

Locust flight

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Under certain environmental and population conditions some species (the locusts) of *Acridid Orthoptera* swarm and are capable of migrating hundreds of miles using flight as the primary means of locomotion. Locust flight is a behavior that lends itself to analysis from many approaches and that has attracted considerable research attention for many years. In particular the role of the nervous system in controlling locust flight behavior has been a focus of investigation since the middle of the twentieth century.

Locust flight is achieved by the movements of two pairs of wings located on the mesothoracic and metathoracic body segments ([Figure 1](#); see also www.zoobotanica.plus.com/GIF%20files/Zoological/locust.GIF). The pairs of wings are not equivalent: the hindwings have a greater surface area and generate most (70%) of the total lift during flight, whereas the forewings are more rigid and show a greater asymmetry in their beat during steering maneuvers (for figure of forewing movement cycle, see [Figure 1 of http://jeb.biologists.org/cgi/reprint/201/5/731.pdf](http://jeb.biologists.org/cgi/reprint/201/5/731.pdf)). During flight the wings beat at a frequency of around 23 Hz, depending on the size and the sex of the individual locust. Rhythmic elevation and depression of the hindwings leads equivalent movements of the forewings by between 5 and 10 ms ([Video 1](#)). Changing the angle of attack (supination or pronation) of the wings during the downstroke provides variation in lift. Steering and maneuvering during flight is performed by changing the relative timing, amplitude, and form of the wing beat on either side of the body ([Video 2](#); [Figure 2](#); [Dawson et al., 1997](#)).

The 10 muscles controlling each wing (see [Figure 1](#)) either attach directly to the base of the wing or indirectly cause wing movements by deforming the thoracic box. Some muscles are bifunctional in that they are also used to move the legs during walking. Electromyographic recordings taken from the wing muscles of flying but tethered locusts have revealed a relatively stereotyped pattern of muscle contractions during flight. This is termed the *flight motor pattern* and consists of alternating activity in elevator and depressor muscles of the wing ([Figure 3](#)).

Wing muscle activity can also be monitored telemetrically, allowing investigation of the motor patterns controlling wing beat parameters during free flight ([Kutsch et al., 1999](#)). Different wing movements underlying flight maneuvers are controlled by changes in the relative timing and strength of contraction of particular wing muscles. The relative timing of the forewing first basalar depressor muscles (M97) is often used as a convenient indicator of steering with earlier firing by as much as 10 to 15 ms on the inside of the intended turn. Perturbing the activity of these muscles during tethered flight has a profound effect on the form of the wing beat ([Hedwig and Becher, 1998](#)).

Locusts are neurogenic flyers in that the pattern of muscle contractions is a replica of the pattern of activity of motoneurons. About 80 motoneurons phasically active with the flight rhythm and located in the three thoracic (pro-, meso-, and metathoracic) ganglia (see [Figure 1](#)) provide excitatory drive to the wing muscles. These neurons have been identified both morphologically and physiologically, and they exist as two apparently identical sets of homologs: one to drive muscles of the forewing and the other those of the hindwing. Motoneurons are driven to fire by premotor interneurons located in the thoracic ganglia. Numerous ($n > 50$) interneurons that are phasically active with the flight rhythm have been identified. Several of these ($n > 15$) are known to produce short-latency excitatory or inhibitory input to either elevator or depressor motoneurons. The flight interneurons that have been described are generally not organized into two homologous groups for the separate control of forewing and hindwing, although specific examples of this sort of organization can be found.

Under the appropriate stimulus conditions (e.g., wind stimulation of the head of the animal) the thoracic ganglia can produce flight rhythms even when the central nervous system is isolated from phasic sensory feedback and from receptors in the wings. This indicates the existence of mechanisms for centrally generating a flight-like motor pattern (i.e., the existence of a central pattern generator). The motor pattern recorded from deafferented preparations is not identical to the flight motor pattern. In particular the frequency of the rhythm is reduced to about 12 Hz. Some debate over the relative importance of central versus peripheral elements in generating the intact flight motor pattern has occurred. Wing hinge stretch receptors, wing tegulae, chordotonal organs, and campaniform sensilla are all proprioceptors that mediate compensatory reflexes necessary for straight and level flight. In addition, some of these are involved in timing the wing beat phase transitions and in setting the wing beat frequency. Peripheral feedback loops are integral components of the circuitry generating flight.

Information on the physiology of interneurons and motoneurons and on the synaptic connections between them has been obtained by recording intracellularly from the neuropil processes of neurons during the short flight sequences expressed by deafferented preparations ([Figure 4](#)). Motoneurons and interneurons can be distinguished physiologically. In motoneurons the recorded spike amplitude is greater and the intraburst spike frequency is lower (about 70 impulses/second compared with about 225 impulses/second for interneurons). Perturbing the activity of single motoneurons by injecting current pulses during the expression of the flight rhythm has no noticeable effect on the timing of the rhythm. Thus motoneurons are generally considered not to have a role to play in pattern generation. However, similar stimuli delivered to some single interneurons ($n > 5$) during flight sequences can reset the rhythm by increasing or decreasing the period of only the cycle in which the stimulus falls. This indicates that the central motor pattern is generated at the interneuronal level.

Bursts of spikes in flight neurons are superimposed upon membrane potential oscillations that can be as large as 25 mV. These oscillations are caused by rhythmic excitatory and inhibitory synaptic input, probably mediated by glutamate and GABA respectively (Figure 5).

Unitary postsynaptic potentials are typically 2 to 4 mV in amplitude, and every presynaptic neuron has so far been seen to have only one type of postsynaptic effect on different neurons. Temporal summation, facilitation, and input from a variety of different neurons all help in creating the membrane potential oscillation of individual neurons. In addition, superfusion of octopamine, a neuromodulator known to be released into the hemolymph during flight, can trigger flight rhythms in dissected preparations and can induce plateau potential generating properties in specific interneurons. Endogenous mechanisms of membrane potential oscillation are probably involved in flight rhythm generation in the intact animal.

The basic unit of activity of the central motor pattern is an elevator followed by a depressor depolarization sequence. Variation in the cycle period tends to result from changes in the depressor to elevator latency. A circuit of interneurons and their synaptic connections has been described that may underlie certain features of the centrally generated motor pattern. It cannot be considered complete; nevertheless, computer simulation of this circuit suggests that it is sufficient to generate the deafferented flight motor pattern. A pathway of connections can be traced from interneurons involved in timing the rhythm to the wing motoneurons. Drive for both forewing and hindwing motoneurons originates, at least partially, in the same source, indicating that most likely a single central pattern generator exists with an output that is distributed to the motoneurons of the different wings. However, hemisection of the mesothoracic ganglion has only a minor effect on flight ability in recovered animals. Peripheral feedback loops may interact with central elements to create separable, wing-specific oscillators.

Numerous sensory systems are involved in controlling the direction of flight. These include the wind-sensitive head hairs, the compound eyes, the ocelli, and the antennae. These systems generate reflexes necessary both for maintaining and for changing course during flight. The neural pathways underlying these reflexes are amenable to intracellular analysis. For example, ocellar stimulation activates two pathways to wing motoneurons. The stronger pathway is via thoracic ocellar interneurons that are phasically modulated with the flight rhythm, thus perhaps providing a means of gating tonic sensory input.

The neural circuitry described previously is not hard-wired but is subject to plastic changes associated with development, functional recovery after a peripheral lesion, and short-term learning. Immediately after the final molt, the winged adult is capable of flight but the wing beat frequency is low (around 14 Hz). The flight system matures during the subsequent 2 weeks. This is partially a consequence of maturation of peripheral elements (muscles and sense organs). Nevertheless, the central flight pattern also increases in output frequency during this period, indicating a maturation of interneuronal circuits. Interneuronal neurites increase in diameter during maturation, probably reducing conduction delays in the circuit (Figure 6). Partial deafferentation by lesioning the hindwing tegulae results in a drop in wing beat frequency. Functional recovery from such a lesion can occur as a result of sprouting of the forewing tegulae afferents and the formation of new connections (Wolf and Büschges, 1997). Finally, short-term changes in the efficacy of muscle-specific proprioceptive input, associated with exteroceptive signals signaling deviation from course, represent a learning mechanism to ensure that the flight system is conformed appropriately for the prevailing condition of the animal.

Awareness is increasing concerning interactions between the nervous system and other aspects of flight behavior important in a broader context. For example, activity in the flight circuit inhibits the normal discharge of certain large neuromodulatory neurons (octopaminergic Dorsal Unpaired Median, DUM, neurons) and this leads to a change in the fuel used by the flight muscles (Mentel et al., 2003). In addition, population conditions have dramatic effects on locusts and their behavior (Simpson et al., 2001), most noticeably as the different polymorphic phases (solitary and gregarious; see figure at http://earthobservatory.nasa.gov/Study/Locusts/Images/locust_comparison.jpg), and concomitant changes occur in neuronal properties. Finally, locusts are poikilotherms living in equatorial regions suggesting that the operation of the flight circuit has to operate successfully in a wide range of temperatures. Temperature has profound effects on membrane, synaptic, and circuit properties (Figure 7), and at extremely high temperatures the system fails. Locusts, like other organisms, have a heat shock response, and prior heat exposure increases the upper temperature limit of the operating range for the flight system (Robertson et al., 1996), possibly via a reduction of potassium conductance to increase the duration of action potentials and prevent the temperature-induced reduction of synaptic potentials below a threshold amplitude required for circuit operation.

The generation of the motor pattern underlying flight in the locust is dependent upon the flexible interaction of central and peripheral elements. Both aspects of this control are amenable to detailed intracellular analysis. The locust flight system thus provides an excellent model for the investigation of mechanisms underlying the control of locomotion, the spatio-temporal patterning of electrical activity, and the interaction of neural circuits with the environment.

1. See also

[Circuits, neural](#)

[Locomotion control](#)

[Motor control, invertebrate](#)

2. Further reading

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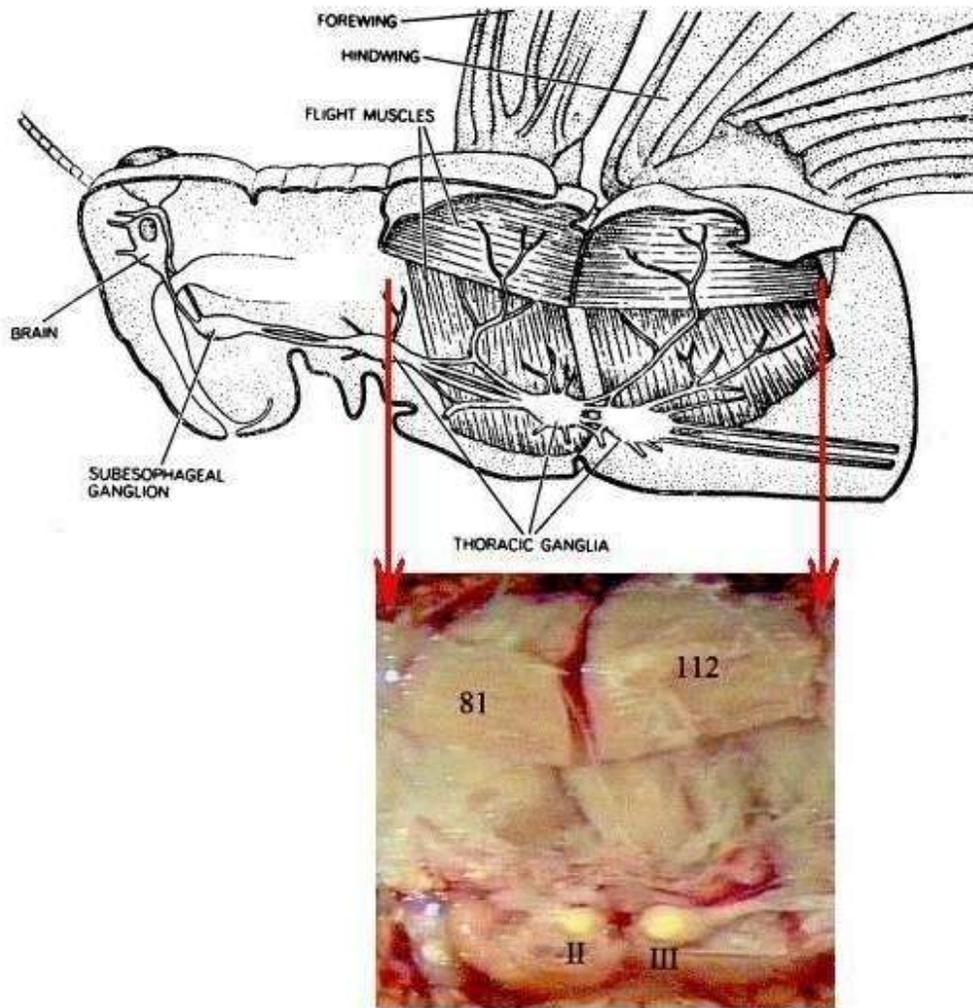
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Figure 1. Nerves and muscle controlling flight in the locust. Parasagittal section through the head and thorax of a locust illustrating the right forewing and hindwing, the flight muscles that move the wings, and the three thoracic ganglia of the ventral nerve cord that contain interneurons and motoneurons responsible for generating flight motor patterns. The inset shows a dissection of *Locusta migratoria*. Muscles 81 and 112 are dorsal longitudinal muscles (indirect wing depressors) of the forewing and hindwing respectively. The mesothoracic (II) and metathoracic (III) ganglia contain most of the neurons of the flight circuitry. (Reprinted from Wilson DM (1968): *The Flight Control System of the Locust*. New York: Scientific American, Inc. All rights reserved. Inset kindly provided by Jeff W. Dawson.)

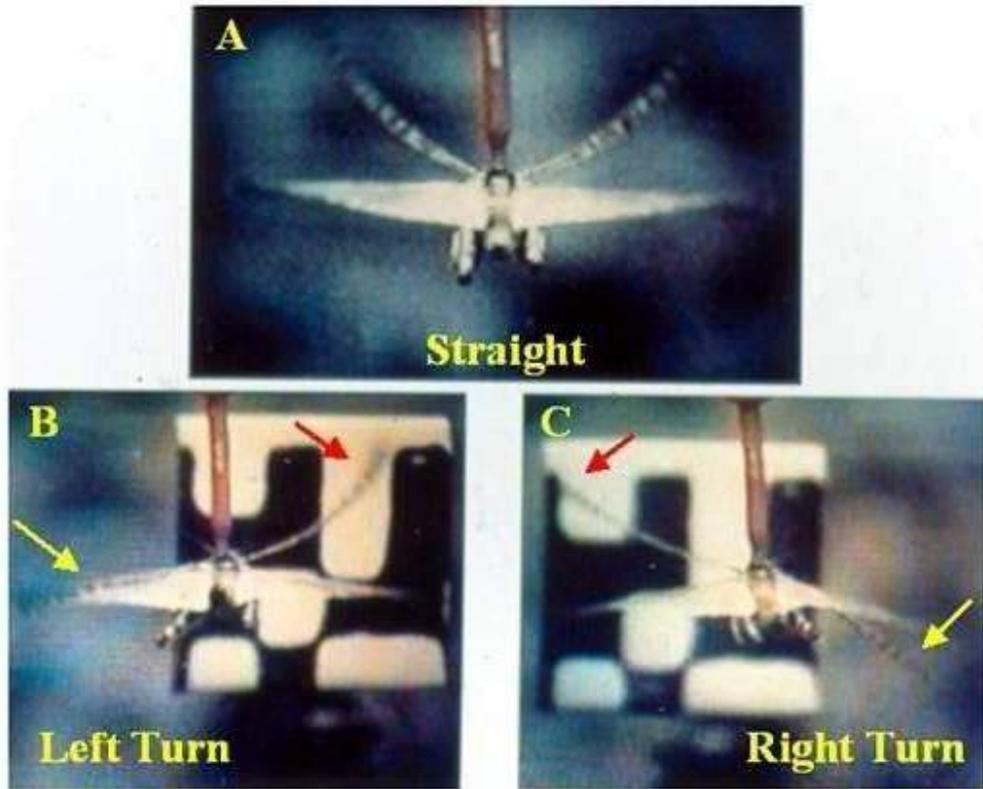


Figure 2. Wing movements during avoidance steering. **A**, Rear view of a locust in straight tethered flight at mid-downstroke. The reader should note that the hindwings are horizontal and slightly lead the forewings that are about 30 degrees from horizontal. Both forewings and hindwings are symmetric. **B**, A steering maneuver to the left to fly around the closest edge of an approaching object (approaching at 0.4 m/second to 1.0 m/second on the bed of an XY plotter). The forewings are now markedly asymmetrically, with the forewing on the inside of the turn (*yellow arrow*) phase advanced relative to the forewing on the outside of the turn (*red arrow*). The timing of the hindwing beat remains relatively symmetric, although an earlier and more pronounced pronation occurs on the inside of the turn. The abdomen and hind legs also extend into the turn and act as rudders and to shift the center of mass. **C**, The mirror image is evident when the locust attempts to avoid an approaching object by steering to the right around it. (Modified from Robertson RM, Reye DN (1992): Wing movements associated with collision-avoidance maneuvers during flight in the locust, *Locusta migratoria*. *J Exp Biol* 163:231-258.)

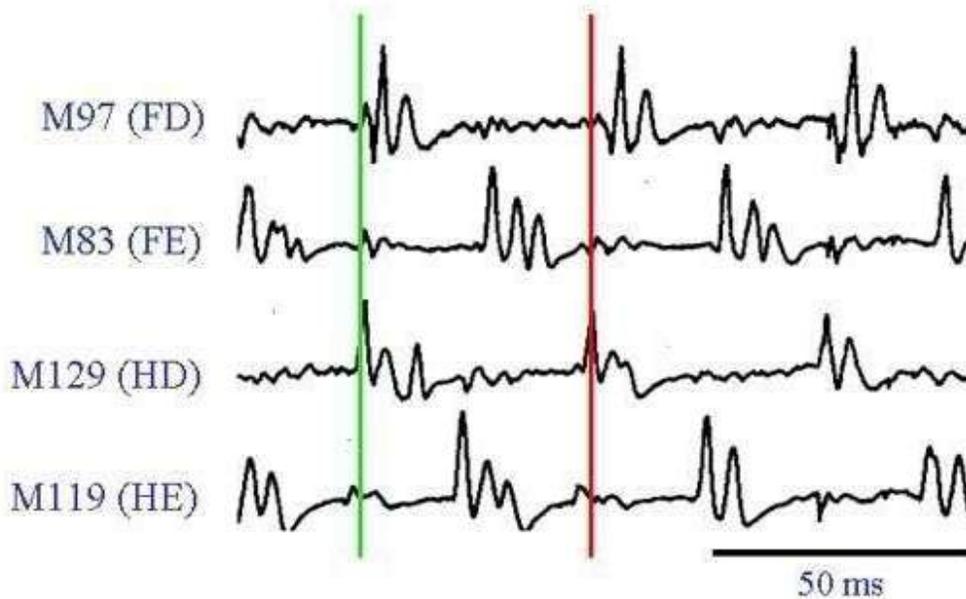


Figure 3. Straight flight motor pattern of a tethered locust. Electromyographic recordings from muscle 97 (first basalar, forewing depressor), muscle 83 (first tergosternal, forewing elevator), muscle 129 (subalar, hindwing depressor), and muscle 119 (first posterior tergocoxal, hindwing elevator) reveal a pattern of activation in which depressors and elevators alternate and hindwing muscles are activated 5 to 10 ms in advance of equivalent forewing muscles. A single wing beat cycle is defined between successive activations of the hindwing depressor (*green line to red line*). Cycle period is about 43 ms (wing beat frequency: 23 Hz).

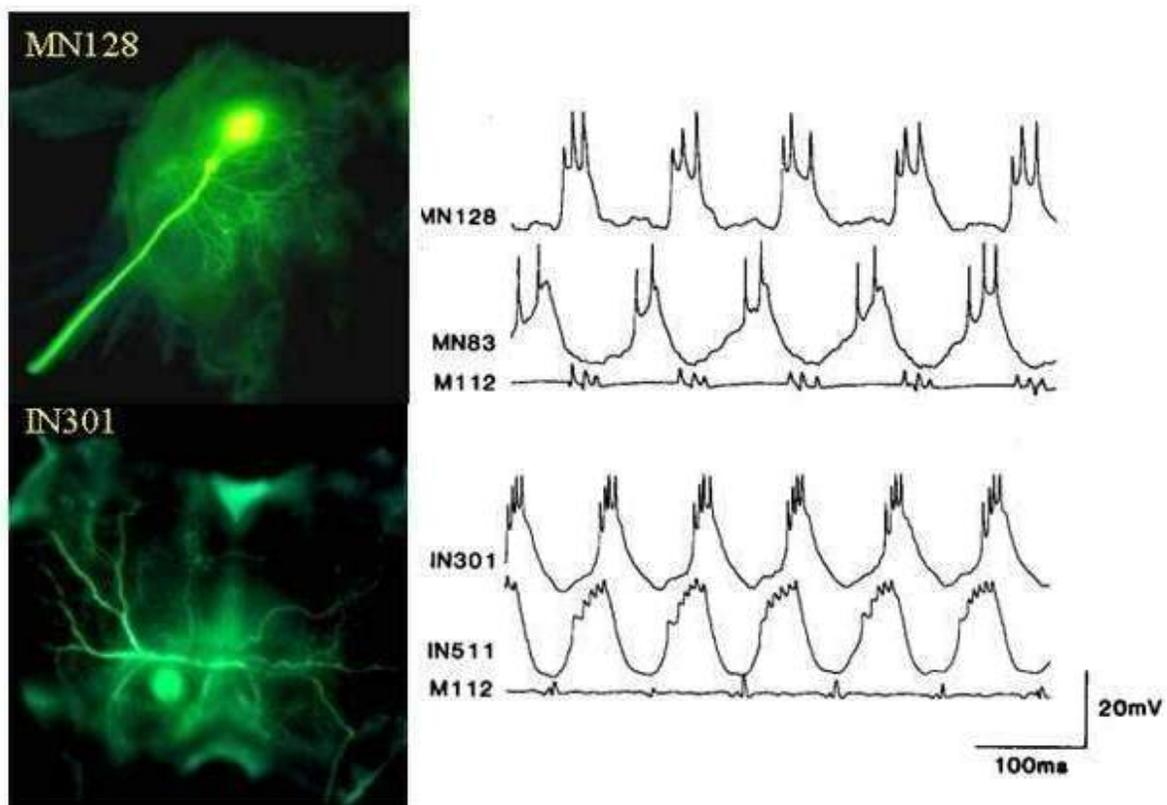


Figure 4. Intracellular recordings from flight motoneurons and interneurons in a deafferented preparation. *Top panel:* Lucifer Yellow fill of motoneuron 128 (second basalar, hindwing depressor) beside simultaneous recordings from this motoneuron and motoneuron 83 (first tergosternal, forewing elevator). The electromyographic recording from muscle 112 (dorsal longitudinal, hindwing depressor) indicates the time of depression in the wing beat cycle. *Bottom panel:* Lucifer Yellow fill of interneuron 301 beside simultaneous recordings from this interneuron and interneuron 511. The reader should note that interneurons tend to fire more spikes at higher intraburst frequencies. As a result of deafferentation the cycle period increases to around 90 ms (rhythm frequency: 11 Hz). (Modified from Robertson RM (1986): Neuronal circuits controlling flight in the locust: central generation of the rhythm. *Trends Neurosci* 9:278-280.)

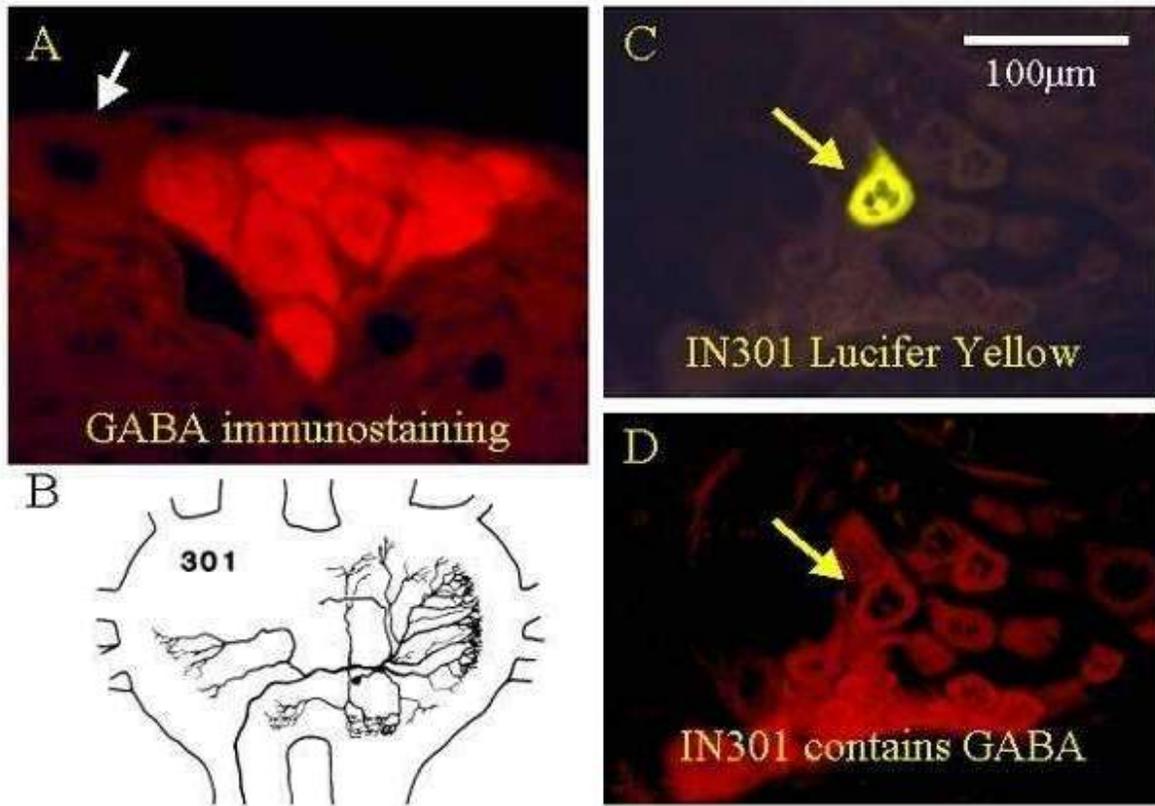


Figure 5. Inhibitory flight interneurons contain GABA. **A**, Localization of neuron somata containing GABA using immunocytochemistry (rhodamine-tagged secondary antibody). A dorsal cluster of somata in the metathoracic ganglion contain GABA. A non-immunoreactive neuron is indicated by the white arrow. **B**, Drawing of a Lucifer Yellow fill of interneuron 301. Section of the mesothoracic ganglion indicating the Lucifer Yellow-filled soma of interneuron 301. Processing the same section for GABA immunofluorescence reveals that interneuron 301 is immunoreactive for GABA (*yellow arrows in C and D*). The reader should note that some other flight interneurons identified as inhibitory on physiologic grounds do not contain GABA (not shown). (Modified from Robertson RM, Wisniewski L (1988): GABA-like immunoreactivity of identified interneurons in the flight system of the locust, *Locusta migratoria*. *Cell Tissue Res* 254:331-340.)

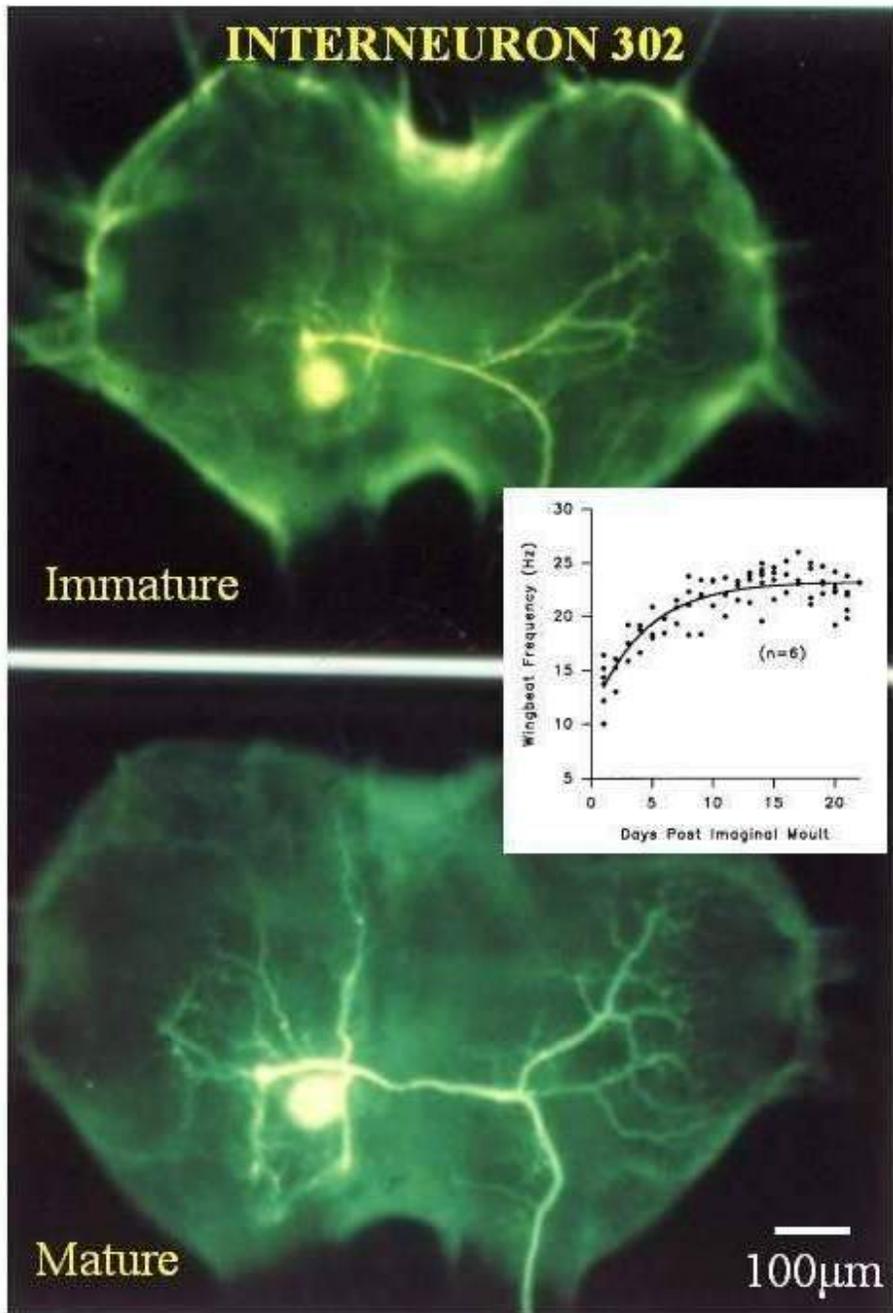
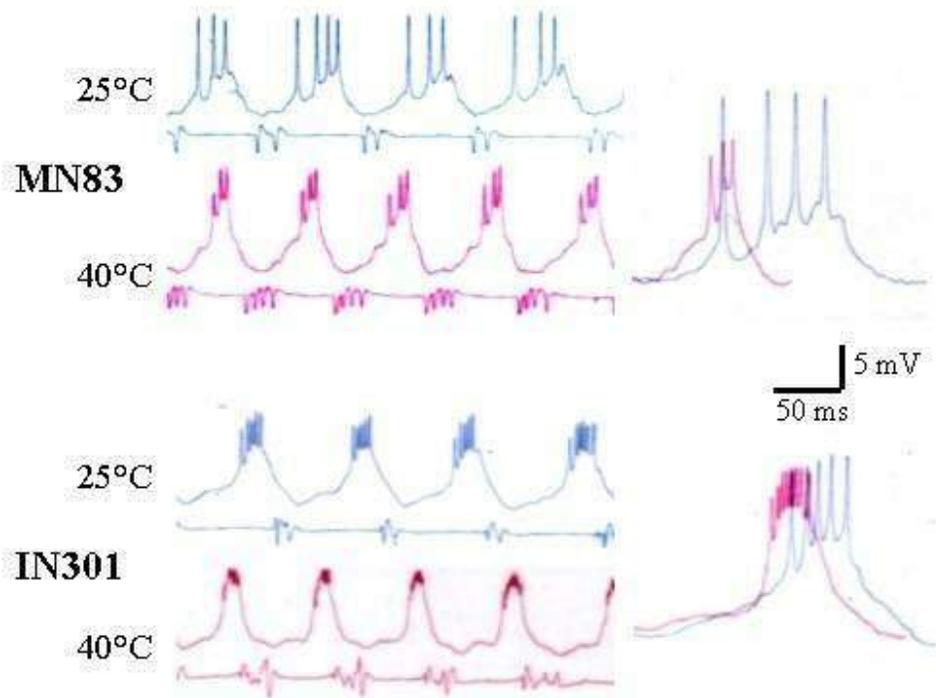


Figure 6. Maturation of flight circuitry. Comparison of Lucifer Yellow fills of interneuron 302 taken from an animal that was 1 day post-imaginal molt (immature) and from an animal 2 to 3 weeks older (mature). The mesothoracic ganglion increases in size. Neurites increase in diameter and in branching. During the same period the wing beat frequency increases from 14 to 23 Hz (*inset*). (Modified from Gee CE, Robertson RM (1994): Effects of maturation on synaptic potentials in the locust flight system. *J Comp Physiol A* 175:437-447; inset modified from Gray JR, Robertson RM (1994): Activity of the forewing stretch receptor in immature and mature adult locusts. *J Comp Physiol A* 175:425-435.)



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Figure 7. Effects of temperature on flight motoneurons and interneurons. Increasing temperature from 25° C to 40° C increases the frequency of the flight motor pattern. Concomitant with this is a marked change in the frequency of firing and membrane potential waveform of both motoneuron 83 (first tergosternal, forewing elevator [*top panel*]) and interneuron 301 (*bottom panel*). To illustrate these differences, single bursts from each neuron recorded at different temperatures are overlaid at the right-hand side of each panel.



Video 1. Straight flight. Rear view of a tethered female locust (*Locusta migratoria*) flying in a wind tunnel (wind speed 3 m/s). The hindwings are larger than the forewings and lead by 5 to 10 ms. Sequence was obtained using high-speed cinematography at 250 frames/s, transferred to videotape from which the movie file was made.



Video 2. Turn right. Rear view of a tethered female locust (*Locusta migratoria*) flying in a wind tunnel (wind speed 3 m/s) and executing a steering maneuver to avoid collision with a target (black cardboard square) that is being propelled directly toward the head of the locust at 0.4 m/s on the bed of an X/Y plotter (see Robertson and Reye, 1992). The target is offset to the left and the locust steers around the closest edge on the right. At the beginning of this sequence the locust has a slight steering bias to the left. Detection of the target is indicated by two shallow wingbeats and elevation of the abdomen. The locust attempts to steer to the right by: ruddering action of the abdomen and right hindleg to the right; increased and early pronation of the forewing and hindwing on the right; increased elevation of the forewings and hindwings on the left at the top of the stroke; and asymmetrical positioning of the forewings during the downstroke with increased elevation on the left. Sequence was obtained using high-speed cinematography at 250 frames/s, transferred to videotape from which the movie file was made.

