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Physical properties of sticky spirals and their connections: sliding connections in orb webs

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Introduction

Typical orb webs made by spiders in the families Araneidae and Uloboridae consist of two types of threads: (1) a scaffold (including hub, frame, temporary spiral, and radial threads) made of strong, non-sticky, and relatively inextensible silk, and (2) a spiral of weaker, sticky silk fastened to the scaffold. In Araneidae, the sticky spiral is a highly extensible and elastic thread coated with droplets of a sticky substance (see DeWilde, 1943; Lubin (in the press) for data comparing physical properties of sticky spiral and scaffold silk in several species); in Uloboridae the spiral is less elastic and less extensible, and is covered with a sticky mat of very fine silk (e.g. Freidrich & Langer, 1969) instead of the semi-liquid glue. In prey capture, the sticky thread functions to stop and entangle prey which encounter the web, while the stronger threads serve to support the entire array (see Witt, 1965, Eberhard, 1972 for detailed discussions of these and other functions).

The stickiness on a sticky spiral thread is generally stronger than the thread itself, and if a relatively large object is attached to a thread of sticky spiral in an orb and then pulled away, the thread itself breaks before it comes unstuck from the object or from the rest of the web (DeWilde, 1943, personal observation). In araneids the sticky spiral is attached to each radial thread it crosses, and in *Araneus diadematus*, the morphology of these junctions is somewhat different from that of other attachments in the orb (Jackson, 1971); in *Uloborus* the sticky spiral is attached to some but not all the radii it crosses (Eberhard, 1972, p. 462).

This note describes what happens when stress is applied to junctions between sticky spirals and radii and to the sticky spiral itself in intact orbs; suggestions are made regarding the functional significance of (1) the form of the attachments in araneids, (2) the lack of attachments in *Uloborus*, and (3) some of the details of the sticky spiral construction behaviour of both araneids and uloborids. Orb webs are seen to be extraordinarily sophisticated traps, even in their microscopic details.

Methods

Araneid webs were observed under a dissecting microscope in the following manner: a plastic loop about 25 cm in diameter covered with double-sided sticky tape was pressed against a portion of an orb, and then this sector was cut free from the rest of the web with a burning cigarette. The loop was placed under the microscope, and a strong light was projected onto a white background to make the threads visible while they were manipulated under medium and high power (30 × and 58 ×). Webs of mature female *Argiope* *argentata*, *Metazygia* sp. (prob. *gregalis*), and penultimate male and female *Eriophora edax* were observed in this way. Unless otherwise specified, the descriptions in the text concerning araneids apply to all three species. These species and those in the table were kindly identified by Dr. H. W. Levi.

Sticky threads from webs of *Uloborus* sp. (ca. *geniculatus*) were collected in both stressed and unstressed states by touching them to microscope slides where they stuck; they were then cut free from the web, and covered with cellophane tape (' Scotch Magic Transparent Tape '), which made the mat of cribellum silk much more visible, and observed under a compound microscope.

The terms ' non-zero ' and ' zero ' of Jackson (1971) are used in the descriptions below in reference to sticky spiral-radius junctions in which the sticky spiral zig-zags lie parallel to the radius for a short distance (' non-zero '—see fig. 2) and junctions in which the sticky spiral continues directly across the radius (' zero ').

Results

Araneidae

Figure 1 represents the macroscopic results of pulling on sticky spiral threads. Although the diagram shows a pull approximately in the same plane of the web, the same results obtained when the sticky spiral was pulled perpendicular to the web plane. At low stress, the segment being pulled was stretched, and the radii on either side were not displaced (fig. 1 (*b*)). At higher stress, the radii were slightly displaced, and the attachments of the sticky spiral to the radii were partially but not completely ruptured; each attachment broke

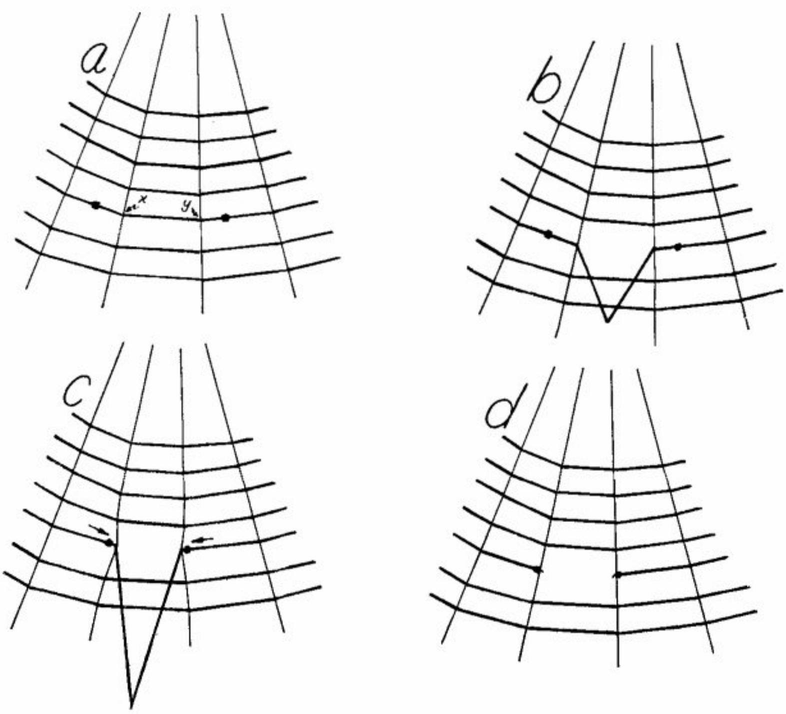

Fig. 1. Conversion of a zero junction to the ' pulley ' form when a segment of araneid sticky spiral is pulled with increasing force. Not to scale.

in a way which did not free the sticky spiral from the radius, but did permit thread from the adjacent segments of the sticky spiral to pass through the attachment (fig. 1 (*c*)), the net effect being as if the sticky spiral passed through pulleys attached to the radii at x and y. As additional tension was exerted, more thread from the two adjacent segments flowed through the attachments, and finally, the stressed segment broke and the two loose ends contracted to a fraction of their former length (fig. 1 (*d*)). Occasionally additional attachments of the same loop of sticky spiral to adjacent radii were also converted to the ' pulley ' form before final rupture occurred.

Apparently sticky spiral-radius attachments which convert to ' pulley ' form are common but not universal in the webs of other araneids (table). Tests with the orbs of species in which there was only a slight tendancy to convert to the ' pulley ' form showed that quicker pulls (the type of stress most likely to be produced by the impact of prey with the web) produced fewer conversions.

Numbers of conversions to ' pulley ' junctions produced by slow pulls of sticky spirals in new (<12 hours old), intact orbs.

Species	Number of pulls	Number of conversions	%
Araneidae			
Acacesia ?hamata (Hentz)	15	15	100
Argiope argentata	15	15	100
Eriophera edax (Blackwell)	15	15	100
Scoloderus tuberculifer	10	10	100
Metazygia sp. prob. *gregalis*	100	97	97
Eustala fuscovittata (Keys.)	15	13	87
Mangora melanocephala (Tac.)	20	11	55
Dolichognatha sp.	14	2	14
Leucauge sp.	40	5	13
Pachygnatha (?) sp.	14	0	0
Tetragnatha sp.	20	0	0
Uloboridae			
Uloborus ca. *geniculatus*			
spiral attached to radius	15	0	0
spiral not attached to radius	15	15	100

Figure 2 illustrates some of the microscopic events associated with the conversion of a sticky spiral-radius junction to the pulley form in a web of *Metazygia* sp. The junction illustrated is the ' non-zero ' type as the conversion of this type of attachment involves the most complex series of events. In *Metazygia* sp. webs, only about 50% (30 of 63) of the sticky spiral-radius junctions were ' non-zero ', the rest, corresponding to Jackson's ' zero ' type in which the spiral runs straight across the radius; the ' zero ' type was essentially the only kind of connection in the webs of *A. argentata* and *E. edax*.

As a segment of sticky spiral was tensed, at first it simply elongated, and no change was produced in the junction (fig. 2 (*b*)). With greater stress, however, the spiral elongated more, and began to rip away from one side of the junction (fig. 2 (*c*)). As it did so, the material which had apparently been cementing the junction (probably consisting of both fibrous and liquid components judging from the figures in Jackson, 1971 and personal observations) accumulated near one end of the junction (y in fig. 2 (*c*)). As the tension increased, the sticky spiral ceased ripping away from the radius, but instead,

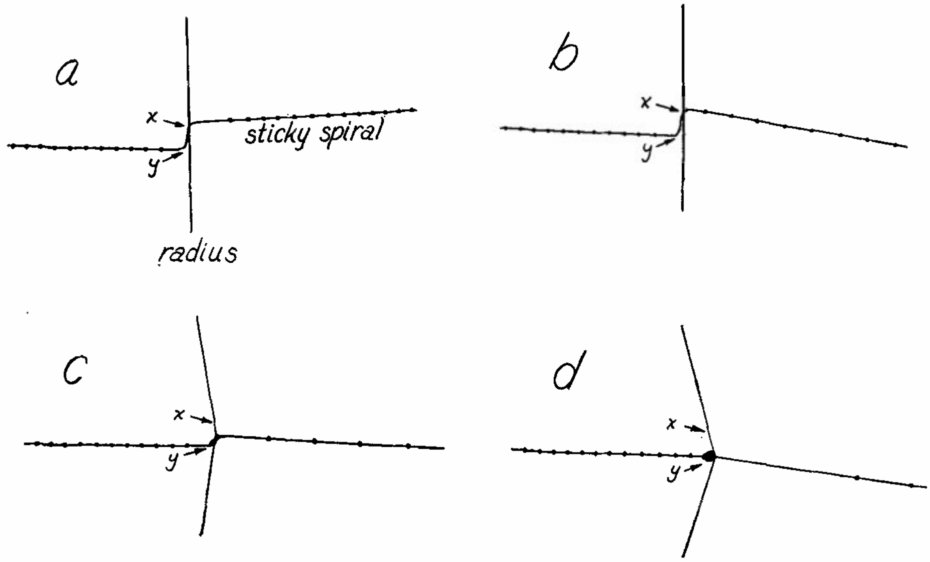

FIG. 2. Conversion of an araneid non-zero radius-sticky spiral junction to the 'pulley' form. Not to scale.

when it was free except for point y, the junction converted to the 'pulley' form and the sticky spiral baseline flowed through it (fig. 2 (d)). The balls of 'glue' on the sticky spiral did not pass through the junction, and accumulated in a growing lump just to the left of the radius (fig. 2 (d)). The 'clean' baseline just to the right of the junction was only very slightly sticky.

'Non-zero' junctions could be converted to 'pulley' forms by pulls from either side. If, as in fig. 2, the sticky spiral segment to the right of the attachment was stressed, the spiral almost always started ripping free from the radius at x and continued to y as in the diagram; but if the other side of such an attachment was stressed, the rip started at y and continued to x. If both sides of the attachment were carefully pulled simultaneously in a direction approximately parallel to the radius, it was possible to create a 'pulley' attachment in the other sense, with the sticky spiral sliding up and down the radius rather than across it.

'Zero' junctions in *Metazygia* orbs converted to the 'pulley' form more readily than 'non-zero' junctions in the same web. When the sticky spiral was seized about 1 cm from its junction with a radius and slowly pulled directly away from the junction (nearly in the plane of the web), it broke before converting to the 'pulley' form in 15 of 31 experiments with non-zero junctions, but in only 3 of 18 with zero junctions (Chi^2 gives $p < 0{\cdot}05$).

Coating the radius and sticky spiral heavily with cornstarch powder prior to stressing invariably prevented the conversion of the attachment to the pulley form, but the mechanism responsible for this is not known.

Slippage along threads also occurred in a second situation in araneid webs. As illustrated in fig. 3, when an object was touched to a sticky spiral segment near an attachment to a radius and then pulled away, the object slid toward the centre of the segment before finally either breaking the spiral or pulling free of the glue.

Uloboridae

Responses similar to that illustrated in fig. 1 were also seen in intact *Uloborus* webs when sticky spiral segments were stressed by pulling them upward (the webs were approximately horizontal), but only at junctions where the spiral was not attached to the radius (table). The *Uloborus* sticky spiral was much less elastic than those of the araneids, and when it finally broke, it did not contract into little blobs as in fig. 1, but remained more or less extended.

Responses similar to that in fig. 3 were also seen in *Uloborus* webs, although in this case the mechanism was quite different, as shown in fig. 4. When a large object was touched to a sticky spiral segment and then pulled away, at first the entire sticky spiral remained stuck to the object (fig. 4 (*b*)); but as the stress increased, the baseline (as in araneids' webs, the baseline is actually composed of two separate strands—see Freidrich & Langer, 1969) ripped away from the mat of sticky silk which remained stuck to the object (fig. 4 (*c*)), and as the object drew farther away, the baseline moved very little but the mat along the baseline ' unfolded ' and the line attached to the object lengthened.

Discussion

Araneidae

Some details of the mechanics of the conversion of a junction to the pulley form are still not clear, but two general statements can be made. First, the material cementing the spiral to the radius apparently sticks more tightly to

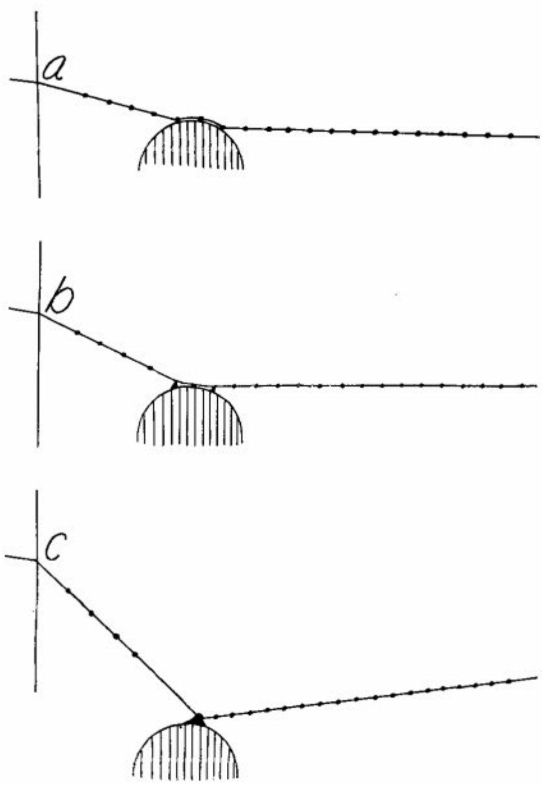

FIG. 3. Movement resulting when an object stuck to araneid sticky spiral is pulled. Not to scale.

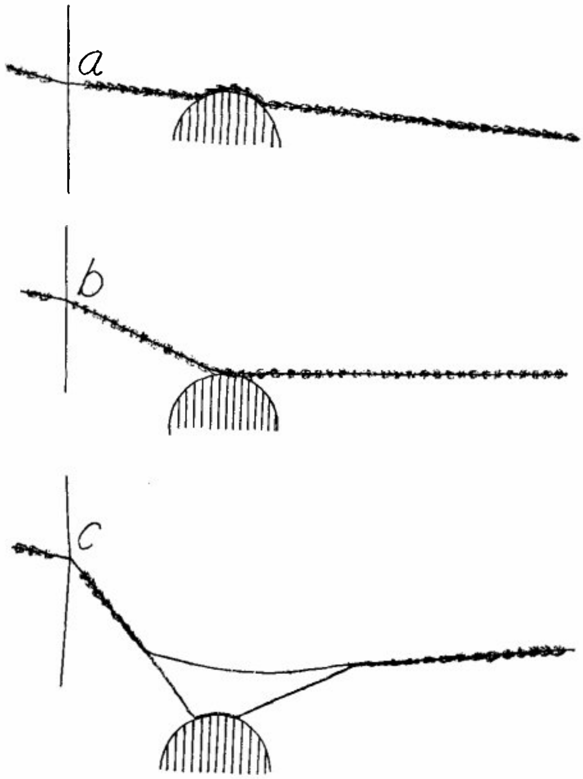

FIG. 4. The results of pulling an object stuck to *Uloborus* sticky spiral. Not to scale.

the radius than to the spiral: when the sticky spiral is pulled on one side of the junction, it is always the sticky spiral rather than the radius which eventually slides through the attachment. The attachment to the radius can only be broken by carefully stressing both sides of the junction at once.

Secondly, the strength of the bond of the cementing substance to the threads at the junction (presumably a function of the amount of cementing material) must be within certain limits. In the case of a stress perpendicular to the plane of the web, the sticky spiral will break free of the radius if the cement's bond to the radius is too weak; if it is too strong, the sticky spiral will rupture before the cement's bond to the sticky spiral breaks (i.e. before the junction converts to the pulley form). The conversion of a 'non-zero' junction (fig. 2) may represent a delicate adjustment of bond strengths: when the junction is first stressed perpendicular to the web plane, the bond to the radius is relatively weak, and the sticky spiral begins to rip away; but then, presumably because the cementing substance accumulates at one point (y in fig. 2 (c) and 2 (d)), the attachment to the radius apparently gets stronger, the spiral ceases to rip away, and eventually the bond between the cementing material and the sticky spiral breaks, converting the junction to the pulley form.

A consideration of what happens when a flexible line stops a moving object shows that the sliding attachments described above probably have considerable functional significance in orb webs. When a moving object strikes a flexible line, its momentum (the product of its mass times its velocity) is dissipated (the object slows down) as it extends the line. If the object is too heavy or is moving too fast, the line elongates to a certain point (its breaking elongation), and breaks, and the object continues with a reduced velocity; the object's velocity is reduced to zero if its momentum is not great enough to over-extend the line. A line's breaking elongation is directly proportional to its length (see Langer, 1969), and all other things being equal, a longer line is thus able to stop larger, faster-moving objects.

The functional significance of pulley form sticky spiral-radius junctions is that sticky spirals are better able to stop prey: before a given segment of spiral is over-extended, it is lengthened by the addition of thread from adjacent segments, and its breaking elongation is thus increased. At the same time, the spiral is not detached from the radii, and the prey is thus kept in the vicinity of the web where it can become entangled in other threads and captured.

It is possible that a puzzling detail in the web building behaviour of many araneids may also be designed to increase the breaking elongation of sticky spiral segments. Just before they attach the sticky spiral to each radius, many species of araneids appear to draw additional spiral silk from their spinnerets with a hind leg (Savory, 1952; personal observations). The function of this behaviour has been thought to be to cause the glue on the sticky spiral to ball up into droplets (e.g. Savory, 1952), but it seems more likely that it serves to elongate the segment of sticky spiral and thus to increase its ability to stop prey. An appreciable pulling force may be necessary to draw the sticky spiral from the spider's spinnerets, and even with the extra pull just before attachment, the sticky spiral of *Araneus diadematus* is normally 5–600% elongated in the intact web (DeWilde, 1943).

This interpretation of the spiders' behaviour is reinforced by the observation that the balls actually form on a given segment of sticky spiral in *Metazygia* sp. and *E. edax* webs many seconds after it has been flexed by the spider's hind leg and attached to the radius. The aggregation into balls is probably a result of the physical properties of the sticky fluid itself.

It should be noted that although sliding attachments increase the spiral's ability to slow and stop moving objects, they do not strengthen the web in the sense that they allow it to support heavier objects hanging in it. The breaking tenacity, as this property is called (Langer, 1969), is a function of a thread's diameter but not of its length. Pulley attachments should thus be taken primarily as adaptations to arrest prey as it moves into and through the web (increasing what Lubin (in the press), calls ' trapping efficiency '), and not as adaptations to enmesh and hold prey which has already been stopped by the web (what Lubin terms ' restraining efficiency ').

Although the mechanical details are different, the way in which an object slides along toward the midpoint of a segment of sticky spiral before breaking away can also be seen to aid in prey capture. In this case the glue which holds the object to the spiral baseline moves along the baseline because less energy is required to flow along the line and extend the longer, relatively slack part of the segment than to further extend the already tight shorter part. As the object moves along the spiral, the shortest arm of the segment is effectively lengthened, and its breaking elongation is thus increased. In addition, a globule of glue accumulates at the point where the object touches the line, and the connection with the object may thus be strengthened. This response would aid both in arresting flying prey and in entangling and holding prey already stopped by the web.

Uloboridae

On comparing the responses of the *Uloborus* web to those of the araneids' webs, one sees that *Uloborus* solves the same mechanical problems involved in stopping prey (conversion of short segments into functionally long lines, and maximization of extensibility of sticky threads), but using different techniques. Their sticky spiral-radius junctions are essentially unbreakable, but provision for functional pulley attachments is made in the central part of the web (where the radii are closer together and the spiral segments would otherwise be very short) by not attaching to each radius, thus leaving weaker junctions through which the sticky spiral can move. This may be the function of the previously unexplained failure to attach the sticky spiral to all radii, a characteristic which is unknown in araneid webs.

In addition the very nature of the loose, wooly mat forming the sticky part of the spiral allows it to pull away from the spiral baseline and elongate greatly before breaking, despite the fact that the sticky spiral components are made of relatively inextensible silk. The sticky mat, which is in effect folded up on the baseline, (probably as a result of the combing action of the spider's calamistrum see Freidrich & Langer, 1969), is 'unreeled' in conditions of high stress, detaching from the inelastic baselines before the latter break, and elongating greatly. When the stress is at a small angle relative to the sticky spiral thread (fig. 4), the unreeling occurs preferentially on the more highly stressed side, thus maximizing the stress the system can take before threads begin to break.

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