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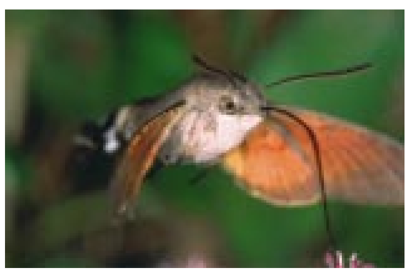
Cover illustration

A dinner dance

Flowering plants must attract birds or insects to help disperse their pollen. The attraction, of course, is usually nectar, but this must be advertised with bright colours and/or scent. The pollinators seek the nectar and usually cooperate, quite innocently, by transporting the pollen. Most insects, like bees, land on a flower, seeking the nutritious reward. Some few insects, like the hummingbird hawkmoth *(Macroglossum stellatarum*), however, do not maintain their end of the unwritten bargain. This interesting creature will hover above the flower, using an unbelievably long coiled tongue that may be three times the length of the insect to extract the nectar and cheat the flower of its pollinating potential. This frenetic Old World moth is a member of the family Sphingidae and is primarily diurnal. These moths have a remarkable hovering flight that resembles that of a hummingbird. They are quite agile and can even fly while coupled during mating. (Hummingbirds are primarily South American, are found exclusively in the New World, and also hover, but they are completely unrelated to this moth.)

This fast flying and fascinating moth is common to European gardens in the summer and deserves more than passing attention. Consider its difficulties. While this moth is hovering above its intended meal, the flower may be caught by a brief gust of wind and move in almost any direction, in any of three dimensions, creating difficulties for the feeding moth. The long proboscis must remain in contact with the small supply of nectar at the base of the flower, and hence the moth must move with the flower, deftly so as to maintain that contact with the base of the flower and the nectar. This aerial positioning is accomplished by sophisticated optical and neural mechanisms that result in surprisingly good visual acuity and movement sensitivity.

To begin with, this hawkmoth has an unusual and complex compound eye that does not have the typical anatomy of most insect eyes. Most of the dipterid species (flies) have neural superposition compound eyes (*BJO* cover, September 2001) that are more complex than, and an evolutionary step up from, the simple apposition compound eyes of more primitive insects (*BJO* cover, March 2001). Each individual unit of the compound, multifaceted eye of the insect is known as an ommatidium. In the classic Exnerian explanation of the compound eye, each ommatidium has a lens as a focusing element and a collection of retinular cells within that ommatidium. Each retinular cell contributes a portion of its folded membrane (rhadomere) that joins with its counterparts from the other retinular cells to create a "rhabdom" along the axis of the ommatidial cylinder. This rhabdom functions as the ommatidium's photoreceptive structure. Although there are variations in the neural mechanisms that occur behind each visual unit, the insect brain receives a mosaic pattern of visual signals that is assembled into a complete image. The



hummingbird hawkmoth has a so called "refracting superposition compound eye," a very sensitive design more typical of nocturnal moths. However, the hummingbird hawkmoth is diurnal, and its bright habitat has allowed remarkable specialisations not known in any other superposition eye. This moth's eye is aspheric and possesses areas of higher resolution and sensitivity that function much like the foveae of vertebrate eyes, features that violate our previous understanding of how superposition eyes function. The optical design of a classic refracting superposition eye allows the lenses of a large number of ommatidia to focus light onto each rhabdom of the retina. According to the classic theory of Sigmund Exner (1891), this requires that the retinular cells are at a set distance behind the lenses (thus resulting in a spherical eye), and that the number of rhabdoms equals the number of facet lenses. But this hawkmoth eye has many more rhabdoms than facets, with the rhabdoms being packed into the retina much more densely than the overlying facets would suggest. Denser rhabdom packing creates a more detailed image at each location where this occurs—in effect creating a fovea. These areas of the eye also have the largest numbers of facets supplying light to each rhabdom. The hummingbird hawkmoth's superposition eyes have thus evolved regions where the visual image is both very bright and highly resolved. This is developed to its greatest extent in the frontal regions of the eyes, which are used for close observation of the flower petals beneath the moth while it hovers (Warrant E, *J Exp Biol* 1999;**202**:497). Looming sensitive neurons, found in the optic lobes of the brain, help to interpret and integrate the expanding and contracting visual image of the moving flower. This results in the necessary lateral arabesque that stabilises flight and allows the moth to maintain its position directly above the flower in a soft summer breeze.

These remarkable moths also have true trichromatic colour vision—that is, they have been shown to discriminate objects on the basis of their spectral information alone, independently of intensity (Kelber A, *et al*, *J Comp Physiol A* 1999;**184**:535). To do this, these creatures have at least three spectral receptor types. These include an ultraviolet type, and there does not appear to be a long wavelength pigment that is stimulated in the redder portion of the spectrum, so the trichromacy is not the same as ours.

A related hawkmoth (*Deilephila elpenor*) has been shown to have nocturnal colour vision and is the only animal known to have it (Kelber A, *Nature* 2002;**419**:922). Furthermore, it has good colour constancy; the quality that allows animals to identify a lemon as yellow in different coloured shades of illumination. Having three different visual pigments, as you might imagine, does decrease the absolute sensitivity of the eye, and in order to see well at night temporal and/or spatial summation of the photic stimulation must occur (Kelber A, *et al*, *Nature* 2002;**419**:922).

So, this moth's aerial ballet becomes its dinner dance.

I R Schwab, E J Warrant
University of California, Davis, Sacramento, CA 95817, USA; irschwab@ucdavis.edu and University of Lund, Sweden

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