

AERIAL MANOEUVRING REFLEXES IN FLIGHTLESS GRASSHOPPERS

By EDMUND A. ARBAS*

Department of Biology, University of Oregon, Eugene, OR 97403, U.S.A.

(Received 24 May 1983–Accepted 21 June 1983)

Aerial locomotion of many insects involves jumping or dropping from elevated positions. Flight and aerobic manoeuvring often follow locust jumps, while jumps from elevated positions can carry flightless grasshoppers several metres through the air. Leg postures and orientation movements associated with aerial locomotion have been studied in the flightless grasshopper, *Barytettix psolus* (Cohn & Cantrall, 1974).

In the present study, adult *Barytettix psolus* of both sexes were tethered by the dorsal pronotum before a movable wind tunnel in a similar fashion to that used previously for the locust (Arbas, 1980). Presence or absence of leg movements was scored visually in some experiments, while in others, vertical components of leg movement were monitored with a capacitive movement transducer (Forman & Brumbley, 1980). To avoid visual influences, compound eyes and ocelli were covered with black (Rapidograph) ink.

Barytettix responded to initiation of airstreams of $3.5\text{--}5\text{ ms}^{-1}$ over their bodies with pronounced elevation and extension of the limbs (Fig. 1A). At the same time, *Barytettix* contracted longitudinally, shortening the abdomen and tucking the head firmly against the pronotum, and moved the antennae together against the wind in an antennal reaction similar to that of locusts (Gewecke, 1970).

Barytettix responded to changes of wind angle caused by moving the wind tunnel in the horizontal plane with rapid postural adjustments of the hindlimbs. If the wind was directed onto the animal from an angle to its left, the right femur was sharply levated and adducted while the left femur was depressed and abducted (Fig. 1B). If the wind tunnel was moved from side to side, *Barytettix* reversed the postures of the two hindlimbs at each change in wind angle (Fig. 1C).

The horizontal component of these leg movements closely resembles the lateral excursions of hindlimbs seen in tethered, flying locusts under similar conditions (Gettrup & Wilson, 1964; Dugard, 1967; Camhi, 1970a; Arbas, 1980). Rapid elevation of the femur contralateral to the oncoming air stream in *Barytettix* is in contrast to the primarily horizontal movements of locust legs and is the most conspicuous feature of its orientation movements.

In locusts, adjustments of hindlimb posture in relation to wind angle are often accompanied by abdominal curling (Gettrup & Wilson, 1964; Camhi, 1970a,b; Arbas, 1980). No similar movements of the abdomen were observed in *Barytettix*.

External mechanoreceptors of *Barytettix* which might be sensitive to air currents

*Present address: Biological Laboratories, Harvard University, 16 Divinity Avenue, Cambridge, MA 02138, U.S.A.

Key words: Grasshopper, jumping, orientation.

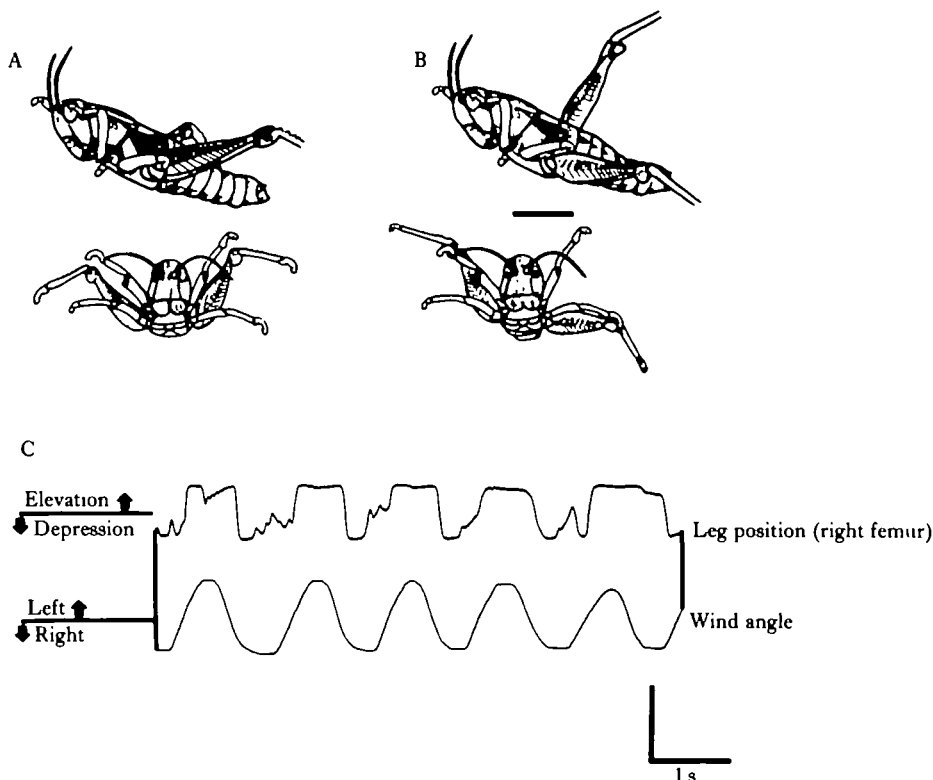


Fig. 1. Aerial posture and orientation movements of *Barytettix*. (A) Representation of 'aerial' posture assumed by *Barytettix* on initiation of air currents along the animal's longitudinal axis. (B) Representation of a postural adjustment elicited by moving the wind tunnel to the animal's left. (C) Movement transducer record (upper trace) of leg movement in response to wind angle changes (lower trace). Calibration: (A, B) 1 cm, (C) vertical, upper trace— 112° , lower trace— 62.5° ; horizontal, 1 s.

include: antennae, cephalic hairplates, caudal cerci and prothoracic spine, as well as distributed body hairs. These were selectively occluded with ink to test their influence on wind-related leg movements. Antennae were sometimes removed irreversibly by cutting at the pedicel, and antennal sockets occluded with ink. At least 10 min was allowed for animals to recover after painting, peeling of ink or cutting of sensory structures.

Air currents were initiated at 35° to the right or left of animals with cephalic hairplates, antennae and cerci occluded in all possible combinations. Leg movements were monitored visually by sighting along animals from behind and observing the postures taken up by the limbs. Two questions were asked on each trial. (1) Is the insect sensitive to onset of wind? Any movement of legs from the rest position towards aerial posture was scored as a positive response. The rest position was one where the legs dangled free in the air with femora parallel to the sternum of the animal. (2) Is the insect sensitive to the direction of the wind? Asymmetrical elevated postures of hind femora were taken as indications of sensitivity to wind direction. In these, the femur contralateral to the wind tunnel was elevated to a greater angle with respect to the rest position than the ipsilateral femur.

Responses to the onset of air currents were scored as asymmetrical, symmetrical or

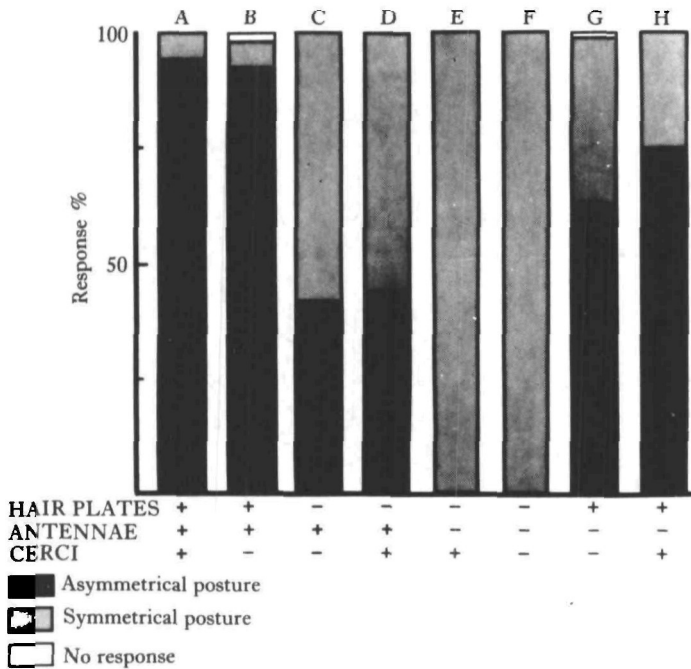


Fig. 2. Effects of sensory ablation on responsiveness of *Baryttix* to air currents. Postural adjustments scored as asymmetrical (black bars), symmetrical (stippled bars) or no response (unfilled bars). (+) Indicates mechanosensory structure exposed to air current, (-) indicates structure occluded by ink or removed by cutting (antennae). Each bar represents 10 trials on each of 10 animals. See text for further explanation.

no movement. Ten trials with 30-s intervals between puffs were performed on each animal. Fig. 2 represents the results of 800 trials on 30 animals.

Significance of the different response levels was assessed by pair comparisons of asymmetrical responses under each condition of sensory ablation. Variances were evaluated for homogeneity and differences between means were tested for significance with the Student's *t*-test or an 'approximate *t*-test' (Sokal & Rohlf, 1969, p. 374). Confidence limits were set at the 5% level. Animals with hairplates, antennae and cerci exposed, responded to air currents with asymmetrical postures (Fig. 2A). Covering the cerci (Fig. 2B) did not significantly reduce sensitivity of animals to air currents, nor to their direction. Covering the hairplates significantly reduced the number of asymmetrical responses obtained, whether or not the cerci were painted (Fig. 2C, D). No asymmetrical responses were observed with both hairplates painted and antennae cut (Fig. 2E, F). Removal of antennae alone also reduced the number of asymmetrical responses obtained (Fig. 2G, H), but less so than covering the hairplates (Fig. 2C, D).

Even with cephalic hairplates and antennae occluded, animals assumed a symmetrical leg posture at the onset of wind. Attempts were made in three animals to eliminate this sensitivity by painting progressively greater areas of the body to eliminate inputs from mechanosensory body hairs. Elimination of responses required painting of the entire body surface except for small areas around spiracles needed for ventilation.

This suggests that a distributed system of surface receptors contributes to the 'wind sense' of *Barytettix*.

These results show that, as in locusts (Weis Fogh, 1949; Camhi, 1970a; Arbas, 1980), cephalic mechanosensory hairs are important in sensing air current direction, and in mediating orientation movements of hindlimbs. The antennae are also capable of mediating directional responses. In *Barytettix*, postural adjustments mediated by antennae have the same orientation with respect to air currents as those mediated by cephalic hairplates. This is in contrast to the situation in locusts, where antennae mediate postures of opposite orientation with respect to air current as compared to those mediated by cephalic hairplates (Arbas, 1980).

Photographic studies (unpublished data) showed that leg postures and movements, corresponding to those described above, are evident in freely jumping animals and in those dropping from elevated positions.

Contact of the tarsi with a firm substrate inhibits flight and aerial orientation movements in locusts (Weis Fogh, 1956; Arbas, 1980). Under experimental conditions, contact of any tarsus is generally sufficient to inhibit wind-angle related postural adjustments in *Barytettix* (Fig. 3), hence the reflexes are 'turned on' the instant the tarsi leave the substrate in a jump or fall, are maintained by airflow over the body, and are 'turned off' again on landing.

Several other species of flightless grasshoppers; *Barytettix paloviridis*, *Barytettix tridens*, *Barytettix nigrofasciatus*, (Acrididae, Melanoplinae); *Brachystola magna*, *Romalea microptera* (Acrididae, Romaleinae) were tested for presence of aerial manoeuvring reflexes, as were flightless juvenile locusts, *Schistocerca gregaria*, and *Schistocerca nitens nitens* (Acrididae, Cyrtacanthacridinae). All but *Romalea* had similar responses, suggesting that a system of aerial manoeuvring reflexes involving the hindlimbs is widespread among saltatory orthopterans. No abdominal curling, described as a yaw-correcting response in adult *Schistocerca gregaria* (Camhi, 1970a,b) was observed in any flightless adults examined.

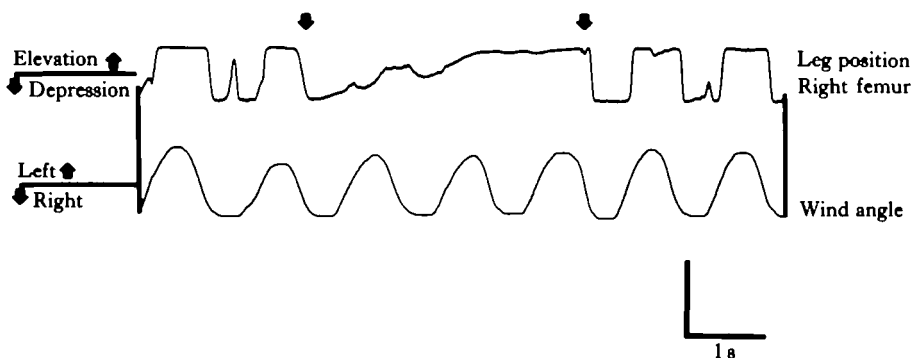


Fig. 3. Inhibition of hindlimb movements by tarsal contact. Upper trace – movements of the right metathoracic femur, lower trace – wind angle. The left prothoracic tarsus of a tethered *Barytettix* responding to wind angle changes was allowed to contact a stick (1st arrow). Although air current velocity was unchanged, and movements of the wind tunnel continued, wind-related hindlimb movements were inhibited until contact with the tarsus was broken (2nd arrow). Calibration: vertical, upper trace – 112°, lower trace – 62.5°; horizontal, 1 s.

The symmetrical aerial posture described for flightless grasshoppers in this report is similar to the 'landing posture' exhibited by early instar hoppers of *Schistocerca gregaria* as described by Cooter (1973). Initiation of this posture is mediated by wind-sensitive cephalic hairs, antennae, cerci and distributed body hairs. Asymmetrical hindlimb reflexes appear to be part of an attitude control system which may be used to compensate for spinning or tumbling or to initiate mid-air turns to face the direction of motion (i.e. to turn the head into the 'apparent' wind) during the aerial phase of jumps or falls. These are mediated by cephalic hairs and antennae. While not examined in detail in this study, optomotor pathways also operate in parallel with air-current mediated pathways in the production of hindlimb movements.

Supported by N.S.F. Grant BNS 75-23786 to Professor Graham Hoyle, a predoctoral fellowship to the author, PHS (5-T-32 GM07257) and the N.S.F. U.S./Mexico Cooperative Science Program.

REFERENCES

- ARBAS, E. A. (1980). A neuroethological study of flight loss and aerial manoeuvring in insects, Ph.D. thesis. Eugene: University of Oregon.
- CAMHI, J. M. (1970a). Yaw correcting postural changes in locusts. *J. exp. Biol.* **52**, 519-531.
- CAMHI, J. M. (1970b). Sensory control of abdomen posture in flying locusts. *J. exp. Biol.* **52**, 533-537.
- COHN, T. & CANTRALL, I. J. (1974). Variation and speciation in the grasshoppers of the Conalcaeni (Orthoptera: Acrididae: Melanoplinae): The lowland forms of western Mexico, the genus *Baryttix*. *San Diego Soc. natl Hist. Mem.* **6**, 1-131.
- COOTER, R. J. (1973). Flight and landing posture in hoppers of *Schistocerca gregaria* (Forsk.) *Acrida* **2**, 307-317.
- DUGARD, J. J. (1967). Directional change in flying locusts. *J. Insect Physiol.* **13**, 1055-1063.
- FORMAN, R. & BRUMBLEY, D. (1980). An improved capacitive position transducer for biological systems. *J. exp. Biol.* **88**, 399-402.
- GETTRUP, E. & WILSON, D. M. (1964). The lift-control reaction of flying locusts. *J. exp. Biol.* **41**, 183-190.
- GEWECKE, M. (1970). Antennae: Another wind sensitive receptor in locusts. *Nature, Lond.* **225**, 1263-1264.
- SOKAL, R. R. & ROHLF, J. F. (1969). *Biometry*. W. H. Freeman Co.
- WEIS FOGH, T. (1949). An aerodynamic sense organ stimulating and regulating flight in locusts. *Nature, Lond.* **163**, 873-874.
- WEIS FOGH, T. (1956). Biology and physics of locust flight: IV. Notes on sensory mechanisms in locust flight. *Phil. Trans. R. Soc. Lond. Ser. B.* **239**, 553-584.