upstroke.

The mechanisms by which such isolated wing rotation can create circulation and lift are not fully understood, and until now this phenomenon has not been experimentally verified. Zanker and Gotz have achieved this by using flies tethered to a force transducer that could pick up a continuous record of the vertical forces produced during the wingbeat. They were able to show that in *Drosophila* peaks of lift production were produced not only after clap-and-fling at the top of the upstroke, but also after isolated wing rotation at the bottom of the downstroke.

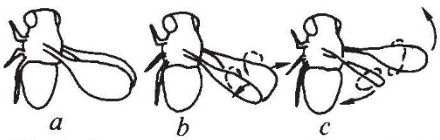

FIG. 2 Wing movements generating unsteady lift during the clap-and-fling. The wings are clapped together (*a*) then rotated, leading edge first (*b*). Air rushes into the gap (broken arrows) and a circulation is set up around the wing for the coming stroke (*c*).

Their results have two important implications. First, it is clear that to solve the problem of how insects control their flight will be extremely difficult; even if we discover exactly how the large numbers of direct flight muscles control the fine details of wing movement, we will not be able to solve this problem until we have a better understanding of unsteady aerodynamics. Second, studies of the aerodynamics of aerofoils in unsteady motion are urgently needed. Such investigation might not only clarify how animals fly, but would help us to improve our own aerodynamic designs; insects and birds are, after all, far more manoeuvrable than helicopters or aeroplanes. □

Roland Ennos is in the Department of Biology, University of York, York YO1 5DD, UK.

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