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Mechanisms of flight steering in locusts

C. H. F. Rowell

Zoologisches Institut, Rheinsprung 9, CH-4051 Basel (Switzerland)

Summary. Steering in flight by locusts provides a well-studied example of the modulation of a rhythmic motor output by unpredictable inputs from outside to produce adaptive behaviour, in this case a form of locomotion. The simplest form, correctional steering, allows the animal to compensate for unintentional deviations from course. Its mechanisms are relatively well understood. The central nervous circuitry which makes this behaviour possible can be thought of as an autopilot. The entire process, from sensory input to the aerodynamic effects of changed motor outputs, is here reviewed. Intentional change of course, either spontaneous or induced by a change in the outside world, is more complex: it demands not only active steering, but also the temporary disablement of the autopilot. The mechanisms by which this could be achieved are discussed.
Key words. Flight; sensory modulation; feature detection; interneurons; sensorimotor integration; locust.

Introduction

Many behaviours are based on centrally generated rhythmic outputs[19]. In order that central circuitry can produce adaptive behaviour, its output must be modified by sensory information. This can derive from proprioceptive or exteroceptive inputs and can be phase-related or phase-unrelated. Insect flight provides an outstanding example of this process, and has been most intensively studied in flies and in grasshoppers, principally locusts. This brief review (for further references see[39,50,53,54]) deals with the latter group. The modulation of the locust flight output by phase-related, usually proprioceptive, inputs has been extensively studied (summarized by Altman[1,2]; see also refs[38,43,44,45,64,77]), but few data are available on the role such inputs play in steering. Modulation by phase-unrelated exteroception is of particular importance in steering, and its central nervous basis has only recently been established[49]. The principles involved are of general applicability.

I define steering as behaviour which induces rotation around one or more spatial axes, thus producing yaw, roll and pitch. Steering demands the production of torques, derived from asymmetric forces produced by the wings and/or asymmetric drag from the wings or from abdomen and hind legs, which are used as rudders. These needs translate into alterations in the activity of the corresponding muscles.

1. *Correctional steering* is associated with involuntary deviations from course, caused by turbulence or motor errors. These cause sensory feedback and the resultant signal makes the motor apparatus produce compensatory torque(s). Classical optomotor reactions of flying insects are part of correctional steering. The circuitry which mediates correctional steering can be referred to conveniently as 'the autopilot'.
2. *Induced change of course* occurs when the animal reorients itself to a new stimulus, and in doing so behaves differently from what is predicted by the autopilot.
3. *Spontaneous change of course* is operationally similar to induced change of course, but is not associated with any known change in external stimulation.

Almost all available data deal with the mechanisms of correctional steering.

Sensory inputs

Visual. The first inputs established as causing steering in locusts were visual[25,28]. It has subsequently been shown that both compound eyes and ocelli are separately capable of mediating visual steering[65,66]. The image-forming compound eyes perceive deviations around all three spatial axes. The non-image-forming ocelli appear to affect steering solely in proportion to their relative illumination[65]. In locusts, the lateral ocelli should be able to detect roll, as the down-side ocellus receives less skylight than the up-side ocellus, thus producing an imbalance in their relative illumination. The ocelli should also detect pitch, since downward pitch decreases and upward pitch increases the illumination of the median ocellus relative to the lateral ocelli. However, the ocelli should be unable in general to detect yaw; since for a locust flying over flat ground yaw would lead to no change in ocellar illumination[76]. Visual inputs have been shown by many subsequent workers to elicit roll and yaw; to date no one has shown behaviourally that flying grasshoppers actively correct for visually perceived pitch, though the physiological data[14,15,55,61,65,79] leave little doubt that this is so.

Wind. Camhi[12,13] showed that tethered locusts, flying in a wind stream in absolute darkness, responded with rudder movements to simulated yaw. The air stream was not laminar or of large cross-section relative to the wing span, but these weaknesses were remedied by Arbas[3], who confirmed the results. The significance in free flight is nevertheless still unclear. Apart from the phasic currents generated by the beating wings[7,33], a form of proprioception, the air flow over the animal is caused by the relative wind (i.e., that resulting from the forward motion through the air). This is of constant direction provided the long axis of the animal is aligned with its direction of movement. An ideal weightless insect could thus steer (i.e., rotational movement) without altering the relative wind. When real insects turn they drift laterally (side-slip, translational movement) owing to their momentum: there is a short period in which their direction of movement through the air is not aligned with their long axis, and probably only then can the animal derive information about a course deviation from the wind hairs alone. However, free flying locusts are on average 5.2° of yaw inclined to their direction of forward movement[10]; that is, there is frequently a side-slip component in straight flight, and this will be continuously registered by the wind hairs. Detection of sideslip may indeed be their major nonproprioceptive role. The best-known wind receptors are hair sensilla located on the head (Weis-Fogh[70], and many subsequent workers). The cercal hairs also influence steering[2,3]. Almost the entire body surface is provided with similar structures; their role in steering, if any, is unknown. The antennae also detect relative wind; this information is used principally for control of flight speed[22], but under some circumstances for steering too[3].

Sensory interneurons involved in correctional steering

Definition. Several neurons have been described which bring the right sort of information from the brain as far as the 'metathoracic ganglion' (which comprises the fused ganglia of the third thoracic and first three abdominal segments). Two criteria have been used to determine whether or not a given interneuron is involved in correctional steering.

a) Most directly: does direct stimulation of the interneuron during flight produce either steering behaviour or the neurophysiological correlates of such behaviour? And, does the effect compensate for the course deviation mimicked by the stimulation? So far this procedure has been applied to only 3 identified interneurons (TCG[40]; DNC and PI(2)5, Hensler and Rowell, in prep.), but has confirmed the role of all.

b) Less directly: does the candidate interneuron have the synaptic effects demanded by hypothesis on flight motor neurons and/or premotor interneurons? This test has been applied succesfully to more interneurons, including the well-characterised DNM and DNI[27,55,61]. The results indicate that there are at least 6 and possibly more than 10 pairs of descending neurons which signal course deviations to the thorax, and that these frequently act synergistically.

Response characteristics. The neurons listed above all respond to both visual and wind inputs, but only TCG is predominantly sensitive to wind. Its wind inputs are derived from cephalic hairs and the antennae[8,6,32]. The three DN units are also directionally sensitive to wind, but receive input from one or more ocelli, and have complex directional responses to whole field movements. The three modalities interact hierarchically, the wind signal being important only in dim light. The DN units act as 'feature detectors', reporting aerodynamically specified deviations from course[55,62]. The response of PI(2)5 is most similar to that of DNI, but it differs in responding to pitch up, having no ocellar input, and in receiving directional proprioceptive input from the neck when the animal rolls its head. Significantly, driving this unit leads not only to modulation of the output to flight muscles but also to rotation of the head[30].

The table lists the nature of the deviations from course which excite the neurons characterised to date. Clearly separated visual channels exist for distinguishing yaw/roll to left and right and pitch up and down. Yaw and roll are imperfectly distinguished by the visual units; perhaps this is because these manoeuvres are rarely performed except together[1], but it is equality possible that the two are separated by integration in the thorax with wind units, which are insensitive to roll. All the above-mentioned neurons have relatively large diameter axons (10–15 μm), and at the elevated body temperatures of flying locusts have a minimum latency of circa 10 ms[55]. Probably other interneurons are involved in correc-

Nature of the deviations from course which excite optimally identified descending interneurons known to mediate steering responses in locusts. The terms ipsi and contra are defined relative to the axon of the interneuron in question. Superscript figures refer to the original descriptions of the neurons in question.

DNI[55]	DNM[55]	DNC[55]	PI(2)5[30]	TCG[6,8]
Diving banked turn ipsi	Dive	Banked turn contra	Climbing banked turn ipsi	Diving turn ipsi

tional steering as well. Candidates driven by the cercal hairs[16,17,58], sternal hairs[47] and antennae[32] are known they have not as yet been tested by the criteria given above.

Connections between sensory interneurons and the motor and premotor neurons of the thorax

Intracellular stimulation of descending interneurons (DNs) leads to modulation of the motor output to muscles moving the head and wings (see above), and presumably abdomen and legs are also affected by these or similar units. How does this occur? The responsible synaptic connections have been investigated only in connection with flight motor neurons (FMNs). Unless otherwise stated, the information in this section is derived from published[49,52] or unpublished (Reichert and Rowell in prep.; Rowell in prep.) work of this laboratory.

Organization of the flight motor. The basic rhythmicity of locust flight is generated by a central oscillator[72] composed of interneurons in the thoracic and anterior abdominal ganglia[51]; the output is modified by proprioception (see Introduction) to produce the functional pattern. The oscillator output is relayed to the FMNs via premotor thoracic interneurons (TINs); some of which are part of the oscillator circuit[51] but most of which are not. There are minimally 30 pairs of TINs, including both local and interganglionic neurons. All are spiking cells, in contrast to the situation found in the premotor organization of the leg motor neurons[60]. Activation of the oscillator leads to rhythmic changes in the membrane potential of the TINs and FMNs, which fire at the top of the depolarising phase. Both are divided into elevator and depressor phase populations; in flight the two populations fire in approximate antiphase to each other, and within a population the neurons fire roughly in synchrony (more detailed descriptions are available elsewhere[45,57,64,68,75]).

Deviation detector inputs. The descending sensory interneurons (see above) make monosynaptic excitatory connections or inhibitory connections, probably disynaptic, with most, possibly all, FMNs[5,52,61]. Synaptic input arriving at MNs during the depolarizing phase of the cycle can affect through summation the number and timing of action potentials; input arriving during the repolarizing phase remains subthreshold. The same is true for the premotor TINs; most, probably all, descending deviation detectors connect with the TINs, which then excite or inhibit the postsynaptic MNs. Experimental manipulations show that the inputs acting via the TINs have more effect on the FMNs than the direct connections, which typically produce very small PSPs. As a result of this summation of oscillator-derived and sensory inputs, the latter affects the FMNs only during predetermined phases of the cycle: the sensory input is gated by the oscillator (fig. 1).

Simulated course deviations which lead to modulation of the FMN discharge have no effect on oscillator interneurons, and these cells receive no inputs from interneurons reporting course deviations. (The oscillator does receive other sensory inputs, as wing beat frequency is sensitive to sensory inputs[11,23,57,69,72]).

Effects on motor output. Summation of the type described affects a) the recruitment of FMNs b) the number of spikes fired by a FMN in its burst c) the time of onset of the burst. These are the same three features which are seen in intact but tethered animals during steering (see below). The most conspicuous effect is the last named, detected as a phase shift within the wingbeat cycle of the first spike of the discharge of any given neuron. The direction of the shift in the FMNs after simulation of a given course deviation is the same as that recorded in tethered flight to the same stimulus (Thüring[66], and Rowell and Reichert, unpubl.).

Other parts of the motor system. Recordings from neck and abdomen motor neurons during fictive flight (the activation of flight-like motor outputs in an animal whose thoracic peripheral nerves have been cut, rendering the wings motionless) show that some units are modulated at flight frequency[15,16,68], but that many are not[4]. Little is known of the premotor organization in these segments. Recordings from TINs of the prothoracic ganglion, probably homologous with mesothoracic TINs known to be presynaptic to FMNs, also reveal little or no modulation by the flight oscillator. This is an interesting functional difference between the segmental replicates of what are probably homologous neural networks. No investigation of the neurophysiology of leg movements during flight has been reported.

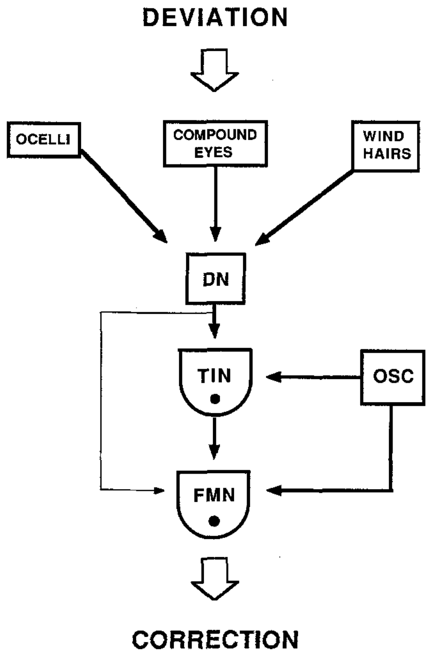

Figure 1. Schema showing the organisation of central circuits mediating flight steering in the locust. Their essence is in the convergence of exteroceptive information and of the oscillator output signal. Both converge on premotor thoracic interneurons (TIN), which are postsynaptic to both the descending sensory interneurons (DN) and the oscillator interneurons (OSC). Summation occurs in the thoracic interneurons, which are all spiking neurons with well-defined voltage thresholds. As the oscillator signal consists of a periodic depolarisation it acts as a gating signal, causing the TINs to influence their postsynaptic flight motor neurons (FMN) only during preset phases of the wingbeat cycle. A similar process takes place in the flight motor neurons themselves, which are also directly postsynaptic to descending neurons and to the oscillator; the sensory input to the motor neurons is however much weaker (symbolised by the thinner line connecting DN and FMN). It must be stressed that the three classes of thoracic neurons shown here are all populations, and that different phase angles of firing (e.g. depressor phase, elevator phase) are represented in all three. Proprioceptive inputs are not shown here, as their role in steering appears to be small, but they affect all the central neural elements shown here. Modified after Reichert and Rowell[49,54].

Changes in FMN and flight muscle output seen during correctional steering

The effects described above are produced by simulated course deviation or by electrical stimulation of sensory interneurons. Similar changes are however seen during steering by tethered but intact locusts. As grasshoppers' flight muscle is of the synchronous variety, most of the experimental work is based on muscle recordings.

The same three effects as were noted above, namely, changes in recruitment, burst size, and phase, were already being reported in the 1960s from tethered steering animals[20, 68, 69, 74]. Möhl and Zarnack[41, 42] were, however, the first to stress that steering is associated with systematic phase shifts in the firing times of virtually all recorded flight muscles, and that this is more consistent and reliable than changes in recuritment or burst length. This has been abundantly confirmed for yaw, roll and pitch by many subsequent workers, several of whom have additionally measured torque or rotation, which was missing in the original reports. The largest shifts, at least in yaw and roll, which demand left/right asymmetry, are invariably between contralateral homologues. Shifts between ipsilateral units, both within and between wings, also occur[57].

A methodological problem with all these experiments is that they measure only relative shifts. For example, a phase shift recorded between left and right homologues does not show whether both units are shifted away from their former relation to the oscillator phase, or only one. This problem has been resolved by recording simultaneously from oscillator INs and FMNs during simulated roll (Reichert and Rowell, in prep.); the results indicate that the neurons of both sides are phase shifted, and in opposite directions, by excitatory or inhibitory inputs respectively.

Changes in wing kinematics during steering and their aerodynamic effects

What changes in wing movements are caused by these changes in recruitment, burst length and phase which are observed in flight muscles? Aerodynamic analysis of locust flight began with Jensen[34, 71], who tried to explain the working of the single wing with steady-flow aerodynamic theory. This states that the fundamental variable controlling lift and thrust is the angle of attack of the wing. Morphologically, this translates as the degree of pronation or supination (i.e., rotation around the longitudinal axis) of the wing. According to Snodgrass[63] this rotation is controlled during the downstroke by the 1st and 2nd basalar muscles, acting as pronators, and the subalar (and possibly the pleurosternal[46]) acting as supinators. If this is so, the angle of attack can be varied by recruitment of motor units (the basalars are innervated by 3 pairs of MNs in all, the subalars and pleurosternals by 2 pairs each), by burst length within each motor unit, and by the relative firing time of pronators and supinators: the earlier the basalar fires relative to the subalar, the more the wing will tend to be pronated during the downstroke, and v.v[46, 67]. There seems no doubt that this theory is essentially valid; systematic changes of the sort predicted in angle of attack and in the activity these muscles are routinely seen during steering. By the middle 1960s it was however already clear that this explanation was not complete. Wilson[73] wrote "For turning, asymmetrical variation in angle of attack and wingbeat amplitude probably suffice", but in the same paragraph went on to point out that the fore- and hind wings in locusts neither function as a single structure, nor are they aerodynamically independent of each other; that is, the aerodynamic performance is influenced by the temporal and spatial relations between the two. He conceived of the forewings as mobile steering elements, leading-edge flaps or pre-wings, altering the air flow over relatively invariable hindwings, which were known to be responsible for most of the lift[21, 73]. This is essentially the position of Zarnack today (1987, pers. comm.). This too seems to be an over-simplification. First, movement of the hindwings *is* modulated in steering[18, 78], contrary to Wilson's belief, and indeed the tethered animal can still steer around the roll axis after amputation of the forewings[66]. Secondly, all the wings can be phase-shifted independently within the wingbeat cycle[9, 78], as can be vividly seen in flash photographs triggered by a particular muscle potential during steering[66] (figs 2 and 3). It seems increasingly likely that these phase shifts between the wings are the most important mechanical variable in steering. This view also fits well with a more modern aerodynamics incorporating vortex shedding and other phenomena.

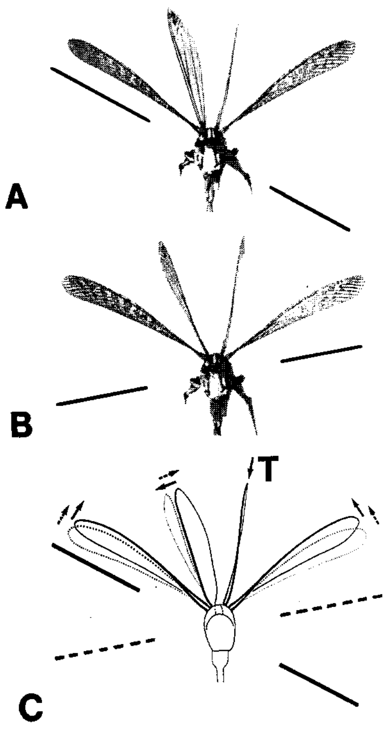

Figure 2. Relative phase shifting of the wings during flight manoeuvres. A locust tethered to a flight balance is surrounded by a cylindrical artificial horizon, the lower half of which is painted black and the upper half white. The animal is viewed head-on in this and the next figure. The subalar muscle of the left hind wing is recorded extracellularly with an implanted electrode, and its muscle potential is used to trigger an electronic flash which produces the photograph shown. In *A* the horizon (symbolized by the heavy line) is rotated to the animal's left, simulating a course deviation of circa 30° roll to the right. The animal accordingly produces a correcting torque to the left (verified by the flight balance torque meter). In *B* a slight (circa 6°) roll in the opposite direction is simulated, and the animal exerts a corresponding small correcting torque to the right. In *C* the traced outlines of the wings from *A* and *B* are superimposed, to show their relative positions at the time of firing of the trigger muscle. The leading edge of the trigger wing (T) is in exactly the same position (near the top of its stroke) in both pictures: that is, the firing of its subalar (a supinator/depressor muscle) is a good indicator of its position. All the other wings are however in different positions. This is most easily seen in the right hind wing, which is pronated and on the down stroke during roll to the left (*A*), and supinated and on the upstroke during roll the right (*B*). Overall, these changes are such that when the animal is exerting torque to the left, the left forewing is phase advanced relative to the right one, and the left hind wing is phase retarded relative to the right one. During torque to the right, these phase differences are reversed. All four wings are phase shifted independently of each other. Modified from Thüring[66].

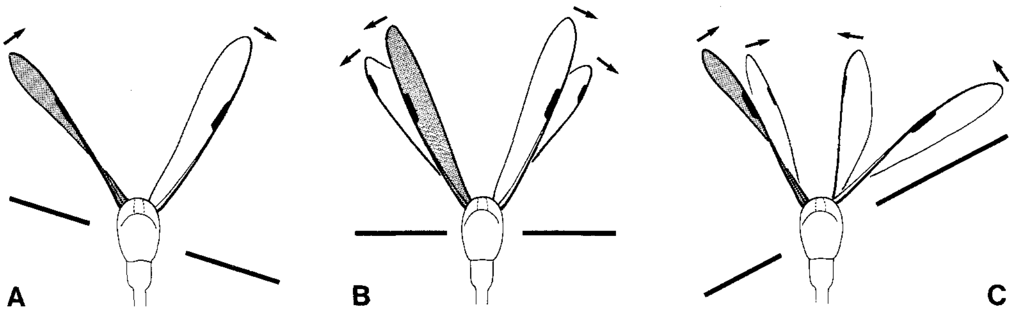

Figure 3. A further example of independent phase shifting of the wings during steering. Technique as in figure 2: here the 2nd basalar muscle (a pronator/depressor) of the right forewing (shaded) is used as the trigger muscle. Once again, the leading edge (black mark) of this wing is in the same position in all three tracings. In straight ahead flight (*B*) both fore and hind wings are symmetrically placed at the time of firing of the trigger muscle. During a torque to the left (*A*), the left forewing is phase advanced relative to the right one (the hind wings are not satisfactorally resolved in this photograph). During a torque to the right (*C*), correspondingly, the left forewing is phase retarded relative to the right one and the left hind wing phase advanced relative to the right one. Modified from Thüring[66].

Apart from pronation/supination and phase shifts of the wings there is a third kinematic parameter which correlates with steering, if not so reliably as the other two[66], and this is wingbeat amplitude. Wilson and Weis-Fogh[75] attributed its control to phase shifting of the elevators and of the dorsal longitudinal depressor, acting as brakes on each other, and this still seems plausible 25 years later.

Three separate kinematic parameters can thus be attributed to phase shifting of the MNs: control of the angle of attack of the individual wing; phase shifting of each wing relative to the oscillator cycle (and thus to each other); and control of wingbeat amplitude. What then of recruitment and burst length? It has long been hypothesized that these control the power of the muscle contraction, and that this in turn would somehow influence the development of force by the wing. The first of these assumptions has been recently substantiated[37]. The second was clarified by Pringle[48], who pointed out that power could be altered only via wingbeat frequency, amplitude, or loading (equivalent to angle of attack). Frequency is not systematically related to steering[57], and amplitude and loading are dependent on phase shifts between the firing times of muscles (above). Thus change in recruitment and burst length should only occur in conjunction with phase shifts and secondary to them. This agrees well with the observation that all three effects are brought about by summation of sensory and oscillator-derived PSPs in the motor and premotor neurones; in such a system the latency of firing of the first AP of the burst is expected to be the most sensitive parameter, followed by change in spike number.

What is the role of head turning?

The currently accepted story, which originated in the 1950s[25, 26, 29, 36], is as follows. During steering the locust first rotates its head with respect to the prothorax to regain symmetrical inputs to head sensilla (e.g. dorsal light response, etc.) thus generating a proprioceptive signal. This signal elicits correctional steering from the thoracic motor centres. As the manoeuvre is completed, the body becomes realigned with the head, and the steering command is negated. This is an elegant hypothesis, but the few critical experiments which have been performed subsequently suggest that it is too simple.

1. Information about course deviation descends directly from the brain to the thoracic ganglia. If the neck proprioceptive input is abolished, wings, abdomen and legs still steer[65].
2. On the other hand, forced movement of the head, in the absence of visual input, elicits steering by the FMNs, as predicted by the hypothesis[65]. This has been confirmed by Hensler[30], who also identified a descending interneuron reporting head movement which influences the FMNs. The tonic component of its response is however subthreshold, and can only be expressed when visual excitation is present.
3. Robert (in prep.) has measured the latency of different components of steering in tethered flying locusts subjected to visually simulated yaw. Movement of the abdomen and/or legs begins within some 50 ms of the onset of the stimulus, while the head movement begins some 30 ms later. The wing beat is modulated within the first complete wingbeat (approx. 50 ms) after stimulus onset (independent unpublished observations by Rowell, Hensler, Thüring). These latencies are incidentally all much shorter than those reported by previous authors[23, 57]. The slowness of the head response may well be the result of its mechanically complicated suspension[31, 59], so that the simplest model is that all components are initiated by the same fast deviation detector interneurons. These experiments clearly do not support the idea that steering is *initiated* by proprioceptive information from the neck. It could however still be *maintained* from this source.
4. When the tethered locust is flying in a closed-loop situation, in which its yaw torques control the rotation of the visual surround (apparatus after Goetz[24]), it can stabilize the surround with respect to itself for long periods, even against an imposed rotatory bias; in free flight this would imply that it maintained a straight course using visual cues. This task can be performed both by control animals and by individuals with fixed heads. However, the latter tend to oversteer and to oscillate somewhat about their mean course; in control animals the oscillations are much smaller or absent (Robert, in prep.). This suggests that the role of head movements is secondary, and is to damp the fast steering reactions (analogous to the suggested[56] function of the halteres of flies). How this is achieved, and whether the unit recorded by Hensler[30] is involved, is currently under investigation.

Induced changes of course

In nature flying grasshoppers can often be seen to change course in response to definite stimuli, for example to approach and land on a particular plant, or to avoid an obstacle in their path. Such behaviour implies that the autopilot circuitry is flexible; indeed, were it not, the locust could only

fly in straight lines! Two initial hypotheses suggest themselves as to how the autopilot could be negated:
a) it could be inhibited by the stimulus that elicits change of course;
b) simple summation between the new input and that derived from the autopilot could occur, in which the new stimulus produces such a large effect on the premotor interneurons that the inputs coming from the autopilot, while themselves unchanged, have temporarily no effect.

We are at present attempting to distinguish between these hypotheses. Some a priori support for the first hypothesis is found in the observation[66] that the autopilot is often inoperative in tethered flight for short or long periods, during which the animal ignores otherwise effective stimuli. Little is known of the precise nature of the stimuli which induce a locust to change course. Locusts make banked turns towards small moving objects in the lateral visual field[18]. This stimulus, like all visual stimuli leading to turning, is practically difficult to separate from the visual aspects of the autopilot. Robert (in prep.) has developed a situation in which the autopilot is driven exclusively by visual input, and the change of course is elicited by an auditory one. As in many other insects[35], acridid grasshoppers (which typically disperse by flying at night) respond to pulsed ultrasound with changes of course, suggesting a bat-avoidance behaviour. We hope that we can standardize this stimulus situation enough to be able to apply it to neurophysiological preparations and distinguish between the two hypotheses present above.

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Control of sequences of movements in crayfish escape behavior

H. Reichert

Laboratoire de Neurobiologie, Département de Biologie Animale, 20 Rue de l'Ecole-de-Médicine, Université de Genève, CH-1211 Geneva 4 (Switzerland)

Summary. Crayfish escape from predators by a series of rapid tailflips. The production of this seemingly simple behavior involves the interaction of multiple neural control mechanisms. The rapid flexion phase of the first tailflip is a fixed action pattern that is always organized by giant command neurons. Subsequent reextension is a chain reflex mediated by sensory feedback from the initial flexion. All following tailflips are produced by a non-giant system which is activated in parallel with the giant system by the escape-initiating stimulus. Proper integration of the giant system and the non-giant system is mediated by a reaction time mechanism.

Key words. Command neurons; crayfish neuroethology; chain reflexes; escape behavior; fixed action patterns; motor control mechanisms; sensory feedback.