FOREWING ASYMMETRIES DURING AUDITORY AVOIDANCE IN FLYING LOCUSTS

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Summary

Flying locusts orient to sounds in their environment. Sounds similar to those produced by echolocating bats cause a flying locust to change its flight path. We used high-speed cinematography and videography to study changes in body posture and wing kinematics of tethered locusts in response to stimulation with bat-like sounds. Locusts showed both negative and positive phonotaxis to this stimulus. Within a few wingbeats of stimulus onset (between 126 and 226 ms), locusts deflected their abdomens to one side, and the angle of the left and right forewings with respect to the dorsal–ventral body axis became asymmetrical during the downstroke. This forewing asymmetry, in which the forewing on the inside of the turn became more depressed, ranged from 20 to 45 ° (37±9.7 °, mean ± S.D.) and was correlated with the direction and magnitude of abdomen deflection, a measure of steering in tethered, flying locusts. Hindwing stroke angle asymmetries were minimal or non-existent after stimulation. Coincident with changes in forewing asymmetry and abdomen deflection was a decrease in stroke amplitude (19±6.5 °) of the forewing on the inside of the attempted turn. Motor patterns from forewing first basalar (M97) muscles showed an asymmetry in the timing of left and right depressor activation that ranged from 10.4 to 1.6 ms (4.23±2.85 ms). The number of spikes per depressor burst increased to a maximum of three spikes in the muscle on the inside of the attempted turn, and depressor frequency (wingbeat frequency) increased by approximately 2 Hz (2.17±0.26 Hz). We suggest that the asymmetry in forewing first basalar activity is causally related to the asymmetry in the timing of the initiation of the downstroke, resulting in an asymmetry in the ranges of the stroke angles of the forewings, which would impart a roll torque to the locust. This would augment the steering torques generated by concurrent changes in the angle of attack of the fore- and hindwings and changes in abdomen position to effect rapid avoidance manoeuvres.

Introduction

Many insects flying at night are susceptible to predation by insectivorous bats. The classic example of this interaction is the in-flight behaviour of tympanate moths in response to the echolocation calls of approaching bats (Roeder, 1962, 1974). An insect successfully negotiating such an encounter must be able to detect and move itself away from the source of the high-frequency sounds. Acoustic startle responses (ASRs) have been described for many tympanate insects, most notably crickets (Moiseff *et al.* 1978), katydids (Libersat and Hoy, 1991), praying mantises (Yager *et al.* 1990; Yager and May, 1990) and lacewings (Miller, 1975; Miller and Olesen, 1979). Ultrasound-sensitive ears have been found in tiger beetles (Spangler, 1988; Yager and Spangler, 1995) and an ASR has been described in scarab beetles (Forrest *et al.* 1995). Acoustic startle responses are typically of short latency and show

directionality to sounds of behaviourally relevant frequencies and intensities occurring in a particular context (e.g. flight) (Hoy *et al.* 1989). Tethered flying *Locusta migratoria* also exhibit an ASR (Hoy *et al.* 1989; Robert, 1989; Robert and Rowell, 1992*b*). When stimulated with short-duration sound pulses with carrier frequencies greater than 10 kHz and intensities greater than 45 dB SPL, locusts increase their wingbeat frequency and deflect their abdomens and hindlegs away from the source of the sounds (Robert, 1989). Abdomen and hindleg deflections increase drag on the side to which they are deflected (similar to the action of a rudder), but they also shift the location of the centre of mass around which the flight forces act (Zanker, 1988). These postural adjustments are accompanied by the production of yaw torques, suggesting that if the locust were flying freely a change in flight path would

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have resulted (Camhi, 1970; Arbas, 1986; Robert, 1989). Together with postural adjustments, changes in wing kinematics also play a role in flight steering.

For a locust in level free flight, lift must equal weight and thrust must equal drag. Lift and thrust are controlled by wing kinematic parameters originating from the coordinated activity of approximately 40 muscles, and changes in wing movements that generate lift may also, coincidentally, generate thrust. When a locust changes the direction of its flight path, it must generate yaw torques or roll torques or both. Torques are generated when thrust and/or lift is changed asymmetrically on either side of the body.

Many of the data for wing kinematic changes during steering are derived from studies of locusts engaged in correctional steering to maintain a straight course (e.g. Thüring, 1986; Waldmann and Zarnack, 1988; Zarnack, 1988). Locusts also engage in intentional steering to change their course (e.g. Baker, 1979*a*; Cooter, 1979; Robert, 1989; Robertson and Reye, 1992; Robertson *et al.* 1996). A comparison of correctional steering (to an artificial horizon under closed-loop conditions) and intentional steering (elicited with high-frequency sounds) reveals that many of the mechanisms are similar; in both types of steering, locusts modulate their wingbeat and use abdomen and hindleg deflections to turn (Robert and Rowell, 1992*a*). However, differences are observed in the two steering modes. In particular, the magnitudes of the changes in wing kinematics and body posture are different between correctional and intentional steering. During collision (Robertson and Reye, 1992; Robertson and Johnson, 1993) and thermal avoidance (Robertson *et al.* 1996), changes are of greater magnitude than during correctional steering. Although abdomen and hindleg deflections, and the resulting yaw torques, in response to high-frequency auditory stimuli have been documented (Robert, 1989), the associated changes in wing kinematics are currently unknown.

During collision and thermal avoidance, the forewings show profound asymmetries during the downstroke, and these are accompanied during thermal avoidance by asymmetries in the timing of activation of the left and right forewing first basalar muscles (M97, wing depressors). We show here that similar changes in wing kinematics and motor patterns are employed by locusts in their steering responses to bat-like sounds, indicating that there may be a common motor strategy underlying rapid avoidance manoeuvres in flight. Current ideas of flight steering in locusts (e.g. Schmidt and Zarnack, 1987; Zarnack, 1988) explicitly discount a role in steering for phase shifts in the timing of transitions to the downstroke. We argue here that such phase shifts are critically important during intentional steering by producing an asymmetry in the range of stroke angles of the forewings, thereby imparting a roll torque that would augment the steering torques produced by other described kinematic asymmetries to increase the rapidity of the manoeuvre.

As with many wing kinematic studies employing stationary cameras and electromyographic recording equipment, it is an unfortunate necessity to tether the animal. The influences of tethering have been dealt with in detail in previous papers (Robertson and Reye, 1992; Robertson and Johnson, 1993; Robertson *et al.* 1996), and they mainly relate to the removal of exteroceptive input that would normally be present during free flight. We therefore anticipated that biases would be present in our data in spite of our efforts to minimize the influences of the tether. Specifically, we predicted that all our locusts would show abdomen deflections away from the sound source, indicating attempts to steer away from the sound source; however, we found that some locusts deflected their abdomens in one direction only irrespective the side of the applied stimulus and that others displayed a steering bias prior to stimulation. In our electromyographic recordings, this bias was manifest as a pre-stimulus asymmetry in the time of depressor activation and an asymmetry in the number of depressor spikes per burst in left and right M97 recordings. In spite of these observations, we are confident that we investigated a real behaviour and not an artefact of the tether for the following reasons. First, abdominal deflections were elicited with behaviourally relevant sound intensities (thresholds between 45 and 55 dB) and deflections occurred within one or two wingbeats after stimulus onset. Second, coordinated, repeatable changes in wing kinematics (e.g. forewing asymmetry) were observed that are similar to those of other avoidance behaviours (collision avoidance, Robertson and Reye, 1992; thermal avoidance, Robertson *et al.* 1996). Finally, the direction of forewing asymmetry was predictable from the direction of abdomen deflection even though the latter was not always away from the sound source. The acoustic stimuli used in the present study were adequate to induce true steering manoeuvres whose direction and magnitude may have been affected by the experimental conditions.

Materials and methods

Animals

Locusta migratoria L. of either sex and at least 2 weeks past imaginal ecdysis were selected from a crowded colony maintained at 31 °C on a 16 h:8 h light:dark cycle. All data were collected at room temperature (approximately 22 °C). Only apparently healthy animals with intact wings were chosen for experiments.

High-speed cinematography and videography

Animals were tethered dorsally with wax by the pronotum to a rigid copper rod and suspended 7 cm in front of a wind tunnel (mouth 20 cm×20 cm, length 28 cm) producing an air flow of $3\,\mathrm{m\,s^{-1}}$ (verified using a hot-wire anemometer). Animals were filmed from behind during sound presentations with either a high-speed 16 mm Locam motion picture camera operating at $250\,\mathrm{frames\,s^{-1}}$ with a shutter speed of 1/1225 s (five animals) or a Hitachi camcorder (model VM5200A) operating at $60\,\mathrm{frames\,s^{-1}}$ with an electronic shutter speed of 1/1000 s (10 animals) (Fig. 1A).

A

Wind tunnel
(3 m s⁻¹)

Speaker

Tethered locust

Camera

B

Speaker

EMG
wires

Tether

Camera

Fig. 1. For kinematic analyses, locusts were tethered 7 cm in front of a wind tunnel equidistant from laterally placed speakers. Sounds were delivered from either the left or the right, and responses were filmed from behind with either a high-speed (Locam) camera or a Hitachi camcorder equipped with a 1/1000 s shutter (A). For motor pattern analysis (B), EMG electrodes recorded activity in the left and right forewing first basalar (M97) depressor muscles while locusts were flying in front of a wind tunnel within a Faraday cage lined with sound-attenuating foam. A single speaker was placed above the animal and one ear was deafened.
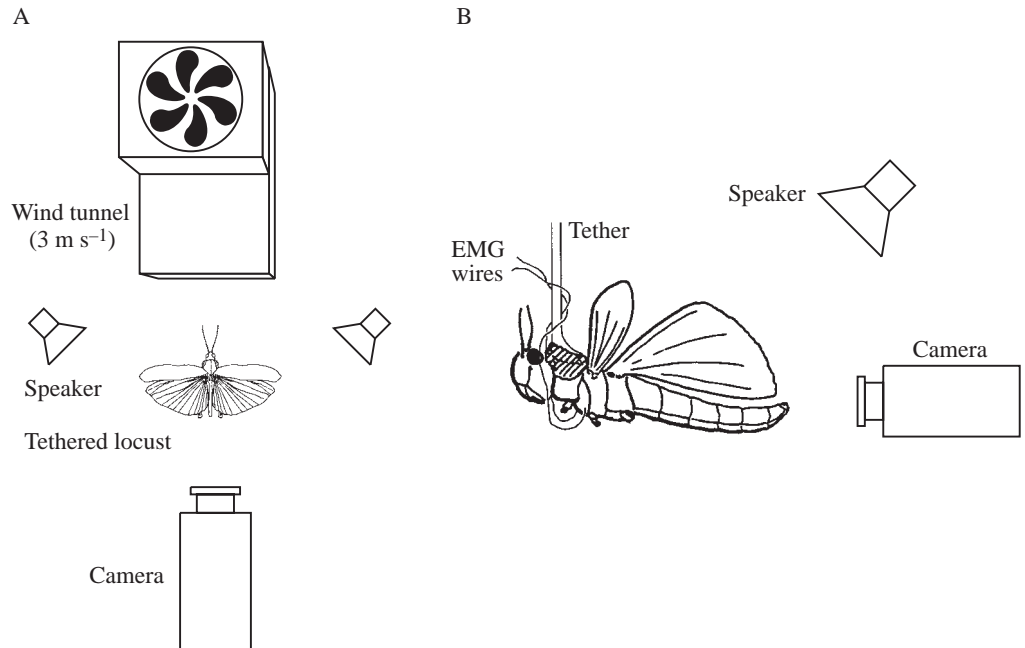
Speakers (ACR Swiss, model FT17H) were placed equidistant (13.5 cm) from the midline of the locust at an angle of 72 ° relative to the long axis of the locust's body. A light-emitting diode was placed in the video frame to monitor the stimulus. When animals were in stable flight, sounds were presented alternately from the left or the right, with the side receiving the first presentation chosen arbitrarily. Sounds consisted of 10 ms, 30 kHz shaped pulses (2 ms rise/fall time) presented with a 20 ms period for a duration of approximately 400 ms. The shaped pulses were synthesised by passing a 30 kHz sine wave from a frequency generator (Dynascan Corporation, model 3011) into a custom-made pulse shaper that was gated by a pulse generator (World Precision Instruments, model 831). The shaped pulses were then amplified (Harman-Kardon, model HK 6100) and passed through a step attenuator (Hewlett Packard, model 350D). Sound intensities ranged from 50 to 90 dB SPL. Sound pressure levels were measured with a Brüel and Kjær sound level meter (model 2209) and a Brüel and Kjær 1/4 inch condenser microphone (model 4135, with protecting grid). A Brüel and Kjær pistonphone (model 4220) was used for calibrating the sound-measuring equipment. Each sound presentation at a particular intensity was considered to represent a trial. Measurements (with the microphone described above) verified that sounds from each speaker produced sound pressure level differences of 3–7 dB SPL across the body at the location of the ears.

Wing movements were analysed using methods described previously (Robertson and Reye, 1992; Robertson and Johnson, 1993; Robertson *et al.* 1996). Briefly, high-speed (Locam) films were analysed by projecting the image of each frame onto a piece of tracing paper on a glass plate and measuring, with a protractor, the angles of each wing relative

to the tether and the horizontal and vertical positions of the abdomen. Care was taken to ensure that the image was not distorted after projection onto the glass plate. Angles were measured to the nearest 5 °, and abdomen position measurements were accurate to 0.5 mm. Approximately 12 frames per wingbeat cycle were captured using the Locam.

Video-taped trials were analysed using software and hardware from Peak Performance Technologies (Englewood, CO, USA), which entailed encoding the video tapes so that each frame could be reliably recalled and measured. Approximately three frames per wingbeat cycle were captured with the video camera. For each video frame, the top and bottom of the vertical tether, the tips of the wings and the position of the tip of the abdomen were marked. From the marked points, the computer calculated wing angles and abdomen position relative to the tether. Angles from video-taped trials were accurate to 5 °; abdomen positions were accurate to 0.5 mm. Forewing and hindwing asymmetries (right wing angle minus left wing angle, respectively, for forewings and hindwings) were then calculated from the wing angles measured when the animal was executing downstrokes. Frames capturing downstrokes were identified when the angular difference (the hindwing angle minus the forewing angle) of the wings on the outside of the turn (direction of turn indicated by direction of abdomen deflection) was greater than 10 °.

For each trial, pre- and post-stimulus measurements of abdomen deflection, abdominal dorsiflexion, forewing asymmetry and hindwing asymmetry were obtained as follows. The pre-stimulus measurement was obtained by averaging 200 ms of data from the period immediately before the stimulus was applied, and the post-stimulus measurement was obtained by averaging 200 ms of data 200 ms after the stimulus was

applied (see boxed regions in Fig. 6). The changes in deflection, flexion and asymmetries were then calculated by subtracting the pre-stimulus measurement from the post-stimulus measurement.

Motor patterns

We examined motor patterns in response to acoustic stimulation in a large (65 cm deep, 125 cm wide, 75 cm tall) Faraday cage lined with sound-attenuating foam. Locusts were dorsally tethered as described above and suspended 5 cm in front of a wind tunnel (mouth 14 cm×14 cm, length 16 cm) producing an air flow of 3 m s^{-1} (verified using a hot-wire anemometer). A single speaker [Technics leaf-tweeter, model EAS10TH400B, response flat (±3 dB) to at least 40 kHz] was positioned 19.5 cm above the animal at an angle of 45° (Fig. 1B). One ear (chosen arbitrarily) was destroyed with an insect pin by completely tearing the tympanic membrane. Care was taken not to disturb the underlying tracheae or to induce bleeding. The eyes and ocelli were painted with opaque nail polish because of the lights required for filming and to eliminate the possibility that locusts were using visual cues for steering.

Sounds were presented when animals were in stable flight. Sounds consisted of 6 ms, 30 kHz shaped pulses (1 ms rise/fall time) presented with a 30 ms period. These stimulus conditions differ from those used for the kinematic experiments described above; however, both stimuli are sufficient for eliciting the reported wing movements. Sounds were generated by passing a 30 kHz sine wave generated by a function generator (BK Precision, model 3010) through a pulse shaper (Coulbourn selectable envelope shaped rise/fall gate, model S84-04) and amplifying with a custom-built amplifier (using a National Semiconductor LM1875T chip). The sound intensity of the shaped pulses was calibrated by measuring the intensity of a pure tone of equivalent frequency and amplitude (Stapells *et al.* 1982) using a Brüel and Kjær (model 2206) sound level meter and a Brüel and Kjær 1/4 inch condenser microphone (model 4135, with protecting grid) placed next to a dead locust, with wings outstretched mimicking flight, and tethered in the experimental position. We used 71, 76, 87, 97 and 100 dB SPL pulses to induce responses from the locusts. Trials consisted of a train of pulses at a particular intensity presented for approximately 500 ms. Each animal was left for at least 2 min between stimulus presentations.

Electromyographic (EMG) electrodes, consisting of fine copper wire insulated except at the tip, were inserted just beneath the cuticle of the sternum into muscles M97 (forewing first basalars, depressors, numbering according to Snodgrass, 1929) and secured with a drop of wax. To prevent the animals from dislodging the electrodes during flight, all the legs were removed at the coxae. Activity from the left and right forewing depressor muscles was referenced to a ground electrode inserted behind the head beneath the pronotum. EMG signals were amplified using Grass Instruments (model P15) differential a.c. preamplifiers and recorded onto video tape for later analysis using a Panasonic video cassette recorder (model

PV-4770-K) and Neuro-corder (model DR-886). Peak times from left and right forewing depressor EMGs were obtained from digitised recordings using software and hardware from Datawave Technologies (Longmont, CO, USA).

Statistical analysis

Statistical tests were performed using Jandel Scientific's SigmaStat software package (Corte Madera, CA, USA). Data were tested for normality and heteroscedasticity, and appropriate parametric or non-parametric measures and tests were employed. All statistical tests assumed significance when $P<0.05$.
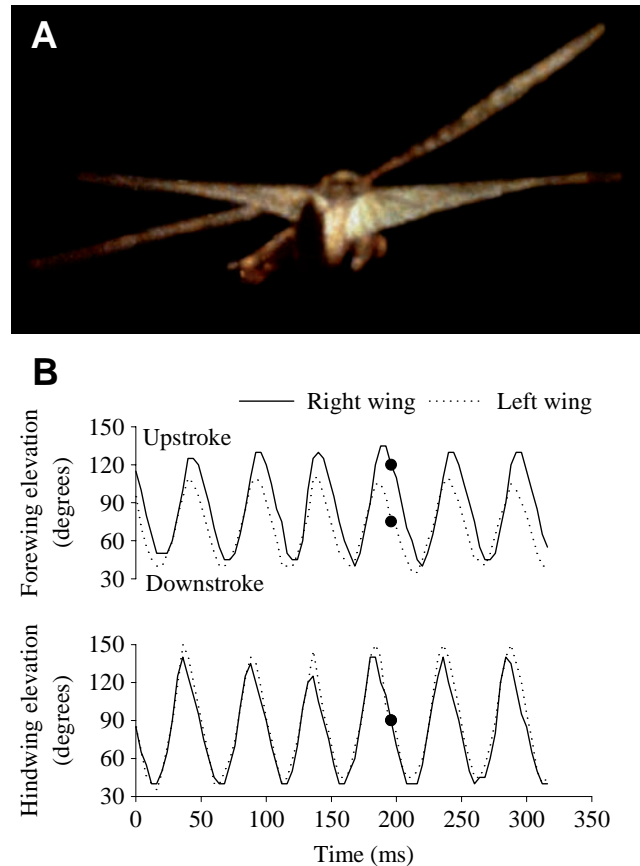

Fig. 2. A single high-speed cinematographic frame capturing a tethered flying locust during its response to a bat-like sound from the right (A), and corresponding measurements of forewing and hindwing elevations from the high-speed film. (B). Large circles in B indicate the frame corresponding to the image in A. Bat-like sounds were present during the entire sequence analysed. A consistent observation in the response to sound was the production of an asymmetry in the angle of the left and right forewings relative to the dorsal–ventral body axis during the downstroke. Although the forewings become strikingly asymmetrical, the hindwings do not. In many instances, forewing asymmetries were so extreme that the forewing on the inside of the turn was depressed to a point below the ipsilateral hindwing. Note that the abdomen and hindlegs deflected away from the sound source with coincident abdominal dorsiflexion. We also observed changes in the angle of attack of the fore- and hindwings (i.e. the relative amounts of wing surface visible).

Definition of terms

All wing angles were measured from behind the animal (i.e. viewing the animal along its posterior–anterior body axis). For calculations of asymmetry and angular difference, 0° is directly above the animal. *Forewing asymmetry* (FWA) is defined as the difference in the angle made by the left and right forewings with the dorsal–ventral axis. It is, by convention, the right forewing angle minus the left forewing angle. A positive FWA indicates that the right wing is depressed more than the left wing. *Hindwing asymmetry* is similarly defined except it is with reference to the left and right hindwings. *Angular difference* (AD) is the angle made between the forewings and the hindwings. It is defined as the hindwing angle (relative to the dorsal–ventral axis) minus the forewing angle, and a positive AD indicates that the forewing is at a greater elevation than the hindwing. *Angular difference asymmetry* (ADA) is the right angular difference minus the left angular difference. Positive ADA values indicate a greater separation of the right fore- and hindwings. *Depressor asymmetry* (DA) is defined as

the difference between the time of activation of the left and right forewing depressor muscles. It is, by convention, the time of the left muscle activation minus that of the right. A positive DA indicates that the right depressor muscle is activated before the left. *Abdominal deflection (ruddering)* is defined as the position of the tip of the abdomen in the right/left axis with zero as the midpoint (pre-stimulus position) and deflections to the right as positive. *Abdominal flexion* is defined as the position of the tip of the abdomen along the dorsal–ventral axis, with positive values indicating an elevation of the abdomen from its pre-stimulus position.

Results

In straight, stationary flight, locusts that were minimally affected by tethering flew with the hindwing stroke leading the forewing stroke and forewing stroke amplitude less than hindwing stroke amplitude. Locusts held their abdomens straight behind them, some with slight dorsiflexion, and

Fig. 3. Detailed description of the wing kinematics from one locust (a different animal from that in Fig. 2) stimulated with a bat-like sound from the left (stimulus bar) filmed using the high-speed camera. Plots of hindwing and forewing elevation are wing tip positions measured every 4 ms (0° is directly below the animal). Before the stimulus was applied, the right and left forewings began their up- and downstrokes at the same time, and the elevation angles of the right and left wing pairs were equal throughout the stroke. After the stimulus was presented, the abdomen lifted (dorsiflexion) and deflected away from the sound source to the right, indicating that the animal was attempting to steer to the right. Further, the right and left forewings developed an asymmetry in elevation angle during the downstroke but not during the upstroke (boxed region). The wing on the inside of the turn path, the right wing, began its downstroke before the wing on the outside of the turn path, the left wing. This is not seen in the hindwings. Asymmetries were quantified by plotting the difference in elevation angles between the left and right wings. Hindwing and forewing asymmetries were calculated for every wing angle measured during the response (solid line in respective asymmetry plots; large circles are asymmetries calculated during the downstroke). Forewing asymmetry during the downstroke was 0° before the stimulus but increased to approximately 40° following the stimulus.
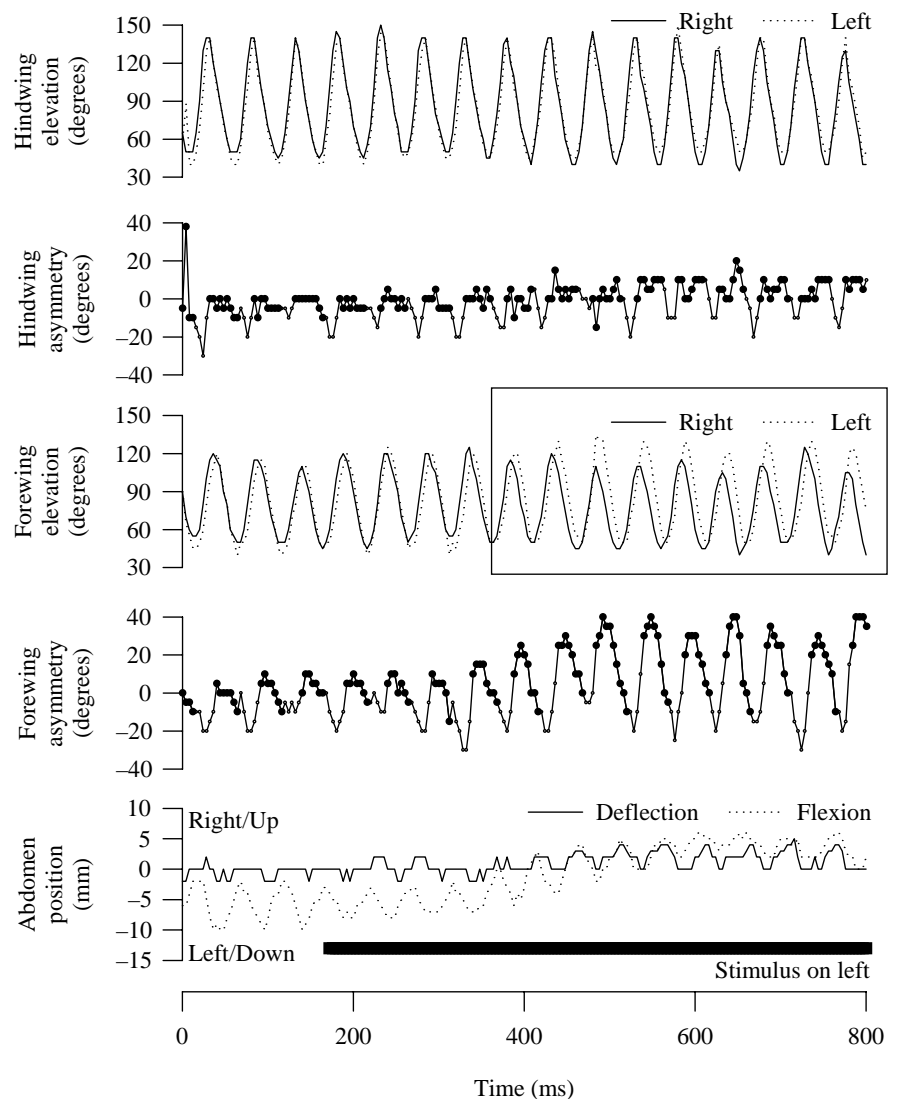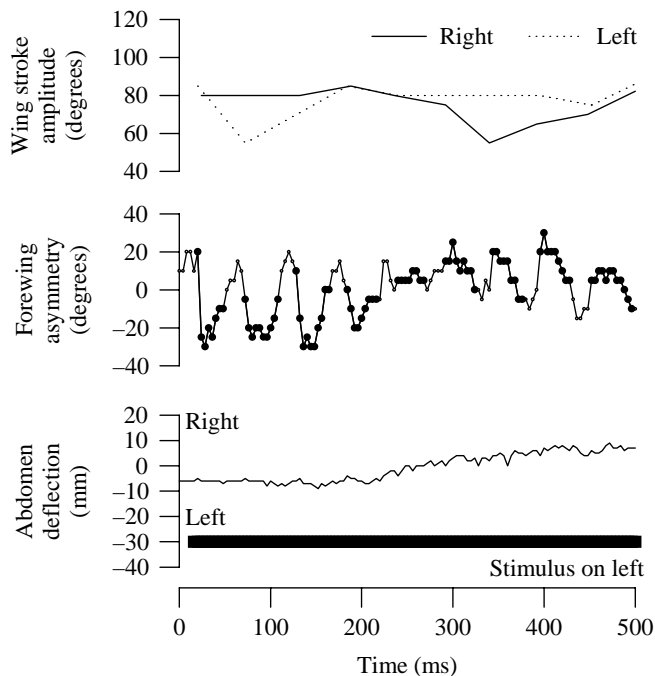
Fig. 4. Wing stroke amplitude on the inside of the turn path (direction of turn determined from abdomen deflection) was less than that on the outside of the turn path. Changes in forewing asymmetry (see Fig. 3 for an explanation of forewing asymmetry) followed the same time course as changes in abdomen deflection. In this trial, a 20° forewing asymmetry was present before the stimulus was applied and is most likely an effect of the tether (see Introduction). The data in this figure are from a different animal from that in Fig. 3.

upstrokes and downstrokes were symmetrical in left and right wing pairs. This posture changed after stimulation with ultrasound. One animal, stimulated from the right (Fig. 2), deflected its abdomen and left hindleg to the left (the inside of the presumed turn) and lifted its abdomen (dorsiflexion). The left and right forewings had asymmetrical positions during the downstroke. In all animals tested, albeit to varying degrees, we observed the characteristic changes in angle of attack with increased pronation of the wings on the inside of the presumed turn. These changes are well established as contributing to steering torques, and we did not analyse their occurrence or magnitude further. Instead, we focus here on observations of forewing asymmetries and abdomen movements.

High-speed cinematography

In the five animals filmed, stereotypical changes in wing kinematics and body posture occurred shortly after the stimulus was applied. We chose one trial from each animal for detailed analysis. Of those trials chosen, two were animals stimulated from the right and three were animals stimulated from the left. Sound intensities ranged from 60 to 90 dB SPL. Four of the five locusts filmed deflected their abdomens to the right (the remaining locust showed no measurable abdomen deflection in response to the stimulus) and, since the direction of abdomen

deflection is correlated with steering direction in tethered, flying locusts (Arbas, 1986; Camhi, 1970; Robert, 1989), we assumed that abdomen deflection indicated an attempt by the locust to steer in that direction. Thresholds for eliciting abdomen ruddering were between 45 and 55 dB SPL as measured from two of the five animals.

Positive forewing asymmetries during the downstroke were observed in all five animals. Two of the five animals filmed showed forewing asymmetries before the stimulus was applied; however, this bias was probably an effect of tethering the animal (see Introduction). Changes in forewing asymmetry (post-stimulus minus pre-stimulus) ranged from 20 to 45° (37±9.7°, mean ± S.D.). Abdomen deflection (and flexion) preceded changes in forewing asymmetry by between 15 and 44 ms. Latency to abdomen deflection was between 100 and 210 ms, and latency to forewing asymmetry was between 126 and 226 ms. Unlike the forewings, appreciable asymmetries were not consistently observed in the hindwings in response to the stimulus. We observed abdominal dorsiflexion in four of the five animals filmed. Left and right forewing and hindwing elevation and calculated forewing and hindwing asymmetries with abdomen positions for one of the five animals filmed are presented in Fig. 3.

In four of the five animals filmed, forewing stroke amplitude on the inside of the turn path decreased by between 15 and 30° (19±6.5°) (Fig. 4). The time course of this decrease coincided with the time course of the change in forewing asymmetry and abdomen deflection. Differences in the period of elevation and depression were not observed between the left and right forewings; however, forewing depression was consistently longer than forewing elevation. Consistent changes in hindwing stroke amplitude were not observed.

Forewing asymmetry was most extreme at the start of the downstroke. We plotted the difference in time between maximum elevation of the left and right forewings (at the start of the stroke reversal) to compare it with the time course of changes in forewing asymmetry (Fig. 5). Even with the 4 ms time resolution of the high-speed camera, a relationship between the difference in the time of initiation (left wing minus right wing) of the downstroke and forewing asymmetry was observed in four of the five animals filmed. The time course of this difference followed the time course of forewing asymmetry. Four of the five animals filmed revealed significant ($P<0.003$) regressions with slopes ranging from 2.26 to 3.28 (Fig. 5).

Videography

Frame-by-frame analysis of high-speed films limits us to detailed examinations of a small number of animals (five in the case of this study). We used a Hitachi video camera (with a fast 1/1000 s shutter) to facilitate data collection and analysis of a larger sample of locusts to verify the consistency of some of the observations made with the high-speed camera. Specifically, we used the video-taped trials to determine how changes in the magnitude and direction of forewing asymmetry were related to changes in abdomen deflection and to

determine how the direction of the sound source affected forewing asymmetries.

Plots of forewing and hindwing asymmetry and horizontal and vertical positions of the abdomen of one locust before and after stimulation are presented in Fig. 6 (see Materials and methods for an explanation of the boxed regions). This figure demonstrates that the videographic method is sufficient for capturing changes in forewing and hindwing asymmetries and abdomen deflection. Measurements of wing angles and abdomen position were made from 85 sound presentations to 10 animals. Of the 10 animals tethered, half (five) showed abdomen deflections in only one direction irrespective of the side of the applied stimulus. Of the remaining five animals (which accounts for 39 % or 33/52 of the trials), 70 % (23/33) exhibited negative phonotaxis.

Scatterplots of abdomen deflection (we discarded 14 trials from the initial 85 and used only trials with abdomen deflections greater than 0.1 cm) and forewing and hindwing asymmetries for all trials, irrespective of the direction of phonotaxis or stimulus intensity, revealed that only seven of 71 trials (9.9 %) showed a discrepancy between the direction of abdomen deflection and the direction of forewing asymmetry (Fig. 7A). Similarly, 25 of 71 trials (35.2 %) showed a discrepancy between the direction of abdomen deflection and hindwing asymmetry (Fig. 7B). Some animals yielded more trials than others, and not all animals showed phonotaxis in one direction; we therefore selected two subsets of data from the 71 trials from 10 animals. The first subset

consisted of trials showing negative phonotaxis to 60 dB SPL sounds (Fig. 7 C,D). Where multiple trials from a single animal were chosen, the responses were averaged to avoid pseudoreplication. The magnitude and direction of forewing asymmetry were significantly correlated with the magnitude and direction of abdomen ruddering (Pearson product moment correlation, $r=0.794$, $N=7$, $P=0.033$), and hindwing asymmetry was correlated with neither abdomen ruddering nor forewing asymmetry (hindwing asymmetry *versus* abdomen ruddering, $r=0.138$, $N=7$, $P=0.769$; hindwing asymmetry *versus* forewing asymmetry, $r=0.337$, $N=7$, $P=0.459$). The second subset of data, consisting of trials from animals showing positive phonotaxis towards 60 dB SPL sounds, found the same relationships (Fig. 7E,F). The magnitude and direction of forewing asymmetry were significantly correlated with the magnitude and direction of abdomen ruddering ($r=0.9$, $N=5$, $P=0.0372$), and hindwing asymmetry was not correlated with either abdomen ruddering or forewing asymmetry (hindwing asymmetry *versus* abdomen ruddering, $r=0.803$, $N=5$, $P=0.102$; hindwing asymmetry *versus* forewing asymmetry, $r=0.805$, $N=7$, $P=0.100$).

Motor patterns

Forewing asymmetries are most extreme at the initiation of the downstroke, and a relationship was found between the difference in the time of downstroke initiation of the forewings and the magnitude of forewing asymmetry (Fig. 5). This prompted us to record motor patterns from left and right
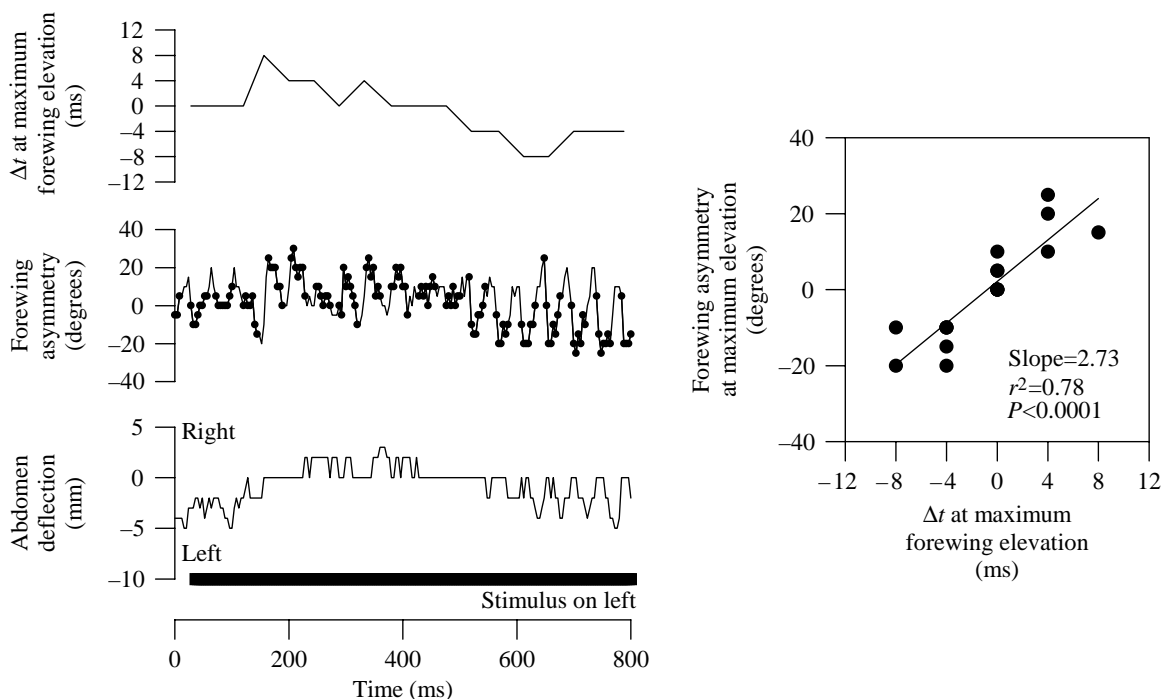

Fig. 5. The time course of changes in downstroke initiation (the difference in the time t between maximum elevation of the left and right forewings) followed the time course of changes in forewing asymmetry. The relationship between the difference in timing of downstroke initiation and forewing asymmetry was linear and predicts that forewing asymmetry, for this animal, increases by 2.73° for each millisecond difference in the time of downstroke initiation between the two wings. (Regression at right for data presented at left.)
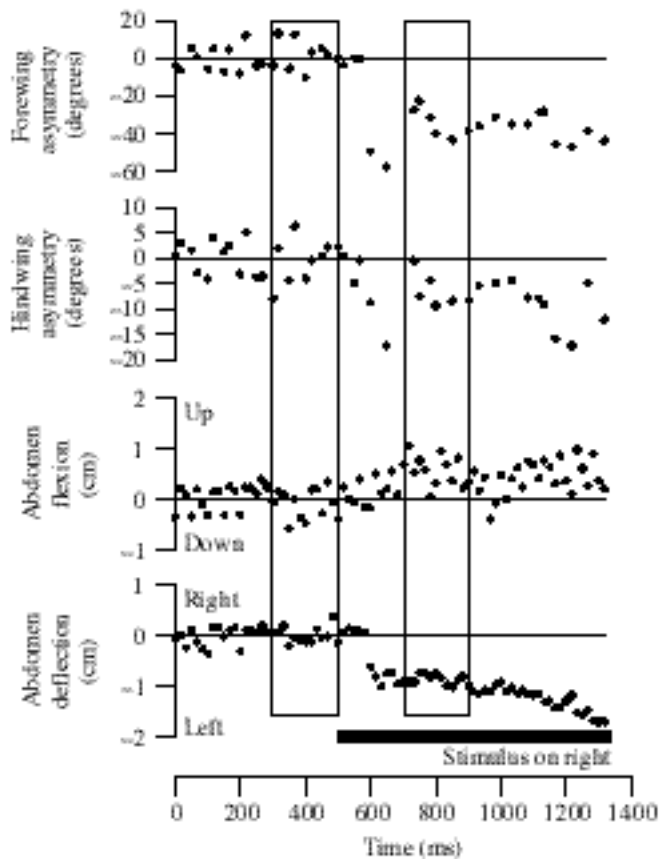
Fig. 6. A sample of the data obtained from a video-taped trial from one locust. We selected frames capturing downstrokes (see Materials and methods for an explanation) and plotted forewing and hindwing asymmetry and horizontal and vertical positions of the abdomen before and after stimulation. Measurements of forewing and hindwing asymmetry and abdomen deflection and flexion were obtained by subtracting a 200ms average of the pre-stimulus data from a 200ms average of the post-stimulus data. The boxes indicate the data windows from which the pre- and post-stimulus measurements were taken.

forewing depressor muscles (forewing first basalars, M97) to determine whether similar asymmetries occur in response to bat-like sounds.

We recorded motor patterns from four locusts. In response to acoustic stimulation, an asymmetry in the timing of left and right depressor muscle activation occurred that ranged from 10.4 to 1.6ms (4.23±2.85ms). The number of spikes per depressor burst also increased in the muscle on the inside of the turn path (turn direction assessed by the direction of abdomen deflection), and the number of spikes per burst in the muscle on the outside of the turn path simultaneously decreased (Fig. 8A). In all animals, an asymmetry in the number of spikes per burst was present before the stimulus was applied and is probaby an artefact of tethering (see Introduction). Wingbeat frequency (frequency of depressor activation) before the stimulus ranged from 15.4 to 18.4Hz and showed an increase of 2.17±0.26Hz following stimulus onset.

The increases were consistent, albeit brief, occurrences that lasted for 3–5 depressor cycles and were coincident with the initiation of changes in abdomen deflection and flexion (Fig. 8B).

Discussion

Stationary, flying locusts attempt to avoid sounds that mimic the echolocation calls of hunting bats (Robert, 1989; Robert and Rowell, 1992b). In the present paper, we describe our investigations of asymmetries of forewing downstrokes of tethered flying locusts attempting to steer in response to auditory stimulation. It is well established that abdomen and hindleg deflections are correlated with the direction of turning in flying locusts (Camhl, 1970; Arbas, 1986; Baader, 1990; Robert and Rowell, 1992a,b), and we used the direction of abdomen deflection as an index of turning direction in our experiments. Our principal findings can be summarised as follows: (1) attempted steering manoeuvres evoked by ultrasound stimulation were accompanied by profound asymmetries in the elevation angles of the forewings during the downstroke, whereas the hindwings remained relatively symmetrical during the downstroke; (2) the magnitude and direction of abdomen deflection correlate significantly with those of forewing asymmetry; (3) the forewing on the inside of the attempted turn was less elevated than the one on the outside; (4) the stroke transition from elevation to depression occurred earlier for the forewing on the inside of the attempted turn; (5) the activation of M97 during a wingbeat cycle occurred earlier, and there was an increase in the number of muscle potentials during each cycle on the inside of the attempted turn. A similar motor strategy has been described for collision (Robertson and Reye, 1992) and thermal avoidance (Robertson et al. 1996) during locust flight. We argue below that a phase shift in the timing of the transition to the forewing downstroke has consequences for steering. This idea has previously been explicitly discounted for correctional steering in locusts (e.g. Zarnack, 1988).

Wing kinematics

Numerous investigations of steering during locust flight (reviewed in Kammer, 1985; Rowell, 1988) have resulted in an emerging consensus of which wingbeat parameters can be altered to produce the required asymmetrical lift and thrust. Asymmetries in angle of attack (inside wings pronated; Dugard, 1967; Baker, 1979a; Waldmann and Zarnack, 1988; Zarnack, 1988), asymmetrical timing of stroke reversals (Thüring, 1986; Schwenne and Zarnack, 1987; Waldmann and Zarnack, 1988) and asymmetrical relative positions of the fore- and hindwings (Schmidt and Zarnack, 1987; Schwenne and Zarnack, 1987) have all been associated with steering manoeuvres and/or the production of steering torques. In the present study and in previous investigations of intentional avoidance steering (Robertson and Reye, 1992; Robertson et al. 1996), the most striking observation was of the production of asymmetries in the forewing elevation angles during the

downstroke. These asymmetries were primarily attained by changes in the relative timing of the initiation of the forewing downstroke on either side of the locust (earlier downstroke on the inside of the turn). We noted, but did not quantify, changes in the angle of attack of the wings (increased and early pronation inside the attempted turn) during the downstroke, and we expect that such changes would have added to any aerodynamic effects of the observed forewing asymmetry. The following discussion concentrates only on the forewing asymmetry as a kinematic mechanism *contributing* to the generation of steering torques.

An important question is whether the described forewing asymmetry on its own could have aerodynamic consequences for steering. It has been claimed (Zarnack, 1988) that such a phase shift in the timing of transitions to the downstroke could alter the generated forces only during the beginning and ending of shifting, or by virtue of the changed interaction with the hindwings (see below). However, the forces generated by the forewings must interact continuously by virtue of the fact that each wing transfers these forces to the body of the locust at the wing hinge, and the relative orientations of the forewings and the body will determine a resultant flight force vector. Assuming that the two forewings are equal in their aerodynamic effect, the resultant lift vector of the forewing pair, considering the pair in isolation, must lie in a plane which bisects the angle between the two forewings. At different
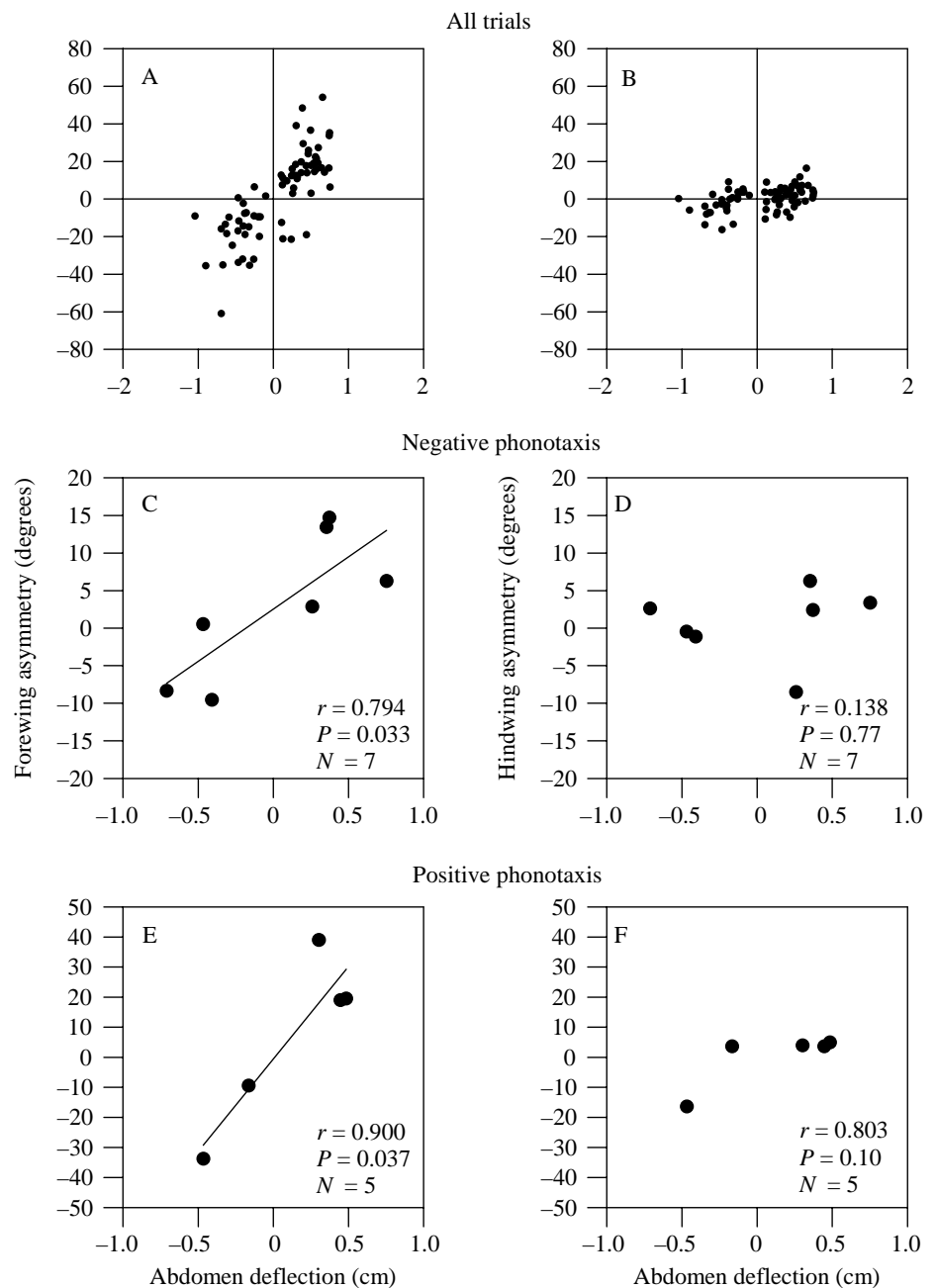

Fig. 7. The magnitude and direction of forewing asymmetry were significantly correlated with the magnitude and direction of abdomen ruddering. Hindwing asymmetry was correlated with neither abdomen ruddering nor forewing asymmetry. Scatterplots of data from all trials combined (*N*=10 animals) show measurements of abdomen deflection with corresponding forewing (A) and hindwing (B) asymmetries (abdomen deflections less than 0.1 cm were omitted). Of 71 trials, only seven (9.9 %) showed disagreement between the direction of abdomen deflection and the direction of forewing asymmetry (A). Hindwing asymmetry does not show the same relationship, 25 of 71 trials (35.2 %) show disagreement with direction of abdomen deflection (B). When examining responses to 60 dB sounds only (data from multiple trials per animal combined), animals turning away from the sound source (negative phonotaxis, C,D) and animals turning towards the sound source (positive phonotaxis, E,F) showed the same results.

A

No stimulus

Left

Right

Sound on left

Left

Right

25 ms

B

Depressor frequency (Hz)

Depressor asymmetry (ms)

Abdomen position (cm)

Right/Up

Left/Down

——— Left

——— Deflection ········· Flexion
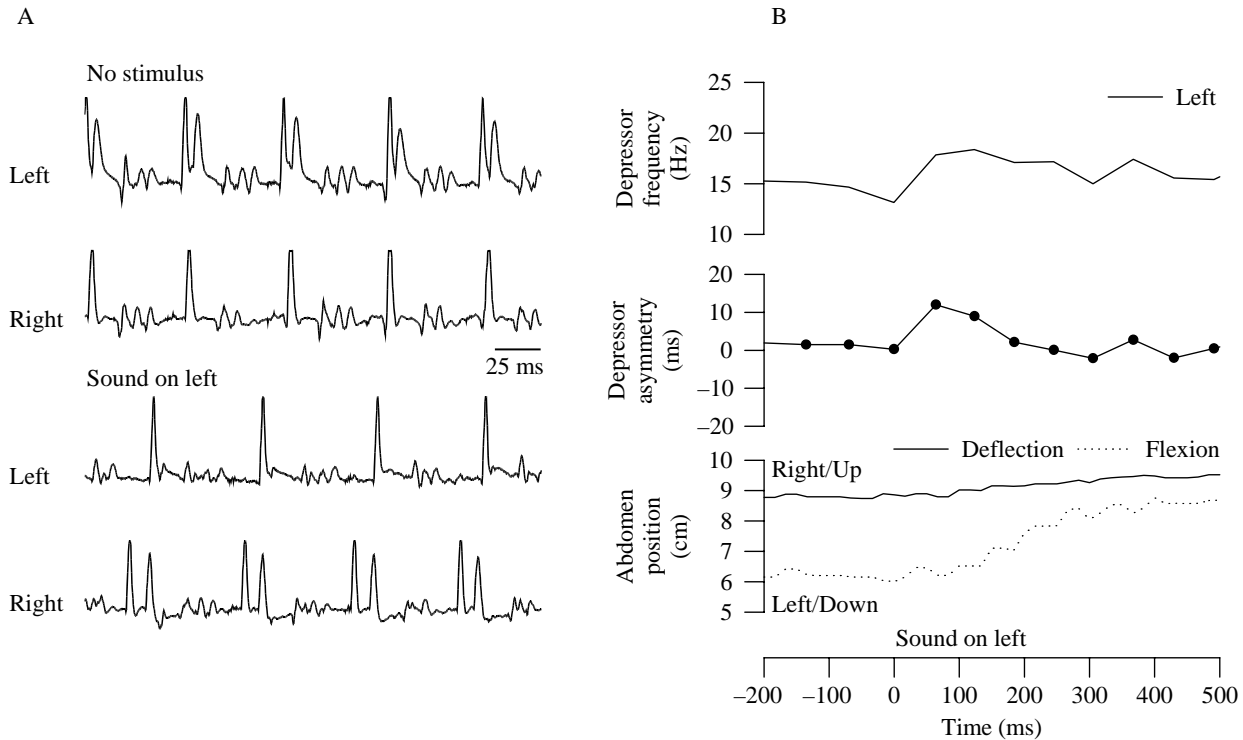
Sound on left

Time (ms)

Fig. 8. Motor patterns from left and right forewing first basalar muscles (larger spikes, M97, depressors; smaller spikes, cross-talk from an elevator muscle) show asymmetries of up to 10.4 ms after stimulation. In addition, more spikes per depressor burst (relative to the pre-stimulus condition) were observed in the muscle contralateral to the stimulus (inside of the turn path as assessed by the direction of abdomen deflection) (A). Asymmetries in depressor muscle activation were accompanied by a 2.17±0.26 Hz increase in wingbeat frequency (measured from depressor bursts). The increase in depressor frequency was brief, lasting for 3–5 depressor cycles, but was coincident with the initiation of abdomen deflection and flexion (B). Note that depressor frequency ranged from 15.4 to 18.4 Hz in all animals and, in the short sequence of spikes selected for A, it appears that depressor frequency has decreased. The motor patterns (A) and changes in depressor frequency and depressor asymmetries (B) are from different animals.

instances during the downstroke, the angle between the forewings changes and, if there is an asymmetry in the elevation angles of the forewings relative to the body, then throughout the downstroke the plane bisecting the angle between the forewings is inclined relative to the dorso-ventral plane of the animal. Thus, although thrust from the forewings may remain symmetrical, the resultant lift vector is directed away from the dorso-ventral plane and towards the side with the lower forewing, and this would occur throughout the force-generating downstroke and not just at the beginning and end of phase shifting. This is inescapably true whether or not locust flight is best considered from a standard quasi-steady perspective (Jensen, 1956) or a vortex-shedding perspective (Brodsky, 1994). The effect of this would be to impart a roll to the locust, and this would allow the larger lift component of the hindwings to contribute to changing the direction of flight. Assuming a symmetrical hindwing beat, hindwing lift would be directed dorsally but, after the forewings impart a roll, dorsal hindwing lift would be directed lateral to the original flight path and would no longer counteract the weight. Clearly, the forewings may not be equal in their aerodynamic effect during steering because of relative differences in their angles of attack (Zarnack, 1988; Robertson and Reye, 1992), but this

effect would add to, and not subtract from, any effect of the forewing angular asymmetry. Given that the hindwings remain relatively symmetrical during steering manoeuvres, a further consequence of a shift in the elevation ranges of the forewings on the two sides could be a difference in the aerodynamic coupling between the fore- and hindwings of the two sides (Schmidt and Zarnack, 1987; Schwenne and Zarnack, 1987; Wortmann and Zarnack, 1987, 1993), and this would also act additively by reducing the lift on the side with the lower forewing. The complexity of unsteady aerodynamic phenomena, if they are present in this situation, makes their effects difficult to predict. In the absence of aerodynamic evidence to the contrary, we conclude that the asymmetry in the elevation angles of the forewings during the downstroke, caused by phase shifting of the transition to the downstroke, makes a significant aerodynamic contribution to the generation of steering torques and that this is aided by changes in the flight forces generated by single wings (changes in the angle of attack) and by changes in the aerodynamic interference between the forewing and hindwing (changes in the separation angle). We propose that the specific aerodynamic effect of the forewing asymmetry described here is to roll the locust and to allow the lift from all four wings to be directed lateral to the

Left wing

Right wing

Right depressor
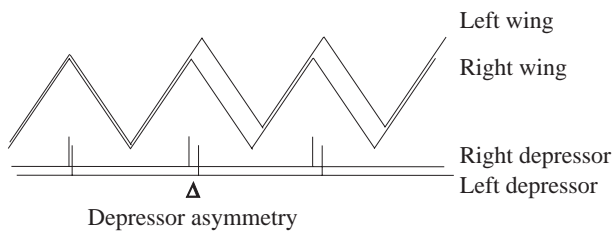Left depressor

Depressor asymmetry

Fig. 9. Model of the effect of changing the relative timing of the forewing stroke reversal on forewing position. The difference in the time of left and right depressor activation (depressor asymmetry) results in a forewing asymmetry during the downstroke. Compare with Fig. 3, boxed region. An asymmetry in depressor activation only affects the downstroke; therefore, the forewings are elevated together for some part of the upstroke.

original flight path. Simply redirecting the hindwings' forces relative to the flight path may provide increased reaction speed compared with reconfiguring the hindwing beat to redirect their forces relative to the animal.

Motor patterns

As described above, the same manoeuvre has the effect of deflecting the resultant flight force vector of the forewing pair towards the side of the lower forewing and increasing the aerodynamic interference between the forewing and hindwing on the side where the separation between the forewing and the hindwing is reduced. There are two motor strategies which would lead to this configuration of the wings during the downstroke during steering: (a) coordination of the beats of the right and left forewings so that they attain asymmetrical elevations during the downstroke (coincidentally, this would affect the separation between the forewings and hindwings on either side); and (b) coordination of the beats of the forewing and hindwing so as to minimise the separation between them (and thus maximise interference) on the inside of the turn and maximise the separation on the other side (coincidentally, this would cause an asymmetry in the elevations of the forewings). Which motor strategy does the animal actually use to change direction during flight? As noted above, a prominent viewpoint in the literature is that asymmetry in the initiation of the downstroke to generate phase asymmetries does not solve the aerodynamic problem of steering in locusts, except in that such an asymmetry will cause the interactions between the forewings and hindwings that are considered to be more important for steering (Zarnack, 1988). However, in the context of avoidance steering, we favour the alternative interpretation of our data that it is the asymmetry in the elevation angles of the forewings that is the parameter under control. This interpretation is reasonable for the following reasons. First, the observation that the forewing on the inside of the turn often appeared below the hindwing (e.g. Fig. 2; see also Fig. 3C in Robertson and Reye, 1992) indicates that the strategy used cannot be described as minimising the separation between the forewing and hindwing on the inside of the turn. Second, when hindwing asymmetries were apparent, they were

in the same direction as the forewing asymmetry (e.g. Figs 6, 7; see also Fig. 9 in Robertson and Reye, 1992, and Fig. 3 in Robertson *et al.* 1996). This would have worked against the generation of steering torques by an adjustment of the forewing–hindwing separations, whereas it would have contributed towards steering torques generated by inclination of resultant force vectors of the forewing and hindwing pairs. Third, this interpretation helps to resolve apparent anomalies in the literature on steering motor patterns. During visually induced rolling, the changes in the phase shift between corresponding contralateral muscles were the largest observed in one particular study (Schmidt and Zarnack, 1987), yet these authors could 'offer no plausible interpretation of this finding', because the degree of aerodynamic coupling between contralateral wings had not been investigated. During the steering reaction of locusts passively yawed in a wind stream, one of the strongest effects was on the timing of the beginning of the forewing downstroke and on the time intervals between contralateral homologous muscles (Zarnack, 1988), yet it was concluded that although 'these alterations of contralateral muscle activity are usually the greatest' they are 'unimportant for the generation of aerodynamic forces'. It is likely that large phase shifts between corresponding contralateral muscles (without changing the relative timing of the activations of a single wing's muscles) would generate phase shifts in the timing of stroke reversals between contralateral wings (without changing the form of the beat of a single wing). One consequence of simply changing the relative timing of stroke reversals of the two forewings by transiently increasing or decreasing the duration of the upstroke or downstroke in one cycle (e.g. Fig. 3; see also Fig. 9 of Robertson and Reye, 1992) is that their stroke angles will occupy different ranges of elevation. Moreover, if the initial change occurs with the beginning of the downstroke (i.e. to change the relative duration of the upstroke during one cycle), then one forewing becomes more elevated than the other, and they remain asymmetrical during the downstroke but return to symmetry for some part of the upstroke (Fig. 9). Thus, bulk shifts in the phasing of contralateral muscles can be interpreted as the motor pattern required to generate forewing asymmetries during the downstroke. Our experiments have confirmed that large phase shifts between contralateral forewing depressor muscles (M97) occur during attempted auditory steering manoeuvres. Such shifts may be involved in generating differences in angle of attack, but would also be required to shift the timing of the transition to the downstroke. Similar, although usually smaller, shifts in the relative timing of M97 across the locust are well described in the steering literature (Zarnack and Möhl, 1977; Baker, 1979*b*; Thüring, 1986; Schmidt and Zarnack, 1987; Zarnack, 1988; Waldmann and Zarnack, 1988; Hensler and Rowell, 1990). Indeed, the relationship between the relative timing of M97 and measured steering torque is so reliable that the timing shift can be used as a monitor of the direction and magnitude of attempted turns to close the feedback loop in a flight simulator (Hensler and Robert, 1990).

We also observed that the burst length of M97 increases on the inside of the attempted turn. This is in accordance with other intentional steering manoeuvres (Baker, 1979*b*; Robertson *et al.* 1996), although there is little or no correlation between M97 burst length and correctional steering (Thüring, 1986; Zarnack, 1988; Waldmann and Zarnack, 1988). Similarly the increase in wingbeat frequency that we observed is probably related to the fact that the locust is responding to an abrupt, startling stimulus in its environment (Cooter, 1979; Wang and Robertson, 1988; Robert, 1989).

General conclusion

Our results suggest that ultrasound information is processed by flight circuitry (see Boyan, 1985, 1989) to produce asymmetries in the flight motor pattern that would elicit turns. One component of the motor pattern change is a shift in the relative timing of M97 (forewing depressor muscles), and this contributes to generating shifts in the timing of transitions to the downstroke and consequently asymmetry in the elevation of the forewings during the downstroke. The alteration in forewing kinematics results in asymmetrical lift to impart a roll to the locust which allows the combined lift of all four wings to be directed lateral to the original flight path. This acts in combination with asymmetries in angle of attack, asymmetrical interference between the forewings and hindwings, postural alterations and an increase in wingbeat frequency to generate rapid banked downward turns. The motor strategy employed by the locust to steer in response to bat-like sounds is very similar to the strategy observed in collision and thermal avoidance. We suggest that these three sensory modalities (visual, thermal and auditory) converge and elicit a common avoidance behaviour mediated by a common neuronal circuit.

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