New and Notable

When Flies Are Flat and Dead

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The sound made by a flying insect can often give us a clue to the identity of the animal. Mosquitoes whine, butterflies flutter, bees buzz, and June-bugs clatter. These onomatopoeias mimic both the dominant frequency and waveform of sounds made by the beating wings of different insects. A whine is a higher frequency than a hum, and a hum has a more sinusoidal waveform than a buzz.

Our ears are very good at identifying frequency characteristics of sounds; in effect, they provide our brains with a Fourier transform of incoming sound vibrations. This reduces the amount of "brain computing time" required to interpret different sounds. Most people can tell if music is out of tune and what instrument is being played, whereas only very few can identify the actual notes being played (by their frequency). Hyatt and Maughan (in this issue) present a method that allows a personal computer to characterize the motion of an insect's wings in the "frequency domain." They use an optical device to detect flashes of light reflected from the wings of a flying fruitfly. Microphones and optical tachometers produce an electrical signal that varies in time and in some way relates to the motion of the wings (the exact relationship is not clear). By calculating the Fourier transform, both fundamental frequency and wingbeat waveform can be assessed.

What can the wingbeat waveform tell us about the flight system? To address this question, something must be said about the unusual nature of the flight muscles and wings of Diptera:

1) Dipterans have only two wings (not four like most insects). This makes acoustic or optical signals easier to interpret.

(To some extent this explains why flies hum whereas bees buzz.)

2) The flight system of Diptera and other insect orders that have species with high wingbeat frequencies (bees and wasps, beetles and true bugs) have flight muscles that are *myogenic*. Muscle contractions are asynchronous with nervous input, and generation of force occurs with a delay after muscle stretch.

3) The wings behave as an inertial mass suspended by the spring-like stiffness of the flight muscles with some additional contribution to mounting stiffness and inertia from the thoracic cuticle. Muscles provide power for flight because the time course of delayed tension rise after stretch matches the period of the wingbeat (Molloy et al., 1987). One would expect wing oscillations to be sinusoidal. However, harmonic distortion can be produced by nonlinear elasticity. Either *catastrophic* elasticity of the thoracic cuticle (known as the "click" mechanism) or nonlinear elasticity of the flight muscles (White and Thorson, 1972)

In such a system, if wing mounting stiffness is reduced then wingbeat frequency falls. Conversely, if wing inertia is lower (e.g., shorter wings) wingbeat frequency will be higher (this is the main reason why small insects have high wingbeat frequency). But what happens if resonance frequency of the wings no longer matches the time course of muscle contraction? This can arise in three ways: 1) wing mutations that affect the moment of inertia leaving muscle kinetics "out of tune" with the changed resonant frequency; 2) muscle mutations that affect muscle stiffness and, thereby, resonant frequency but in which contraction kinetics remain wild-type; 3) muscle mutations in which muscle stiffness is close to wild-type but in which contraction kinetics are changed. Mutations of types 2 and 3 have been reported previously (Molloy et al., 1993; Drummond et al., 1990). Hyatt and Maughan identify a myosin light chain mutant that seems to fall somewhere between classes 2 and 3 in which both muscle stiffness and kinetics are

changed. The wingbeat frequency is reduced by nearly 30% from 210 to 150 Hz, and spectral broadening about the resonant frequency (characterized by an arbitrarily defined parameter H) is caused by reduced "coupling-efficiency" between the optimum driving frequency for the muscles and wing resonance frequency. Wing vibrations are more highly damped or acoustically "deadened."

A limitation of the technique presented here is that optical tachometers do not measure wing angle, so the method should be used with some caution. It will be of great value to those who wish to screen for *Drosophila* flight muscle mutants produced by random mutagenesis where several thousand individuals need to be tested.

As an historical end note: the first person to make an extended study of insects' "flight tones" (Sotavalta, 1947) used no electrical transducers or sophisticated computation; he used his ears! He possessed perfect pitch and could calibrate his hearing to within less than 6% of the dominant frequency that he heard. We are all not fortunate enough to have perfect pitch, and the method of Hyatt and Maughan will be useful to those interested either in identifying different insects at a distance or screening for and studying the in vivo effects of *Drosophila melanogaster* muscle mutations.

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