support of the latter hypothesis, Saito, Kratzat *et al.* and Cerullo, Filbeck *et al.* provide evidence that collided ribosomes are targeted for rescue even in the absence of SmrB or MutS2. The phylogenetic conservation of SmrB and MutS2 also suggests that these factors may be critical for growth under some natural environmental conditions. Identification of the conditions that lead to ribosome collisions that are resolved by SmrB and MutS2 is likely to provide exciting answers to these questions.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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Biomechanics: Passive forces set the stage for stick insects

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https://doi.org/10.1016/j.cub.2022.03.042

For small animals like insects, passive elastic forces within their joints are extremely important to control of limb motion. A new study shows that these passive forces are tuned to the needs of individual joints.

When an animal's nervous system controls movement, it must do so in the context of the underlying physics of the animal's body[1]. In the case of large animals, such as humans or horses, the physics of movement is dominated by the inertial forces on the animal, a function of the animal's mass. The dominance of these forces for large animals is such that locomotion is often parameterized in terms of the ratio of two opposing inertial forces — centripetal forces and gravity — while other forces within the limbs, such as joint elasticity or internal damping are often ignored[2]. For small animals, however, it is a different story: at the size of an insect, inertial forces within the limbs are very small, while passive

elastic forces within the joint are relatively much larger, making these elastic forces extremely important to the control of a small animal's limb[3,4]. For small animals, these passive elastic forces can be so (relatively) large that they can generate motions of their own, either by restoring a perturbed limb to an initial position[5] or by restoring a maximally extended (or flexed) limb back to rest during a locomotion cycle[6,7]. With elastic forces being so important for insect locomotion, Guschlbauer, Hooper et al.[8] were curious, did evolution tune these passive forces to the individual use of a given limb? The results of the experiments inspired by that curiosity, reported in this issue of Current Biology, indicate that indeed it did.

To answer this question, Guschlbauer, Hooper et al.[8] needed an animal with limbs that have similar sizes but that are used differently from each other during a single behaviour — and their perfect model organism was the stick insect Carausius morosus. The stick insect has three pairs of similarly sized legs: front (prothoracic), middle (mesothoracic) and hind (metathoracic). Each of these legs is used when the animal walks, but they are used differently during a step: specifically the angular range of motion of each leg is very different. The authors first measured the specific range of motion for each of the three sets of legs, quantifying the angular movements during walking. Measured relative to the orientation of the body, the front leg moved through an arc of 38°–78°, while the middle leg moved through an arc of 76°–114° and the hind leg through an arc of 116°–137° (Figure 1, left). Importantly, while each leg is rotated a similar number of degrees — 43°, 38°, and 21° for the front, middle, and hind legs, respectively — both the starting angle and ending angle of each leg's motion are very different. Once they had measured the walking kinematics of each leg, the authors could test if the passive forces within each leg were tuned to these individual leg angles.

To test this hypothesis, each leg was brought to its forward-most position and then released, allowing the passive forces to bring the leg back to a forward-most resting position. Likewise, each leg was brought to its backward-most position, and released, so that the passive
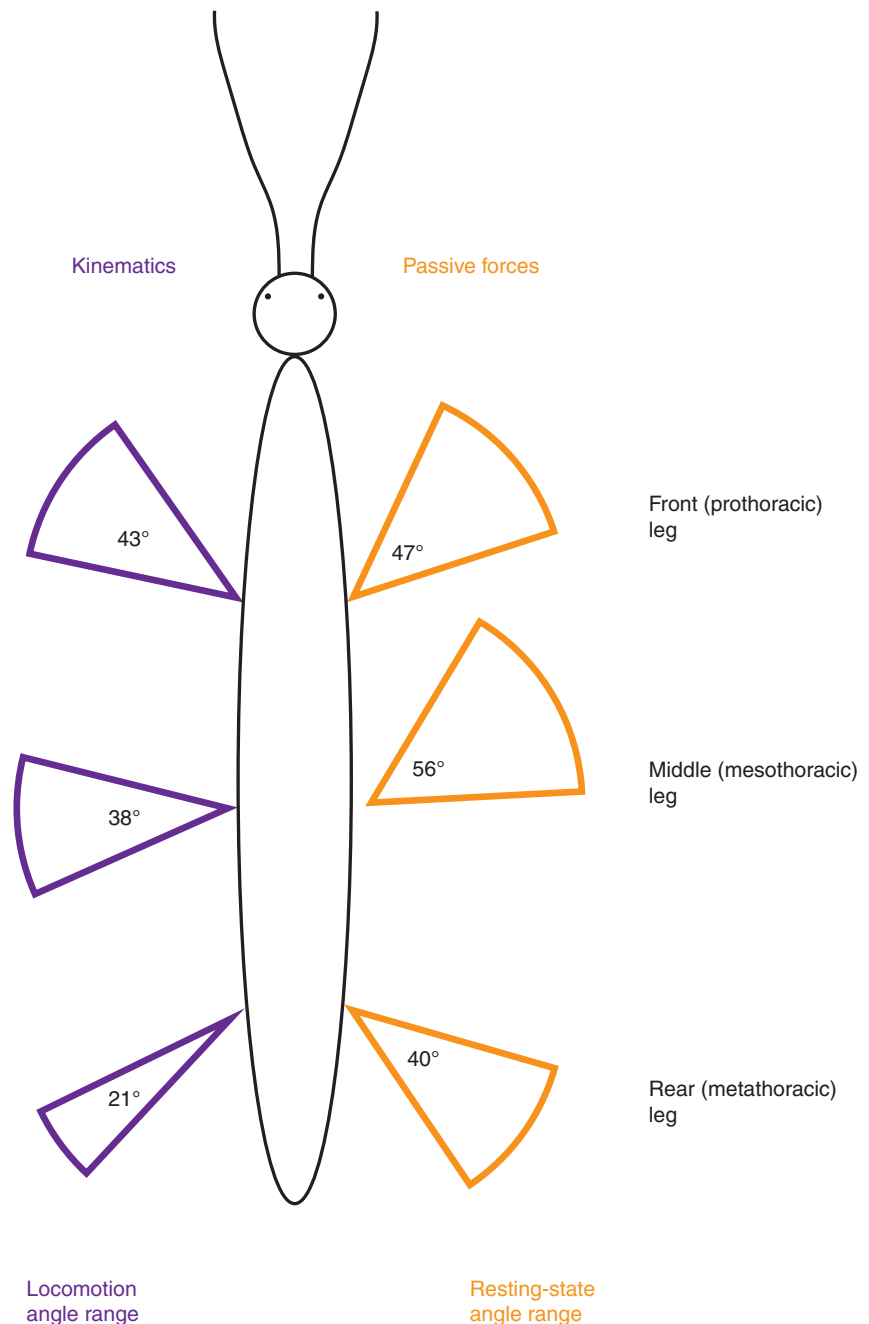
Figure 1. Leg angle ranges during locomotion of *Carausius morosus*.
The angle ranges were measured for each type of leg of the stick insect during locomotion (left, in purple), and during the action of passive forces (right, in orange). The movement ranges of the legs were found to correlate with the resting-state angle range defined by the passive forces. (Data from Guschlbauer, Hooper et al.[8].)

forces would return the leg to its backward-most resting position. The range between the forward-most and backward-most resting angles for each leg defined a range of 'resting-state

angles' — the angles at which passive forces allow leg motion. If passive forces are simply a matter of size, each of these forward-most and backward-most resting positions will be the same for

each leg. But if the passive forces are tuned to the use of each leg, the forward-most and backward-most resting positions will match the angular excursions of the leg observed during walking.

When Guschlbauer, Hooper *et al.*[8] measured the forward-most resting positions of the legs, they found that the front, middle, and hind legs returned to very different resting positions (25°, 38°, and 106°, respectively; Figure 1, right). Likewise, when they measured the backward-most resting positions, the legs returned to very different resting positions (72°, 94°, and 146° for the three pairs of legs, respectively). It was clear to see that the passive forces within each leg pair were tuned differently, but did these angles match the joint angles observed during the walking experiments?

For the front legs, the resting-state angle range was 25°–72°, almost a complete match with the observed angle range of motion during walking (35°–78°). For the middle legs, the resting-state angle range was 38°–94°, relatively close to the range observed in walking (76°–114°). Finally, for the hind legs, the resting state range was from 106°–146°, very similar to the angular range observed for

those legs during walking (116°–137°). The passive forces for each leg pair were not only different from each other but also tuned to the angular movements of those legs during locomotion.

The passive elastic forces within the leg joints were not just a consequence of the animal's small size: these forces were tuned to the movement of the leg at each joint, providing a quantitative demonstration that elastic forces were tuned to the behavioural range over which the leg moved. This illustrates that elastic joint forces not only get relatively stronger as animals get smaller, but also are tuned to the needs of individual joints. These forces are very dominant in small insect motions and are keyed to the movement of each joint, giving evolution another tool for generating intricate movements in small animals.

DECLARATION OF INTERESTS

The author declares no competing interests.

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Neuroscience: Reliable and refined motion computations in the retina

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We can distinguish between the direction and speed of a moving object effortlessly, but this is actually a very challenging computational task. A new study demonstrates that this process begins at the first stages of visual processing in the retina.

Anyone who has ever driven a car can attest to the importance of accurately judging the trajectory of the other cars on the road. This need to precisely estimate the direction that other cars are moving remains important whether one is racing

along the Autobahn or stuck behind the Sunday joyrider traveling well below the speed limit. Confounding the speed and direction of other cars on the road could have disastrous consequences. Indeed, humans can judge the direction of

moving objects with similar accuracy across a wide (~100-fold) range of stimulus speeds[1]. This ability to represent direction information separately from other pieces of information is a type of *invariant* neural