Thus Palaeodictyoptera nymphs support the theory that the ancestral pterygote had three pairs of veined thoracic lobes, enabling it to warm up and become more active faster. Extended lobes with some articulation enabled the insect to glide, perhaps to escape predators and to aid dispersal. The final step was for the articulation and musculature to develop to allow two pairs of wings to be actively flapped. This major development allowed insects to colonise the world.

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Motor Control: Winging It with a Few Good Muscles

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A recent study reveals how flies achieve their remarkable aerodynamic agility with only a small number of wing muscles.

Few flying animals are as agile as flies. Centuries of frustrated fly swatters can attest to that. In a split second, a fly can change direction at will or react to turbulence to stay on course. Amazingly, this agility is achieved along *three* axes of rotation [1]. While terrestrial animals only rotate about the vertical axis and turn left or right, flies can also rotate nose-up or nose-down and roll from side to side. To manoeuver rapidly and stably along these three axes requires a highly sophisticated flight control system. Anatomists have long recognized, however, that flies control their flight with a strikingly small number of wing muscles: the fruit fly *Drosophila*, for instance, uses only a dozen wing muscles to control flight, each supplied by a single motoneuron. How such a sparse motor system can allow flies to fly with such finesse has eluded neuroethologists for decades.

That is, until now. In this issue of *Current Biology*, Lindsay *et al.* [2] report the secret to a fly's remarkable aerial agility. They discovered that the wing musculature of *Drosophila*, while consisting of only a few muscles, is functionally organized in a far more 'stratified' and logical fashion than we previously appreciated.

To crack the mystery of fly flight, neuroethologists have sought to understand how each wing muscle contributes to flight stability and steering. Traditionally, this problem has been approached using electrophysiology: a fly is tethered to the tip of a tiny rod, and an electrode is inserted into an individual muscle to record the muscle's firing pattern during flight. By correlating patterns of muscle activity with changes in wing kinematics during flight, scientists can infer the role of that muscle in flight control.

These types of experiments have provided great insights into how wing muscles control flight, particularly during rapid turns [3]. Most muscles examined were found to be inactive during straight flight, but transiently activated when the fly steered. Moreover, the activity of each wing muscle was associated with specific changes in the motion of the wing located

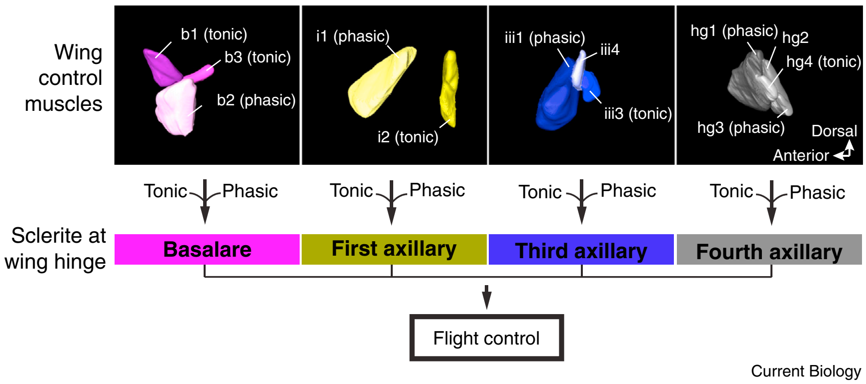

Figure 1. Functional and anatomical organization of the wing musculature in *Drosophila*.
Twelve wing control muscles are subdivided into four groups of muscles that insert directly onto one of four sclerites at the wing hinge. Each wing muscle group contains at least one 'tonic' and one 'phasic' muscle, which provide continuous, fine-scaled and transient, gross inputs onto each cuticular element at the wing hinge, respectively. These inputs displace sclerites at the wing hinge in precise ways, thereby regulating wing kinematics during flight manoeuvres and stability.

on the inside or outside of the intended turn.

Electrophysiology is a powerful way to investigate wing muscle function during flight, but it nevertheless has its limitations. Most notably, not all wing control muscles can be studied by electrophysiology. Some muscles are located at sites on the fly's thorax that obstruct wing movement when occupied by an electrode. As a result, electrophysiological studies on wing musculature have provided data on only *half* of the fly's wing control muscles [3], and several aspects of flight control have remained elusive. For instance, if most wing muscles are recruited only during turns, how does the fly *continuously* adjust wing motion to fly straight and stably in spite of perturbations? To get a more complete picture of flight control, neuroethologists would have to figure out a way to expose the activity of the *entire* wing motor network.

By leveraging the genetic tools available in *Drosophila*, Lindsay *et al.* [2] were able to visualize the activity of all twelve wing control muscles *simultaneously* in intact, flying flies. They engineered transgenic flies that expressed the genetically encoded fluorescent calcium indicator, GCaMP6f [4], in all wing control muscles. The fluorescence of each wing muscle was then monitored as the fly flew and steered in response to optomotor stimuli. The authors were able to infer muscle activity from changes in the intensity of GCaMP6f fluorescence as a result of changes in intracellular calcium levels.

Lindsay *et al.* [2] discovered that a fly's twelve wing control muscles generally fall into two anatomically and functionally distinct groups (Figure 1). One group of relatively large 'phasic' muscles displayed patterns of activity that were associated with large, ephemeral changes in wing motion, like those seen during rapid turns. The authors also discovered a group of smaller 'tonic' muscles that influenced wing motion in a continuous, graded fashion. By making continuous fine-scaled adjustments in wing motion, these tonic muscles allow flies to fly stably and remain on course during flight perturbations.

These wing control muscles exert their effects on wing motion through the wing hinge, an exceedingly complex and specialized mechanical joint. The wing hinge is composed of several minuscule cuticular elements called sclerites, four of which are directly influenced by wing control muscles [5] (Figure 1). By mechanically displacing these four sclerites in specific ways, wing control muscles produce precise changes in wing kinematics during flight manoeuvres and stabilizations [3,6].

Anatomical studies have shown that a fly's twelve wing control muscles are subdivided into four motor units that each insert onto one sclerite at the wing joint [5]. Interestingly, Lindsay *et al.* [2] found that each of the four motor units contains at least one 'phasic' and one 'tonic' wing muscle. Thus, each motor unit can independently influence separate elements of the wing hinge (and thereby flight) continuously *and* transiently with fine-scaled and gross adjustments, respectively.

These findings suggest that a fly's wing musculature is far more 'functionally stratified' and logically organized than we had previously anticipated. This organization allows a sparse wing motor system to function with a broader and more precise range of flight control than one might anticipate based on the number of elements that compose the system. Lindsay *et al.* [2] thus provide the elusive skeleton key to the mystery of fly flight that has puzzled insect neuroethologists for so long.

This pattern of functional organization may also suggest that during evolution, it is easier and faster to expand the function of a motor system by "stratifying" existing substrates than by evolving new ones. It is noteworthy, in this regard, that the same set of wing control muscles in *Drosophila* has been co-opted for use in other behavioral contexts, such as courtship [7,8]. How the wing motor system is functionally organized in these other contexts is an intriguing question for future work.

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