Radius orientation in the cross spider *Araneus diadematus*

FRITZ VOLLRATH[1,2,3], THOMAS NØRGAARD[3,4] & MICHAEL KRIEGER[1,2,5]

[1]*Department of Zoology, South Parks Rd, Oxford OX1 3PS, UK (fritz.vollrath@zoology.oxford.ac.uk)*

[2]*Zoologisches Institut, Rheinsprung 11, CH-4051 Basel, Switzerland*

[3]*Department of Zoology, Universitetsparken B135, DK-8000 Århus C, Denmark*

[4]*Department of Zoology, Winterthurerstrasse 190, CH-8057 Zürich, Switzerland*

[5]*Laboratoire de Micro-informatique, Swiss Federal Institute of Technology, CH-1015 Lausanne, Switzerland*

Abstract
We studied radius building in the orb-weaving spider *Araneus diadematus*. Distorting webs during construction did not affect radius placement indicating that tensions were not a major factor in orientation. However, locally and specifically displacing part of the spider's walking thread did affect radius placement and led the spider to shift its radius attachment point predictably, and thus the hub angle. We conclude that path integration could be a mechanism by which the spider determines a radius attachment point on the web frame.

Key words: Orb web, orientation, path integration, web construction, web tension

INTRODUCTION

Orb webs like that of the garden cross spider *Araneus diadematus* are examples of animal design that can be studied in great detail, both for ontogeny (building behaviour) and final morphology (web architecture). The construction of the frame (the 'rim' in analogy with a wheel) and radius threads (the 'spokes') are crucial parts of the building behaviour since here the animal determines the working platform on which to fashion the rest of the web (Peters 1937a, 1939; Tilquin 1942; Eberhard 1990; Vollrath 1992; Zschokke 1996). This stage can be divided into two principal phases: (1) construction of the frame threads, guy lines and primary radii, and (2) filling in the remaining radii following a characteristic pattern (Peters 1937a, 1937b; König 1951; Mayer 1953; Reed 1969a; Eberhard 1982; Zschokke & Vollrath 1995a). Web-building proper starts from a star of threads (Mayer's 'Fadenstern' 1953) or proto-web (Eberhard 1972; Zschokke 1996) consisting of a proto-hub with 3-7 radiating threads (Petrusewiczowa 1938; Mayer 1953). These proto-radii will become the original guy threads of the future web and define it's plane (Zschokke & Vollrath 2000). Only when the spider has completed this proto-web will it commence constructing the frame together with the primary radii (Zschokke 1999). This is followed by filling in the orb-space with the remaining radii which are often placed in opposing directions, although in this pattern there is much irregularity on top of species-specific traits (McCook 1889; Peters 1937b; Petrusewiczowa 1938; Mayer 1953; Reed 1969b; Zschokke & Vollrath 1995b; Eberhard 1972, 1981; Zschokke 1996, 1999, 2000).

When constructing a secondary radius, *Araneus diadematus* clambers along existing radius

and frame threads (Fig. 1 A, B). In the early stages, existing radii can be cut and replaced; and in the process the radius wheel (such as it is) can be greatly distorted and the hub be moved several times (Mayer 1953; Zschokke 1996; Zschokke & Vollrath 2000). In the later phases, radii are only added, never removed, and there is no visible distortion. However, the possibility remains that underneath the visible radius wheel there lies — invisible to us but highly tangible to the spider — a wheel of tensions that is altered by the spider adding radii. Radii under unusual tension are replaced or re-strung (Dahl 1885; Nielsen 1932) and cut radii replaced with tensions taken into account (Wiehle 1927; Le Guelte 1969). Wiehle (1927) and Le Guelte (1969) interpret the replacement of a cut radius as evidence that the underlying guiding principle of radius construction is tension. Eberhard noted that in certain orb webs tensions are equilibrated (Eberhard 1972, 1981) but he also demonstrated that they are unlikely to be used as guide in orientation (Eberhard 1988). We have confirmed this in our experiments with *Araneus diadematus*.

Tensions would provide local landmarks for orientation during web construction. Hans Peters (1937b) took a very different view and hypothesised that the spider might use some form of spatial map. To test this idea Peters (1937b) displaced a radius thread with a match stick in a way that enlarged the gap between two adjacent radii. When the spider, after circling the hub, arrived at this new 'oversized' opening, it built a new radius thread to fill this gap, resulting again in a radius interval typical of this web segment. Peters (1937b) only did a few pilot experiments and interpreted his results as evidence that the spider may orient not by tension but by path integration, i.e. by constantly recalculating the vector pointing home. There is strong evidence that spiders use medium range orientation by path integration, e.g. funnel spiders hunting in their webs (for reviews see Görner & Glaas 1985; Mittelstaedt 1985), jumping spiders hunting in a bush (Hill 1979; Tarsitano & Jackson 1994), egg-sac

searching in wolf spiders (Görner & Zeppenfeld 1980), return to lost prey in ctenid spiders (Seyfarth et al. 1980) and orb spiders during prey capture (Peters 1932). There is additional evidence that orb spiders use it in the short range (millimeters) during spiral construction (Peters 1937b; Eberhard 1988). Our study investigated the possibility that such a mechanism might also be used by orb weavers in the medium range (10-15 cm) during radius placement.

MATERIAL AND METHODS

We used juvenile (ca. 20 mg) *Araneus diadematus* garden cross spiders acclimatised to our laboratory conditions (45-55% rH, 24 ± 2 °C); and we used the same set of individuals for repeated measures on subsequent webs. The spiders were kept in open ended PVC frames (30x30x5 cm); they were watered daily and fed a fruit fly after web construction. The web-building behaviour was recorded on videotape from its early beginning and analysed frame by frame (25 fps). Webs were also photographed and digitised using our standard lab procedures (Vollrath et al. 1997). We conducted three experiments using either 3 or 5 spiders for series of repeated measurements:

(i) In the first experiment, on the effect of local tensions, we changed the local structure of tension by displacing a single vertical radius in the lower part of the web sideways by 1 cm. For the displacement we used a fine metal pin (1 mm diameter and 15 cm long) attached to a micro manipulator.

(ii) In the second experiment (on the effect of global tensions) we used standard frames hinged in the corners that could be sheared by 30° which distorts the entire web anchored to the sides of the frame to such an extend that untensed radii completely relaxed and sagged.

(iii) The third experiment (on the issue of detour integration) built on an analysis of natural detours which the spider did in the corners of the web. In the actual experiment we shifted the spider's out-radius using a fine metal rod, just before the animal turned from this radius
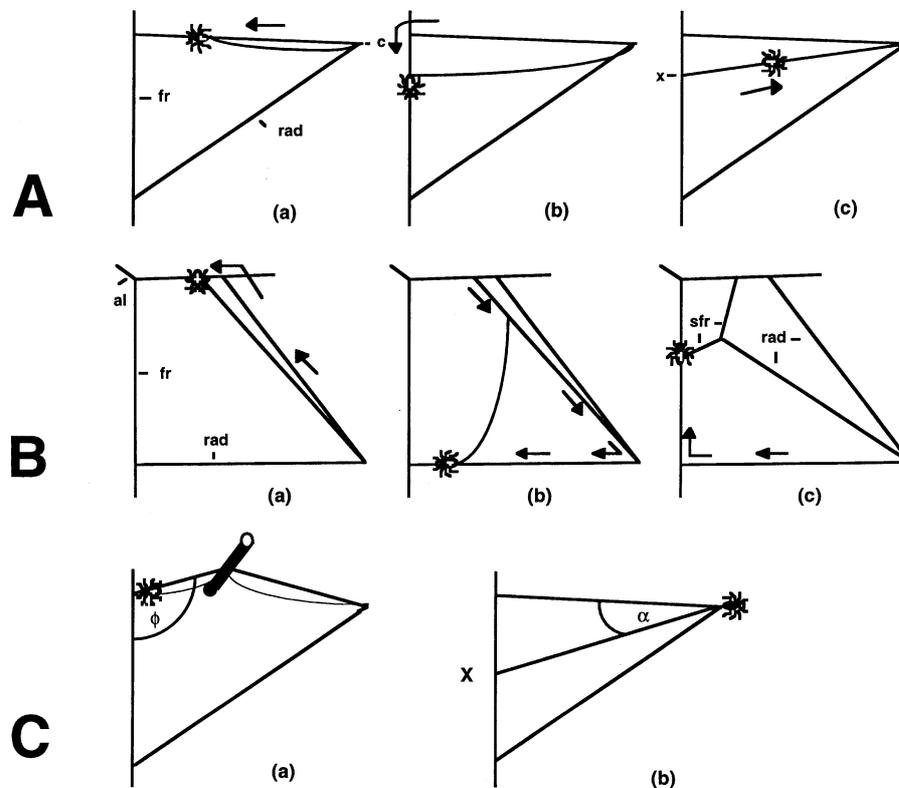
Fig. 1 Attachment of a radius thread to a frame thread in the orb of *Araneus*. **A**. Radius construction without detour. **(a)** The spider walks on the higher radius thread to the periphery. **(b)** It attaches the trailing line to the frame. **(c)** The spider returns to the centre on this line. **B**. Radius construction with detour. **(a)** The spider walks on the higher radius thread to the periphery and attaches the thread. **(b)** On the way back to the centre, the spider connects a second thread to the new radius **(c)** The spider walks now on the lower radius again to the frame. There, it first tightens and then attaches the trailing line (al: anchor line, c: centre, fr: frame, rad: radius, sfr: secondary frame, x: attachment point of new radius). **C**. Radius construction during experimental manipulation. The spider walks along the existing out-radius dragging along the new radius thread (stippled). **(a)** The out-radius is shifted carefully a few millimeters upwards behind the spider with a small metal rod altering angle ϕ. **(b)** The spider attaches the new radius at point X, resulting in the angle α at the hub.

onto the frame thread. We shifted it only a few millimeters (to minimise affecting tensions) and always upwards (Fig. 1C). Since the spider always moves downwards on the frame thread, this served to increase the spider's detour angle (ϕ in Fig. 4). On the whole this manipulation did not seem to irritate the spiders. However, since the spider moves fast, one had to react quickly which introduced a variable degree of error. This crucial experiment was repeated twice. In our first set of trials (n = 21) photos where taken and analysed, and the expected hub angle was calculated from the neighbouring angles; our analysis of radius geometry showed that this was possible. In our second trials (n = 70) the behaviour was filmed on video (25 f.p.s.) and analysed frame by frame, and all angles measured on the screen (mag. 2 times) using a customised analysis program. In this set of trials the last radius put into place by the spider was cut and the experiment performed when the spider replaced it. The angle

pairs compared in this case were (i) the experimental hub angle (which was the result of the manipulation) and (ii) an angle predicted from a possible algorithm that models path integration (Fig. 2).

Unless otherwise noted, all comparisons were made with 1-factor ANOVAs. If the degree of freedom was greater than one (df > 1), then a multiple comparison procedure (SNK, α = 0.05) was additionally used. The data on experimental radius displacement (first set) were analysed by first noting the sign of the angle (smaller, larger, indifferent to the calculated normal angle, i.e. the local set angle); thus the detour to the set value was calculated for each web using the average angle for that sector. We then performed sign tests both for all data pooled (with and without the confidence limits given by the standard deviation) and for the measurements repeated during one web-construction process averaged. The data on experimental radius displacement (second set), the control, and experimental angle pairs were analysed using a t-test after normality had been established by probit analysis.

RESULTS

To establish baseline data on the radii, we measured and analysed radius geometry and examined the sequence in which radii were laid down. To study the role of tensions we determined experimentally how accurately the spider could replace a radius that had been removed, both in control webs and in webs with distorted tensions. To examine the possibility of path integration we compared angular regularity between radii that were built with, and without, the spider walking a natural as well as an experimental detour.

Detailed description of radius construction

The spider begins adding radii to the initial radial cross by circling the web's centre, holding on to the hub with the legs on the inward-facing side of its body and measuring the angle between two neighbouring radii with its first and second leg on the outward-facing body

Fig. 2. Sides and angles used in the calculation of the predicted angle at the hub. In the equations small letters x, y and z refer to angles and capital letters X, Y, Z, T and A refer to sides (line segments) in the web. The arrow illustrates the point behind the spider where the out-radius and the new radius thread was lifted during the experiments. The algorithm used to calculate the predicted hub angle: (1) $x_{predicted} = x + (\arcsin T * \sin (180 - z) / A)$ where (2) $T = (\sin x / \sin (180 - y2 - x) * Z) - X$ and (3) $A = (T2 + Y2 - 2TY * \cos(180 - z))^{1/2}$.

side. If this radius angle exceeds the spider's set value it clambers out along a radius towards the frame trailed by its omnipresent drag line, clambering always on the upper (with respect to gravity) of the two radii (Fig. 1). It walks along the frame and, at one point X, attaches a thread to become the new radius. It reels in its drag line until this is taut, and returns straight to the hub on this line, thus drawing the new radius from the point X of attachment on the frame to the centre, where it is attached to the thread circling the hub. The point X on the frame thread determines the angle at the hub between the new radius and the out-going radius. Thus point X is reached by a detour from the hub along a neighbouring radius to the frame and along the frame to this attachment point. The experiment manipulated the spacial relationship of the radii and frame threads and thus affected the various outer angles between the radii and frame threads as well as the inner angles between the radii at the hub (Fig. 2).

Radius geometry

We found that individual spiders (N = 5) building webs under our controlled conditions made webs (n = 96) with a fairly predictable radius geometry. Radius number was 32.1 ± 0.5 with significant differences (F = 13.66, P < 0.0001, df 4/91) between spiders. Inter-radius angles (the angles between adjacent radii) varied within each web according to their position: the north (above the hub) had significantly larger angles (= fewer radii) than the south (below the hub), east and west (either side of the hub) lay between. Again there were significant individual differences (2-factor ANOVA, F = 187.28, orientation P < 0.0001, spiders P < 0.0001, interaction P = 0.09). We could normalise for the individual differences by expressing the number of radii per sector as percent of all radii in a web. The up/down asymmetry and left/right symmetry of the web's radius numbers and angles was repeated in the length of the radii in the different sectors: longest in the south and shortest in the north. The difference between the sectors was significant, and there were significant differences between spiders (2-factor ANOVA, F = 63.80, orientation P < 0.001, spiders P < 0.0001, interaction P = 0.40).

Radius construction behaviour

In three spiders we filmed and analysed radius construction (n = 12, 10, 12 webs). Here we observed between 5 and 8 primary radii, with spider specific means of 6 ± 0.74, 6.8 ± 0.68 and 5.9 ± 0.58 . There were no significant differences between individual spiders (F = 1.36, df = 2, P = 0.27). However, there was a significant difference (F = 20.14, P < 0.0001) in the numbers of primary radii between north and south sectors (north = 2.2 ± 0.64, south = 1.71 ± 0.8) but none between the east and west sectors (east = 1.09 ± 0.67, west = 1.15 ± 0.61). We analysed the construction sequence of the remaining radii, using a 'coefficient of radius construction' which is composed of the rank of each radius in the sequence of construction (the radius index) divided by the total number of all radii (to normalise for radius numbers between webs). We
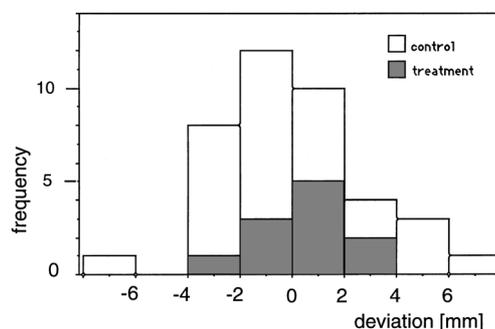
Fig. 3. Displacement of radial attachment points under normal (control) conditions and under conditions of slight distortion.

observed significant differences (F = 59.32, P < 0.0001) in the coefficients between different sectors: radii in the lower sector (south) were built later than those in the other sectors (north, east and west). The coefficients of radius construction were (n = 30) : north = 0.41 (n = 113), south = 0.71 (n = 226), east = 0.41 (n = 185) and west = 0.46 (n = 196).

Local tension experiment

If the spiders were to use tensions in order to determine the placement of a radius, then distorting the tensions in a web should lead to a different placement of a focal radius when compared with normal conditions. We allowed a spider to build its last radius before it would have proceeded to spiral construction. We then continued to cut this radius until the spider stopped replacing it and began auxiliary spiral construction. As long as the spider did replace this radius (N = 7 webs, n = 38 cuts), it did so accurately, attaching it within a range of a few mm (1.9 ± 1.5 mm), in a normal distribution around the original (control) attachment point (Fig. 3).

When we distorted the web slightly with a tripod-mounted micro manipulator pulling the frame sideways, this radius was still always replaced in the typical fashion. Attachment points in such distorted webs were not placed differently (F = 0.30, P = 0.59) from the control attachments that had been made previously while the web was undisturbed.

Global tension experiment

In the 15 cases where we distorted the web grossly by shearing its holding frame by 30°, the spider either kept on building (9 times) or it stopped (6 times) for an average of 5 minutes (4'52" ± 4'65"). This kind of extreme distortion had some radii stretched by 20% and others relaxed so much that they sagged. In the nine cases where the spider continued without interruption it either did nothing about the situation (6 times) or else it connected two adjacent threads (3 times). On the six occasions where it interrupted its behaviour, the spider always readjusted the tensions by laying what appeared to be a single reinforcement radius in the area of highest distortion.

Detour analysis

We assumed that the spider attempts to place the attachment point on the frame thread in such a way that each radius receives its particular hub angle specific to each sector. If the spider uses path integration to determine the placement of a radius, then we would expect that the regularity of the radius angle at the centre would be negatively affected by the length of the detour. *Araneus diadematus* builds two types of radii: those that involve only a minor detour along the outgoing radius and the frame, and those where a secondary piece of frame is laid down (Fig. 1). We analysed 21 webs of two spiders (n = 10, 11) for the different web parameters (Fig. 2). The difference between the two spiders was significant, therefore they were treated separately in our statistics. The variances of the angle in both spiders was always significantly larger (F = 1.73 resp. F = 1.57, P < 0.05) when the animals had walked a detour (n = 34 resp. n = 45) than when they had not done so (n = 207 resp. n = 184).

Displacement experiments

If the spider uses path integration for radius placement then changing one parameter of the path in a specific way would affect the point of attachment X in a predictable manner (Fig. 4). We increased the angle ϕ between the outgoing radius and the frame from $\phi1$ to $\phi2$ by slightly lifting the out-going radius upward just before the spider walked over this junction A. We observed that this resulted in the spider shortening its path section A-X on the frame thread which led to a decreased hub angle α.

For the first set of trials we measured this angle and compared it to the average set-angle for this particular web and web section. These experimental angles were on average smaller, sometimes marginally, sometimes considerably. Since we had a variable number of repeated measures for each spider and web, and since the experimental setup had some uncontrollable variables (exact repeatability of displacement, spider's detection of our interference), we decided to use a conservative measure of impact. Therefore, for each spider we only used one trial (i.e. the first) of a sequence. We tested the distribution of differences between the observed angle α and the expected angle α for normality using the Kolmogorov-Smirnov-Lilliefors test (Legendre & Vaudor 1991) with the result that the null-hypothesis of normality could not be rejected. A non-directional 1-sample t-test was then performed on the distribution of differences with P = 0.031, indicating (at the 5% level) that our manipulation might have had an effect. We likewise examined the data for interactions between the observed angles α (at the hub) and ϕ (at the frame) and again found a weak positive correlation.

For the second set of trials we modified our analysis because we filmed the experiment and behaviour. This allowed us to do pairwise comparisons of a calculated angle (computed from the control angle and the size of the out-radius displacement) and the actual experimental angle (built in the experiment); the data were obtained from digitised measurements of single-frame video pictures. From the 70 superficially good trials (where the spider only stopped briefly) we took the 46 best trials (where the animal continued without a stop and where the image was so good that we could clearly distinguish all threads). For this

Fig. 4. Path integration experiment. The new radius thread being actually or hypothetically drawn is shown as a fine grey line. **(a)** From the hub H the spider exits via the out-radius and when it encounters the turns the frame thread at A, it moves towards the intersection of an already existing radius at B. Before reaching this point it places a thread at point X on the frame which gives a typical angle α at the hub. In our experiments, when the spider was just before A, the out-radius behind it was displaced a given amount (using a small metal rod) at S. Such radius displacement resulted in changes in the radius-frame angle ϕ from $\phi1$ to $\phi2$ which in turn affected the position of X moving it from X1 to X2 with resulting changes of the hub angle α from $\alpha1$ to $\alpha2$. The experiment has different predictive outcomes depending on whether the original angle ϕ at A is smaller than 90° **(b)** or whether it is larger than 90° **(c)**. The dotted line shows the spider's dragline as it links the points of experimental displacement S and frame-fixation X2.

data set, our results showed that the estimated angle deviated from the calculated angle by an average of +1.46 degrees (variance estimate: 11.45). Thus, with a probability of P < 0.0017 (t = 3.45), we have to reject the null-hypothesis that there was no difference between the experimental and the calculated angle. We then reanalysed our data after taking out all values where the deviation was greater than 5 degrees. The reasoning behind this adjustment was the thought that, to make such large 'mistakes', these spiders perhaps were disturbed imperceptibly by our measurements (we could only detect the stopping of building). In this potentially more conservative dataset of 41 trials the average angle was +0.68 degrees larger than the calculated angle (variance estimate: 3.78) which was significant at P < 0.0303 (t = 2.246).

DISCUSSION

Orb spider web-building behaviour is fine-tuned orientation coupled to manipulation of threads. During web-construction orb weavers might conceivably use path integration (or its leg-positioning equivalent) over the short distances spanned during capture spiral construction (Eberhard 1988). During radial construction the distances over which the spider would
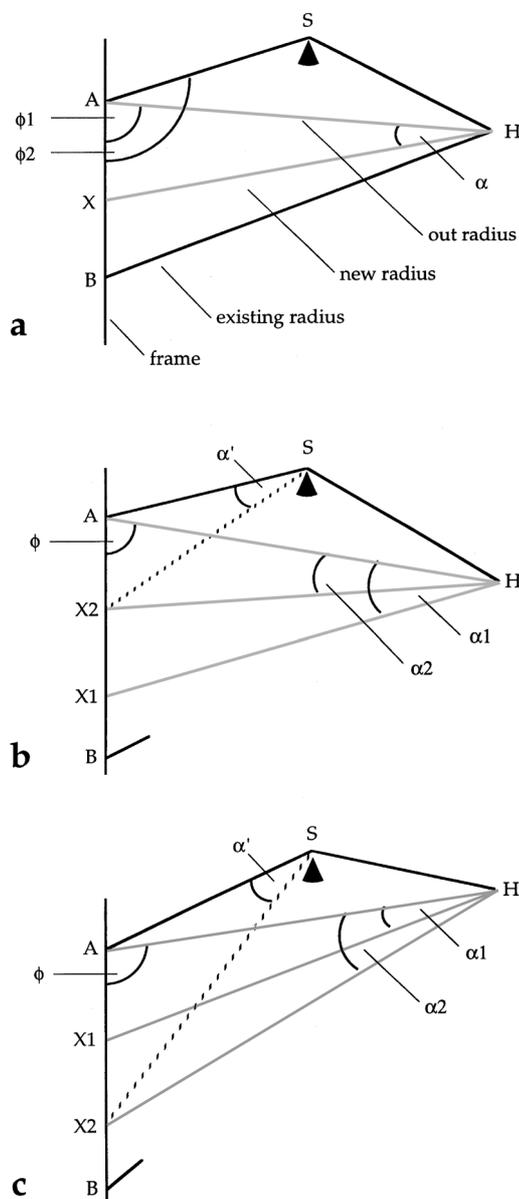
have to integrate are considerably larger indeed, they are over 10 times the spider's length. If here path integration were used then this could radically alter our interpretation of all other phases of site-exploration and orb-construction. This would have serious repercussions for the assumptions presently made in interpretations of orb web-construction (Eber-

hard 1981, 1982, 1988; Coddington 1986; Vollrath 1992; Hormiga et al. 1995), and in computer simulations where, so far, memory — but not path integration — has to be invoked to model realistic web-geometries (Eberhard 1969; Gotts & Vollrath 1991, 1992; Krink & Vollrath 1997, 1999, 2000).

Our detour analysis, tension experiments, and displacement experiments were designed to determine the likelihood that an orb spider might use such a mechanism as opposed to tensions during radius construction. We show that web parameters like radius positioning can be normalised and that radius angles can be predicted for each sector; this allowed us to interpret our perturbation experiments.

We conclude that tensions are not used as major landmarks during web construction. The first experiment showed that slightly altering the tension had no effect. Even when the web was grossly distorted and a reaction could be observed (9 out of 15 cases), in each web only one single radius thread was adjusted (or in the case of the connection of two threads, two). The other radii were left untouched whether they were highly tensed or slack to the degree of flapping. The spider simply continued laying new radii. If tensions were a major guiding principle, we would expect a more notable adjustment after our perturbance of the distribution of tensions in the whole web. Note that in windy conditions in nature webs do flap about without apparently perturbing the spider. Spider silk is a viscoelastic material (Denny 1980) and the initial tension in a thread will decrease rapidly after installation in the web. This would make it difficult for the spider to use thread tensions as a reliable aid during web construction. However, for web-engineering and prey capture, tensions are of course important (Craig 1987; Wirth & Barth 1992; Linn et al. 1995). The orb web spider *Zilla diodia*, for example, seems to adjust radius morphology to balance tensions by doubling the outer part of many, if not all, radii (Zschokke 2000).

Our data support the use of path integration during web building although it falls short of proving it. The aim of these experiments was to alter spatial parameters of the path walked by *A. diadematus* during the placement of new radius threads. This was done by lifting the existing radius thread (along with the silk dragline) at a point just behind the building spider and before it turned from this radius thread to the frame thread. However, manipulation of the existing radius in this manner would increase the spider's silk payout as well as its detour angle. And the spider might use silk payout as a measure of distance walked.

The outcome of the first set of trials was in favour of path integration. According to the initial predictions, the angle α at the hub should be smaller than expected if angle ϕ were equal to, or smaller than, 90° and larger than expected if angle ϕ were greater than 90° (Fig. 4 b,c). However, we must consider that the spider's dragline was lifted together with the existing radius thread - which should have resulted in the spider shortening the path section at the frame and hence reducing angle α accordingly. If this effect was fairly consistent, we would still expect a correlation (if only a weak one); this we see.

In the second set of trials we actually calculated the expected angle assuming path-integration. The outcome was a significant shift of angular dimensions in the right direction. If (e.g., by measuring its payout of silk) the spider used the distance it actually travelled on the lifted radius to determine the cut angle, then this could explain a certain mismatch between calculated and observed angles.

On a note of caution, we want to point out that our experimental interference will certainly have been sensed by the spider, and we do not know whether it has affected its behaviour. Nevertheless, we deduce from the results of all our experiments and from comparison with orientation behaviour in other spiders where path integration has been shown to exist (Görner & Glaas 1985; Mittelstaedt 1985) that, as Hans Peters had thought (Peters 1937b), the use of path integration during radius construction in orb weavers is now a likely possibility.

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