Compliant threads maximize spider silk connection strength and toughness

Avery Meyer1, Nicola M. Pugno2,3 and Steven W. Cranford1

1Laboratory for Nanotechnology in Civil Engineering (NICE), Department of Civil and Environmental Engineering, Northeastern University, 400 Snell Engineering, 360 Huntington Avenue, Boston, MA 02115, USA
2Laboratory of Bio-Inspired and Graphene Nanomechanics, Department of Civil, Environmental and Mechanical Engineering, Università di Trento, via Mesiano 77, 38123 Trento, Italy
3Center for Materials and Microsystems, Fondazione Bruno Kessler, Via Sommarive 18, 38123 Povo (Trento), Italy

Millions of years of evolution have adapted spider webs to achieve a range of functionalities, including the well-known capture of prey, with efficient use of material. One feature that has escaped extensive investigation is the silk-on-silk connection joints within spider webs, particularly from a structural mechanics perspective. We report a joint theoretical and computational analysis of an idealized silk-on-silk fibre junction. By modifying the theory of multiple peeling, we quantitatively compare the performance of the system while systematically increasing the rigidity of the anchor thread, by both scaling the stress–strain response and the introduction of an applied pre-strain. The results of our study indicate that compliance is a virtue—the more extensible the anchorage, the tougher and stronger the connection becomes. In consideration of the theoretical model, in comparison with rigid substrates, a compliant anchorage enormously increases the effective adhesion strength (work required to detach), independent of the adhered thread itself, attributed to a nonlinear alignment between thread and anchor (contact peeling angle). The results can direct novel engineering design principles to achieve possible load transfer from compliant fibre-to-fibre anchorages, be they silk-on-silk or another, as-yet undeveloped, system.

1. Introduction

The field of biomimicry has undoubtedly motivated many studies in an attempt to learn from Nature [1–5]. Advancements have been made in both the understanding of the natural function of biological materials and systems (i.e. protein-based materials [3]), as well as the synthesis and regeneration of certain tissues (such as collagen and bone [5]). In particular, spider silk and webs are fascinating examples of natural structural engineering essential for an animal’s survival [6,7]. Spider silk and webs present a seemingly endless platform for mechanistic discovery while the synergy between material, structure and function presents a complex problem to biologists, materials scientists and engineers alike [7–12]. Yet, while we currently understand relatively well the mechanical properties of silk [13,14] and the biological function of a web [15–19], less clear is how the web itself behaves from a structural mechanics perspective. In structural engineering, for example, failure of a load-bearing system typically occurs at the junction of beams and columns, i.e. the load-transfer joints [20,21]. The following question therefore arises: how does a complex geometric structure such as a spider web transfer load across silk threads?

Complicating analysis, recent work suggests that both silk (as a material) and webs (as a structure) are intimately connected—material properties govern the structural performance and vice versa, creating heightened functionality through synergistic interactions [22–24]. For example, a spider may vary the properties of a piece of thread depending on its placement in the web [16,25]. With such considerations, a need for robust and adaptable connections for load transfer is presumed. One recently explored structure used to anchor webs to their physical surroundings (cementing dragline silks to a variety of solid supports such as wood, concrete or other surfaces during web
construction) is the so-called attachment disc [26–28]: dragline silk has been observed to fuse with a disc-like structure, providing a secure anchor point to assist prey capture and predator evasion [26,27]. A previous study has elucidated both a ‘staple-pin’-like attachment for structural anchorage and branching ‘dendritic’ structures for prey capture [27]. In both cases, a splayed thread configuration facilitates transfer of load from the anchored thread to a substrate. Such splayed attachment discs display remarkable adhesive properties and hold great potential to guide the design of bioinspired and biomimetic anchorages and adhesives [29].

Attempting to learn from the attachment disc, another recent study used the theory of multiple peeling [30] to explore the adaptation of the strength of attachment of such an anchorage [28]. Using complementary theoretical and computational means, a novel mechanism of synergistic material and structural optimization was demonstrated, such that the maximum anchorage strength was achieved, regardless of initial anchor placement or material type. An optimal delamination (or peeling) angle was facilitated by the inherent extensibility of silk, and attained automatically during the process of delamination.

However, silk thread attachment is clearly not limited to rigid substrates. In the construction of a web, structurally robust ‘bridge’ lines are typically used to anchor the web structure [31,32]. The dragline thread attachments to these threads is not fully understood, but poses an interesting mechanical question: what are the effects of attachment if the supporting material is compliant? Inspired by such thread-adhered connections in spider webs (figure 1a,b), here we explore the case of silk-on-silk attachment; that is, when silk threads are adhered to a similar, compliant silk ‘anchor line’ (figure 1c and see Methods section).

While the anchorage rigidity can be directly controlled by variation in constitutive behaviour, in addition, the intrinsic compliance (or ‘stretchiness’) of the anchor line introduces a new potential control variable—pre-stretching or pre-tensioning the anchorage. This is especially critical for spider webs in situ, wherein changes in humidity and silk moisture content can imbue significant pre-tension in silk threadlines (a phenomenon known as supercontraction [34–37]). Stresses owing to supercontraction have been measured and found to be of the order of 10–100 MPa [38]. Here, we explore the effect of stiffness variation (through both constitutive response and pre-strain) on the anchor thread in terms of silk-on-silk adhesion strength. Readers should note that our goal is not to exactly replicate the silk attachment, but rather to learn the physics underwriting Nature’s success. Indeed, owing to the diverse speciation of spiders and varying mechanical responses of silks [24,39,40], the developed model here is intended to be a general representation of an idealized mechanical system, not reflective of a particular silk, but rather an adhered compliant thread-on-thread system. As such, we implement a general hyperelastic law that deviates from the more complex response of silk [41–46], but facilitates an analytical solution to the delamination process [28]. Indeed, the transfer of ideas from biology is not limited to the ultimate form and function of a biological system, but the understanding of such connections may translate to robust structural engineering designs of cable bridges or structural fuses. We hence propose to explore the silk-on-silk attachment with a general elastic theory of a multiple-branched adhesive anchorage, from both a general material and structural perspective.

2. Theoretical and computational models

2.1. Theory of multiple peeling

In an earlier work [30], an elastic model was proposed for a simple anchorage system with adhesive forces at a branch–substrate interface, and confirmed by a recent silk-inspired computational study [28]. Here, the governing equations are outlined only for brevity. We note that, for the peeling model configuration, the applied force induces both a normal force and a shear force at the intersection of the two threads (e.g. mix-mode loading), where the ratio of normal and shear forces is dependent on the contact angle. Both normal and shear contributions are included in the peeling model—the formulation is based on the theory of multiple peeling [30], an extension of the energy-based single peeling model of Kendall [47]. While the ratio of normal/shear stresses is a function of the angle at the interface, the two contributions can be reduced to an effective stress, which itself can be reduced to a critical strain in the delamination thread [30]. Here, we are only quantifying the strength(force) required to detach. The spider, it is presumed, is not concerned with the variation of angle or

Figure 1. Images of silk-on-silk connections and model schematic. (a) SEM image of a silk-on-silk junction, wherein a (typically) smaller adhered thread splay and is connected to a larger anchor thread. (Reproduced with permission from Work [33]. Copyright © 2013, John Wiley & Sons, Inc.) (b) Microscope image of a small section of Nephila clavipes spider web, depicting numerous radial and spiral thread silk junctions, including splayed connections considered here. (Reproduced with permission from Koski et al. [25]. Copyright © 2013, Nature Publishing Group.) (c) Ideal model of silk-on-silk connection, with a symmetric adhered thread attached to a laterally fixed anchor thread at a prescribed angle, $\alpha$. Variation in anchor thread stiffness can be achieved directly through stress–strain response or indirectly through applied pre-strain. (Online version in colour.)
stress state of the attachment, but only the limit state—e.g. the detachment force. It can be easily shown that for a linear-elastic system, the critical delamination force for detachment can be calculated as

\[ F_d = 2YA_s \sin \theta \sin \xi, \]  

(2.1)

where \( Y \) is the elastic modulus, \( A_s \) is the cross-sectional area of a delaminated section and thus \( YA_s \) is the elastic thread rigidity or stiffness (e.g. an equivalent 'spring stiffness'). Because the above reflects a force balance, for nonlinear materials such as spider silk, we can substitute the secant modulus, \( F_t/\varepsilon_{ult} \) for the stiffness, \( YA_s \), where \( F_t \) is the tensile force in an adhered branch at the critical strain, \( \xi \). The critical level of strain at which an adhered branch will delaminate or detach can be expressed as

\[ \varepsilon_d = \cos(\alpha) - 1 + \sqrt{(1 - \cos(\alpha))^2 + \lambda}, \]  

(2.2)

where \( \alpha \) is the contact angle (figure 1c and see [30] for detailed derivation). Here, a non-dimensional parameter, \( \lambda \), is introduced representing the competition between adhesion energy per unit length, \( \gamma \), and elasticity, where \( \lambda = 4\gamma/YA_s \) or equivalently \( 4\gamma/(F_t/\varepsilon_d) \): we note that in [30] a slightly different definition was adopted. The contact angle \( \alpha \) is a parameter that can change the critical delamination force through strain \( \varepsilon_d \), and finding where the derivative of the structural delamination force with respect to \( \alpha \) is equal to zero (corresponding to a force maximum),

\[ \cos(\alpha_{max}) = \frac{1}{\cos(\alpha_{max}) + \sqrt{(1 - \cos(\alpha_{max}))^2 + \lambda}}. \]  

(2.3)

The force required for delamination is here geometrically restricted by the peeling angle, \( \alpha_{max} \). Equation (2.2), derived from pure mechanical considerations, has also a geometrical interpretation (as the reader could easily prove): during delamination, the contact angle is invariant, as we also observe in simulation.

### 2.2. Representative constitutive behaviour

Evolutionary diversity of spiders has resulted in a vast array of material properties and behaviours [19,39,40], web structures [15,17,19] and, not surprisingly, associated means of attachment [27,48]. While the exact mechanical behaviour in a particular silk is species-dependent, this does not eliminate the possibility to explore the behaviour of silk-on-silk attachment using an idealized model. We wish to accurately capture generic silk-like behaviour and assess the mechanisms of detachment. Thus, for the current investigation, as a simplification, we implement a model previously developed for silks [9,28,49]. For the constitutive stress–strain behaviour of the attachment, we introduce a generalized hyperelastic constitutive law (most similar to the behaviour of capture, or viscid, silks [40,50]), where

\[ \sigma(\varepsilon) = k\sigma_{ult} \left( \frac{\varepsilon}{\varepsilon_{ult}} \right)^{\beta}, \]  

(2.4)

defined by the ultimate stress \( (\sigma_{ult}) \), strain \( (\varepsilon_{ult}) \), a hyperelastic parameter \( (\beta) \) and a scaling factor, \( k \). We note that the above constitutive behaviour results in either zero stiffness (for \( \beta > 1 \)) or infinite stiffness (for \( \beta < 1 \)) at zero strain (i.e. \( \varepsilon = 0 \)). However, the relation is adequate for a system subjected to pure tension, where \( \varepsilon > 0 \), as is the current case. See the Methods section for additional description. The above relation can efficiently reflect a relatively strong, stiff, brittle response, to a relatively weak, yet highly compliant, extensible response, encompassing a range observed across many spider species with few parameters. To directly vary stiffness, for the 'anchor line', we further scale the stress–strain relation through \( k \) by factors of three-quarters \(( \times 0.75 \), \( \times 1 \), \( \times 2 \) and \( \times 4 \), respectively (figure 2), to reflect connections to both weaker/thinner and stronger/thicker anchor threads (e.g. viscid silk to dragline, or dragline to bridge line) and thus variable stiffness. Effective stiffness upon initial loading of the anchor thread is also controlled indirectly through the addition of pre-strain (see Methods section). For each scaling factor of anchor thread, we implement pre-strains of 0% to approximately 11%. We note that these pre-strains result in pre-stresses of the order of 1 MPa, which is easily achieved through supercontraction [38].

### 3. Results and discussion

#### 3.1. Embrittled force–displacement

Simulations of four models (with anchor thread stress–strain scaling factors of \( \times 0.75 \), \( \times 1 \), \( \times 2 \) and \( \times 4 \)) are undertaken at various anchor thread pre-strains (example simulation depicted in figure 3; additional movies of the peeling simulation are provided in the electronic supplementary material). The performance of each anchorage is then assessed by the force–displacement behaviour \( (F - D) \), detachment strength \( (F_d) \) and toughness \( (T) \). The angles at delamination \( (\alpha, \alpha^*) \) are also determined to confirm the prediction of the theory of multiple peeling (equation (2.3)).

Readers should note that, other than delamination, failure of the anchorage can occur by either (i) fracture of...
The failure modes are governed by the adhesion energy, as theoretically expected, between the adhered thread and the anchor thread—the structure delaminates and deforms upwards in equal measure (again, see figure 3). We see, however, that, in these cases, extensibility is an asset. Both an increase in rigidity (i.e. anchor thread scaling; figure 4c,d) and pre-stain, individually contributing to a higher anchor stiffness, result in a decrease of load capacity of the connection and, correspondingly, the associated displacement of the initiation of detachment. The opposite is true for a weaker anchorage—scaling the anchor thread by $\times0.75$ results in the strongest observed detachment forces.

In terms of pre-stretch, for threads of equivalent stress-strain response (figure 4b), the detachment force, $F_d$, varies from approximately 230 to 70 $\mu$N (a decrease of approx. 70%) by pre-staining the anchor thread 11%. Similarly, keeping a pre-stain value constant, we see load capacity drop by variation in anchor thread response, from 312 $\mu$N for 0% pre-stain, a factor of $\times0.75$, to 230 $\mu$N (0%, ×1), to 170 $\mu$N (0%, ×2) to 140 $\mu$N (0%, ×4), or changes of +36%, −26% and −39% accordingly, when compared with equivalent stiff threads (e.g. normalized by $\times1$ results; figure 5a). Simply put, increasing the structural stiffness embrittles the anchorage arising from the geometrical constrain of the peeling angle, a restriction commonly adopted by engineers but relaxed by spiders. At the same time, the variation between compliant and rigid systems decreases as the level or pre-strain increases—i.e. from 79 $\mu$N (8%, ×1) to 72 $\mu$N (8%, ×2) to 58 $\mu$N (8%, ×4), or decreases of only −9% and −27%, respectively (figure 5a). These trends hold for all values of pre-strain. Also noted is that, regardless of system stiffness, the force–displacement response exhibits the least variation when the pre-stain is high. The anchor thread (though pre-tension) converges towards a ‘rigid’ substrate, with respect to the compliance of the adhered thread. In effect, the adhered thread cannot ‘feel’ the compliance of the anchorage, and the behaviour is more akin to rigid substrate peeling [28].

In consideration of the tensile forces, $F_b$, in the adhered thread at the delamination point, in both rigid and compliant substrates, these can be shown to be strongly dependent on the contact angle, e.g. $\alpha = \alpha^*$, where, in the case of rigid anchors, $\alpha^* = 0$. As an initial approximation, we can consider a rigid geometrical rotation of the peeling interface (using the thread–thread contact at $\alpha = \alpha^*$ rather than using thread–substrate contact at $\alpha$ and assuming the strain at delamination, $e_d$, for both cases is approximately equal) and, for a given system, the load capacity of a compliant anchorage approaches scales according to

$$F_{d, \text{approx}} \approx F_{d, \text{rigid}} \frac{\sin \alpha}{\sin (\alpha - \alpha^*)},$$  \hfill (3.1)

where the effect of compliant anchorages is contained in $\alpha - \alpha^*$; as for more rigid threads ($\alpha^* \rightarrow 0$), the dependence from the contact angle is lost, and $F_{d, \text{compliant}} \rightarrow F_{d, \text{rigid}}$. We note that

The delamination process. The detachment load also corresponds to a constant peeling angle, as theoretically expected, between the adhered thread and the anchor thread—the structure delaminates and deforms upwards in equal measure (again, see figure 3). We see, however, that, in these cases, extensibility is an asset. Both an increase in rigidity (i.e. anchor thread scaling; figure 4c,d) and pre-stain, individually contributing to a higher anchor stiffness, result in a decrease of load capacity of the connection and, correspondingly, the associated displacement of the initiation of detachment. The opposite is true for a weaker anchorage—scaling the anchor thread by $\times0.75$ results in the strongest observed detachment forces.

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$$F_{d, \text{approx}} \approx F_{d, \text{rigid}} \frac{\sin \alpha}{\sin (\alpha - \alpha^*)},$$  \hfill (3.1)

where the effect of compliant anchorages is contained in $\alpha - \alpha^*$; as for more rigid threads ($\alpha^* \rightarrow 0$), the dependence from the contact angle is lost, and $F_{d, \text{compliant}} \rightarrow F_{d, \text{rigid}}$. We note that
this scaling is constrained by the symmetric two-branch arrangement, where \( \alpha > \alpha^* \) and \( \alpha < 90^\circ \) by definition. Equation (2.4) gives an idea of the huge increment in the load capacity expected for a compliant anchor (when \( \alpha - \alpha^* \) tends to zero). Comparison of this approximation and the measured load capacities are plotted in figure 5 and given in table 1, clearly illustrating the effect of anchorage compliance. While providing a simple approximation, the scaling relation in equation (3.1) is not exact, as \( \epsilon_{cb} \) vary between rigid and compliant conditions, and we outline a solution approach in subsequent sections.

Analogous to force, we also see a decrease in the thread displacement at detachment, \( \Delta_d \). Increase in the system rigidity (be it through scaling the anchor thread stress–strain response or addition of pre-strain) results in a continuous decrease in the detachment displacement—an effective measure of the flexibility of the connection (similar, for example, to the ductility of structural steel beam–column joints). Unlike the detachment force, there is no convergence in the detachment displacement, which continues to decrease with pre-strain and anchor thread strength. Owing to the function of a spider’s web—i.e. catching and maintaining prey—lack of connection ductility could result in catastrophic failure, especially in consideration of impact loadings. In webs, as in engineered structures, brittle-like small deformation failure should be avoided.

Finally, with the addition of pre-stretch, we note a distinct transition from a nonlinear stiffening response to a more softening-like response. The hyperelastic character of the global response changes from an extreme stiffening-like behaviour at low pre-strains (most similar to the constitutive law; figure 2) to a near-constant stiffness with sudden yield at high pre-strains. This is counterintuitive, as the material law for both threads is always a stiffening behaviour (\( s \propto \epsilon^2 \), with \( \beta = 3 \)). However, the initial rigidity/stiffness is imbued by the applied pre-strain, and amplified by the geometric configuration of the connection—interaction between both material and structure. Again, we can propose a benefit of not only compliance of the structure, but also a stiffening-like behaviour wherein the force required to both deform and break the connection increases [9,28]. Upon sudden loading (from prey capture, for example), a web is subjected to some finite load. The spider, presumably, would want to anticipate if such a load decreases the structural integrity of the web, with ample warning of failure. Stiffening connections—such as those with limited pre-strain—would both deform considerably and yet have sufficient capacity to withstand the loading force. The connection can be evaluated based on extreme sagging, or loss of thread tension. In effect, the spider would be clearly warned of impending failure. A rigid connection in contrast would give no such warning—only small deformation would occur until a failure event is initiated.

It could also be postulated that a tension structure such as a web would necessitate some geometric flexibility at the connections, owing to uncertainties in environmental conditions.

![Figure 4](https://rsf.royalsocietypublishing.org/journal/rsif)
Figure 5. Load capacity and toughness. (a) Delamination load, $F_d$, as a function of applied pre-strain. When the anchor thread is stretched, the increase in rigidity results in a decrease in load capacity as the adhered thread is geometrically constrained. The effect is heightened for more compliant anchor threads (scale factors $k$ of $\times 0.75$ and $\times 1$). (b) Approximated load capacity versus observed load capacity, determined by angles and scaling relation (equation (3.1)). (c) Connection toughness, $T$, as a function of pre-strain, depicting an inverse relation between toughness and system rigidity, similar to load capacity. (d) Approximate toughness versus observed toughness (equation (3.2)). (Online version in colour.)

Table 1. Delamination forces, toughness, measured and scaled/approximated via equations (3.1) and (3.2).

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(such as anchorage sites). If a spider must reconstruct portions of the web, for example, and slightly modify the architecture of the web, then a modest ‘tightening’ of the silk junctions would provide the required extensibility and facilitate geometrical variation.

### 3.2. Toughness

Next, we assess the systems in terms of toughness, $T$, or elastic energy capacity of the connection, evaluated numerically by integrating the $F-\Delta$ curves until ultimate detachment. We note that this includes the plateau regions of the $F-\Delta$ response (figure 4), where the delamination force is relatively constant. Again, there is a clear influence on system rigidity, be it through the addition of pre-strain or scaling of stress–strain (figure 5c), amplified by the joint effect on ultimate load ($F_d$) and displacement ($\Delta_d$). For example, with threads of equivalent stress–strain response (figure 4b), the toughness varies from approximately 2.4 to 0.8 $\mu J$ across the values of pre-strain. Similarly, with constant pre-strain, we see toughness decrease by variation scaling factor, from 3.2 (0%, $0.75$) to 2.4 $\mu J$ (0%, $1$) to 1.9 $\mu J$ (0%, $2$) to 1.4 $\mu J$ (0%, $4$). This has critical implications for such connections: while the adhesion strength between threads is constant ($\gamma_a = 5.0 \times 10^{-2}$ m$^{-1}$), the length of the adhered thread connection is constant (40 mm), and the direction of the applied force is constant, the toughness of the connection—that is, the required energy to detach one thread from the other—is dependent on both the structural and material response of the silk-on-silk connection. Moreover, the toughness is increased by an increase in system compliance (e.g. no pre-strain, equivalent behaviour) while increasing system rigidity has the adverse effect—it weakens the system in terms of both load capacity and toughness. Accounting for the angle of the anchor thread, similar to the load capacity, the increase in toughness can also be approximated according to

$$T_{\text{approx}} \approx T_{\text{rigid}} \frac{\sin \alpha}{\sin (\alpha - \alpha^*)}. \quad (3.2)$$

Comparison of this prediction and the measured toughness values is plotted in figure 5d and given in table 1. In general, the more extensible the anchorage (and thus $\alpha^* \rightarrow \alpha$), the tougher the connection.

### 3.3. Ideal peeling angles

Finally, we analyse the detachment geometry—specifically the angles of both the adhered thread ($\alpha$) and the anchor thread ($\alpha^*$), as shown to vary in figure 6 as a function of anchor rigidity. Upon initiation of delamination, both angles remain constant until the adhered thread is completely detached (again, refer to figure 3). The optimal angle, $\alpha_{\text{max}}$, was shown to maximize delamination force, $F_d$, and can be predicted by equation (2.3) for rigid substrates, based on the effective stiffness of the adhered thread, and the adhesion energy (through the parameter $\lambda$).

First, we check the validity of equation (2.3) for compliant anchorages. As mentioned, owing to the nonlinear behaviour of the silk, we calculate the value of $\lambda$ substituting the secant stiffness, or $YA_e = F_l/e_d$, where $F_l$ is the force in the adhered thread at the onset of delamination (via the measured value of $F_d$) and $e_d$ is the associated strain in the silk at the limiting force. Using $\lambda$, we can solve equation (2.3) for $\alpha_{\text{max}}$.

The measured values of $\alpha$ and $\alpha^*$ are reported in table 2. However, using equation (2.3) and presuming a rigid anchorage, the calculated values of $\alpha_{\text{max}}$ consistently underestimate the actual peeling angle, $\alpha$. This can be understood by considering the increase in energy required to deform the more compliant anchorage—rather than just stretch the adhered thread until the critical delamination force surpasses the adhesion energy barrier (expressed through $\gamma_a$), the load must also deform and stretch the compliant anchorage. This allows more energy to be absorbed by the system, thus requiring additional force to delamate, and subsequently increasing the delamination angles. As a result, the exact values for $F_d$ can be solved only after calculation of $\alpha^*$. It represents an additional unknown in the coupled nonlinear problem, and can be derived geometrically. We find

$$\cos(\alpha^*) = \frac{1 + \varepsilon_{\text{pre}}}{1 + \varepsilon_{\text{total}}}, \quad (3.3)$$

where $\varepsilon_{\text{pre}}$ is the prescribed pre-strain, and $\varepsilon_{\text{total}}$ is the total anchor strain accounting for the applied total load in the anchor thread $F_{\text{anchor}}$. From the anchor–thread system equilibrium, we find

$$F_{\text{anchor}} = F_{\text{pre}} + \frac{F_d}{2\sin^2 \alpha^*}, \quad (3.4)$$

where $F_{\text{pre}}$ is the force in the anchor thread owing to the pre-strain (solved via the constitutive law; equation (2.4)). With high pre-strain (or anchor to thread stiffness ratio $k$), $F_{\text{anchor}} \approx F_{\text{pre}}$, $\varepsilon_{\text{total}} \approx \varepsilon_{\text{pre}}$ and $\alpha^* \rightarrow 0$, i.e. the anchor thread does not deform vertically and the gain in the load capacity is lost. The measured and predicted values of $\alpha^*$ are plotted in figure 7a,b.
Table 2. Delamination angles, measured and predicted.

<table>
<thead>
<tr>
<th>anchor scaling factor, $k$</th>
<th>pre-strain</th>
<th>peeling angle ($\circ$), $\alpha$</th>
<th>anchor angle ($\circ$), $\alpha^*$, $\gamma_{\text{pred}}$ equations (3.3) and (3.4)</th>
<th>$\lambda^a$ equation (3.5)</th>
<th>contact angle ($\circ$), $\Delta\gamma_{\text{pred}}$ equation (3.6)</th>
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<tbody>
<tr>
<td>$\times 0.75$</td>
<td>0.111</td>
<td>34.35</td>
<td>11.20</td>
<td>17.55</td>
<td>0.0139</td>
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<td>34.15</td>
<td>16.95</td>
<td>21.02</td>
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<td>35.88</td>
<td>22.20</td>
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<td>36.39</td>
<td>26.41</td>
<td>29.51</td>
<td>0.0021</td>
</tr>
<tr>
<td></td>
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<td>37.72</td>
<td>28.03</td>
<td>32.81</td>
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<tr>
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<td>35.27</td>
<td>23.45</td>
<td>23.69</td>
<td>0.0053</td>
</tr>
</tbody>
</table>

We note that the prediction for $\alpha^*$ slightly deviated from the measured value as the rigidity of the anchorage is increased—the measured values are consistently lower than the predicted. This can be attributed to the relaxation of the threads—upon delamination, the portion of the anchor thread no longer in contact with the adhered thread undergoes relaxation as it is no longer subjected to the applied load and the anchorage angle is reduced from the predicted value. A similar trend was observed in a previous study [28].

Clearly, increasing the rigidity of the anchor results in less extension of the anchor thread and smaller deformation, and thus detachment occurs at lower forces (as shown in figure 5a). A compliant anchorage increases the effective adhesion between threads, by increasing the work required to achieve the critical delamination strain and angle, via the deformation of the anchorage (in comparison with a rigid substrate with the same adhesive properties). Through the anchor deformation, the compliance of the anchorage can increase the ‘adhesion capacity’ significantly. In terms of a robust connection, a spider would desire a very stretchy system, amplifying the adhesion strength between two silk threads.

To account for the variation in anchor stiffness and the increase in adhesion capacity in terms of the theory of multiple peeling, we must account for the force at the contact peeling angle, $\Delta \alpha = \alpha - \alpha^*$, rather than at the adhered thread angle, $\alpha$ (figure 7c). We see that the contact peeling angle consistently increases with relative stiffness, $k$, as well as applied pre-strain. Because the adhered thread here is constant, the variation of the anchor thread properties (i.e. pre-strain and stiffness) results in variation in work required to delaminate. Moreover, we observe that an increase in $\Delta \alpha$ corresponds to a decrease in delamination force. This effect can be understood through equation (2.3) by considering the parameter $\lambda$—an increase in angle corresponds to an increase in $\lambda$, which can be considered a ratio of the work required to delaminate to elastic stiffness of the adhered thread. An increasing $\Delta \alpha$ corresponds to a decreasing delamination force, as by the secant stiffness, $\lambda \propto 1/F_d$. As a result, by increasing the contact angle, we can expect lower delamination forces.

In terms of the theory of multiple peeling, we can introduce a modification to the definition of $\lambda$ in equation (2.3). We capture the effect of compliant anchor thread by letting

$$
\lambda^a \equiv \frac{\lambda}{1 + \Omega}
$$

where $\Omega$ is the ratio of adhered thread stiffness ($F_{\text{anch}}/\gamma_0$) to anchor thread stiffness ($F_{\text{anch}}/\gamma_{\text{total}}$) at delamination, accounting for the increase in stiffness owing to scaling, $k$, and pre-strain through equations (3.3) and (3.4). We note that, while similar, the scaling factor, $k$, is not equivalent to $\Omega$, as $k$ reflects variation of constitutive relation (equation (2.4)), whereas $\Omega$ reflects the relative stiffness at the strains of each thread. This $1 + \Omega$ adjustment represents the influence of a finite value of the anchor rigidity on the load capacity and represents a previously derived solution for an aligned double joint [51] (where $\Delta \alpha = 0$; note a slightly different definition in [51]). Clearly, as the anchor thread becomes more rigid ($\Omega \to 0$), rigid substrate conditions are approached, and $\lambda^a = \lambda$. This modified form is substituted...
into equation (2.3) along with the contact peeling angle, $\Delta \alpha$, or

$$\cos(\Delta \alpha) = \frac{1}{\cos(\Delta \alpha) + \sqrt{(1 - \cos(\Delta \alpha))^2 + \lambda^*}}$$  \hspace{1cm} (3.6)

and the optimal contact peeling angle, $\Delta \alpha$, can then be calculated. Values of $\lambda^*$ are given in table 2, and the measured and predicted values of $\Delta \alpha$ are plotted in figure 7d showing a relevant agreement. Finally, the force can be predicted by modifying equation (2.1), accounting for $\Delta \alpha$ instead of $\alpha$. The predicted forces are plotted in figure 7e.

3.4. Variation of constitutive law

The computational results clearly indicate an increase in load capacity with anchorage compliance, which can be calculated through equations (3.3)–(3.6). In practice, engineering materials are typically neither as extensible as spider silks nor do they exhibit the same magnitude of hyperelastic stiffening (represented by $\beta$; equation (2.4)). The rigidity ratio, $k$, however, can easily be manipulated through geometrical design of connections, such as increasing the cross-sectional area of the anchor (for a given material, $k \propto A$). Similarly, the pre-strain, $\varepsilon_{pre}$, can be easily manipulated in practice through the application of pre-tension. The key question then arises: what is the effect of varying the constitutive law? Or more specifically, what is the effect of varying the hyperelastic parameter $\beta$?

To explore the variation, we use the formulation developed here to predict the peeling strength as a function of $\beta$ for the anchor thread (the properties of the adhered thread are assumed constant). The solution requires an iterative approach described in the Methods section. We repeat the process for $\beta = 0.5, 1.0, 1.5, 2.0, 2.5, 3.0$ and $3.5$ (figure 8a) while modifying the pre-strain from 0% to 15%. The resulting factors are plotted in figure 8c. The trends clearly depict a drastic increase in load capacity and toughness with compliance, which decreases as the material law approaches linearity ($\beta \to 1$). Stiffening behaviour in the anchorage is desired, owing to the relative initial compliance. As the material transitions from linear-elastic to softening behaviour, there is little change in the connection.
capacity for the strain regime explored. This can be attributed to relative stiffness of a plastic softening-like behaviour at small strains (for the case here, where $\alpha_{ult} = 2$, at $\varepsilon = 0.15$, the ratio of anchor thread tangent stiffness with $\beta = 0.5$ to adhered thread tangent stiffness with $\beta = 3$ is greater than 100; see Methods section). In effect, using the constitutive law expressed by equation (2.4), the anchor thread approaches the rigid condition for $\beta < 1$ at small strains. Of note, the specific delamination strengths and behaviours are dependent on both the constitutive law and the adhesion model implemented (see Methods section). One would expect different delamination forces if other material responses and interaction rules were applied. Again, as silk and silk-on-silk behaviours are not fully understood, we have relied on a simplified representation to enable both modelling and analysis. The procedure can clearly be repeated upon determination of more accurate laws.

### 3.5. Significance of pre-strain and supercontraction

We have shown that the addition of pre-strain or rigidity in an anchor thread effectively embrittles a silk-on-silk connection. However, a key motivation for the exploration of the pre-strain effect is in consideration of supercontraction. Unique to silk, the process of supercontraction [34–37] involves the uptake of water by silk—and thus a function of environmental humidity—and results in significant shrinkage if the silk fibres are unrestrained [37,52,53]. It is proposed that the addition of H$_2$O molecules disturbs the fibrous or axial predominance of the molecular structure of silk (controlled by specific motifs in the silk proteins [35,54]), and facilitates a self-folding effect (e.g. entropy-driven recoiling of molecular chains [55,56]), resulting in marked changes in mechanical properties [34,37,52,53]. If the fibre/thread is restrained from contraction, intrinsic stresses build up within the thread—i.e. a post-tensioning mechanism controlled by wetting. The exact physiological function of supercontraction (if any) is still unresolved [36], but has been postulated to enable tailored mechanical properties [57], or pre-tensioning a web [53], as examples.

It would be an oversimplification to claim that supercontraction merely ‘pre-tensions’ the silk threads, as the addition of water induces an effective phase-change of the silk nanostructure. Indeed, while there is a resulting build of intrinsic stress, the constitutive behaviour of supercontracted/humid/wet silk changes from the dry state, and is dependent on numerous factors. That being said, a recent study using Brillouin scattering measured how the elastic stiffnesses of spider silk change when it supercontracts [25], reporting an increase in longitudinal stiffness with humidity, and there is a clear connection between silk’s internal stress, stiffness and extensibility with humidity. It was hypothesized that supercontraction helps the spider tailor the properties of the silk during spinning, because the spider may be able to tailor the particular elastic constants by pulling and restraining the silk threads and adjusting the water content. Clearly, this has a subsequent effect on the silk connections, which are highly sensitive to pre-tensioning and stiffness. That being said, readers should note that supercontraction not only acts as a post-tensioning mechanism, but also fundamentally changes the constitutive law of the silk (via molecular changes in the nanostructure). Here, we apply a tension to our model without any variation of constitutive law as a simplification to facilitate theoretical treatment. To accurately reflect supercontraction, the constitutive law would be a function of humidity [58], which is beyond the scope of this study.

With supercontraction as a consideration—potentially resulting in a pre-strain and thus a weakening mechanism for silk-on-silk connections—it could be hypothesized that the ‘glue’ silk [59,60] present at the thread junction within a web may not only serve as a mechanical adhesive (depicted in figure 1a), but also potentially as a ‘protective coating’ that prevents/controls local hydration (and thus can suppress or amplify the effects of supercontraction). Uncertainty in the changes in humidity could have adverse effects in the web, but, at the same time, silk connections should maintain structural integrity. Perhaps, by means of ‘glue’ coating key connections, the ever-impressive spider inadvertently ‘weather-proofs’ its structure.

### 4. Conclusion

Extending from previous work on rigid substrates [28], here we explore the load transfer, ultimate strength and deformation behaviour of thread-adhered silk-on-silk attachments. Before concluding remarks, we note that there may be other physiological roles of ‘compliant connections’, but we intentionally maintain a structural perspective in our analysis and discussion. Our aim is to learn a mechanical lesson from Nature, relying on general representative computational and
toughness (extreme properties. Common engineering materials (elasto-
structure (here, a silk connection) that benefits from these
of a simple thread-adhered silk-on-silk connection. The simple
We consider the structure depicted in figure 1
5.1. Ideal connection
simplification—based on the web geometry) and pre-tensioning (based on
rigidity in the anchor thread) significantly degrades the ulti-
anchor stiffness (from either an introduction of pre-strain or
virtue for such silk-on-silk attachments—the increase in
throughout silks). The key finding is that compliance is a
the hyperelastic stiffening response (which is common
to enable theoretical treatment—it is not intended to reflect the
exact behaviour of either dragline or capture silks, but rather
the hyperelastic stiffening response (which is common
Herein, we presented the underlying design principles and
mechanisms that determine the possible load transfer from compliant fibre-to-fibre anchorages, be they silk-on-silk
or another, as-yet undeveloped, system.

5. Methods
5.1. Ideal connection
We consider the structure depicted in figure 1c: that shows a model of
a simple thread-adhered silk-on-silk connection. The simple
anchorage is colarchic, two-branched, symmetrical and homoge-
neously adhesive across a similar, compliant thread. It is an
adhesive anchor because it allows a force, \( F \), to be transmitted
or a solid substrate through adhesive forces at the material interface
(e.g. no penetration of material entanglement), symmetrical
because the initial angles, \( \alpha \), on both sides are equal, and it is
colarchic because it has no hierarchy (e.g. a single connection).
The model represents the most basic geometry of splayed silks
connections that engage adhesive forces at a silk thread interface.
We again note that the model is not representative of any particular
spider species or silk type by design, to maintain generality and
potential transferability of the findings to similar systems.
We proceed to describe the theoretical formulation of multiple
peeling [30] and the general silk-based material model to explore
the silk-on-silk connections.

5.2. Constitutive model
We consider the general stress–strain relation expressed by
equation (2.4), defined by the ultimate stress (\( \sigma_{ult} \)), strain (\( \epsilon_{ult} \)), a
hyperelastic parameter (\( \beta \)) and a scaling factor (\( k \)). For stiffening,
\( \beta > 1 \), whereas softening occurs for \( \beta < 1 \), and linear-elastic
behaviour when \( \beta = 1 \). Because we are interested in forces, we
simply multiply by cross-sectional area, and rearrange to separate
the constants

\[
F(\epsilon) = A_0 \sigma(\epsilon) = kA_0 \sigma_{ult} \left( \frac{1}{\epsilon_{ult}} \right)^\beta \epsilon^\beta (5.1)
\]

For modelling purposes, we want the force to be a function of
distance (\( r \)), and not strain, so we substitute

\[
\epsilon = \frac{r - r_0}{r_0} \quad \text{and} \quad \epsilon_{ult} = \frac{\sigma_{ult} - r_0}{r_0}. (5.2)
\]

From which we attain

\[
F(r) = kA_0 \sigma_{ult} \left( \frac{1}{\left( \frac{r}{r_0} - 1 \right)} \right) ^\beta (r - r_0)^\beta. (5.3)
\]

For the elastic potential energy, we integrate once with respect to \( r \)

\[
\varphi(r) = kA_0 \sigma_{ult} \left( \frac{1}{\left( \frac{r}{r_0} - 1 \right)} \right)^\beta \left( \frac{1}{\beta + 1} \right) (r - r_0)^{\beta + 1}. (5.4)
\]

The final potential is effectively defined by four parameters,
where (i) \( kA_0 \sigma_{ult} \) captures the ultimate strength (or maximum
force) of the threads, (ii) \( r_0 \) the ultimate strain or maximum extension,
and (iii) \( r_0 \) prescribes the equilibrium condition
(which can be manipulated for pre-stretch) and \( \beta \) the hyperelastic
parameter (where \( \beta > 1 \) implies hyperelastic stiffening). For the
model here, the hyperelastic parameter is set at \( \beta = 3.0 \). We use
\( \sigma_{ult} = 1400 \text{ MPa} \) [28] and assume a cross-sectional diameter of
approximately 20 \( \mu \text{m} \) for the attached silk threads, resulting in
an ultimate strength of the order of 0.5 N. We also implement
\( \epsilon_{ult} = 2.0 \), such that \( \sigma_{ult} = 3r_0 \) and \( r_0 = 0.1 \text{ mm} \).

The tangent stiffness can be expressed as the derivative of the
stress with respect to strain

\[
\frac{d\sigma}{d\epsilon} = k\beta \left( \frac{\sigma_{ult}}{\epsilon_{ult}} \right) \epsilon^{\beta - 1}. (5.5)
\]

For all cases without pre-stretch, regardless of the scaling
factor, the initial stiffness of the threads is zero (e.g. \( \sigma_{ult} = 0 \)
for \( \epsilon = 0 \)). However, the addition of pre-stretch increases the
initial effective stiffness of the anchor thread to a finite non-
zero value. Pre-stretch is controlled by varying \( r_0 \) and the initial
geometry of the model, where

\[
\epsilon_{pre} = \frac{\epsilon_{initial} - r_0}{r_0} \quad \text{and} \quad \epsilon_{initial} > r_0. (5.6)
\]
5.3. Thread adhesion
Adhesion between threads is achieved with a Lennard–Jones (LJ) interaction of the type
\[
E = 4e_{12} \left( \frac{\sigma_{12}}{r} \right)^{12} - \left( \frac{\sigma_{12}}{r} \right)^6 \quad \text{for} \quad r < r_{cut},
\]
where \( E \) is the energy of the interaction, \( e_{12} \) is the adhesion parameter, \( \sigma_{12} \) is an interaction-range parameter, \( r \) is the distance between the two particles and \( r_{cut} \) is the cut-off distance beyond which the interaction no longer has effect. An LJ interaction is implemented to facilitate the use of molecular dynamics software, typically applied in full atomistic studies. While the scale is much larger here, the LJ interaction provides an adequate representation of non-instantaneous delamination—that is, there is some give at the adhered interface before complete fracture (and zero force or detachment)—e.g. silk thread attachment is not assumed brittle. The LJ interaction also decays relatively quickly, so it does reflect long-range adhesion. We use \( \sigma = 0.009 \) mm, leading to an energy minimum at a spacing 0.1 mm and \( r_{cut} = 0.50 \) mm. The adhesion parameter, \( e_{12} \), is proportional to the energy of adhesion per unit length of silk, \( \gamma_s \), whereas high adhesion results in thread rupture (2.2) and (2.9)), but the relation remains the same.

5.5. Peeling simulations
We used steered molecular dynamics (SMD) with a constant pulling velocity as the protocol for simulating the force-induced deformation of attachment structure. The SMD approach applies a moving spring force (pulled at a constant rate of 0.05 mm s\(^{-1}\) and with a spring stiffness of 0.1 N m\(^{-1}\), similar to previous simulations [28]), such that the structure can behave in a manner not captured by either force or displacement loading alone, allowing induced conformational changes in the system. We note that trial cases with pulling rates of 0.5 and 0.01 mm s\(^{-1}\) were implemented to check for any rate dependence, with negligible effect on the observed results. Upon loading, we measure the attachment angle, \( \alpha \), and applied force, \( F \) (example plotted in figure 3).

5.6. Iterative solution
To solve the critical delamination force, \( F_d \), as a function of pre-strain and \( \beta \), an iterative solution is implemented. We first set \( k = 1 \), and through equations (2.1)–(2.3) determine the critical delamination force, \( F_{d,\text{rigid}} \), and peeling angle, \( \alpha_{\text{rigid}} \), for rigid substrate conditions. Through \( k \) and the applied pre-strain, we can predict both the total force in the anchor thread at delamination (equation (3.4)), and the anchorage angle, \( \alpha^* \) (equation (3.3)). From \( \alpha^*, \alpha_{\text{rigid}} \) and \( F_{d,\text{rigid}} \) the secant stiffness for both the anchor thread and adhered thread can be determined. We can then calculate \( \lambda^* \) through equation (3.5) through \( \Omega \) and use equation (3.6) to calculate the optimal contact peeling angle, \( \Delta \alpha \). From \( \Delta \alpha \), we can update both the adhered thread angle, \( \alpha \) (where \( \alpha = \Delta \alpha + \alpha^* \)), as well as the delamination force, \( F_d \) (equation (2.1)), which differ from the initial rigid solution. These updated values serve as the initial values for a subsequent solution, requiring a recalculation of \( \alpha^*, \Omega, \Delta \alpha, \alpha \) and \( F_d \). The process is repeated until convergence is attained, and the necessary delamination force is predicted, \( F_{d,\text{compliant}} \). Finally, the ratio of \( F_{d,\text{compliant}} / F_{d,\text{rigid}} \) is calculated to determine the amplification effect of compliant anchorages.

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References


