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Rapid mid-jump production of high-performance silk by jumping spiders

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Jumping spiders (Salticidae) do not rely on webs to capture their prey, but they do spin a silk dragline behind them as they move through their habitat. They also spin this dragline during jumps, continuously connecting them with the surface they leapt from. Because spiders cannot spin silk in advance, this silk must be spun at the same speed as the spider jumps — in effect, requiring spin speeds over ten times faster than typical. And while many spiders can move rapidly, for example when running or rappelling, previous research on silk has found that silk spinning rates in excess of walking and web-building speeds (~2–20 mm/s) result in lower quality silk and even dragline failure[1]. Here we report that, despite being spun at high speeds (~500–700 mm/s; 100–140 body lengths/s), jump-spun salticid silk shows consistent, uniform structure as well as the high-performance qualities characteristic of silk spun by other spiders, including orb-weaving species, at low speeds[2]. The toughness of this jump-spun silk (mean = 281.9 MJ/m^3) even surpasses reported values for all but the toughest orb-web draglines[2]. These results show that salticids are capable of spinning high-performance silk and are able to do so extremely rapidly under natural conditions.

Spiders produce silk through specialized spinnerets near the anterior of the abdomen. Silk properties vary based on species, silk type, spinning conditions, and other factors[1,3,4]. The silk spun by salticids during jumps is dragline silk produced by the major ampullate (MA) silk system[3]. MA silk is the most well-studied type of spider silk, renowned for its role as the energy-absorbing radial lines of capture webs spun by orb-web spiders (Araneae), and is among the toughest tensile materials known[3]. As spiders move, they periodically anchor draglines to substrates using spinneret-derived attachment disks of silk and adhesives[5]. During jumps, salticid draglines act as a safety-line should the jump fail and may enable mid-jump orientation control[6,7]. Although spiders can control silk-production rate and anchor location, since silk only takes its solid form by being pulled from the spinnerets, silk cannot be made and stored ahead of time, nor can it be reeled back in. Slow-spun jumping spider MA silk is generally thought to be of intermediate quality[2,4,8], but nothing was previously known about rapidly produced jump-spun silk.

Working with the mid-sized (~5 mm) zebra jumping spider *Salticus scenicus*, we used high-speed cameras (2500 frames/s) to quantify the velocities of spiders jumping across 3 cm gaps

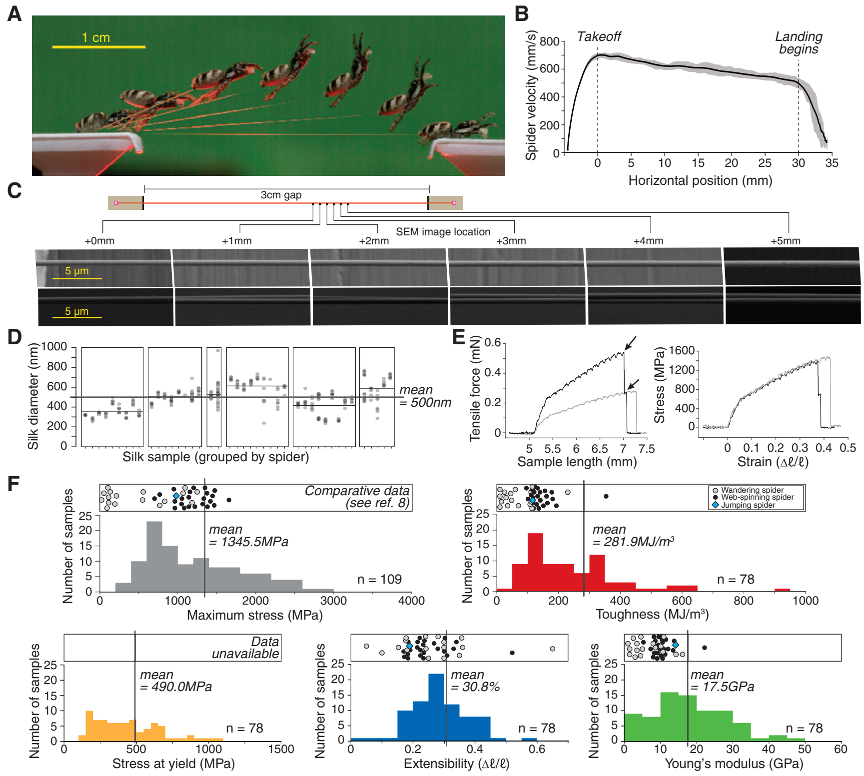

Figure 1. Analysis of dragline silk spun by the jumping spider *Salticus scenicus* (Salticidae) during jumps across 3 cm gaps.

(A) Pseudo multi-exposure image from high-speed video of a spider jumping across a 3 cm gap (video = 2500 frames/second, displayed time intervals = 12 ms). (B) Velocity of *S. scenicus* during 3 cm jumps. Thick line shows mean velocity, shading extends to 25th and 75th percentiles (n_{jumps} = 35; $n_{spiders}$ = 9). (C) Scanning electron microscopy (SEM) images of jump-spun dragline samples with single (top) or dual-lines (middle) present, imaged at 1 mm intervals across each sample. Images shown were rotated and cropped, but otherwise unaltered. Schematic (above) showing approximate sampling sites along a dragline sample (pink) in silk-collection experiments. (D) Silk diameter based on SEM images (n_{images} = 356; $n_{samples}$ = 42; $n_{spiders}$ = 6); circles show mean diameter from each image. X-axis entries each represent a single dragline sample from independent jumps, grouped (in rectangles) by individual spider. Thin horizontal lines show spider-specific means, the thick line shows overall mean (mean of spider-specific means). (E) Representative tensile test results showing (left) sample length versus force and (right) stress versus strain (values normalized by initial sample cross-sectional area and initial length) for a single-filament sample (gray) and a dual-lined sample (black). Arrows indicate primary and secondary ruptures in black example, direct evidence of dual lines. (F) Histograms showing quantification of tensile properties for jump-spun silk from the current study, calculated using the overall mean diameter (see D). Black vertical lines indicate means (mean of spider-specific means). Sample-size differences reflect additional data due to dual-lined samples. Circles in the boxes above each histogram show previously published silk dragline data (see[2]), for comparison with other spider species.

(Figure 1A and Video S1). We then designed an assay where spiders jumped across a series of 3 cm gaps, allowing us to collect samples of jump-spun silk that spanned each gap (Figure S1). Working with these samples, we used scanning electron microscopy (SEM) to examine the external characteristics of draglines. To quantify the tensile properties of the material, we then used quasi-static tensile testing, in which each sample was slowly pulled while measuring the forces present.

Analysis of high-speed videos revealed that spiders travel at high speeds during 3 cm jumps with takeoff velocities near 700 mm/s and average mid-jump velocities of 599.3 mm/s (n_{jumps} = 35; $n_{spiders}$ = 9; Figure 1B). Our SEM images (n_{images} = 356; $n_{samples}$ = 42; $n_{spiders}$ = 6; Figure 1C,D) showed that jump-spun draglines are smooth, uniform cylinders, as is typical of draglines produced by other spider species[9]. By taking multiple images across each sample (Figure S1), we found that dragline diameter does not systematically vary, suggesting that mid-jump spin speed has minimal effect on silk diameter. Spider draglines typically consist of two filaments[9] — products of a left–right pair of spinnerets. This dual-lined nature was evident in many of our SEM samples (Figure 1C), as well as in our tensile tests where samples often showed two breaking points (Figure 1E). Thus, when calculating tensile properties, the number of filaments present was used to determine the effective sample cross-sectional area (see Supplemental information).

Most of the tensile properties of jump-spun silk ($n_{samples}$ = 78; $n_{spiders}$ = 12) are similar to values reported for dragline silks of other spider species, with the notable exception of toughness (Figure 1F). The toughness measures that we observed are among the highest values reported for silk in any spider species, exceeding the vast majority of orb-web spiders, and just below the silk produced by the Darwin's bark spider (*Caerostris darwini*), which builds meter-wide orb webs that are among the largest recorded[2]. Toughness aside, even the seemingly ordinary tensile and physical properties of jump-spun salticid silk become extraordinary once the high speeds at which they are spun are taken into account.

These results raise a number of exciting questions. From a mechanistic perspective, it is not clear whether salticids possess specific physiological adaptations that enable rapid silk production while maintaining high-performance material properties. At the genetic and molecular levels, silk protein composition is known to influence its material properties[3,4]; thus, comparisons between salticids and other species might further our understanding of high-performance silk. Additionally, the fact that salticids produce such silk might also inform our understanding of evolution across the group by changing how we think about the presence/absence of high-performance silk across the spiders.

It is possible that the jump-spun silk of other salticids might surpass the values reported here, as *S. scenicus* tends to have average properties among salticids: their size and jumping ability are typical of the group, and they do not show any noteworthy jumping- or silk-related specializations. Yet salticids are the most species-rich spider family[10], showcasing a wide range of specialized behavioral, morphological, and ecological adaptations, thus increasing the likelihood that more exceptional salticid silks remain to be found.

Our results provide direct evidence against the widely held view that prey capture and the production of high-performance silk are functionally and evolutionarily linked in spiders[2]. Although there is support for this hypothesis[4], our work demonstrates that there are species — and behavioral contexts — that may provide important exceptions, especially since salticids are thought to use tension on the dragline to control in-flight angle during jumps[6,7]. Thus, whereas high-performance, high-toughness silk may be maintained in orb-web spiders through selection for its ability to slow fast-moving prey, it may instead be maintained in salticids for its ability to slow a fast-moving self mid-jump. Alternatively, another aspect of salticid biology, or even the mechanical demands or consequences of jump-spun silk, might result in the production of high-toughness draglines.

SUPPLEMENTAL INFORMATION

Supplemental information includes one figure, experimental methods and results, additional discussion, Inclusion and diversity statement, one video, and one data file and can be found with this article online at https://doi.org/10.1016/j.cub.2021.09.053.

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