

Lyriform organs on regenerated spider legs

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Summary

This biometrical study of a lyriform sensory organ showed that those on regenerated legs had different dimensions from those on normal legs. Since form and function is correlated in these sensors, and since they are implicated in the co-ordination of the spider's legs, I argue for a case of sensory adaptation. My hypothesis of "clever leg vs. clever brain" states that, when legs are regenerated, evolutionary modifications in the morphology of these peripheral sensors relieve the need for central adaptations in the spider's web-building algorithm.

Introduction

Most spiders easily autotomise legs, which they re-grow in a succession of moults. In some species the regenerated legs are fully functional shortly after moulting (Vollrath, 1990). A striking example is *Araneus diadematus* Clerck, the garden cross spider, which can build a typically regular orb web only 24 h after regenerating up to four legs, even if they are all on one side of the body (Vollrath, 1987). This is remarkable as the regenerated legs are at first only half the length of their normal counterparts, yet co-ordinate perfectly with one another in both prey capture and web construction (Vollrath, 1987). The regenerated legs are used for measuring during web construction, when they have to follow a rigid pattern of synchronised movements that involves sensory feedback of leg positioning (Vollrath, 1992). Such sensory feedback (Hergenröder & Barth, 1983) may come from proprioceptors at the leg joints or in muscles, such as the lyriform organs (Barth, 1985a) or stretch-receptors (Seyfarth, 1978).

Lyriform organs are skeletal slits, often grouped into sensory fields that resemble a harp with strings of variable length (Vogel, 1923). There is evidence for the implication of lyriform organs in positional control and idiothetic orientation (Seyfarth, 1985). Since they are mechanoreceptors recording the strain in the cuticle (Pringle, 1955) their functional response (i.e. the signal generated) is thought to be determined by each organ's size, shape and location on the leg (Barth, 1985b; Barth & Pickelmann, 1975). Because of the hypothetical strict causal relationship between morphology and signal, I was puzzled to read in the literature (Vogel, 1923) that regenerated spider legs are thought to carry visibly deformed lyriform organs. In the light of my observations that such legs can be used to build fine webs, this would suggest that lyriform organs are either (i) not as important as often assumed or (ii) not so deformed as to be functionally impaired.

Material and methods

To examine Vogel's (1923) statement, I measured the external morphology of particular lyriform organs on normal and regenerated legs of *A. diadematus*. Leg specimens were taken from the exuviae of normal, immature spiders and of those that had regenerated a previously autotomised leg. Leg autotomy was induced by pinching a leg with forceps. Such legs regenerated underneath the wound crust before they were expressed at the next moult. Leg exuviae were carefully broken into sections and mounted in Canada balsam on microscope slides. It was ensured that the sections were thoroughly filled with the balsam. The coverslip was spaced on glass rods to avoid deformation and allow proper orientation of the specimen. Before mounting, leg diameter was measured at the widest point of the patella on the flat-lying, slightly bent leg (at the pair of lyriform organs), and length was measured dorsally at the longest projection of both the patella alone and the patella+tibia (compare Fig. 1). These measurements correlate perfectly with all other measurements of leg dimensions (Vollrath, 1983).

The legs were measured under a light microscope at 115× magnification (before mounting), and selected lyriform organs were traced on paper (after mounting) at 440× magnification using a Zeiss drawing attachment. The number of slits was counted, and selected measurements of each organ were taken from the tracings with the help of a digitising tablet (Houston HiPad attached to an Apple IIe computer). One of two adjacent organs was examined more closely. Slits were counted and the triangular outlines of the organs were measured using the length of two sides, the kathetes. Some legs were examined under a scanning electron microscope. This method produced good photographic evidence, but for collecting empirical data the light microscopic approach proved superior. The statistical

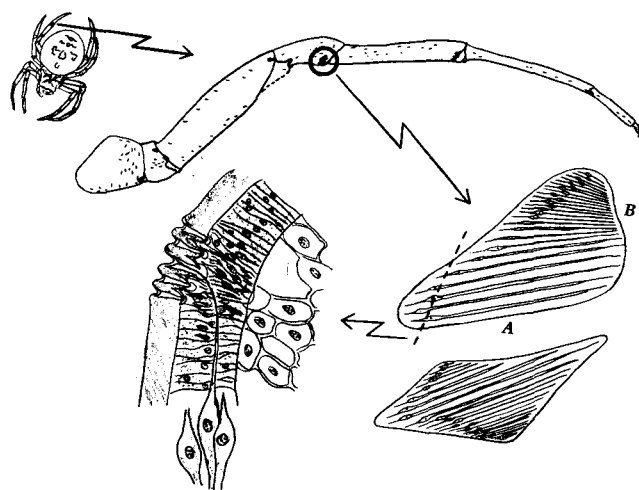


Fig. 1. Diagram of the spider, the two lyriform organs studied, their position on the spider's leg, and a cross-section of the triangular organ showing 4 slits (one innervated). The triangular organ was measured along its height (A) and width (B). Leg length was measured from joint to joint along the mid-dorsal surface either of the patella and tibia combined or of the patella alone, leg diameter was taken at the widest point of the patella at the lyriform organs.

analysis was done using an Analysis of Covariance (ANCOVA) with regenerated vs. normal legs as treatment and the various measured parameters as variants and covariants. It was not possible to obtain good measurements of all parameters on all specimens; thus, the sample size varied.

Results

I examined 51 normal and 26 regenerated legs taken from the exuviae of immature *A. diadematus* with a wide range of body sizes. Regenerated legs are on average about half the length of their normal counterparts (Vollrath, 1990). The present study showed (Fig. 2a) that they had significantly greater diameters compared with normal legs of equivalent length (ANCOVA interaction term $F=7.28$, $p<0.01$). Comparison of the colour and firmness of the cuticulae suggests that they were also thinner on regenerated legs (exuviae were much paler, and broke and buckled more easily).

A survey was conducted of 5 prominent lyriform organs on the patella, tibia and metatarsus. A more detailed analysis examined a cluster of 2 — here termed triangular and rhomboid (numbers 6 and 7 respectively of Barth & Libera (1970)) — situated on the patella close to its joint with the tibia (Fig. 1). On the 26 regenerated legs the rhomboid organ was badly deformed (with slits interconnecting) in 12 cases, while the triangular organ with one exception was always well formed ($n=23$). The difference in quality of regeneration was significant (sign test $p<0.001$). Since I was primarily interested in the possibility of measurable (and possibly adaptive) changes I concentrated my examination on the triangular organ.

The triangular organs on regenerated legs were significantly smaller in area than those of comparable normal legs when regressed against leg length (Fig. 2b) ($F=18.28$, $p<0.0001$). But they were of similar size when regressed against leg diameter (Fig. 2c) ($F=0.710$, $p=0.497$, n.s.). This suggests that the "triangle" formed by the regenerated organ was wider at its base (B) and not as high at its apex (A) as that of the normal organ (see Fig. 1). There was no significant difference in the relationship between the area and the number of slits (Fig. 2d) in the triangular lyriform organ on normal and regenerated legs ($F=0.147$, $p=0.894$, n.s.). There was, however, a difference in the shape of organs on normal and regenerated legs (Fig. 2e); the regenerated organ was significantly stouter ($F=7.795$, $p<0.01$), which confirms the interpretation of the previous correlations (organ area against leg length and diameter).

Discussion

My measurements showed that Vogel (1923) is partly right and partly wrong: regeneration in *A. diadematus* produced both malformed and well-formed lyriform organs. The novel observation of my study concerns the dimensions of the well-formed organs, which differ significantly from those on normal legs of the same size.

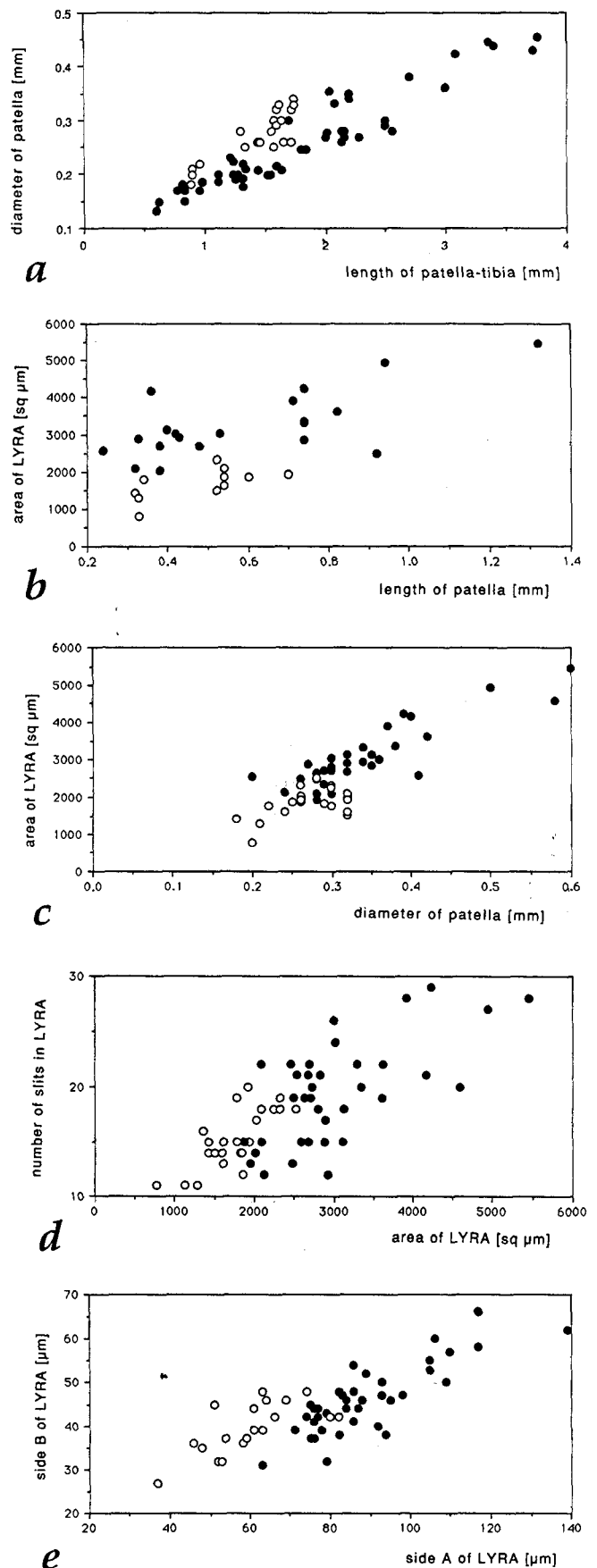


Fig. 2. (a) Patella+tibia length and patella diameter of normal and regenerated legs (normal legs=filled circles, regenerated legs=open circles); (b,c) Area of triangular organ on normal and regenerated legs in relation to patella length (b) and patella diameter (c); (d) Relationship between area of triangular organ and number of slits; (e) Shape of the organ; sides A and B indicated in Fig. 1.

It is this observation that demands an explanation, or at least a hypothesis.

Malformed organs are accounted for easily by assuming developmental problems during regeneration, especially as regenerated legs carry an impoverished set of sensory hairs (Vollrath, unpublished). The presence of well-formed but abnormally dimensioned organs is more difficult to understand. Is this the outcome of constraints during development or might there be a functional explanation? As an evolutionary biologist I believe it is the second and in the following shall argue my case. As yet the evidence for the proposed hypothesis is slim but I hope that neurophysiologists might be able to collect data which could test it.

Most spiders easily autotomise legs, which they regrow in a succession of moults. In some species the regenerated legs are fully functional shortly after their emergence. A striking example is *A. diadematus*, which can build a typically regular orb web only 24 h after regenerating up to four legs, even if they are all located on one side of the body (Vollrath, 1987). This is remarkable because the regenerated legs are at first only half the length of their normal counterparts, yet both co-ordinate perfectly with one another during prey capture and web construction. The regenerated legs are used for measuring during web construction, when they have to follow a rigid pattern of synchronised movements that involves sensory feedback of leg positioning (Vollrath, 1992).

Such sensory feedback may come from proprioceptors at or in the leg joints or muscles, such as muscle stretch-receptors or lyriform organs (Barth, 1985b; Seyfarth, 1978, 1985). There is evidence for the implication of lyriform organs in positional control and idiothetic orientation (Seyfarth, 1985). Since they are mechanoreceptors recording the strain in the cuticle, their functional response (i.e. the signal generated) is thought to be determined by each organ's size, shape and location on the leg (Barth, 1985b). My measurements showed that at least some lyriform organs on regenerated legs are well-formed and thus in a state to act as fully functional sensory organs. However, they are positioned and shaped differently from those on normal legs. Accordingly, their signals should also be different. It is tempting to speculate that this could pose a problem for the inherited behaviour pattern of web-building with its stringent requirements for leg co-ordination.

It is possible, indeed likely (see above), that the observed modifications of lyriform morphology are correlated to modifications in signals. Is it possible that evolution has tinkered at a peripheral level to allow the production of modified signals? This hypothesis would make sense if peripheral preconditioning would relieve the need for modifications at the higher levels of the web-building algorithm. After all, these modifications are only temporary (instar dependent) as well as tightly linked to the anatomical structure (a leg and its length) that carries both the sensory organs and executes the central command.

Peripheral filtering of information would relieve central control (Wehner, 1987). In a "clever leg" scenario,

such as I propose, signals would be modified sensibly at their source and the CNS could ignore the real position of a regenerated leg. In a "clever brain" scenario, on the other hand, the central web-building program would receive true bearings of each leg and then would have to apply the right correction factors for both the efferent and afferent signals to and from each regenerated leg. Peripheral preparation of sensory data would reduce the number of necessary calculations in the decision algorithm which consequently could be simpler and also run faster. Simulations of spider web-building behaviour show that functional construction programs can consist of few rules (Eberhard, 1969; Gotts & Vollrath, 1991); incorporating allowances for varying leg lengths would complicate these programs. Accuracy matters during web-building, since any reduction in regularity negatively affects a web's capture rate (Rhisiart & Vollrath, 1994) and consequently reduces its builder's fitness. Not surprisingly, all orb spiders can build regular webs even when several legs are missing (Weissmann, 1987). Not all spiders regenerate lost legs. One group, the metids-tetragnathids, suppress the regeneration of lost legs; this is not an obvious cost-benefit function of life-history traits (Vollrath, 1990). Could it be that they suppress regeneration because their legs never evolved the ability to regenerate peripheral filters, or is it because their web-building algorithm lacks the ability to compensate for shorter legs?

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A new genus and species of linyphiid spider from south-west England (Araneae: Linyphiidae)

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Summary

Nothophantes horridus, n. gen., n. sp., is described from a limestone quarry in south-west England, and its taxonomic affinities and habitat are discussed.

Introduction

A single female of an unknown species of linyphiid spider was collected from a disused limestone quarry at Shapter's Field, Cattedown, Plymouth, Devon in 1989. A second specimen was collected from the rock face of the same quarry on 12 March 1991 and, on this occasion, was recognised as being clearly new to Britain. At first it was thought to be possibly a species of *Lepthyphantes* Menge (and was provisionally listed as "*Lepthyphantes* sp." in the BAS Members' Handbook checklist issued in March 1992). Several further visits to the site failed to produce any more specimens. In early 1994, it was learnt that development of the site was likely to proceed during the summer of 1994 and that much of the limestone quarry face was going to be removed and used for reclamation purposes. The developers agreed to support an invertebrate survey as part of a nature conservation mitigation programme on the site during March and April 1994. This led to the capture of four more females, but unfortunately no males.

More detailed examination of the specimens has shown that it is not possible to include the species in *Lepthyphantes* or in any other known genus, and it is

therefore described here in a new genus as *Nothophantes horridus*, n. gen., n. sp. All measurements are in mm.

Genus *Nothophantes*, new genus

Type species: Nothophantes horridus, new species.

Etymology: The generic name is derived from the Greek *nothos*, spurious, and *hyphantes*, a weaver; gender masculine.

Diagnosis: The female is diagnosed by the epigyne (Figs. 1–2), with its large transverse atrium and broad dorsal scape attached to the ventral plate, and by the numerous long spines on the legs and prominent bristles on the abdomen. The chaetotaxy is similar to that of some species of *Lepthyphantes* and *Troglohyphantes* Joseph, but the epigyne is very different. The male is unknown.

Description: The female has total length *c.* 2–3 mm. The carapace is unmodified, and the eyes moderately small, with posteriors *c.* 1.25–1.5 diam. apart. The abdomen may be uniform pale grey, or sometimes darker with pale yellow on lateral sides anteriorly. Legs moderately long, with tibia I l/d *c.* 7.5, and femora I and IV equal to or longer than carapace. Metatarsus IV almost as long as tibia IV. Femora I–II with 1 dorsal spine, femur I also with a prolateral spine. All tibiae with 2 dorsal spines and 1 prolateral and 1 retrolateral spine; tibia I, and occasionally tibia II, also with a ventral spine. All metatarsi with 1 dorsal spine. Spines very long; dorsal tibial spines 3–5 × diam. of tibia. Metatarsi I–III with a trichobothrium, Tm I *c.* 0.2. Palp with numerous strong spines, and tarsus with a claw. Epigyne (Figs. 1–2) with a large transverse atrium. The ventral plate does not extend far posteriorly, but attached to its dorsal surface there is a broad scape which curves first anteriorly and then posteriorly to lie just ventral to the dorsal plate. The posterior extension of the scape carries a large socket distally on its ventral surface. The copulatory ducts (Fig. 3) follow a wide loop from the lateral spermathecae through the ventral plate, before turning sharply dorsally and posteriorly to terminate on the ventral surface of the scape just anterior to the distal edge of the dorsal plate.

Included species: Only the type species.

Distribution: Known only from Plymouth, UK.