Control of hindlimb posture by wind-sensitive hairs and antennae during locust flight

Edmund A. Arbas
Arizona Research Laboratories, Division of Neurobiology, 611 Gould-Simpson Science Building, University of Arizona, Tucson, Arizona 85721, USA

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Summary. 1. Steering movements of tethered, flying locusts, Schistocerca gregaria, subjected to simulated yaw were examined under open-loop conditions. Lateral movements of hindlimbs or curling of the abdomen were monitored with a capacitive movement transducer and were interpreted as indicating the tendency of the animal to turn.

2. Three responses to simulated yaw were noted: 1) Yaw-correcting upwind turning tendencies (Figs. 1, 2, 3). 2) Downwind turning tendencies (Figs. 2, 3, 4, 5), and 3) transient adjustments of hindlimb position consistent with an upwind turning tendency occurred in animals that made either no sustained postural adjustments of hindlimbs, or that exhibited sustained downwind turning tendencies (Figs. 4, 5).

3. Ablations of certain mechanoreceptors tested their roles in wind detection and wind angle determination. The expression of upwind turning tendencies, whether sustained or transient, depends on inputs from cephalic mechanosensory hairplates (Figs. 2, 3, 4, 5). With hairplates occluded, all locusts exhibited downwind turning tendencies. All downwind turning tendencies depend on inputs from the antennae (Figs. 2, 3).

4. Antennae and hairplates operate in an apparent antagonism in the steering responses they produce, which may provide the control flexibility required for complex flight maneuvering.

Introduction

The locust flight system can be considered to comprise two kinds of interacting mechanisms: those that generate propulsive forces; and those that orient the resultant movement of the animal. A great deal is known about elements of the first category, including: aerodynamics (Weis Fogh 1976; Nachigall 1976); kinematics of free flight (Baker and Cooter 1979a, b); properties of wing muscles (Pringle 1976) and aspects of their motor control (Burrows 1977; Hedwig and Pearson 1984; Möhl 1985a, b); as well as features of the central flight oscillator (Robertson and Pearson 1984, 1985). Mechanisms of the second category are generally less well understood and are the subject of this report.

Flying locusts use several mechanisms to correct for disorientations and to initiate turns, including: (1) asymmetries of the timing or burst structure of action potentials to the wing muscles of the two sides (Zarnack and Möhl 1977; Möhl and Zarnack 1977; Taylor 1981); (2) curling of the abdomen in a rudder-like fashion (Camhi 1970a); and (3) lateral excursions of the meso- and metathoracic legs (Gettrup and Wilson 1964; Dugard 1967; Rowell and Reichert 1985). Asymmetrical production of lift or thrust by the wings will impose a torque on the animal and cause a turn. Asymmetrical postures of the legs, or curling the abdomen to one side causes asymmetrical aerodynamic drag, a shift of the center of mass of the animal’s body, and altered moments of inertia about the animal’s rotational axes, all of which may contribute to the execution of turns in flight.

Sensory basis of steering movements

With the exception of the antennae (Gewecke 1970), all known air current sensors of locusts and grasshoppers are hair sensilla. Mechanosensory hairfields on the frons and vertex of the locust head are the most intensively studied of the air current sensors (Weis Fogh 1949, 1956; Smola 1970; Camhi 1969, 1970a, b; Bacon and Tyrer 1979; Tyrer et al. 1979; Bacon and Möhl 1983;
Möhl and Bacon 1983); they are involved in steering through movements of the abdomen (Camhi 1970a, b), wings (Gewecke and Philippen 1978; Möhl and Bacon 1983), and legs (this study). Wind-sensitive hair sensilla of other body parts may also play a role in flight (Pflüger and Tautz 1982). The antennae are sensitive to air currents (Gewecke 1970), and are involved in the control of flight speed and certain wing stroke parameters (Gewecke 1974, 1975, 1977) and are known to feed onto interneurons that have a role in steering (Bacon and Möhl 1983; Möhl and Bacon 1983). In locusts, previous studies have examined yaw-correcting postural adjustments of the abdomen (Camhi 1970a) and resulting torque production (Gewecke and Philippen 1978) in response to changes in the angle of airflow over the body as well as aspects of their sensory control. This report describes the leg movements of tethered, flying locusts in response to simulated yaw under open-loop conditions, and presents evidence for the involvement of cephalic hairplates and antennae in mediating several types of postural adjustments of legs and abdomen associated with orientation to wind.

Materials and methods

Animals used in this study were adult male Schistocerca gregaria (Forskål) obtained from a stock maintained at the Department of Zoology, University of British Columbia. Animals were kept in crowded cages at 32°C on a 16:8 h light:dark cycle. They were fed lettuce daily and provided a mixture of bran and alfalfa meal ad libitum.

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The roles of cephalic hairfields and antennae were tested by monitoring responses to wind angle changes with these structures ablated. Vibrations of cephalic hairs in their sockets, or movements of the proximal antennal joints were prevented by allowing ink to harden around each respective structure. This procedure was reversible in most cases (see Results) and the ink could be removed without apparent damage. Each animal was used for only one series of sensory ablations, was induced to 'fly' for short periods during which its responses to wind angle changes were tested. Except where noted otherwise, responses to wind angle changes were consistent over several bouts of flight in each condition of sensory ablation.

Results

Flight posture and steering movements

Initiation of an air current along the longitudinal body axis of tethered locusts elicited wingbeating and arrangement of the limbs into symmetrical flight posture similar to that depicted in Fig. 1 A.

When the wind tunnel was moved in the horizontal plane, flying locusts responded with postural adjustments interpreted as indicating a tendency to turn (Weis Fogh 1949; Dugard 1967; Camhi 1970a; Baker 1979) (Fig. 1 B). In a turn to the right, for example, the head often rolled to the right, the right metathoracic leg was abducted, the left leg adducted, and the abdomen curled to the right. The mesothoracic legs often adopted a posture similar to that of the metathoracic legs. One or both of the prothoracic tibiae were occasionally extended, especially during changes in wind angle, suggesting that they may also be used in some steering maneuvers.

If the wind tunnel was moved from side to side, locusts followed the change in wind angle with lateral movements of the legs (Fig. 1 C) and abdomen (Camhi 1970a, Fig. 3). The orientation of steering movements was usually such that induced turns would re-center the wind on the head. Not all animals responded with this type of reaction. Five of thirty-three animals tested prior to any sensory ablations (except for the painting of the compound