ULTRASOUND-INDUCED YAW MOVEMENTS IN THE FLYING AUSTRALIAN FIELD CRICKET (*TELEOGRYLLUS OCEANICUS*)

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Summary

An ultrasonic stimulus induced negative phonotactic steering in the yaw axis of tethered, flying Australian field crickets. The forewings, hindwings and twisting of the thorax generated the forces which induced the yaw turn. However, abdominal ruddering did not contribute to yaw turns. Each aspect of the yaw steering response depended upon the stimulus intensity. At higher ultrasonic intensities, the magnitude and average angular velocity increased while the latency of the yaw turn decreased. Each of these factors varied in a graded manner, revealing that this behavior is more complex than a simple reflex.

Introduction

Flying Australian field crickets (*Teleogryllus oceanicus*) respond to suprathreshold ultrasound by steering away from the sound source. This steering response, negative phonotaxis, is a complex act that includes several aerodynamic changes from steady-state flight: abdominal ruddering, tilting the forewings into the turn, an increase in hindwing wing beat amplitude on the outside of the turn, and a general increase in wing beat frequency (May *et al.* 1988*a*; Moiseff *et al.* 1978). Each of these changes should contribute to steering the cricket away from the sound source, and modeling based on ultrasound-induced changes in pitch and roll indicates that crickets do move in this way (May *et al.* 1988*b*). We now extend our investigations to ultrasound-induced changes in yaw in flying crickets, which have not been systematically studied.

Yaw is produced by applying torque around the vertical axis through an animal's center of gravity. Such yaw torque has been observed in many insects, including dragonflies (Alexander, 1986), fruitflies (Mayer *et al.* 1988), houseflies (Wagner, 1986) and locusts (Cooter, 1979). Several studies have suggested that abdominal ruddering makes an important contribution to yaw steering (Baker, 1979; Camhi, 1970; Zanker, 1988). Yet, there are other ways to induce yaw. Modulation of wing beat amplitude has been shown during yaw turns in fruitflies (Götz, 1983) and locusts (Cooter, 1979). Cooter (1979) showed kinematic changes in both the fore-

and hindwings of locusts during yaw. Temporal changes may also affect yaw. Möhl and Zarnack (1977) found time shifts between the forewing and hindwing muscles during yaw-corrective steering. Thus, yaw torque may be produced through a combination of kinematic and temporal changes.

Earlier studies have predicted that ultrasound-induced yaw turns should occur in the Australian field cricket. First, Moiseff et al. (1978) showed that a flying field cricket swings its abdomen away from the source of an ultrasonic stimulus. This abdominal ruddering might increase body drag contralateral to the stimulus and, thus, contribute to negative phonotactic yaw. Second, Pollack and Hoy (1981) found ultrasound-induced firing in the mesothoracic second basalar muscle, 98, contralateral to the sound source. Firing of muscle 98 should produce increased pronation of the forewing on the inside of the turn. This probably induces roll but may also affect yaw movements. Finally, May et al. (1988a) showed an increase in hindwing wing beat amplitude ipsilateral to an ultrasonic stimulus. This increased stroke amplitude could provide increased thrust ipsilateral to the sound source and, thereby, contribute to negative phonotactic yaw. Taken together, these studies indicate that ultrasound-induced yaw in the Australian field cricket is an elaborate behavior.

Materials and methods

Preparation and recording set-up

All experiments used adult female crickets, Teleogryllus oceanicus, 1–4 weeks after the adult molt. The animals were obtained from Hawaii and have been cultured for 3 years in our laboratory colony where they were maintained at a high density and on a reversed light cycle. Crickets were flown during the first three hours following the onset of darkness. All these factors enhance tethered flight (M. L. May, personal observation).

In all experiments, the crickets were tethered dorsally and flown upright. The tether was attached with a small amount of dental wax at the intersection of the thorax and the first abdominal segment (i.e. near the cricket's center of gravity). The tethered cricket was placed in a laminar-flow wind stream which was adjusted to the average cricket flight speed, $2.1\,\mathrm{m\,s^{-1}}$ (May et al. 1988a). The wind speed was measured by a digital anemometer (Omega model HH 30). Only those crickets which aligned their flight path with the wind stream were used in experiments.

The tether apparatus, designed to measure yaw angle, allowed free rotation around the cricket's vertical axis (Fig. 1). The tether, an aluminum welding rod, was connected through an offset attachment to a small aluminum cylinder which was balanced, through its vertical axis, on needle points. Effectively, crickets making yaw movements in flight rotated the small cylinder. A 4 cm length of aluminum welding rod was attached to the rotating cylinder. This rod conducted a 30 kHz sine wave and served as the wand for a capacitative measuring device (Sandeman, 1968). Yaw movements made by the cricket rotated the cylinder

swinging the wand between two capacitative sensors. Thus, displacement of the wand produced a d.c. voltage. This d.c. voltage was calibrated in degrees of yaw, to an accuracy of ±1°, by using a circular protractor. Moreover, the d.c. output was linearly related to the angle of yaw for 50° in either direction relative to wind direction. To avoid problems with electronic drift, the capacitative measuring device was recalibrated in degrees after each experiment. The d.c. voltages for all experiments were recorded on tape (Vetter model 420) for off-line analysis.

All ultrasonic stimuli were electronically produced. The 20 kHz output of a sine-wave generator (Brüel & Kjaer model 3011) was shaped (custom-built trapezoid shaper) and temporally adjusted for duration (WPI pulse module model 831). The 20 kHz tone was attenuated (Hewlett-Packard 350D), amplified (Nikko NA-790), and then delivered to one of two piezoelectric speakers. In all experiments, the speakers were located in the cricket's horizontal plane and at 90° to the left or right of the cricket's long axis. The sound pressure levels were measured with a sound level meter (Brüel & Kjaer 2209) and a 1/4″ microphone (Brüel & Kjaer 4135) and are given in dB relative to 20 μPa (dB SPL). Spectral prints of the stimulus were measured by a real-time spectrum analyzer (Nicolet 444A) and all harmonics were at least 40 dB less intense than the carrier frequency. In all experiments, the ultrasonic stimulus was a pure tone pulse with a carrier frequency of 20 kHz.

Experimental procedure

The first set of experiments was designed to assess the effect of pulse repetition
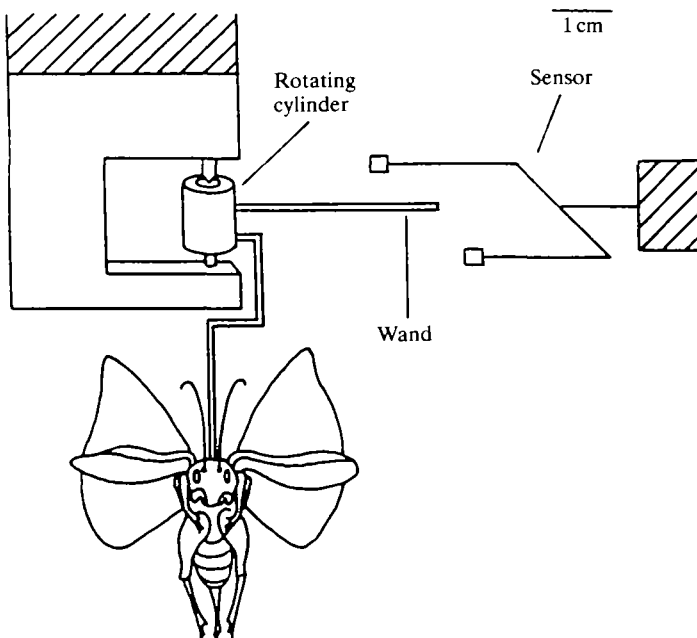

Fig. 1. Tether apparatus and sensing device. Yaw motion produced by the cricket is transduced into a d.c. voltage recorded by the sensor. Scale bar applies to the mechanical apparatus. See text for details.

rate on yaw steering. Flying crickets were stimulated with 300 ms duration trains of 20, 40, 60, 80 or 100 pulses s^{-1}. In each case, the pulse was 5 ms in duration with a 0.5 ms rise–fall time. For comparison, a 300 ms pulse was also used. The criterion for threshold was the lowest stimulus intensity which induced forewing tilt (May *et al.* 1988*a*) in at least three out of four trials. For each stimulus condition, we measured the behavioral threshold, the latency to yaw onset, and the maximum yaw angle. For latency and maximum angle, we used a stimulus intensity which was 15 dB over threshold. Two trials were performed for each stimulus condition to determine the latency and the maximum angle. Then, we performed three one-way analysis of variance tests (i.e., ANOVA's) – for response threshold, latency and maximum yaw angle – to compare the effects of the different pulse trains and the trapezoid pulse on a series of crickets (*N*=7).

The second set of experiments was designed to determine the effect of stimulus intensity on yaw steering. For these experiments, the ultrasonic stimulus was a 100 ms trapezoid pulse with a rise–fall time of 5 ms. The stimuli were delivered at 0, 2, 5, 8, 10, 15 and 20 dB over threshold. The average threshold was 72±1 dB (mean±s.e.m.; *N*=10). For each stimulus, we measured the latency to yaw onset, the time from yaw onset to maximum yaw (i.e. time-to-peak, T_{pk}), and the maximum yaw angle in 10 crickets. At each stimulus intensity, we performed two trials which were later averaged.

To determine how the crickets produce yaw torque, we also performed amputation experiments. The crickets were flown in full flight (FW+HW) (i.e. no wings amputated), forewing flight (FW) (i.e. hindwings amputated), hindwing flight (HW) (i.e. forewings amputated), and no-wing flight (NW) (i.e. both fore- and hindwings amputated). In each of these conditions, we tested 10 crickets with the series of stimulus intensities described above.

To isolate the effect of abdominal ruddering on the production of yaw turning, we performed an additional manipulation (*N*=5). As in the NW condition, we amputated both the fore- and the hindwings. Then, a stiff wire was attached at the base of the tether and waxed to the dorsal surface of the pronotum. This stabilized the thoracic segments but still allowed the cricket to move its head and legs. Further, this condition left the abdomen free to swing in the normal manner.

Statistical analysis

An interpretation of the amputation experiments required statistical analyses. The maximum yaw angles produced by the HW and the FW condition were compared using a two-way ANOVA with a replicated design (Sokal and Rohlf, 1981). In this test, one factor was flight condition (i.e. HW and FW) and the second factor was stimulus intensity. A similar two-way ANOVA was designed to compare the FW with the NW condition.

May *et al.* (1988*a*) showed that negative phonotactic pitch in crickets is produced by a non-linear combination of forces from the hind- and forewings. Is yaw also produced by a non-linear relationship between the two pairs of wings? To check for linearity, we compared the maximum yaw angle produced in full flight

FW+HW, with the sum of the angles produced by two of the amputation conditions, FW and HW. If yaw is generated by a linear combination of forces from the two wing pairs, then the yaw angles produced by the intact condition, FW+HW, should be equal to the sum of the angles produced by the forewings alone (i.e. FW condition) and the hindwings alone (i.e. HW condition). For this comparison, we used a two-way ANOVA of unreplicated design (Sokal and Rohlf, 1981). The factors were flight condition (FW+HW and the sum of FW and HW) and stimulus intensity. For FW+HW, we used the average angle of yaw produced at each stimulus intensity by 10 intact crickets. For comparison, we summed the average angles from the amputation experiments, FW and HW, for each stimulus intensity from the 10 crickets tested in each condition. This allowed us to determine if the yaw angle produced by the sum of the FW and the HW amputation conditions equalled the angles produced in the intact condition.

We also computed the average angular velocity (maximum yaw angle/T_{pk}) at each stimulus intensity in each flight condition. Then, unpaired t-tests were used to compare the average angular velocity in the HW, FW and NW conditions relative to the FW+HW condition. These tests were performed at both 5 and 15 dB over threshold. The same statistical design was used to compare latencies in the various flight conditions.

Throughout the results, values given are the mean±S.E.M. from the 10 crickets tested.

Results

Visual observation suggested that the crickets were able to adjust their flight direction through yaw steering. However, the crickets tended to fly straight into the wind stream. Most of the crickets could maintain stable tethered flight for approximately 45 min, although some flew for over an hour.

Pulse repetition rate did not affect yaw. Whether the stimulus was one of the 300 ms pulse trains or the single 300 ms pulse, there was no difference in behavioral threshold ($P>0.1$), latency to onset of yaw ($P>0.25$) or maximum yaw angle ($P>0.25$).

Yet, removal of one or the other pair of wings did affect yaw steering (Fig. 2). In the intact condition, an ultrasonic stimulus induced a fast turn away from the stimulus (Fig. 2A). Following the negative phonotactic yaw, the crickets turned back into the wind stream, although not always returning to the pre-stimulus baseline (Fig. 2A). The response to ultrasound for the HW condition, although slower and of a lower magnitude, was similar to that for the FW+HW condition (Fig. 2B). The FW and NW conditions showed the largest differences relative to FW+HW fliers (Fig. 2C and D). In both the FW and the NW fliers, the yaw response was slow relative to the intact condition. Further, FW and NW fliers never turned back into the wind stream as seen in both the FW+HW and HW conditions.

Yaw angle

The intact condition, FW+HW, produced the largest yaw turns over the stimulus range (Fig. 3A). A 20 dB suprathreshold stimulus induced an average turn of 23.7±5.2° and a maximum of over 50° (*i.e. out of the capacitative sensor's linear range*). The intensity–response curve for the FW+HW condition was nearly linear from 0 to 20 dB over threshold. Comparison of the FW+HW and HW conditions (Fig. 3A) showed a significant difference in maximum yaw angle.

The stimulus–response curve comparing HW and FW fliers showed comparable yaw angles for both conditions (Fig. 3B). At 20 dB over threshold, the average angles of yaw were 9.7±0.7° and 9.2±1.4° for HW and FW fliers, respectively. The results of the two-way ANOVA comparing the maximum yaw angles for the HW and FW conditions showed no significant difference in magnitude ($F=1.20$; $P>0.25$) although both conditions were affected by stimulus intensity ($F=10.65$; $P<0.005$). Therefore, both the FW and HW conditions contribute equally to the intact yaw response.

The isolated contributions to yaw turning from FW and HW fliers explained the magnitude of the response in intact crickets. When comparing the yaw magnitude produced by intact fliers, FW+HW, with the summed magnitudes from HW and FW fliers, there was no significant difference ($F=1.20$; $P>0.25$).

The NW fliers produced the smallest angles of yaw relative to intensity (Fig. 3C). At 20 dB over threshold, the average angle of yaw was 5.8±0.9°. Further, the angle of yaw produced by the NW condition was significantly smaller
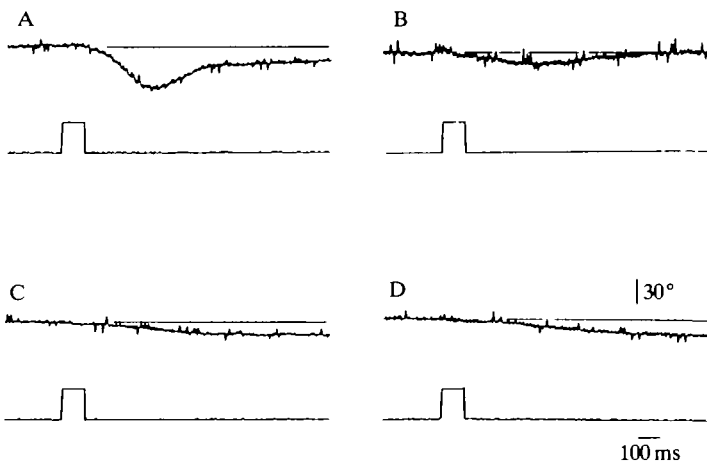

Fig. 2. Effect of wing amputation on yaw steering. (A) The FW+HW condition. (B) The HW condition. (C) The FW condition. (D) The NW condition. In each part of the figure, the upper trace is the d.c. voltage from the yaw-sensing device. The straight line represents the pre-stimulus d.c. baseline. The lower trace represents the duration of the ultrasonic stimulus. In each case, the stimulus delivered from the cricket's left side was a 20 kHz tone of 100 ms in duration at an intensity of 20 dB over threshold. The downward deflection of the d.c. voltage indicates a turn to the right. The scale bars for time and degrees apply to all parts of the figure.

than that of the FW condition ($F=10.87$; $P<0.005$). Yet, the angle of yaw induced in both NW and FW fliers depended upon the stimulus intensity ($F=7.28$; $P<0.0001$), as in intact and HW fliers.

When testing crickets in the NW condition with the thoracic segments fixed, there was no ultrasound-induced angle of yaw. This reveals that the abdominal ruddering alone produces little or no yaw torque.

Response latency

In the FW+HW fliers, the latency to the onset of yaw decreased with increasing stimulus intensity (Fig. 4A). At threshold, the average latency was 166 ± 17 ms. This value decreased to an average of 108 ± 9 ms at 20 dB over threshold. The minimum latency recorded for the FW+HW condition at 20 dB suprathreshold was an unexpectedly short 45 ms.

In the HW condition, the average latencies were 186 ± 10 ms and 115 ± 9 ms at threshold and 20 dB suprathreshold, respectively (Fig. 4B). But this was not significantly different from the latency in the FW+HW condition at either stimulus intensity.
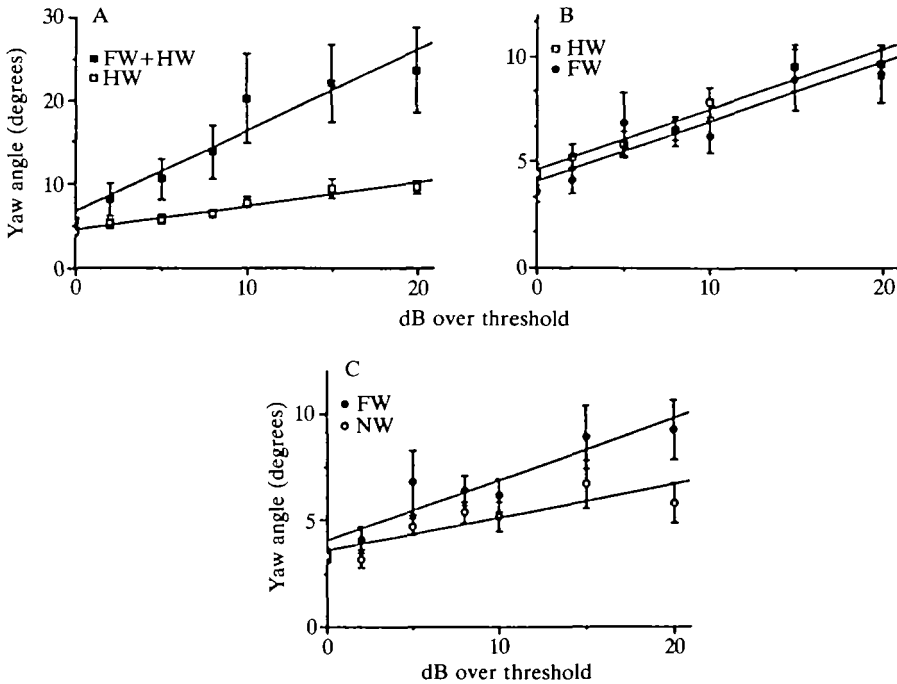

Fig. 3. The effect of stimulus intensity and wing amputation on the maximum yaw angle. (A) FW+HW compared to HW fliers. Both data sets fitted with a least-squares line [(FW+HW: $y=6.6+0.97x$; $r^2=0.92$) (HW: $y=4.5+0.29x$; $r^2=0.96$)]. (B) HW compared to FW fliers. HW data fitted as in A. FW data fitted with a least-squares line ($y=4.1+0.28x$; $r^2=0.88$). (C) FW compared to NW fliers. FW data fitted as in B. NW data fitted with a least squares line ($y=3.5+0.16x$; $r^2=0.76$). For each part of the figure, the sample size was 10 crickets.

Both the FW and NW conditions showed longer latencies than the FW+HW condition (Fig. 4B). There was a significant difference between the latencies for both the FW ($P<0.0005$) and the NW ($P<0.0005$) fliers relative to the FW+HW fliers at 5 dB over threshold. This difference was also significant at 15 dB over threshold (FW: $P<0.0005$; NW: $P<0.0005$).

Time-to-peak and angular velocity

Increasing stimulus intensity induced an increase in the time from yaw onset to the time of peak yaw angle (i.e. T_{pk}). This is shown for the FW+HW condition in Fig. 5. At threshold, the average T_{pk} for the FW+HW condition was 139 ± 10 ms. By 20 dB suprathreshold, the average T_{pk} increased to 252 ± 17 ms. Further, the increase in T_{pk} was linearly related to stimulus intensity.

The stimulus intensity affected the average angular velocity of yaw turns (Fig. 6). In the FW+HW condition, there was an increase in average angular velocity with increasing stimulus intensity (Fig. 6A). The average angular velocity for the FW+HW condition was $37.2\pm6.2°s^{-1}$ at threshold. The fitted line plateaud at approximately $90°s^{-1}$ by 8 dB over threshold.

Wing amputation decreased the average angular velocity (Fig. 6B). At 5 dB over threshold, the only significant difference was between FW+HW and NW fliers ($P<0.025$) where the average angular velocities were 59.2 ± 13.8 and $24.1\pm2.4°s^{-1}$, respectively. By 15 dB over threshold, the angular velocity in the FW+HW condition was significantly larger than the HW ($P<0.025$), FW ($P<0.01$) and NW ($P<0.005$) conditions (Fig. 6B). At 15 dB suprathreshold, the
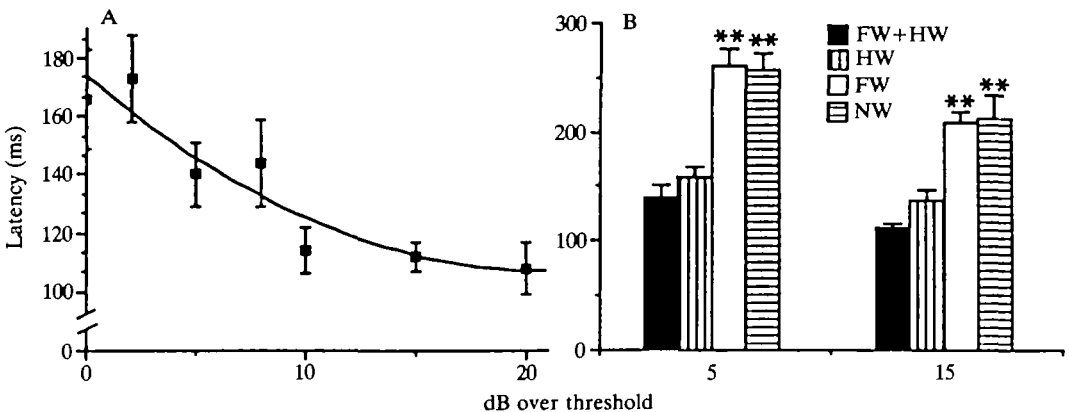

Fig. 4. The effect of stimulus intensity and wing amputation on latency. (A). The relationship between latency and stimulus intensity for intact, FW+HW, fliers ($N=10$). The fitted line is a second-order polynomial ($y=173.6-6.4x+0.2x^2$; $r^2=0.885$). Note the discontinuity on the ordinate. (B) The effect of FW+HW, HW, FW and NW conditions on latency at 5 and 15 dB over threshold. HW, FW and NW latencies were compared with the FW+HW latency at both stimulus intensities with t-tests. A double asterisk indicates $P<0.01$. For each amputation condition, the sample size was 10.

average angular velocity for FW+HW fliers was $115.3\pm25.8°\,s^{-1}$ and only $35.3\pm3.3°\,s^{-1}$ for NW fliers.

Discussion

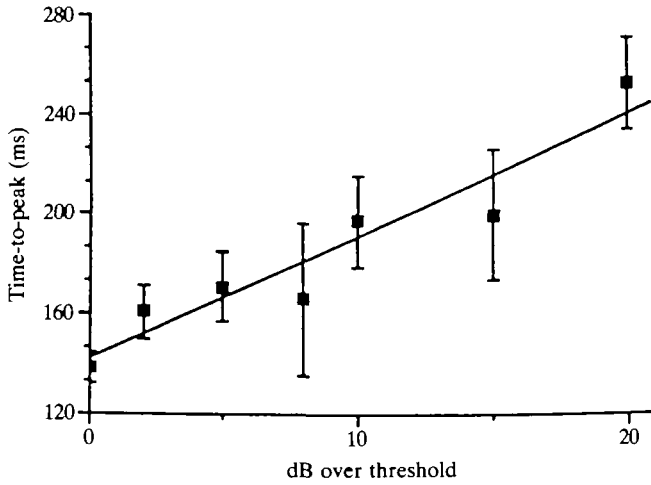The results in this paper reveal that ultrasound-induced yaw turning in crickets

Fig. 5. The effect of stimulus intensity on the time from yaw onset to the peak angle (i.e. T_{pk}). The data shown are for the FW+HW condition ($N=10$) and are fitted by a least squares line ($y=141.6-4.9x$; $r^2=0.901$).
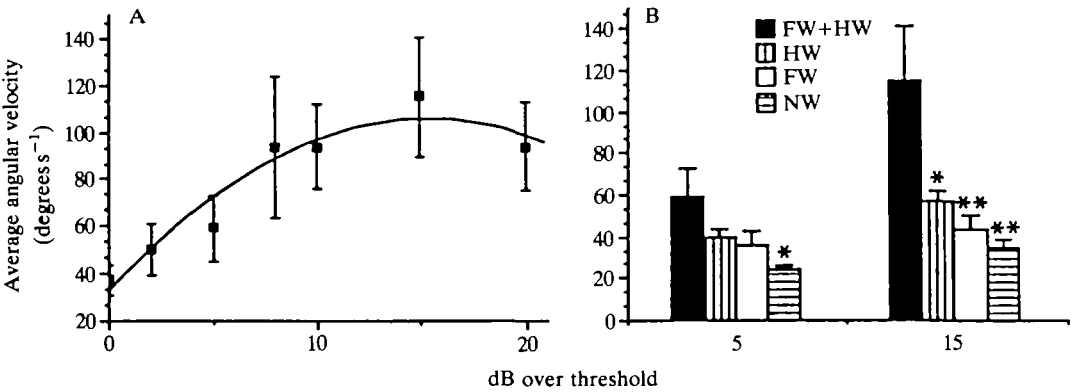

Fig. 6. The effect of stimulus intensity and wing amputation on the average angular velocity. (A) Average angular velocity *vs* stimulus intensity for FW+HW fliers ($N=10$). The fitted line is a second-order polynomial ($y=31.9+9.6x-0.3x^2$; $r^2=0.391$). (B) The effect of HW, FW and NW conditions on average angular velocity at 5 and 15 dB over threshold. HW, FW and NW average angular velocities ($N=10$ for each condition) were compared with that of the FW+HW condition at both stimulus intensities with *t*-tests. A double asterisk indicates $P<0.01$, while a single asterisk indicates $P<0.05$.

is a graded, not all-or-none, behavior. Several parameters of yaw turning – maximum angle, latency, time-to-peak and angular velocity – are functionally related to the stimulus intensity. Moreover, both the fore- and hindwings as well as twisting the thorax contribute to the generation of yaw torque. This suggests that the production of yaw turning in crickets results from the aerodynamic interaction of several forces.

In crickets, yaw turns are produced by an array of forces. Removing either the fore- or the hindwings dramatically decreases the magnitude of yaw turning (Fig. 2B and C). Yet even with both wing pairs removed, crickets still perform ultrasound-induced yaw turns (Fig. 2D). This suggests that yaw forces are produced by general body movements as well as by changes in both the fore- and hindwings.

The effect of the forewings on yaw turning may be less apparent than that of the hindwings. For example, the single case shown in Fig. 2C may lead to the impression that the forewings have only a slight role in yaw turning. Nevertheless, statistical analysis of the full data set leads us to conclude that the forewings do contribute to the turn. By comparing the magnitude of yaw turns over an intensity range of 0–20 dB over threshold, we found the following relationships: (1) intact fliers produce significantly more yaw than HW fliers; (2) HW and FW fliers produce similar levels of yaw; and (3) FW fliers produce significantly more yaw than do NW fliers. Therefore, the forewings do contribute to yaw turning.

In the tethered, intact flight condition, ultrasound induces negative phonotactic yaw which is followed by a second yaw in the opposite direction (Fig. 2A). This second turn, seen in both the FW+HW and HW condition, is probably a realignment with the wind stream. But, the second turn is not observed in the FW and NW conditions. This suggests that the second turn is an active response rather than a passive aerodynamic consequence and that the hindwings produce the realignment turn. Further, this suggests that the fore- and hindwings perform different tasks in yaw turns. The hindwings participate in both the initial yaw response and the following course correction. However, the forewings are involved only in the initial yaw turn.

The magnitude of the yaw turn in intact fliers is nearly linear from threshold to 20 dB suprathreshold (Fig. 3A). This corresponds with other aspects of cricket negative phonotaxis – tilting the forewings, pitch and roll – which show a linear dependence on stimulus intensity (May *et al.* 1988*a*). Moreover, the linear relationship between the stimulus intensity and the angle of yaw in the intact animal can be explained by the simple summation of the yaw angles from crickets flying with just their forewings and just their hindwings. This suggests that there is a linear interaction between the aerodynamic forces generated by the two wing pairs when they are both present. This is similar to the results obtained for ultrasound-induced changes in roll, but pitch is different. Amputation experiments indicated that pitch in an intact cricket is produced by a non-linear interaction between the fore- and hindwings (May *et al.* 1988*a*).

In all cases, threshold was defined as the onset of forewing tilt. However, th▄

magnitude *versus* intensity plots (Fig. 3) show yaw angles of roughly 5° at threshold. This suggests that changes in yaw may occur at intensities below the threshold for forewing tilt. Given that all flight conditions, even NW fliers, show this 'jump' at threshold, thoracic twisting may be the primary source of yaw at the lowest intensities.

The results from the present experiments show that both pairs of wings and thoracic twisting contribute to ultrasound-induced yaw. But, how do the wings and body produce yaw torque? Yaw torque could be generated by the hindwings through differential thrust. Since the hindwing ipsilateral to the ultrasonic stimulus shows an increased upstroke elevation (May *et al.* 1988*a*), this could suggest an increase in wing beat amplitude. Such an amplitude increase could induce increased thrust ipsilateral to the stimulus, which would turn the cricket away from the ultrasound. Modulation of the wing beat amplitude has been shown to induce yaw torque in *Drosophila* (Götz, 1983).

There are also ultrasound-dependent kinematic changes in the cricket's fore-wings. Ultrasound-induced firing in muscle 98 induces increased forewing pro-nation contralateral to the stimulus (Pollack and Hoy, 1981). Changes in forewing pronation have been correlated with yaw turns in locusts (Cooter, 1979). Similar pronation may affect yaw in crickets. The other primary ultrasound-induced change in a cricket's forewings, forewing tilt (May *et al.* 1988*a*), is not likely to contribute to yaw. Banking the forewings into the turn probably induces roll, although there may be some secondary yaw.

The importance of body movements in steering by crickets has been postulated for years. Several studies (Moiseff *et al.* 1978; Pollack and Plourde, 1982) have suggested that abdominal ruddering produces turning in crickets. We have shown here that body movements alone can induce yaw turns when a flying cricket is stimulated with ultrasound. But when only the abdomen is free to move, there is no quantifiable yaw turn. The conclusion is that abdominal ruddering plays no significant role in the production of yaw torque in tethered, flying crickets.

There is a possible explanation for the controversy between earlier hypotheses and the present findings concerning abdominal ruddering. The conflict may result from experimental procedure. In earlier studies of cricket flight, the animals were tethered dorsally on the pronotum but then flown upside down. In this arrange-ment, the abdomen rests horizontally, supported by the metathorax. In the present study, the crickets were tethered near their center of gravity and flown upright. In this configuration, the cricket's abdomen hangs slightly ventrally until the onset of flight. With the beginning of flight, the cricket raises the abdomen in line with the rest of the body. Although the possible neuromuscular and mechanical differences between the two preparations have not been examined, a qualitative visual observation suggests that abdominal ruddering is decreased in the upright flight preparation compared with the upside down arrangement (M. L. May and P. D. Brodfuehrer, personal observation).

Abdominal ruddering may, however, affect other aspects of turning. This paper shows that abdominal ruddering produces no significant yaw but does not consider

other aspects of turning. Therefore, abdominal ruddering may induce other turning forces. The abdominal swing causes a lateral displacement of weight relative to the long axis of the cricket's body. This asymmetry of weight distribution could affect turning in the roll axis.

Given that abdominal ruddering produces no yaw in NW fliers, what did induce the yaw? While watching a tethered, flying cricket, one can see the cricket twist the thorax away from an ultrasonic stimulus. This twisting, anterior to the center of gravity, appears to induce a yaw torque which plays a role in negative phonotaxis.

One of the most interesting aspects of yaw turns in cricket negative phonotaxis is the time course of the response. The latency decreases with increasing stimulus intensity and this temporal effect is primarily produced by the hindwings (Fig. 4). Although the average latency at 20 dB suprathreshold in the FW+HW condition was 108 ms, a minimum latency of 45 ms was recorded. This minimum value is a particularly fast onset by comparison with neuronal constraints. The minimum latency in the brain of Int-1, the first interneuron in the negative phonotactic circuit, is about 15 ms (P. D. Brodfuehrer and R. R. Hoy, in preparation). Further, ultrasound-sensitive neuronal information descending from the brain can be recorded in the cervical connectives within 20 ms after an ultrasonic stimulus (Brodfuehrer and Hoy, 1989). This suggests that the neuromuscular mechanisms generate movement in the yaw axis in less than 25 ms.

Both time-to-peak and angular velocity increase with increasing stimulus intensity (Figs 5 and 6A). The increase in angular velocity could provide sufficient momentum to prolong the turn, thereby producing the increase in time-to-peak. The angular velocity appears to be dependent upon both the fore- and hindwings but not on thoracic twisting (Fig. 6B). The maximum average angular velocity recorded was $308° s^{-1}$. This is slow compared with instantaneous angular velocities of over $1500° s^{-1}$ recorded in *Drosophila* during yaw turns (Mayer *et al.* 1988); however, crickets certainly generate instantaneous angular velocities which exceed the $300° s^{-1}$ average.

It has been suggested that the negative phonotactic response of flying Australian field crickets is a bat-avoidance response (Moiseff *et al.* 1978). If this response is indeed an escape behavior, the dynamics of yaw turning are well suited to the job. An increasing stimulus intensity could denote increasing proximity of the source, perhaps a bat. This study shows that as the stimulus intensity increases so does the effectiveness of the yaw turn. At higher stimulus intensities, the yaw turn's speed and magnitude increase. These factors suggest that cricket negative phonotaxis is both a complex and a robust behavior.

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