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Ultrafast launch of slingshot spiders using conical silk webs

Symone L.M. Alexander and M. Saad Bhamla

In the Theridiosomatidae spider family, at least three genera (Epeirotypus, Naatlo and Theridiosoma) use their three-dimensional cone-shaped webs as ultrafast slingshots that catapult both the spider and the web towards prey [1-3]. Also known as slingshot spiders, theridiosomatids build three-dimensional conical webs with a tension line directly attached to the center of the web. In 1932, Hingston [1] hypothesized that the slingshot spider releases the tension line using its front legs, while holding the web with its rear legs. Coddington [2] detailed how female spiders meticulously build their webs line-by-line. But lacking to date has been quantification of spider kinematics, such as displacement, velocity and acceleration. Here we report the first quantification of theridiosomatid motion, revealing that slingshot spiders generate the fastest arachnid full body motion through use of their webs for external latch-mediated spring actuation

Field portable high-speed cameras coupled with high resolution macro lenses were used to visualize slingshot spider motion in the Peruvian Amazon Rainforest (see Supplemental Information for methodological details). Our observations of slingshot spider web release agree with the earlier work of Hingston and Coddington (Figure 1A,B,D). To achieve the threedimensional cone configuration, the slingshot spider grips the center of the orb with its four posterior legs while pulling the tension line with its four anterior legs and holding the bundled silk of the tension line with the pedipalps (Figure 1B and Video S1). This motion extends the orb web into a cone, with the slingshot spider facing the tension line. Upon sensing an external stimulus, the slingshot spider rapidly releases the bundled tension line (6.0 \pm 0.8 ms), flinging both the spider and the web

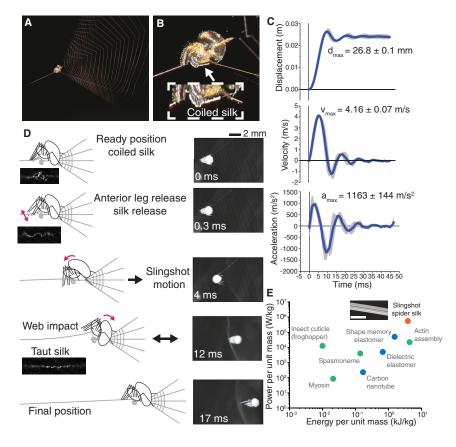


Figure 1. Ultrafast motion and latch-mediated spring actuation performance of slingshot spiders.

(A) A slingshot spider holding its three-dimensional conical web in tension. (B) The 'ready' position of the slingshot spider. The tension line is connected to the center of the web. To extend the web, the slingshot spider grips radial web lines with the back four legs and uses the front four legs to bundle the tension line that it then holds in place using its pedipalps. (C) Kinematic values obtained from high speed video analysis reveal peak displacement of 26.8 ± 1.0 mm, peak velocity of 4.16 ± 0.07 m/s, and peak acceleration of 1163 ± 144 m/s². The data displayed are for the fastest observed slingshot spider, slingshot spider 1, with n = 3 web releases (Figure S1). (D) Schematic representation of slingshot spider web release. Insets show still frames of full body motion (Videos S2, S3; scale bar = 2 mm) and silk uncoiling (Video S4). (E) Slingshot spider silk exceeds the power output of some biological (green symbols) and synthetic (blue symbols) materials. Symbols represent maximal values, with spider slingshot spider 3 achieving the highest power and energy density (E_{silk} =3 .92 kJ/kg, P_{silk} = 5.53 x 10^5 W/kg, t = 7.1 ms). Maximal and average numerical values and calculation methods for slingshot spider silk are provided in the SI. Inset shows SEM of a radial silk line (scale bar = $5 \mu m$).

backwards (Videos S2,S3). In contrast to Hingston's hypothesis that the entire bundled tension line is released, we observed that the spider only releases a small section of the tension line (Video S4) [1]. To reset the trap, the spider extends an anterior leg to re-grip the tension line and restarts the process of pulling and bundling the tension line (Video S1).

Latch-mediated spring actuation systems are united by their use of biological springs and latches to achieve powerful motion at short timescales [4,5]. The slingshot spider is one of few

examples where an organism uses an externally built tool (a web) and not an anatomical structure as a spring to achieve ultrafast motion, motion that is too fast for the organism's neurons to monitor or modify (Figure S1). To quantify the slingshot spider's performance as a latch-mediated spring actuation system, the web release kinematics of slingshot spider were determined. Slingshot spiders were triggered via a finger snap near the web cone and recorded using a high-speed camera (Video S3). Four slingshot spiders were observed with n = 3, 2, 3, and 7 web releases, dependent



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on spider responsiveness (Figure S1). The fastest observed slingshot spider achieved velocities of up to 4.2 m/s $(v_{max} = 4.2 \pm 0.1 \text{ m/s in t} = 6.0 \pm 0.8 \text{ ms})$ and accelerations exceeding 1300 m/s² (a_{max} = 1163 ± 144 m/s²) or about 130 g (~10x faster than cheetah sprint) (Figure 1D; see Supplemental Information for more kinematics). The observed spiders vary in mass, though the initial web displacement has a greater effect than mass on peak velocity and acceleration (Figure S1). Similar to the loading of a spring, the total displacement of the web is the primary source of elastic energy storage and the driving force for peak velocity and acceleration. This effect can be described using the expression $E = k x^2$, where E =stored elastic energy, k = spring constant, and x = displacement. Thus, by adjusting the degree to which they extend their webs (increase or decrease x), slingshot spiders of different mass can achieve similar kinematics (Figure S1).

Trap-jaw spiders have appendages that exhibit faster speeds and accelerations, but so far as we know slingshot spiders exhibit the fastest full body motion for an arachnid (Table S1) [6]. The closest comparisons are ballooning spiders and the triangle spider Hyptiotes. Ballooning spiders utilize their webs for aerial dispersion, but wind speeds used for this behavior are most favorable when less than 3 m/s (v_{max} < 3 m/s) and no acceleration data have been reported [7]. Recent work on the triangle spider reports web release speeds up to 2 m/s and accelerations up to 530 m/s² (v_{max} = 1.2 ± 0.4 m/s, a_{max} = $371 \pm 158 \text{ m/s}^2$) [8]. These species have comparable speeds to slingshot spiders, but slingshot spiders can instantly and repeatedly slingshot their webs, even if they are not allowed time to reload (Video S5). High-resolution high-speed imaging revealed that this control over displacement is achieved by the slingshot spider releasing small sections of the bundled tension line, rather than releasing the entire tension line at once (Video S4; see Table S1 in the Supplemental Information for a comparison to other ultrafast biological systems).

To further quantify latch-mediated spring actuation performance, the power and energy density generated by the slingshot motion were calculated. The slingshot spider acts as the engine pulling along the tension line and uses

four anterior legs as latches, while the radial web lines are the primary propulsive force (spring) driving the slingshot motion (Figure S1). As such, measured properties of the radial silk diameter, cross-sectional area, number in the web — were used to calculate energy (E_{silk}) and power (P_{silk}) density (see Supplemental Information). Slingshot spider silk outperforms several natural and synthetic materials in power/mass and energy/mass (Figure 1E, Figure S1, maximum observed values are Esile = $3.92 \text{ kJ/kg}, P_{\text{cilk}} = 5.53 \times 10^5 \text{ W/kg}) [9].$ The force distribution in the web may be more complex because of the threedimensional topology of the web. The use of specific silk lines in spider webs for energy dissipation is well known [10], but our findings suggest the slingshot spider web is also highly effective for elastic energy storage and release. Furthermore, unlike most latch-mediated spring actuation systems where often the spring structures are unknown or impossible to extract non-destructively for testing, the slingshot spider's use of its viscoelastic silk for spring-like motion is advantageous for future structural and molecular studies of elastic energy storage due to its abundance and easy

Our quantitative descriptions of slingshot spiders have identified a latch-mediated spring actuation system that uses a web as an external tool for ultrafast motion. Our work raises questions about the biological function of the slingshot spider's ultrafast motion as well as the molecular and mechanical properties of slingshot spider silk springs that enable high power densities.

SUPPLEMENTAL INFORMATION

Supplemental Information includes experimental procedures, one figure and one table can be found with this article online at https://doi. org/10.1016/j.cub.2020.06.076; supplemental videos can be seen at https://www.youtube. com/playlist?list=PLFN0kHHXDcj3grfHgXcWjlV mvMTrsK9II.

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AUTHOR CONTRIBUTIONS

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Chemical and Biomolecular Engineering, Georgia Institute of Technology, Atlanta, GA 30311, USA.

E-mail: s.alexander@gatech.edu (S.L.M.A.); saadb@chbe.gatech.edu (M.S.B.)