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Flight and hearing: ultrasound sensitivity differs between flight-capable and flight-incapable morphs of a wing-dimorphic cricket species

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Summary

We studied frequency sensitivity of flight-capable and flight-incapable forms of the wing-dimorphic cricket *Gryllus texensis*, using both behavioral and neurophysiological measurements. Behavioral thresholds for negative phonotaxis in response to ultrasound stimuli are lower for long-winged (i.e. flight-capable) crickets than for short-winged (flight-incapable) individuals, whereas thresholds for positive phonotaxis in response to a calling-song model do not differ. Similarly, thresholds of the identified interneurons ON1 and AN2 differ between flight morphs for high sound frequencies but not for the frequency of calling song. Our results show that sensitivity to ultrasound is closely linked to flight ability, and thus to the risk of predation from aerially hawking bats. We suggest that sensitivity to ultrasound is one of a suite of flight-associated characteristics, the development of which may be under common hormonal regulation.

Key words: bat predation, phonotaxis, juvenile hormone.

Introduction

Predation by echolocating bats has been an important selective pressure on insects, favoring the evolution of ultrasound-sensitive ears (Hoy, 1992; Jones and Rydell, 2003). Aerially hawking bats emit ultrasonic probes and detect flying insect prey by the echoes that return from their bodies. In some hearing species flight is restricted to one gender, and sensitivity to ultrasound is reduced in the non-flying gender, e.g. moths (Cardone and Fullard, 1988) and mantises (Yager, 1990). These observations suggest that sensitivity to ultrasound is closely linked to flight physiologically, as well as evolutionarily.

Many cricket species are flight dimorphic, occurring both as long-winged and short-winged forms (Zera, 2004; Roff and Fairbairn, 2007). The long-winged form is initially capable of flight, but individuals may lose this ability when flight muscles undergo histolysis, which becomes increasingly probable with advancing adult age (Shiga et al., 1991). The short-winged form is incapable of flight throughout life. Unlike the cases cited above, in flight-dimorphic crickets the risk of bat predation varies within a single gender and, for long-winged crickets, within a single individual. Moreover, crickets use hearing not only to detect bats but also, in a lower range of frequencies, for intraspecific communication (Moiseff et al., 1978). We compare auditory sensitivity between flight-capable and flight-incapable forms of the cricket *Gryllus texensis*, both to ultrasonic stimuli and to the sonic frequency of intraspecific signals. We find, using both behavioral and neurophysiological measures, that sensitivity to ultrasound, but not to low sound frequencies, varies according to the ability to fly. Our findings suggest that ultrasound sensitivity is one of a suite of developmental and physiological phenotypes that are linked to flight, and thus to the risk of predation by aerially hawking bats.

Materials and methods

Animals

Gryllus texensis (Cade and Otte) were reared in the laboratory at 25–28°, on a 12 h:12 h photoperiod, with *ad libidum* access to Purina™ Cat Chow and water. Under these conditions, approximately half the males develop as long-winged, and half as short-winged individuals. The frequency of short-winged females is much lower, approximately 10%. We studied males aged 7–21 days after the final molt. Both long- and short-winged males were selected from the same cohorts, the adult ages of which were known to within 1 week. Thus, both wing morphs were represented approximately equally over the entire range of ages. Experiments were performed during the animals' scotophase.

Sound stimuli

Stimuli were produced by National Instruments (Austin, TX, USA) digital-to-analog boards (AT-MIO 16E4, 12-bit resolution or PCI-6251, 16-bit) with sampling rate of 100 kHz. Sound level (r.m.s. of a constant tone with the same peak amplitude as actual stimuli) was adjusted by a programmable attenuator (PA4, Tucker-Davis, Alachua, FL, USA or 50P-076, JFW Industries, Indianapolis, IN, USA) and calibrated with Bruël and Kjaer instruments (Naerum, Denmark; 4135 microphone, 2610 sound-level meter).

Behavioral measurements

Flying crickets flex the abdomen in the direction of an

intended turn (Moiseff et al., 1978). We monitored abdominal position as an indicator of phonotactic responses. Crickets were attached to an applicator stick at the pronotum using a wax-colophonium mixture and placed ventral side uppermost in a wind stream to induce flight. The abdomen was illuminated with a fiber-optic source so as to cast a shadow onto a pair of photocells, which were connected together to provide a differential output. The photocells were masked by a V-shaped covering, so that the area covered by the shadow of the abdomen varied as the abdomen was flexed to the left or right. Experiments were performed in a plywood chamber (0.6 m×0.6 m×1.2 m) lined with echo-suppressing foam. Sound stimuli were either 5 s-long models of the species' calling song (6 ms-long sound pulses, with 2 ms linear onset and offset ramps, pulse period of 12.8 ms, and carrier frequency of 5.2 kHz) (Walker, 2000), or 60 ms pulses (including 5 ms onset and offset ramps) with carrier frequency of 30 kHz, a frequency that occurs within the echolocation calls of many bat species (Fenton et al., 1998), including some that are sympatric with *G. texensis* [e.g. *Eptesicus fuscus*, *Myotis thysanodes*, *Antrozous pallidus* (Fenton and Bell, 1981)]. Duration of the ultrasound pulse was longer than that typical of bat calls, but was chosen to be consistent with the stimuli used in neurophysiological experiments, where long pulse duration facilitates measurements of threshold. Photocell output and stimulus marker were recorded to computer files using a DigiData 1322A interface (Molecular Devices, Sunnyvale, CA, USA), with a sampling rate of 1 kHz.

Stimuli were presented in blocks of 5 trials, with 9 s between trials and at least 1 min between blocks; sound frequency and sound level was constant within each block. Stimulation began at 60 dB SPL for the song model, and at 80 dB SPL for the ultrasound pulse, with the expectation that these would be above threshold; if they were not, stimulus level was increased successively, in 10 dB steps, until threshold was exceeded. Stimulus level was then decreased in 10 dB steps until it fell below threshold, and then increased in 2 dB steps until threshold was again reached. A stimulus was scored as above threshold if it evoked a response on at least three of the five trials. The criterion for a response on each trial was that the recording of abdominal position during the period 10 ms to 200 ms after stimulus onset for 30 kHz pulses, or 10 ms to 5 s for the song model, departed from the mean pre-stimulus value (recorded for 1 s immediately before stimulus onset) by at least four standard deviations (s.d.). Responses were analyzed during the intervals between blocks of trials using custom-written software running under Scilab 3.0 (www.scilab.org). Thresholds were measured for each of two loudspeakers (Radio Shack 40-1310, Fort Worth, TX, USA), one on the left and one on the right, each at an angle of 72° from straight ahead and at a distance of 22 cm from the cricket. Thresholds for the two loudspeakers seldom differed by more than 2 dB (maximum difference 8 dB); threshold was taken as their mean.

Neurophysiology

Crickets were affixed to a support and their forelegs were held flexed against the sides of the pronotum in a position similar to that adopted during flight. The prothoracic ganglion and cervical connectives were exposed by ventral dissection and bathed in physiological saline (Strausfeld et al., 1983). ON1 was recorded extracellularly with a glass microelectrode (5–10 MΩ, 1 mol l^{-1} NaCl) from its soma-contralateral processes in the auditory neuropil, where its spikes can be recognized unambiguously by response preference for electrode-contralateral (i.e. soma-ipsilateral) stimuli (for details, see Pollack, 1986). AN2 was recorded extracellularly from the cervical connective using either a hook (stainless-steel or tungsten) or suction electrode. AN2 spikes were recognized by their large amplitude and lower threshold to ultrasound stimuli. Stimuli were 60 ms sound pulses, including onset and offset ramps of 5 ms duration, presented at rates of 0.5 Hz (ON1) or 0.33 Hz (AN2). Stimuli were generated (National Instruments AT-MIO16 E4, sampling rate: 100 kHz), and responses recorded (sampling rate: 10 kHz), using custom Matlab programs (Mathworks, Natick, MA, USA). As for behavioral measurements, threshold was defined as the lowest sound level that evoked a response on at least three of five stimulus presentations, with a response defined as occurrence of at least two spikes within 70 ms following stimulus onset. For ON1, threshold was determined on-line using the same algorithm for adjusting sound level as described above for behavior (except that resolution was 1 dB rather than 2 dB). For AN2, stimuli were presented at intensities ranging from 50–90 dB SPL in steps of 5 dB, and threshold was determined off-line.

Flight-muscle condition

At completion of an experiment, flight-muscle condition was assessed visually after exposing the metathoracic muscles 112a, 118 and 119 (Shiga et al., 1991) by dorsal dissection. Non-histolyzed muscles are pink, whereas histolyzed muscles are white (Zera, 2004). This distinction is obvious and unambiguous, as indicated by 100% agreement among a group of four individuals who scored muscle condition for a subset of crickets (7 pink, 8 white) (Guerra and Pollack, 2007).

Statistics

Statistical tests were performed using R (www.r-project.org).

Results

Behavior

The majority of work on phonotaxis in crickets has focused on females; however, males also perform phonotaxis during flight (Pollack, 1982). Like females, males attempt to steer towards the side from which a model of their species' calling song is broadcast, and away from a source of ultrasound. Although short-winged males are incapable of true flight (as are long-winged individuals that have undergone histolysis of flight muscles), they exhibit flight-like behavior when tethered and placed in a wind stream, as indicated by adoption of a characteristic flight posture, with the front and mid legs flexed against the side of the body, the hind legs extended backwards, and the antennae extended anteriorly. We did not examine wing musculature of the crickets used for behavioral tests; thus the long-winged group almost certainly includes some individuals with histolyzed muscles. Both long- and short-winged crickets respond to a model of the species' calling song during tethered flight by attempting to steer towards the sound source, as indicated by flexion of the abdomen to the side from which the

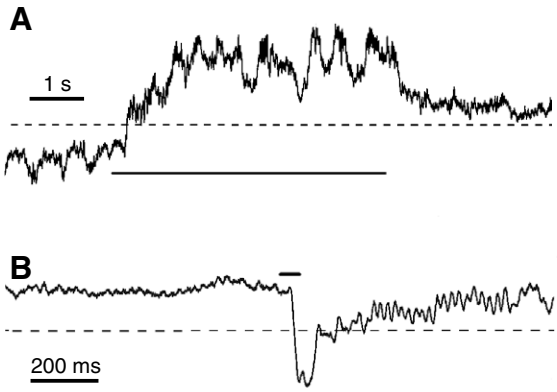

Fig. 1. Examples of positive and negative phonotactic steering responses in crickets. Traces reflect abdominal position; upward deflections indicate movements to the right. (A) Response to a model of the species' calling song, broadcast from the cricket's right at 60 dB SPL (indicated by horizontal bar). The broken line indicates the threshold level for detection of a response (mean +4 s.d. of pre-stimulus position). (B) Response of the same cricket to a single, 30 kHz pulse (indicated by the horizontal bar above the trace) presented from the right at 80 dB SPL. The broken line shows mean pre-stimulus position –4 s.d. Note the difference in time scale from A.

sound is broadcast (Fig. 1A), and they attempt to steer away from ultrasound pulses (Fig. 1B). Thus, both flight-capable and flight-incapable *G. texensis* perform positive and negative phonotactic steering movements during tethered flight.

Thresholds for positive phonotactic responses are similar for the two morphs (*t*-test, P=0.75). Threshold for the negative phonotactic response to ultrasound is approximately 8 dB lower for long-winged than for short-winged individuals (P=0.003; Fig. 2).

Frequency sensitivity of interneurons

ON1 and AN2 are two identified interneurons that have been studied in several cricket species (Pollack and Hedwig, 2007). ON1 is broadly tuned; it is most sensitive to the dominant

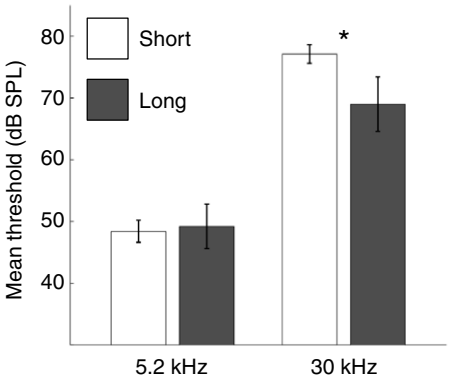

Fig. 2. Thresholds for phonotactic steering responses of long- and short-winged crickets for a model of the species' calling song with the species-typical carrier frequency (5.2 kHz) and for single 30 kHz sound pulses. Values are means ± s.e.m., N=10 for each wing morph. *Mean threshold differs significantly for 30 kHz (*t*-test, P=0.003), but not for 5.2 kHz (P=0.75).

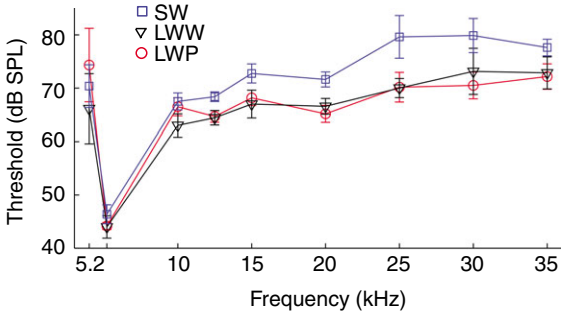

Fig. 3. ON1 tuning curves for crickets of three wing-muscle classes: short wings (SW); long wings, white muscles (LWW), and long wings, pink muscles (LWP). Only LWP individuals are capable of flight. Values are means ± s.e.m.; sample sizes: SW, 8; LWW, 7; LWP, 6.

frequency of calling song, but its responsiveness extends to ultrasonic frequencies. AN2 is most sensitive to a broad range of high frequencies. AN2 functions as a 'conditional command neuron' for negative phonotaxis; when firing at a sufficiently high rate, it evokes steering responses directed away from the sound source (Nolen and Hoy, 1984; Marsat and Pollack, 2006). ON1 influences activity of AN2 through contralateral inhibition (Selverston et al., 1985; Faulkes and Pollack, 2000; Marsat and Pollack, 2005; Marsat and Pollack, 2007).

Crickets were classed as short-winged (SW), long-winged with pink (i.e. non-histolyzed) muscles (LWP), and long-winged with white (histolyzed) muscles (LWW). As expected, sensitivity of ON1 varies with sound frequency, but also differs between flight classes (Fig. 3; two-way ANOVA, frequency effect, P<0.0001; flight-class effect, P<0.0003). The flight-class effect is accounted for by the elevated thresholds of SW individuals. *Post-hoc*, pair-wise two-way ANOVAs among the three flight classes show that threshold curves do not differ between the two long-winged classes (flight-class effect, P=0.51), but each of these differs from the short-winged class (LWP *vs* SW, P=0.0012; LWW *vs* SW, P<0.0002).

Differences in threshold between short- and long-winged crickets are evident only for high sound frequencies. Because there was no difference in sensitivity between LWP and LWW crickets, we combined these into a single, long-winged group for further analysis. Thresholds are significantly lower (*post-hoc* *t*-tests, P<0.05) for long-winged crickets for all tested frequencies above 10 kHz except 30 kHz, where the difference is nearly significant (P<0.07). Thresholds of the long- and short-winged groups are nearly identical for 5.2 kHz, the dominant frequency of the species' calling song (long-winged: 44.1±1.1 dB SPL; short-winged: 46.4±1.8, P=0.30).

Sensitivity of AN2 also varies with both sound frequency and flight class (Fig. 4, frequency effect, P<0.0001; flight-class effect, P<0.003). Unlike ON1, where sensitivity correlates with wing length independently of muscle condition, for AN2 sensitivity is determined by flight ability, independently of wing length; thresholds for high frequencies are elevated for SW and LWW individuals. *Post-hoc*, pair-wise ANOVAs among the three flight classes show that LWW and SW crickets do not differ in sensitivity (flight-class effect, P>0.1), but each of these classes differs from the LWP group (SW *vs* LWP, P<0.02;

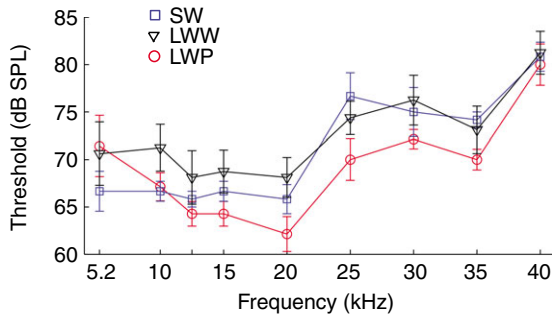

Fig. 4. AN2 tuning curves for crickets with short wings (SW; *N*=8), with long wings and white muscles (LWW; *N*=7), and with long wings and pink muscles (LWP; *N*=7) crickets. Values are means ± s.e.m.

LWW *vs* LWP, $P<0.003$). *Post-hoc* comparisons of threshold between flight-incapable (LWW and SW treated as a single group) and flight-capable (LWP) individuals revealed significant differences at 20 kHz and 35 kHz (*t*-test, $P<0.05$), and nearly significant differences at 15, 25 and 30 kHz ($P<0.06$, $P<0.08$ and $P<0.07$, respectively). Thresholds are similar for 5.2 kHz (flight-incapable, 68.3±2.0 dB SPL; flight-capable, 71.4±3.2, $P>0.4$). Because all long-winged individuals have pink muscles early in adult life, these results imply that sensitivity of AN2 to high frequencies changes along with, or following, wing-muscle histolysis.

Discussion

The link between flight and hearing in insects is long established. Comparisons between long-winged and short-winged insects, both across species and within wing-dimorphic species, have often found that tympana are present exclusively, or are better developed, in the long-winged forms (Knetsch, 1939; Ingrisch, 1976). A few studies have focused more specifically on the relationship between flight, with its attendant risk of predation from aerially hawing bats, and sensitivity to ultrasound. Female gypsy moths do not fly, whereas males do. Thresholds of auditory receptor neurons to ultrasonic frequencies are up to 20 dB higher in females than in males (Cardone and Fullard, 1988), despite any obvious difference in ear anatomy. In many mantis species only males fly, and ultrasound sensitivity of females, measured at the interneuron level, is reduced or absent (Yager, 1990). In mantises, there is a close correlation between sensitivity to ultrasound and the external anatomy of the ear. In both moths and mantises, then, the sexual difference in ultrasound sensitivity originates, at least in part, peripherally. Among orthopterans, a relationship between flight and sensitivity to ultrasound has so far been sought only in the ground cricket, *Eunemobius carolinus*. Like *G. texensis*, *E. carolinus* may be either short- or long-winged. In addition, long-winged individuals may undergo dealation, thus losing the ability to fly. Frequency sensitivity of flight-capable and flight-incapable forms was generally similar, as assayed by recording from unidentified multiple units in the cervical connective (Farris and Hoy, 2000). However, as the identity of the neurons recorded was not known, these findings cannot be compared directly with ours.

The mechanisms underlying the poorer ultrasound sensitivity of flight-incapable *G. texensis* are not yet known. One possible explanation lies in the mechanics of auditory transduction, whether at the level of the tympanum or of the cellular elements of the inner ear. Any mechanical differences between the flight morphs must be restricted to high sound frequencies, as differences in sensitivity to low-frequency stimuli were not found. It is also possible that flight-incapable forms have fewer receptor neurons tuned to high frequencies, or that these differ in their electrophysiological properties (e.g. voltage threshold for production of action potentials; firing rate). Electrophysiological and biomechanical experiments directed at these issues are currently underway.

Threshold of AN2 for high frequencies is higher in long-winged crickets with histolyzed flight muscles than in those that have not yet undergone histolysis. Peripheral changes cannot account for this shift, as there is no corresponding change in sensitivity of ON1. A caveat here is that this conclusion rests on the assumption that ON1 and AN2 receive input from the same high-frequency receptors. However, earlier work, albeit on another species (*Teleogryllus oceanicus*), suggested that this is indeed the case (Pollack, 1994; Pollack, 1997). It is likely, then, that central mechanisms also play a role in regulating sensitivity to high frequencies, at least for AN2.

Because the frequency of histolyzed muscles increases with age, the loss of high-frequency hearing in individuals with histolyzed muscles may be an indirect consequence of aging, rather than being more directly related to muscle condition. However, even if this is the case, the functional result is the same; ultrasound hearing is poorer when flight is no longer possible.

The decision to develop as a short- or long-winged morph is made during the last larval instars, and is determined by a combination of genetic and environmental influences (Zera, 2004; Roff and Fairbairn, 2007). The genetic contribution is polygenic (Roff and Fairbairn, 1991). Under constant laboratory conditions, genetics can account for up to 98% of the phenotypic variation in wing morph [*G. rubens* (Roff and Fairbairn, 1991)]. Under natural, more variable, conditions, however, heritability may be as low as 21% [*G. pennsylvanicus* (Roff and Simons, 1997); heritability of wing morph has not yet been measured for *G. texensis*]. Environmental factors that bias development towards one morph or the other include temperature, photoperiod, density and diet (Harrison, 1980). Proximately, wing morph is determined by juvenile hormone (JH) titre, which is elevated in larvae that will develop with short wings, compared to their long-winged counterparts (Zera, 2004). Long- and short-winged crickets differ in a number of other characters, including flight-muscle condition, gonad growth and lipid metabolism (Zera and Denno, 1997). Collectively, these have been referred to as a ‘migratory syndrome’ (Roff and Fairbairn, 2007). Experimental manipulation of hormone levels suggest that all of these characters are regulated in concert by JH (Zera et al., 1998). Our findings suggest that enhanced sensitivity to high sound frequencies may be yet another component of the migratory syndrome.

Moths that live in bat-free habitats tend to lose sensitivity to ultrasound, a phenomenon that has been interpreted as evolutionary loss of a specialization that is no longer being maintained by selection (Fullard, 1994). In the current case,

however, the loss of sensitivity by flight-incapable individuals occurs on a developmental, rather than an evolutionary, time scale. Both long- and short-winged individuals may issue from a single mating (Roff and Simons, 1997), in which case they would share identical histories of selection pressure. Nor can relaxed selection explain the loss of high-frequency sensitivity of AN2 in long-winged crickets that have undergone wing-muscle histolysis. The question thus arises: why is high frequency sensitivity poorer in flight-incapable individuals? There is no obvious advantage accompanying decreased high-frequency sensitivity (e.g. there is no increase in sensitivity to lower frequencies).

We suggest that poorer sensitivity to ultrasound may simply be a consequence of the physiological mechanisms responsible for enhanced sensitivity in flight-capable individuals. That is, rather than poor sensitivity in flight-incapable individuals representing a decrease in sensitivity, it may instead reflect the absence or reversal of an increase. Acoustic communication among conspecific crickets predated the appearance of bats (Hoy, 1992). A plausible scenario is that selection pressure exerted by bat predation led to enhancement of the moderate sensitivity to ultrasound that was already present in the auditory system. This might have been implemented physiologically through a JH-regulated mechanism, which was already in place as a regulator of other flight-associated characteristics such as wing length and the other components of the migratory syndrome. According to this view, lower sensitivity to high frequencies of flight-incapable individuals would reflect a mechanistic link, through JH, to the other characteristics associated with inability to fly, rather than being adaptive itself.

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