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Interacting Gears Synchronize Propulsive Leg Movements in a Jumping Insect

Malcolm Burrows† and Gregory Sutton*

Gears are found rarely in animals and have never been reported to intermesh and rotate functionally like mechanical gears. We now demonstrate functional gears in the ballistic jumping movements of the flightless planthopper insect *Issus*. The nymphs, but not adults, have a row of cuticular gear (cog) teeth around the curved medial surfaces of their two hindleg trochanters. The gear teeth on one trochanter engaged with and sequentially moved past those on the other trochanter during the preparatory cocking and the propulsive phases of jumping. Close registration between the gears ensured that both hindlegs moved at the same angular velocities to propel the body without yaw rotation. At the final molt to adulthood, this synchronization mechanism is jettisoned.

Many insects jump prodigiously by rapid and powerful movements of their hindlegs. Two arrangements of the hindlegs are found; those of grasshoppers and fleas move

in separate planes at the side of the body; those of the champion jumping insects, froghoppers and planthoppers, move counterrotationally in approximately the same near-horizontal plane beneath

the body. In the latter, synchronous movements of the hindlegs are necessary to avoid rapid spinning in the yaw plane (1, 2).

To reveal the mechanism of this precise synchronization, we made high-speed videos of jumping in nymphs (Fig. 1A) of the planthopper *Issus coleoptratus* (Hemiptera: Fulgoroidea: Issidae) and analyzed the anatomy of the proximal hindleg joints. The most rapid take-off occurred in 2 ms [2.01 ± 0.1 ms (mean \pm SEM) for eight nymphs] [supplementary material (SM) and movie S1] with a velocity of 3.9 m/s (mean 2.2 ± 0.56 m/s, $n = 8$). The two propulsive hindlegs started moving within 30 μ s of each other. Such precise synchrony would be difficult to achieve by 1-ms-long neural spikes. The hind coxae are opposed to each other at the ventral midline, and propulsive thrust was generated by large thoracic muscles that rotated

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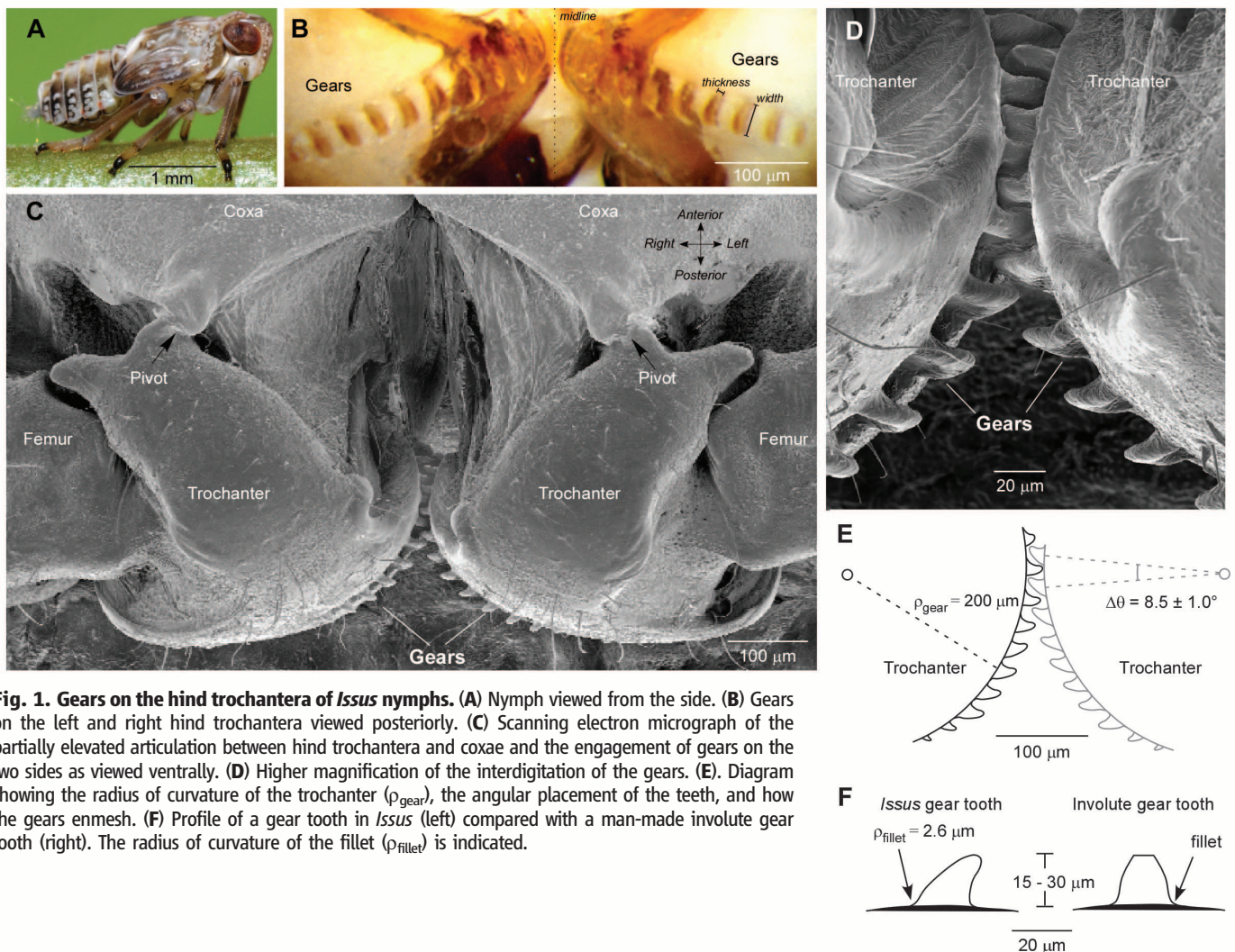


Fig. 1. Gears on the hind trochanters of *Issus* nymphs. (A) Nymph viewed from the side. (B) Gears on the left and right hind trochanters viewed posteriorly. (C) Scanning electron micrograph of the partially elevated articulation between hind trochanters and coxae and the engagement of gears on the two sides as viewed ventrally. (D) Higher magnification of the interdigitation of the gears. (E) Diagram showing the radius of curvature of the trochanter (ρ_{gear}), the angular placement of the teeth, and how the gears enmesh. (F) Profile of a gear tooth in *Issus* (left) compared with a man-made involute gear tooth (right). The radius of curvature of the fillet (ρ_{fillet}) is indicated.

the trochantera about the coxae. Each hind trochanter of nymphs had a curved strip of gear teeth (Fig. 1B), a feature that extends to other nymphal Fulgoroidea (3, 4). The gear on one trochanter enmeshed with a corresponding gear with teeth of the same size and shape on the other trochanter (Fig. 1, C and D). These gears are not present on the front or middle legs.

Each gear strip was 350 to 400 μm long, contained 10 to 12 teeth, and had a radius of curvature (ρ) of about 200 μm (Fig. 1, E and F). The left and right trochantera had the same number of teeth, which gives a gearing ratio of 1:1. One tooth occurred for every $8.5^\circ \pm 1.0^\circ$ ($n = 9$ nymphs) of rotation (Fig. 1, D and E). In final instar nymphs, the width of an individual tooth was 80 μm at the anterior end, tapering to 30 μm posteriorly (Fig. 1B). Each tooth was 9 μm thick, was separated from the next tooth by 30 μm , and projected from the surface by 15 to 30 μm , again tapering from the anterior to the posterior end. The dark coloration of the teeth, in contrast with the lighter

color of the underlying cuticle, suggests that the teeth are heavily sclerotized (Fig. 1B). Each gear tooth had a curved fillet at its base (Fig. 1E), a feature which, in man-made gears, reduces the likelihood of shearing. In *Issus*, however, the teeth were asymmetric (Fig. 1, D to F), whereas those of man-made gears often have a symmetric shape called an involute designed to work in both rotational directions (5). *Issus* gears only have one direction of powered rotation.

To determine the action of the gears in jumping, we captured high-speed images of a nymph restrained on its back but with its legs free. Rapid and synchronous movements of the hindlegs, which have all the characteristics of natural jumps (6), could then be induced by gently touching the abdomen. In preparation for a jump, the hindlegs were raised (levated) at their coxo-trochanteral joints so that both hindlegs were rotated forward (7) (Fig. 2, A and B; SM; and movie S2). In the propulsive jumping movements, both hindlegs were depressed at the coxo-trochanteral joints

with angular velocities as high as 200,000°/s (Fig. 2C, SM, and movie S3). During both the preparatory and propulsive movements, the gear teeth clearly engaged so that both hind trochantera were mechanically constrained to move within 21 μs of each other (Fig. 2, A to C). Two further experiments showed that gears ensure synchronous movements of the hindlegs. First, when the hindlegs were cocked in readiness for jumping, experimental manipulation of the tendon of the large jumping muscle of one hindleg led to the synchronous and rapid movement of the other leg, even in a dead animal. Second, the gears occasionally failed to engage at the start of the propulsive phase of a jump so that some teeth spun past each other. After these few misses, one tooth engaged with a tooth on the other hindleg, which then depressed rapidly, delayed only by a few microseconds relative to the first hindleg. This emphasizes that the gears play a critical role in ensuring close synchrony.

The body mass and measured accelerations predict that the torque generated was about

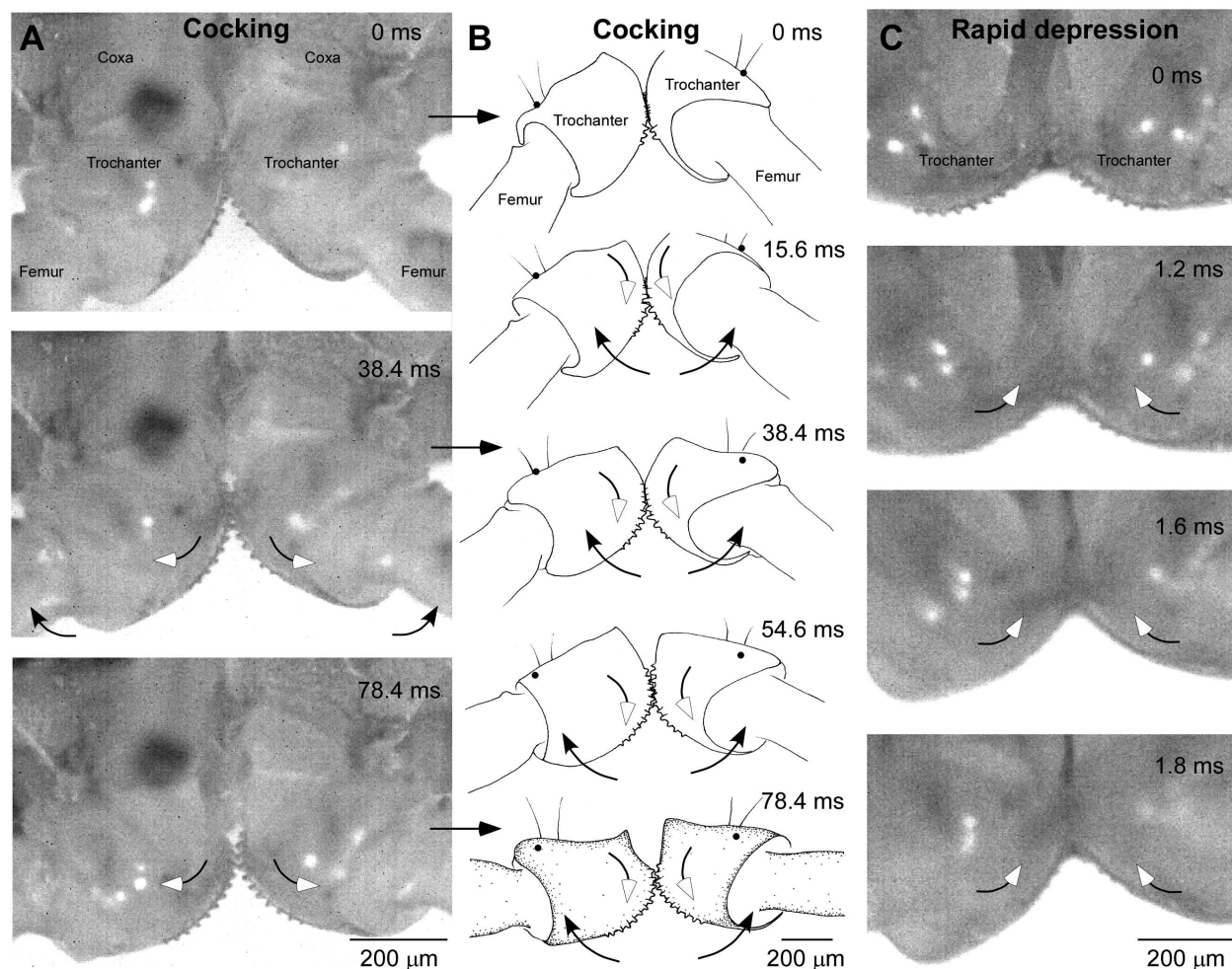


Fig. 2. Engagement of the gears during jumping. (A). Three images, at the times indicated (captured at a rate of 5000 images per second) show the levation of the hind trochantera and proximal femora into their cocked position in preparation for a jump (see movie S2). The trochanter starts moving at time 0 ms, and cocking is completed 80 ms later. (B) Drawings of the progressive movements of the gears and joints during cocking. The horizontal black arrows

indicate the correspondence between the frames in (A) and the drawings. (C) Rapid and synchronized depression of the two hindlegs that power jumping (see movie S3). Four images starting from the first detectable depression movement of the hind trochantera (time 0 ms). Full depression was completed 1.8 ms later. The curved, black arrows show the direction of movement of each hindleg and the curved, open arrows, the direction of gear rotation.

0.7 mN·mm. Each hindleg, and hence each gear, is controlled by separate sets of levator and depressor muscles so that not all the torque goes through each tooth. When one leg moves first at the start of a jump, its gear teeth will engage with and transmit power to the other stationary leg inducing it to move. The left and right power-producing muscles are innervated by independent sets of two motor neurons each, but all four motor neurons carry highly synchronized spike patterns that should help to ensure that the same amount of force is generated in each leg (7). This neural mechanism assists the synchrony of the leg movements but cannot deliver the level of synchrony measured during jumping. Thus, the primary role of the gears is to ensure that the hindlegs move synchronously within microseconds of each other.

The gear teeth are lost at the final molt into adulthood. This biomechanically important change in morphology is likely to be triggered by the changed hormonal environment during the larval-to-adult transition (8). Adults are, nevertheless, better jumpers than the nymphs; they reach take-off velocities as fast as 5.5 m/s (mean 3.2 ± 0.2 m/s for 10 males) in less than 1 ms (mean 1.5 ± 0.04 ms) and experience forces of 700 g (9). The adults use frictional contact between the more proximal coxae to ensure synchronous movements of the hindlegs (1). Their improved performance may be due to other factors, rather than a consequence of abandoning the gear mechanism. An inherent limitation of gears is that if one tooth breaks, their synchronizing action is degraded. In nymphs, a breakage could be repaired at the next molt, but this is not possible after the final molt to adulthood. Alternatively, the larger size of adults may mean that friction between the trochantera is a more effective synchronization mechanism.

Elsewhere in the animal kingdom, apparently ornamental cogs occur on the shell of the cog

wheel turtle *Heosemys spinosa* and on the pronotum of the wheel bug *Arilus cristatus* (Hemiptera, Reduviidae). The hearts of crocodilians have a cog wheel valve (10–12) that closes during each heart beat and can increase the resistance in the pulmonary outflow (13). In some insects, a row of regularly spaced protrusions work like clockwork escapement mechanisms to produce sound (14, 15). In such stridulation mechanisms, a plectrum is moved across the row of teeth (16, 17) at a rate of 2500 to 5000 teeth per second (16, 18), whereas the similarly sized gear teeth of *Issus* spin past each other at almost 50,000 teeth per second. Despite working under very different mechanical conditions, the similar tooth morphologies of the two structures suggest constraints that enforce a particular geometry.

The mechanical gears in *Issus* enhance the synchrony between leg movements to the level of microseconds, so that they are more tightly coupled than most limbed motions. By contrast, but at similar time scales, the parasitoid fly *Ormia ochracea* uses a mechanical linkage to amplify microsecond intra-aural time differences 50 times, so that the azimuth source of sound can be detected more easily (19, 20). The gears in *Issus*, like the screw in the femora of beetles (21), demonstrate that mechanisms previously thought only to be used in man-made machines have evolved in nature. Nymphal planthoppers have interacting gears that play an essential functional role in a natural behavior.

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Supplementary Materials

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Materials and Methods
Movies S1 to S3
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