SHORT COMMUNICATION

LEG-INDUCED STEERING IN FLYING CRICKETS

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Over the past 50 years, researchers have speculated that flying insects use their legs as part of the steering mechanism. This hypothesis developed from observing that insects making a right turn, for example, swing their right metathoracic and sometimes mesothoracic leg in the direction of the turn. Several insects exhibit this behaviour, including crickets (Moiseff *et al.* 1978), locusts (Gettrup and Wilson, 1964; Dugard, 1967; Baker, 1979; Cotter, 1979; Taylor, 1981), flies (Hollick, 1940; Götz *et al.* 1979; Nachtigall and Roth, 1983) and bugs (Govind and Burton, 1970; Govind, 1972). In locusts, Camhi (1970) noted that the inside metathoracic leg (i.e. on the same side as the turn) moves out from the body and into the path of the hindwing during yaw steering; however, the aerodynamic effect was untested. Here we demonstrate that in the Australian field cricket (*Teleogryllus oceanicus*) the metathoracic leg produces a significant aerodynamic effect on yaw steering by impeding the downstroke of the hindwing on the inside of the turn.

Flying crickets were tethered upright and stimulated with ultrasonic pulses to induce negative phonotaxis (i.e. steering away from the sound source). The crickets were restricted to rotations in the yaw axis by a device which indicated the instantaneous angle of yaw during flight in a laminar flow wind stream (see May and Hoy, 1990, for details). Then, we determined the latency, maximum angle ($\pm 1°$) and average angular velocity of the yaw steering. The ultrasonic pulse had a carrier frequency of 20 kHz, a duration of 100 ms and rise/fall times of 5 ms. All stimuli were 15 dB above threshold, as defined by ultrasound-induced forewing tilt (May *et al.* 1988).

To investigate the role of the metathoracic leg in yaw steering, we tested 10 crickets under the following experimental conditions. First, we delivered five ultrasonic stimuli from each side of the flying cricket to establish the existence of a robust steering response (May *et al.* 1988). Then, we amputated one metathoracic leg at the joint between the coxa and trochanter and repeated five stimulus trials from each side. Stimuli were delivered contralateral to the amputated leg to test whether the inside metathoracic leg has an aerodynamic effect on yaw steering. Stimuli ipsilateral to the amputated leg served as controls for possible side effects caused by amputation. Amputation did not obviously diminish the quality of the
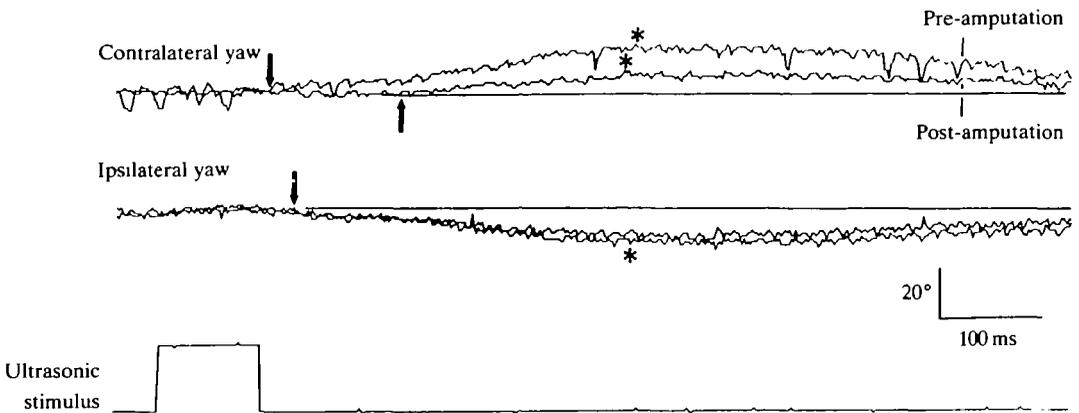
Fig. 1. Effect of the metathoracic leg on yaw angle. The traces labeled contra- and ipsilateral yaw show the instantaneous yaw angle for stimuli from either side of the cricket. The traces for ipsilateral stimuli, before and after amputation, are overlapping. The solid lines indicate baseline (i.e. flying straight) in both the ipsi- and contralateral traces. The arrows indicate the onset of yaw (i.e. latency) and the asterisks denote the time at which maximum yaw angle is attained. The time calibration line applies to all traces, including the stimulus trace. The angular calibration line applies to the yaw angle traces.

flight behavior. Throughout this paper, the terms contra- and ipsilateral are used with respect to the amputated leg. Using a one-way analysis of variance (ANOVA) test, we assessed the effect of amputation on the latency, maximum angle and average angular velocity of yaw steering. All values are given as mean±S.E.M.

Our experiments show that removing the metathoracic leg affects yaw steering in response to contralateral stimuli, but not to ipsilateral stimuli (Fig. 1). For contralateral stimuli, amputation significantly increased ($P<0.01$) the latency for yaw steering (from 98.2 ± 3.2 ms to 137.6 ± 5.6 ms), significantly decreased ($P<0.01$) the maximum yaw angle (from $17.1\pm2.1°$ to $9.2\pm1.5°$), but had no effect ($P>0.25$) on the average angular velocity. Although these average values were determined from 10 crickets, there is considerable variation between individual trials. For example, the average values predict that amputation will induce an approximately 40 ms increase in latency to contralateral stimuli. However, in Fig. 1 this increase is approximately 130 ms. For ipsilateral stimuli, amputation produced no significant effect on latency ($P>0.05$), maximum angle ($P>0.25$) or average angular velocity ($P>0.10$) of yaw steering. Therefore, removing the metathoracic leg on the side of a turn affects yaw steering and the amputation does not produce additional side effects.

To explore the temporal effects of amputation, we examined the duration from stimulus onset to maximum yaw angle. Using a one-way ANOVA, we compared the duration for contra- and ipsilateral stimuli both before and after amputation. The results show no significant difference ($P>0.05$). Thus, the time from stimulus onset to peak yaw angle is constant. Given that the average angular velocity is also

constant, this implies that the primary effect of amputation on yaw steering in response to contralateral stimuli is an increase in latency which decreases the maximum yaw angle through a secondary effect.

These experiments show that the inside metathoracic leg affects yaw steering but not that the effect is *via* the hindwing–leg interaction. Therefore, using the same protocol as before, we conducted a series of experiments on 10 crickets which had their hindwings removed. These results, also compared with one-way ANOVAs, show that, if the hindwings are absent, amputation induces no significant effect on latency ($P>0.25$), maximum yaw angle ($P>0.25$) or average angular velocity ($P>0.25$). Thus, the metathoracic leg by itself has no aerodynamic effect on yaw rotation.

We conclude from our experiments that the metathoracic leg on the inside of the turn affects yaw steering through an interaction with the hindwing. To provide pictorial evidence for this effect, we photographed tethered, flying crickets and then made line drawings from the negatives (Fig. 2). During straight flight (Fig. 2A), there is no interaction between the hindwing and the metathoracic leg. However, during steering (Fig. 2B), the extended metathoracic leg on the inside of the turn blocks the hindwing from completing the downstroke. It appears that this interaction is primarily between the femur and the posterior edge of the wing, or the vannus. Once the inside metathoracic leg is removed (Fig. 2C), the inside wing again completes a full downstroke during steering.

While many insects appear to use their legs during steering, the effect does not always involve the hindwings. In particular, some dipterans, which have no hindwings (Hollick, 1940; Götz *et al.* 1979), swing their metathoracic leg into a turn. It is thus possible that swinging a leg, by itself, into a turn may have aerodynamic effects. However, this effect is not observed in our experiments on yaw in crickets.
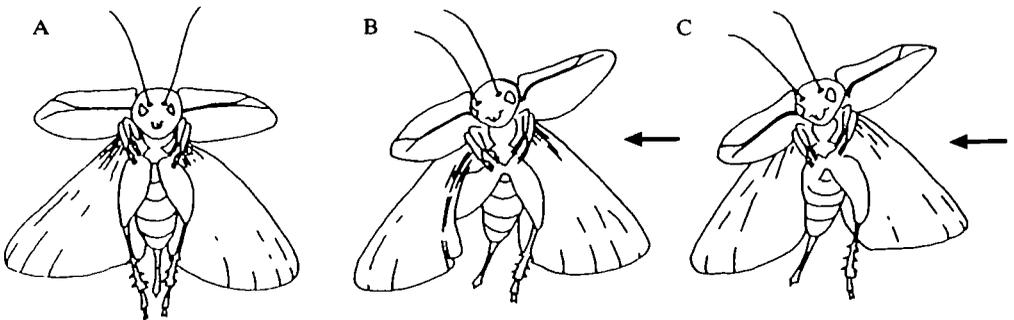

Fig. 2. The interaction between the inside metathoracic leg and the hindwing during yaw steering. All three illustrations, nearly identical in hindwing phase, are from photographs of the same cricket. (A) Normal flight in the intact state. (B) Steering flight in the intact state (C). Steering flight with the left (with respect to the viewer) metathoracic leg removed. Note that, in B and C, the arrows show the direction of the stimulus and the forewing tilt indicates active steering.

The conclusions drawn from these experiments are particularly pertinent to crickets avoiding ultrasound. Given that ultrasound-induced negative phonotaxis in flying crickets may be a bat-avoidance response (Popov and Shuvalov, 1977; Moiseff *et al.* 1978), the latency of steering is critical. As shown here, the primary effect of the metathoracic leg on yaw steering is to decrease the latency of the aerodynamic result. Furthermore, although crickets also swing their leg during calling-song-induced positive phonotaxis, the ultrasound-induced swing appears faster and of a larger magnitude. Thus, blocking the hindwing may be particularly well developed in the negative phonotactic escape response.

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