Sci Nat (2015) 102:41
DOI 10.1007/s00114-015-1291-6

SHORT COMMUNICATION

Adhesion of dry and wet electrostatic capture silk of uloborid spider

Hervé Elettro[1] · Sébastien Neukirch[1] · Arnaud Antkowiak[1] · Fritz Vollrath[2]

Received: 24 April 2015 / Revised: 22 June 2015 / Accepted: 24 June 2015

Abstract We demonstrate the impressive adhesive qualities of uloborid spider orb-web capture when dry, which are lost when the nano-filament threads are wetted. A force sensor with a 50 nN–1 mN detection sensitively allowed us to measure quantitatively the stress–strain characteristics of native silk threads in both the original dry state and after wetting by controlled application of water mist with droplet sizes ranging between 3 and 5 μm and densities ranging between 10^4 and 10^5 per mm^3. Stress forces of between 1 and 5 $\mu N/\mu m^2$ in the native, dry multifilament thread puffs were reduced to between 0.1 and 0.5 $\mu N/\mu m^2$ in the wetted collapsed state, with strain displacements reducing from between 2 and 5 mm in the dry to 0.10–0.12 mm in the wetted states. We conclude that wetting cribellate threads reduce their van der Waals adhesion with implications on the thread's adhesive strength under tension. This should be considered when discussing the evolutionary transitions of capture silks from the ancestral dry-state nano-filaments of the cribellate spider taxa to the wet-state glue-droplets of the ecribellate taxa.

Communicated by: Sven Thatje

Electronic supplementary material The online version of this article (doi:10.1007/s00114-015-1291-6) contains supplementary material, which is available to authorized users.

✉ Fritz Vollrath
fritz.vollrath@zoo.ox.ac.uk

[1] Sorbonne Universités, UPMC Paris 06, CNRS, UMR 7190, F-75005 Paris, France

[2] Department of Zoology, University of Oxford, South Parks Rd, Oxford OX1 3PS, UK

Keywords Spider · Web · Glue · Electrostatic · Evolution · Prey capture

Introduction

Orb-web spiders use two very different mechanisms to entrap insects in their capture threads. The evolutionary more ancestral cribellate technique requires the spider to slowly and laboriously hackle thousands of fine filaments, while the more advanced (i.e. derived) ecribellate technology deploys highly cost-efficient self-assembling glue droplets (Vollrath 2005). Molecular profiling suggests that the two mechanisms have dissimilar evolutionary histories with strong evidence for independent origins of the two types of orb webs (Fernández et al. 2014; Bond et al. 2014) despite many similarities in architecture and ecology (Shear 1986; Bond and Opell 1998; Foelix 2011; Opell and Bond 2001). The two opposing mechanisms of prey capture rely on fundamental differences between the two types of silk used by the two weaver types, cribellate and ecribellate, in their orb-web capture threads.

Indeed, these two different prey-capture systems are functionally opposed and comprise very different technologies (Peters 1987, 1995; Vollrath 2005; Opell and Schwend 2009; Opell et al. 2011; Sahni et al. 2011), i.e. the hackled-and-puffed nano-thread-adhesion capture system of the cribellate spiders (Peters 1984; Opell 1994) and the two-component-extrusion glue-adhesion system of the ecribellate spiders (Vollrath and Edmonds 1989; Opell and Hendricks 2007). The hackled threads relies on the spider to comb and electrostatically charge the threads, which are understood to attach and adhere to the insect by van-der-Waals forces (Hawthorn and Opell 2002, 2003). The aqueous glue threads carry droplets that self-assemble via a Rayleigh-Plateau transition upon water adsorption from the atmosphere (Edmonds and Vollrath

Published online: 07 July 2015

1992) and attach by surface wetting and glycoprotein adhesion (Vollrath et al. 1990; Vollrath and Tillinghast 1991; Opell and Hendricks 2007). Consequently, it has been deduced that the glue threads only work when wet while hackled threads work best when dry (Peters 1987; Opell 1994) or dryish (Hawthorn and Opell 2003).

It seems from the literature (cited so far as well as see also, e.g. Blackledge and Hayashi 2006) that the cribellate system would fundamentally depend on its original, non-wetted, highly puffed-out configuration state for the nano-fibrils to retain their function. Indeed, the very spinning mechanism of the cribellum fibre composite is specially adapted to an electrostatic spinning process that leads to the configuration of hackled puffs of dry silk nano-filaments astride core carrier threads (Kronenberger and Vollrath 2015). One must argue that the puffs, in turn, would rely on dryness for their continued function, if indeed, electrostatic forces and nano-adhesion sites are keys to their functionality. Confusingly, it has also been shown that high ambient humidity seems to increase the adhesive properties of some (nano-noded) cribellum threads, perhaps by adding capillary forces to electrostatic forces (Hawthorn and Opell 2003), strange as that might sound considering potentially conflicting physical dynamics.

Here, we test the hypothesis that cribellate capture threads are indeed much more sticky when dry as opposed to when wetted. *Uloborus* cribellum threads were exposed to high-density mist and their adhesion to a nano-force tensile tester measured before and after wetting. Imagery of both dry/puffed and wetted/collapsed threads complemented the force measurements.

Materials and methods

Uloborus plumipes spiders were collected at the Paris Jardin des Plantes greenhouse and taken into the laboratory where they spun webs in appropriate frames. The experimental apparatus consisted of a combination of microscope and stress–strain gage with the added ability of controlled application of water mist. *Uloborus* capture thread samples were carefully taken from a web using calipers to avoid deformation, straining and stressing. The samples were then tested at T 20 °C using a FemtoTools, FT-FS1000 detection capacitive force sensor with a 50 nN–1 mN measurement range in two different ways. Press-in is meant to approximate forward contact loading resulting from an insect hitting the web straight on. Press-on is meant to approximate a more a side-ways hit with shear loading generated by lateral body contact and flapping wings. Contact areas were calculated from the cross-section area of the sensor in contact with the sample. For the press-in setup, this is the full cross-section area of the sensor tip along its main axis, which is square with border size 50 μm, i.e. 2500 μm^2. For the press-on setup, the full width of the sample (that is 100 μm for the dry case) is in contact with the edge of the sensor (that is 50 μm), i.e. 5000 μm^2. These contact areas are used for normalizing forces to allow comparison between press-in and press-on forces. Even though the contact area in not the same for the dry and wet threads, we use the same normalisation area for the wet case to account for the physical differences between the samples.

Wetting was achieved by controlled mega-sonic misting of distilled water at controlled droplet sizes ranging between 3 and 5 μm and at densities ranging between 10^4 and 10^5 per mm^3. We note (i) that threads dried out very quickly (see also video in Suppl. Material and/or www-link) and (ii) that it made no difference to dimensions and adhesive properties whether prior to the measurements pre-wetted threads were left at room humidity (50 % rH) or thoroughly desiccated by exposure to dry air surrounding a small dish of exposed phosphorus-pentoxide P_2O_5, which is an excellent way of drying silk threads (Vollrath and Edmonds 1989). SEM images were taken at a range of magnifications with 10 nm of Gold/Palladium coating.

Results and discussion

Our experiment demonstrated that wetting destroys the adhesive properties of the threads. We conclude that rain or even heavy mist would render the *Uloborus* capture threads unable to retain any prey that they may intercept (Fig. 1).

In its native state, the cribellate silk studied showed the typical uloborid puffs. These collapsed during even brief 5 min wetting (see Suppl Materials and www-link for video).

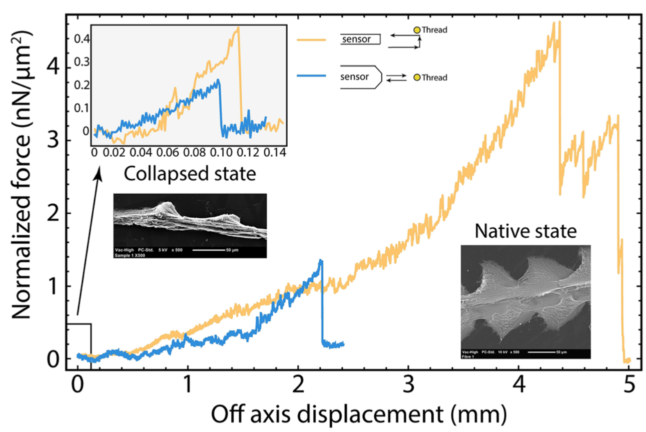

Fig. 1 Representative stress–stain graphs of native and collapsed cribellate capture silk adhering to a sensor. Measurements were taken subsequently on the same piece of capture thread of *Uloborus plumipes*, and images were taken from adjacent sections of the same thread. The sensor was either pushed into the thread or lowered onto the thread before being pulled away; in both cases, the force of contact was equivalent. Please note that these two curves are representative for 14 individual stress–strain tests, further explanations and significances in the text. Inserts: SEM images of a capture thread in the native puffed state and collapsed after wetting

The measured adhesion forces differed significantly between native-puffed and wetted-collapsed threads (Fig. 1), and this was irrespective whether the sensor was pushed (pressed) forward into the capture thread or pushed (pressed) down unto it (one tailed t tests, p=1.0 and 0.75 % respectively, N=4, n=14). For the dry threads, pushing onto a thread followed by pulling away showed stronger adhesion than pushing into a thread, again this was highly significant (Fig. 1, one tailed t test p=1.4 %). We assign this difference in force to the concurrent difference in contact between the sensor and the individual filaments. In the case of push-in/pull-out, the contact area of the sensor would have been about 2500 μm^2 and adherent threads were pulled away at more or less 90 degree. In the case of push-down/pull-away, the contact area of the sensor would have been about 5000 μm^2 and the threads are pulled in the area of contact and in a very oblique angle, which would allowed for much longer periods of contact over the same pulling distance. Of course, the differences of actual filament contact area between sensor and threads would change when the filaments are all collapsed into one-another, as happens when they are wetted (Fig. 1 left inset), which is in stark contrast to their native state when they are fully puffed out (Fig. 1 right inset).

The experimental wetting may or may not have affected electrostatic charges of the thread by temporary grounding of the otherwise insolating threads via the applied aqueous mist coating. However, it is much more likely that the wetting-induced collapse of the filament puffs significantly decreased the number of surface contact area/points and that this alone would account for the significant drop in adhesion after wetting. As our images show, and as Peters 1987 predicted which Zheng et al. 2010 confirmed, wetting the submicron capture filaments of *Uloborus* causes them to coalesce, which is an important phenomenon in fibre physics and hence reasonably well understood (Bico et al. 2004). As we have shown here, fine mist accumulates quickly and effectively destroys the adhesive effectiveness of hackled silk. For the spider, this means that fog (or perhaps even dew) may radically decrease the capture efficiency of an *Uloborus* web. As is well known, all orb weavers, cribellate and ecribellate alike, tend to take down their webs in rain. In the ecribellates, this is a response to droplet overloading, which leads to sagging threads that can snap and compromise the integrity of the whole structure. Overloading might also be a problem for cribellate capture silks but even a fine mist, as we have now demonstrated, leads to an irreversible loss of function which in turn would require web rebuilding.

We believe that our observations contribute to recent developments concerning our understanding of the evolution of spider capture threads. Two recent publications provide evidence for 'independent origins for the two types of orb webs' (p 1772, Fernández et al. 2014) and 'reject the prevailing paradigm of a monophyletic Orbiculariae' clade (p 1765, Bond et al. 2014). Both studies used state-of-the-art gene sequencing coupled to other analyses of lineage relationships. Our discovery that wetting renders in-operable the evolutionary older cribellum capture threads suggests that a simple transition to the obligatory wet droplet threads of the ecribellate orb-weavers would have been far from straightforward, if at all possible, and thus strongly supports the notion of independent evolution of orb spider capture threads and, by extension, perhaps also of web spiral geometries and web-building behaviour patterns. Last but not least, our observations challenge the deductions of Zheng et al. (2010) who see wetting as such an integral part of cribellate capture thread function that it bio-inspired them to design supposedly derivative synthetic water collectors (Zheng 2014).

Acknowledgments We all thank the Royal Society of London (International Exchange grant IE130506), the Paris group also thanks the Agence Nationale Reseaux (grant 09-JCJC-0022-01), La Ville de Paris (grant Programme Emergence) and the CNRS (grant PEPS PTI) while FV also thanks the US Air Force (AFOSR grant FA9550-12-1-0294) and the European Research Council (ERC grant SP2-GA-2008-233409). Last but not least, we thank the journal's reviewers for improving comments. Data accessibility: All data and methods are reported within this paper and with the electronic supplementary material.

References

Bico J, Roman B, Moulin L, Boudaoud A (2004) Elastocapillary coalescence in wet hair. Nature 432:690

Blackledge TA, Hayashi CY (2006) Unraveling the mechanical properties of composite silk threads spun by cribellate orb-weaving spiders. J Exp Bio 209:3131–3140

Bond JA, Opell DB (1998) Testing adaptive radiation and key innovation hypotheses in spiders. Evolution 52:403–414

Bond JE, Garrison NL, Hamilton CA, Godwin RL, Hedin M, Agnarsson I (2014) Phylogenomics resolves a spider backbone phylogeny and rejects a prevailing paradigm for orb web evolution. Curr Biol 24: 1765–1771

Edmonds D, Vollrath F (1992) The contribution of atmospheric water vapour to the formation and efficiency of a spider's capture web. Proc Roy Soc London 248:145–148

Fernández R, Hormiga G, Giribet G (2014) Phylogenomic analysis of spiders reveals nonmonophyly of orb weavers. Curr Biol 24:1772–1777

Foelix R (2011) Biology of spiders, 3rd edn. Oxford Univ. Press, Oxford

Hawthorn AC, Opell BD (2002) Evolution of adhesive mechanisms, in cribellar spider prey capture thread: Evidence for van der Waals and hygroscopic forces. Biol J Linn Soc Lond 77:1–8

Hawthorn AC, Opell BD (2003) Van der Waals and hygroscopic forces of adhesion generated by spider capture threads. J Exp Biol 206:3905–3911

Kronenberger K, Vollrath F (2015) Spiders spinning electrically charged nano-fibres. Biol Let 11(1):20140813. doi:10.1098/rsbl.2014.0813

Opell BD (1994) Factors governing the stickiness of cribellar prey capture threads in the spider family Uloboridae. J Morphol 221:111–119

Opell DB, Bond JE (2001) Changes in the mechanical properties of capture threads and the evolution of modern orb-weaving spiders. Evol Ecol Res 3:567–581

Opell DB, Hendricks ML (2007) Adhesive recruitment by the viscous capture threads of, araneoid orb-weaving spiders. J Exp Biol 210:553–560
Opell BD, Schwend HS (2009) Adhesive efficiency of spider prey capture threads. Zoology 112:16–26
Opell BD, Tran AM, Karinshak SE (2011) Adhesive compatibility of cribellar and viscous prey capture threads and its implication for the evolution of orb-weaving, spiders. J Exp Zool 315:376–384
Peters TM (1984) The spinning apparatus of Uloboridae in relation, to the structure and construction of capture threads, (Arachnida, Araneida). Zoomorph 104:96–104
Peters HM (1987) Fine Structure and Function of Capture Threads in Ecophysiology of Spiders. pp187-202 in (ed.) W. Nentwig Springer-Verlag Berlin Heidelberg
Peters HM (1995) Ultrastructure of orb spiders' gluey capture threads. Naturwissenschaften 82:380–382
Sahni V, Blackledge TA, Dhinojwala A (2011) A review on spider silk adhesion. J Adhes 87:595–614
Shear W (1986) Spiders, Webs, Behavior and Evolution. Stanford University Press
Vollrath F (2005) Spiders' Webs. Curr Biol 15:R364–R365
Vollrath F, Fairbrother WJ, Williams RJP, Tillinghast EK, Bernstein DT, Gallager KS, Townley MA (1990) Compounds in the droplets of the orb spider's viscid spiral. Nature 345:526–528
Vollrath F, Edmonds D (1989) Modulation of the mechanical properties of spider silk by coating with water. Nature 340: 305–307
Vollrath F, Tillinghast E (1991) Glycoprotein glue beneath a spider web's aqueous coat. Naturwissenschaften 78:557–559
Zheng Y, Bai H, Huang Z, Tian X, Nie FQ, Zhao Y, Zhai J, Jiang L (2010) Directional water collection on wetted spider silk. Nature 462:640–443
Zheng Y 2014 <http://www.rsc.org/chemistryworld/2014/08/interview-yongmei-zheng-spider-silk-water-droplet>