

Neuronal circuits controlling flight in the locust: how sensory information is processed for motor control

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Animals abstract relevant information from a profusion of diverse stimuli and then organize appropriate behavioral responses. How is this done? A partial answer comes from studies on the flight steering system of the locust where multiple sensory systems have been shown to interact and shape the response properties of deviation-specific detector neurons. These sensory detector neurons project to a population of segmental premotor interneurons, which, gated by the flight central oscillator, then phase-couple and distribute integrated sensorimotor information to specific flight motoneurons, thus producing the motor program modifications which underly corrective steering responses.

The locust must perform corrective steering reactions in order to maintain a stable course in the face perturbations such as air turbulence or faulty motor performance. Course deviations are detected by three exteroceptive sensory systems¹⁻³: the compound eyes; the three simple eyes or ocelli; and the numerous aerodynamic windhairs (Fig. 1A). Sensory input from these systems ultimately results in phase-specific modification of flight motoneuron firing and thus produces a corrective behavioral response^{4,5}.

How is this sensory information processed and encoded by the CNS? Are there feature detector neurons that are selective for those types of course deviations which occur during flight? If deviation is encoded as specific neural activity, how then is this error signal integrated with the activity of the central flight oscillator in order to produce the correct motor response? These questions are actually relevant to the study of any locomotor system⁶. We prefer to study them in the locust because there we can record intracellularly with dye-filled microelectrodes from identified neurons involved in ongoing motor activity. Furthermore, due to the work of Robertson and Pearson⁷⁻⁹ we know quite a lot about the central oscillatory circuits with which exteroceptive sensory information must interact.

Detectors of course deviation

We have identified a small population of interneurons which receive sensory information in the brain and then convey it to the thoracic ganglia where the flight motor pattern is organized. Three of these cells have been studied in detail¹⁰⁻¹² (Fig. 1B). Each of these interneurons encodes a very specific type of course deviation. For example, the neuron DNI in Fig.

1B responds to an angular rotation around the animal's longitudinal axis only if this roll is clockwise and directed away from the natural horizontal flying position. The neuron will not respond to a clockwise roll if it is directed towards the horizontal instead of away from it, nor will it under any condition respond to a roll in the opposite direction. The cell also encodes information about yaw and pitch deviations in

the other two axes of angular rotation, and responds best to the stimulus configuration that signals the occurrence of a diving banked turn to the ipsilateral side. Thus this neuron is not a simple movement detector, it is an absolute deviation detector, pre-programmed to detect the sensory consequences of a well-defined situation in nature¹².

All three sense organs, compound eyes, ocelli and windhairs, contribute to these specific detector features^{10,12}. If a given deviation detector is excited by the visual input that the compound eyes receive during a roll to the right, then it is also excited by a darkening of the right ocellus. This makes sense, since the ocelli are wide-field luminance receptors, which in nature function as horizon detectors. A roll to

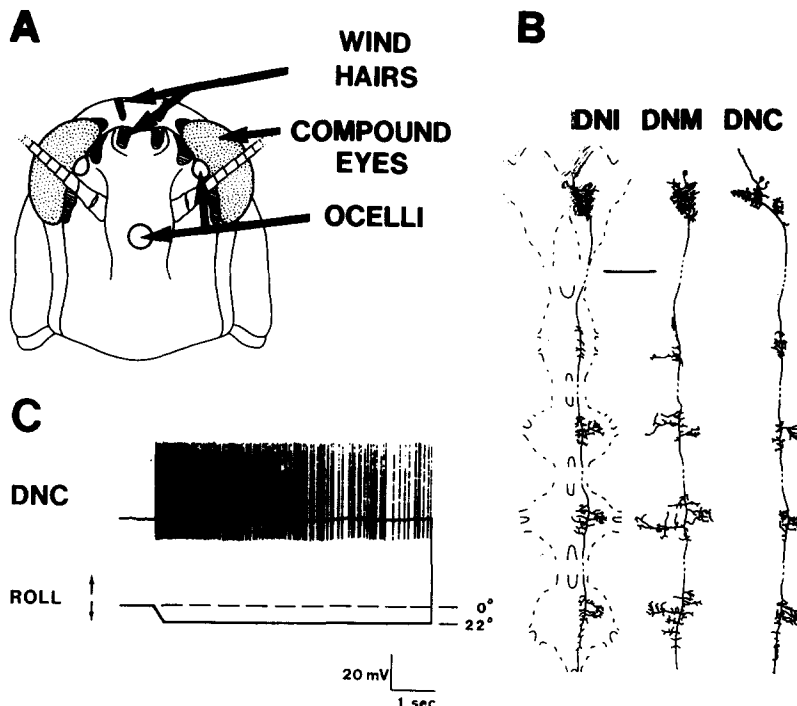


Fig. 1. Deviation detector neurons convey processed sensory information to segmental ganglia. (A) Three exteroceptive sensory systems on the head of the locust detect consequences of course deviations. The two large compound eyes and the three simple ocelli monitor course stability visually. The mechanoreceptive windhairs are aerodynamic detectors and are arranged in fields of specific directional sensitivity for flight wind (here indicated as striped areas). (B) Large descending deviation detector neurons, three of which have been uniquely identified (DNI, DNM, DNC), receive convergent sensory input in the brain from all three sensory systems. This input is integrated in the DN neurons and then relayed to the segmental ganglia, where the flight motor is organized. For DNI, the brain, the subesophageal ganglion and the three thoracic ganglia are shown in outline. Scale bar: 800 μ m (C) The response of a DNC neuron to a simulated roll deviation, which was presented to the animal by an artificial horizon. The dotted line (0° ROLL) indicates the horizontal horizon position.

the right would thus always be accompanied by a darkening of the right ocellus. In the same manner, if a neuron is visually excited by a yaw movement to the right, then it is also excited by a wind directed towards the animal's head from the left. Flight wind from the left would in nature accompany a yaw to the right. Thus, although these deviation detectors are multimodal, they actually detect a specific type of course deviation.

The response properties of a deviation detector are not due simply to summation of excitatory input from the three sensory systems. Mutual inhibition also occurs and prevents a response if there is a conflict in information content. Thus, much like modern day aviation autopilots, the overall organization is 'fail safe'. It not only has several interacting and mutually reinforcing back-up systems, it also has features that prevent inappropriate responses. When all three sensory systems deliver information compatible with a specific deviation, then the response of the detector can be a massive, quasi-tonic discharge as shown in Fig. 1C.

Processing this information for motor control

The error signal must be integrated

with the flight motor pattern to produce an appropriate corrective steering response. How is this signal phase-coupled to the flight cycle and delivered to the appropriate flight motoneurons?

The process of combining and matching sensory information with a centrally generated flight rhythm is carried out by a population of interneurons located in the three segmental ganglia of the thorax^{11,13}. These thoracic interneurons (TINs) are postsynaptic to specific descending deviation detectors and project to specific flight motoneurons. Thus these segmental interneurons channel descending sensory information to motoneurons.

However, the TINs are not simply central relay stations¹³. The evidence for this is as follows. First, when the locust is not flying, deviation detector information is not passed on to the flight motoneurons and thus will not affect the flight muscles. (Since the descending deviation detectors do make weak synaptic connections with flight motoneurons, some deviation information will reach the motoneurons even when the animal is not flying. However, this 'direct' input is not sufficient to fire the motoneurons.) Second, TINs are under the control of

the flight central rhythm generator. They receive rhythmically alternating excitatory and inhibitory drive from the circuitry of the flight oscillator, without themselves being able to affect the rhythm. They are thus members of the subpopulation of thoracic premotor interneurons whose prime responsibility is not the driving of oscillations (see previous article by Robertson).

This second feature is very important. It effectively matches the phase-independent, quasi-tonic signal of a deviation detector presynaptic to a TIN, to the phase-specific activity of flight motoneurons postsynaptic to that TIN. This is because the transmission of sensory information through the TIN to the motoneurons is phasically gated by the signal from the oscillator. Figs 2A and B show this for one identified TIN. In a non-flying animal, firing the deviation detector (here via current injection through the recording microelectrode) evokes excitatory postsynaptic potentials (EPSPs) in the TIN but does not fire the cell (Fig. 2A). In contrast, during flight motor activity, the TIN receives phasically alternating excitatory and inhibitory drive at flight rhythm from the flight central oscillator (Fig. 2B). If the deviation detector is again fired, temporal summation occurs such that the EPSPs add to the

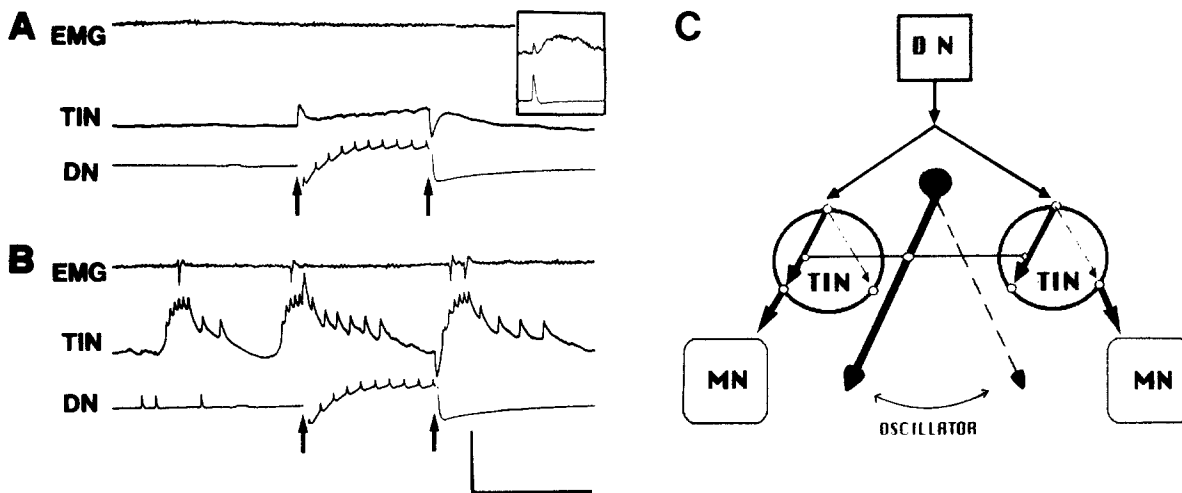


Fig. 2. Premotor thoracic interneurons, gated by the central oscillator, phase-couple and distribute descending deviation information. (A) Simultaneous intracellular recordings from a deviation detector neuron (DN) and a premotor thoracic interneuron (TIN). In a non-flying animal (no activity in the flight muscle electromyogram, EMG), the firing of the DN neuron evokes only 1:1 EPSPs in the postsynaptic TIN. Since the TIN does not generate action potentials, DN information is not passed on to motoneurons. The DN neuron was activated by intracellular injection of depolarizing current during the time indicated by the arrows. The inset shows the EPSP evoked in the TIN (top trace) by a single action potential in the DN (bottom trace) at a higher gain and expanded time scale. The initial transient on the top trace is a coupling artefact. (B) The same experimental situation as in (A), but now during flight motor activity (note EMG activity). The flight oscillator rhythmically excites and inhibits the TIN. Firing the DN neuron now causes EPSPs in the TIN which summate with this rhythmic drive and evoke spikes in the TIN. However, these additional DN-induced spikes occur only during the depolarizing phase of TIN modulation, not during the hyperpolarizing phase. Thus in this 'flying' animal, DN information is passed on to flight motoneurons postsynaptic to the TIN, but only during one phase of the flight cycle. In (A) and (B) the large polarizations at stimulus onset and stimulus end are artefactual. Scale bars for (A) and (B) are 20 mV (TIN), 100 mV (DN) and 100 ms. (C) Simplified summary scheme for the way in which the central oscillator gates descending sensory information at the TIN level. The oscillator is represented by a mechanical pendulum, which rhythmically switches the flow of information from the deviation detecting DN neurons to flight motoneurons (MN) at the level of the TINs.

depolarization phase of the TIN membrane potential. However, this does not happen during the hyperpolarizing phase. Thus the TIN produces an increased number of action potentials, but only during the depolarizing phase of its activity pattern. Consequently, a motoneuron postsynaptic to the TIN will receive additional synaptic input during the depolarizing phase of TIN modulation but not during the opposite hyperpolarizing phase. In this way, a tonic descending signal is phase-coupled to the flight rhythm and delivered to appropriate flight motoneurons in one and the same step. The behavioral results of this additional phase-coupled synaptic drive to flight motoneurons are the changes in wingbeat phase and wingbeat amplitude that produce correctional flight steering responses.

It is important to realize that there are numerous TINs in the flight control system of the locust¹⁴. Some drive elevators, others drive depressors; some are excitatory, others are inhibitory. Since the deviation detector neurons make synaptic connections with a number of different TINs, the effects of a deviation signal will be diverse and depend both on the motoneuron in question and on the phase of the flight cycle¹⁵. To illustrate this, Fig. 2C shows a simplified summary scheme in which a 'pendulum-type' central flight oscillator mechanically gates descending signals at the TIN level. This scheme illustrates the following points about interactions between the central oscillator and the TINs:

(1) When the oscillator is not operating, sensory information does not reach the flight motoneurons via the TINs. Thus the steering circuitry is operative only when the animal produces flight motor activity.

(2) Due to rhythmic gating of the TINs by the oscillator, the same sensory signal is transmitted to different motoneurons intermittently during the flight cycle. The oscillator selects

and switches the direction of sensory information flux. Also, sensory information can have profound effects on the flight motoneurons without influencing the central oscillator.

(3) Since different TINs can have opposite synaptic effects on different motoneurons, the same sensory information can cause excitation of one motoneuron and inhibition of another.

(4) The phase-coupled signal is applied to the appropriate group of motoneurons automatically by this circuitry, thus obviating the need for further 'decision-making' in the brief time between stimulus and response.

The role of segmental interneurons in sensorimotor integration may be even more general than indicated by our experiments. There is evidence in the locust flight system that proprioceptive information from certain wing sense organs is also channeled to motoneurons through the TINs¹⁶. Again, a copy of the centrally generated motor rhythm could be used to control sensory information flow. Other forms of proprioceptive input can, in addition, influence elements of the oscillation generating circuitry directly¹⁷.

In the locust, the flight central oscillator not only generates the basic rhythmic motor pattern, it also rhythmically opens and closes the sensory pathways that can in turn modify that motor pattern. Thus the central rhythm-generating circuitry helps to adaptively adjust motor behavior to environmental variability. This central phenomenon of interneuronal gating by neuronal oscillators together with the overall arrangement of sensorimotor integration circuitry may be of general significance. The locomotor control systems of vertebrates involve descending pathways from projection areas in the brain to segmental motor centers in the spinal cord and thence to spinal motoneurons¹⁸. Central neuronal oscillators are located in the spinal cord and gating processes have been documented and ascribed to the segmental inter-

neuronal level^{19,20}. It would not be surprising if similar principles of neuronal organization were found in all animals that need to integrate a rhythmic motor output with non-phase-locked sensory input.

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