J. comp. Physiol. 103, 39—54 (1975)

Lyriform Slit Sense Organs

Modelling an Arthropod Mechanoreceptor

Friedrich G. Barth* and Peter Pickelmann

Zoologisches Institut der Universität München, München, Federal Republic of Germany

Received June 3, 1975

Summary. 1. In lyriform organs of arachnids several innervated cuticular slits are closely arranged in parallel. The mechanical consequences of this arrangement were studied in model experiments with regard to their importance for the organ's stimulus conducting properties (Fig. 1).

2. Groups of parallel slits were cut into plexiglass disks. On these static pressure loads were applied from varying directions. The resulting deformation of the slits was measured in terms of compression and dilatation, respectively. It was compared to that of a model with only one slit.

3. *Simple models* with three or five slits of equal length: A slit's deformation is drastically reduced by the presence of neighbouring slits closely arranged in parallel. Differences between various slit areas and the effect of load direction on deformation are reduced as well. The peripheral slits of a group take up much more load than the intermediate slits. In large groups they are deformed even more than a single, isolated slit. Different areas of the same peripheral slit vary markedly with regard to the effect of load direction (Figs. 2a and 5).

4. *More elaborate model* with seven slits copying a lyriform organ on the spider leg tibia: Again considerable differences are found in the degree of deformation. It is positively correlated with both slit length and peripheral position of the slit within the group. The majority of slits is most compressed in that area where the dendrite attaches in the original receptor. This is not always the mid portion of the slit, however (Figs. 2b, c, 6 and 7).

5. According to previous studies compression is the adequate deformation of the slit leading to nervous activity. It is most effectively achieved by loads perpendicular to its long axis. *Photoelastic experiments* with model tibiae show that pressure stresses roughly perpendicular to the long axes of the slits have indeed to be expected under natural stimulus conditions. They also provide a basis for understanding topographical features pertinent to the majority of the lyriform organs on the spider leg: their proximity to a joint, their location on the lateral surface of the leg, and their orientation roughly parallel to the long leg axis (Figs. 4 and 8).

6. The main physiological consequences deduced from these model studies for a close parallel arrangement of slits are: a) a considerable enlargement of the range of stimuli accessible for sensory analysis at a specific site and b) a marked stimulus intensity fractionation by different slits within the same group.

Introduction

Spider skeletons must be considered quite rigid structures where fully sklerotized. Only minimal deformation can be expected to occur under natural load. Nevertheless spiders are capable of measuring such minute deformations. They

---

* Supported by a grant of the Deutsche Forschungsgemeinschaft. Many thanks are due to Drs. H. Marwitz and E. Ficker of the Technische Universität München for generous help with the photoelastic experiments. Ing. K. Steinmaßl, Philips Company at München, kindly introduced us to strain gauge techniques. Mr. E. A. Seyfarth made valuable comments on the manuscript.

occur during locomotion, during substrate vibration and presumably at a number of other behaviorally significant occasions (Barth, 1972; Barth and Libera, 1970; Barth and Seyfarth, 1971; Liesenfeld, 1961; Pringle, 1955; Seyfarth and Barth, 1972; Walcott and van der Kloot, 1959). The sense organs serving in this capacity are the slit sensilla, peculiar to arachnids and analogous to the companiform sensilla of insects and crustaceans.

In previous studies their fine structure was found to be well intelligible in terms of functional design (Barth 1971, 1972a, b, 1973a).

From a morphological point of view the lyriform organs are the most spectacular type of slit sense organs. In contrast to both the isolated and grouped slits they are composed of up to about 30 slits lying closely side by side and forming a multitude of outline shapes due to differences in their respective lengths (Fig. 1) (Vogel, 1923; Barth and Libera, 1970). From the physiological point of view and with particular regard to the compound organ's stimulus conducting properties we were mainly intrigued by two sets of questions: 1. What are the functional consequences of the neat parallel arrangement of the slits? 2. What is the distinctive feature of the sites on the legs, where these multichannel mechanoreceptors are found, both in terms of stimulus patterns and the importance of their detailed sensory analysis?

The present paper deals with these questions. Our model experiments point to the functional significance of a number of mechanical properties specifically attributable to the type of slit arrangement found in lyriform organs. A photoelastic experiment was carried out with regard to the second set of questions. Its results provide an explanation for topographical features peculiar to the majority of lyriform organs on the spider leg. Some of the main results are considered relevant for an understanding of "compound" campaniform sensilla of insects like those on the halteres of dipteran flies.

Material and Methods

Deformation of Model Lyriform Organs. We used two types of models in order to learn about the deformation of slits lying side by side: a. simple ones with three or five slits of equal length cut into plexiglass disks as shown by Fig. 2a; b. a more elaborate model copying the lyriform organ HS 8 on the tibia of the spider *Cupiennius salei* Keys. (Fig. 1) with regard to the number of slits, the distribution of slit lengths, the troughlike shape of the exocuticular portion of the slits, and the length-to-width and depth ratios of the slits (Fig. 2b).

Arguments for the special suitability of plexiglass as model material were given previously (Barth, 1972a, b). In a recent paper on the microfiber reinforcement of spider cuticle (Barth, 1973b) the fine structural basis of the exocuticle's mechanical isotropy in its plane is given in detail.

The models were carefully loaded parallel to their surface and from varying directions as described earlier (Barth, 1972a). Shear movements of the slit were not considered since they are not the adequate stimulus (Barth, 1972b)[1].

In case of the simple models the deformation of the slits could readily be measured under a microscope with a calibrated ocular grid. The more elaborate model called for the application of strain gauge techniques, because even under heavy load deformation of some of the slits was extremely small. Fig. 2c shows the ring-shaped device inserted into the slits for that purpose. Two strain gauges were glued onto the opposite surfaces of its upper flattened part

---

[1] Dilatation of the slit is not effective either (Barth, 1972b). Its measurement was included in the experiments because it elucidates the compression effect and is easily accomplished.

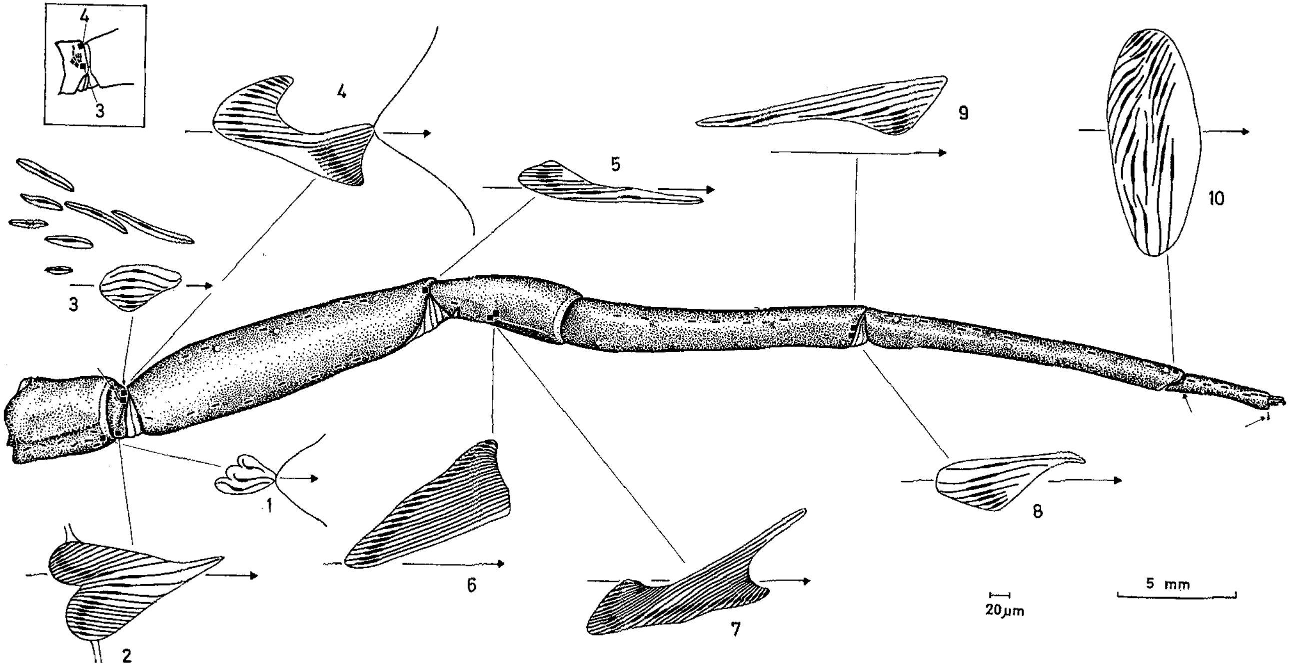

Fig. 1. Posterior view of the walking leg of a spider (*Cupiennius salei* Keys.). Besides the isolated slit sensilla (—) there is a multitude of lyriform or compound slit sense organs (■). The majority of them is found close to a joint, on the lateral surface of the leg, and oriented roughly parallel to the long leg axis. The detail drawings show that they vary considerably, however, in outline shape and patterns formed by the dendrite attachment sites (see widened part of slits) (from Barth and Libera, 1970)

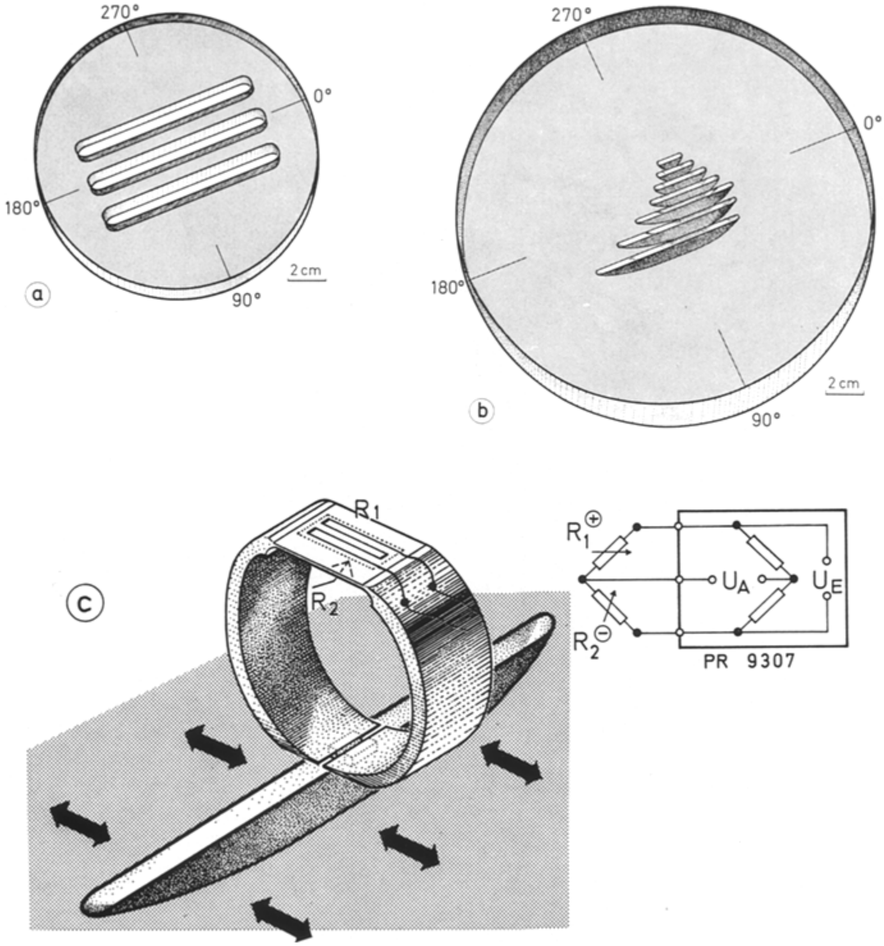

Fig. 2a—c. Models used for the study of deformation of lyriform organs under load. (a) simple. (b) more elaborate type. Angles as defined for load directions. (c) method used to measure deformation with two active strain gauges and a carrier frequency bridge (PR 9307). See text

which was bent during slit deformation. Thus the sensitivity of the measuring system was greatly enhanced by adding the effects on the two strain gauges. The compliance of the ring was chosen very big as compared to that of the model slits. Mechanical interference with slit deformation was thus kept negligible. The strain gauges were wired to form parts of a Wheatstone bridge. Voltages were measured with a Philips carrier frequency bridge (PR 9307). The whole system was calibrated and checked for linearity by observing the voltage output caused by deformations of the ring which were controlled with the light microscope. Dilatation could be measured by inserting the ring into the slits in a slightly pre-compressed state.

Photoelastic Analysis. Photoelastic experiments were carried out in the "Institut für Mechanik und Spannungsoptik" of the Technical University at München. Details of the techniques applied are found in the textbook of Föppl and Mönch (1972). Araldite B (CIBA AG) was used to cast model tibiae (ca. 35:1).

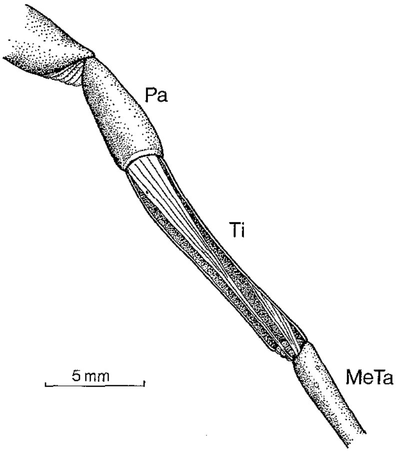

Fig. 3. Arrangement of the two paired flexor muscles (numbers 23/24 and 25/26 according to Parry, 1957) in the spider leg tibia, which lacks extensors

Initial stresses were avoided by proper annealing. The models were heated up to 150° C, then loaded and cooled down to 70° C under load at 3° C/hr. Thus the stresses were frozen and the models could be cut into pieces for further inspection under polarized light.

Loading of the models was done as explained by Fig. 4. This arrangement allowed to imitate the load conditions to be expected whenever the flexor muscles of the tibia (which lacks extensor muscles) are active against some mechanical resistance such as the body weight or hemolymph pressure, which is used for leg extension at this joint (Parry and Brown, 1959) (Fig. 3). Forces will then be acting on the tibial exoskeleton introduced via the articular condyli and the tibial muscle attachment sites. The force generated by muscle contraction is represented by weight P in the model experiment. The angle between force vector P and the long leg axis of the araldite tibia could be varied.

Isoclinics were measured by viewing the pieces cut from the model in light successively polarized in different directions. Lines of principal stresses could then be drawn by the standard graphical procedure (Föppl and Mönch, 1972). The "nail test" was used to identify the sign of the stresses in the different areas of the model *surface*. The surface is the most interesting part of it; here the dendrite of the slit sense organ terminates in the covering membrane and transduction takes place (Barth, 1971, 1972a, b).

Results

Our previous experiments on the functional morphology of the individual slit (Barth, 1972a, b, 1973a) clearly pointed to the fact that the structural variation of slit sense organs is paralleled by a variation in deformability. Since we know that compressional deformation of the slit is the mechanical event leading to an electrical response of the sensory cell attached to the slit (Barth, 1971, 1972b), it seems conclusive to ascribe differences in sensitivity to those in deformability.

In slits of lyriform organs a special effect on the deformability must be expected to result from their parallel arrangement[2]. The first set of experiments deals with this aspect. In a second experiment the combined effects of the various structural features is studied in a more refined model built in accordance with the

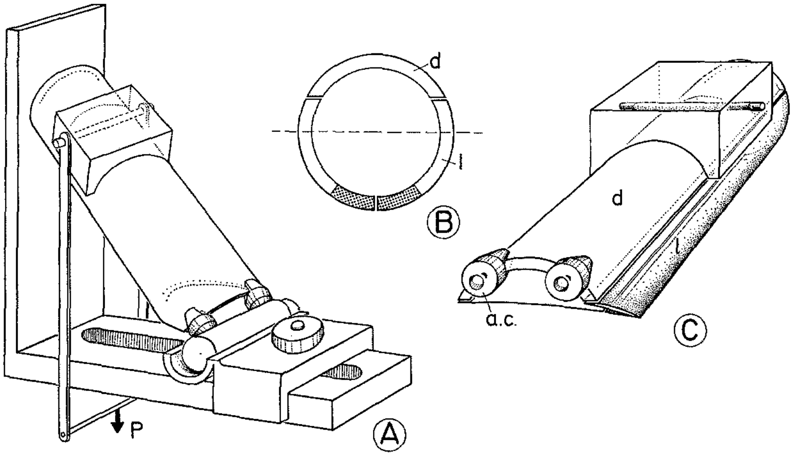

Fig. 4. Type of model used for the photoelastic experiments. A model tibia with two articular condyli (a.c. in C) was put into the device shown in A. By tilting it through various angles the direction of the load vector P could be varied. After freezing the stresses the models were cut into a dorsal and two ventrolateral pieces (d and l in B) for the analysis with polarized light

structure of a lyriform organ found on the spider leg tibia. Finally, the results of a photoelastic study are presented. They further an understanding of topographical features peculiar to the majority of lyriform slit sense organs on the spider leg.

I. *Deformability of Simple Model Slits Arranged in Parallel*

The deformation of groups of three and five slits arranged in parallel and cut into plexiglass disks as shown by Fig. 2a was measured under load applied from various directions. The results are summarized as follows (Fig. 5):

1. As expected slits in the periphery of a group behave quite differently from those in its middle.

2. The *median slits* of both the three- and five-slit system behave the same way as do isolated slits with regard to the range of load directions resulting in compression and dilatation of the slit, respectively. In all cases about 72% (260°) of the possible load directions result in compression (Fig. 5a–c; see insert circles). As to the amount of deformation, however, there are spectacular differences between isolated slits and the median slits of a group. The neighbouring parallel slits of a group reduce compression considerably. This applies to all load directions as well as all three slit areas distinguished (Fig. 5, ●, ▲, ■). Whereas in isolated slits compression greatly depends on the direction of load and is greatest at 90° (270°) the directionality of the median slit's deformation in a group is much less pronounced and in fact hardly seen. In addition its maximum

---

2 Variations in slit length, curvature of the covering membrane, and position of the dendritic end apparatus within the covering membrane are found as well. Their effects on a single slit's deformability were described earlier (Barth, 1972a, b, 1973a). They apply to the individual slits of a lyriform organ as well.

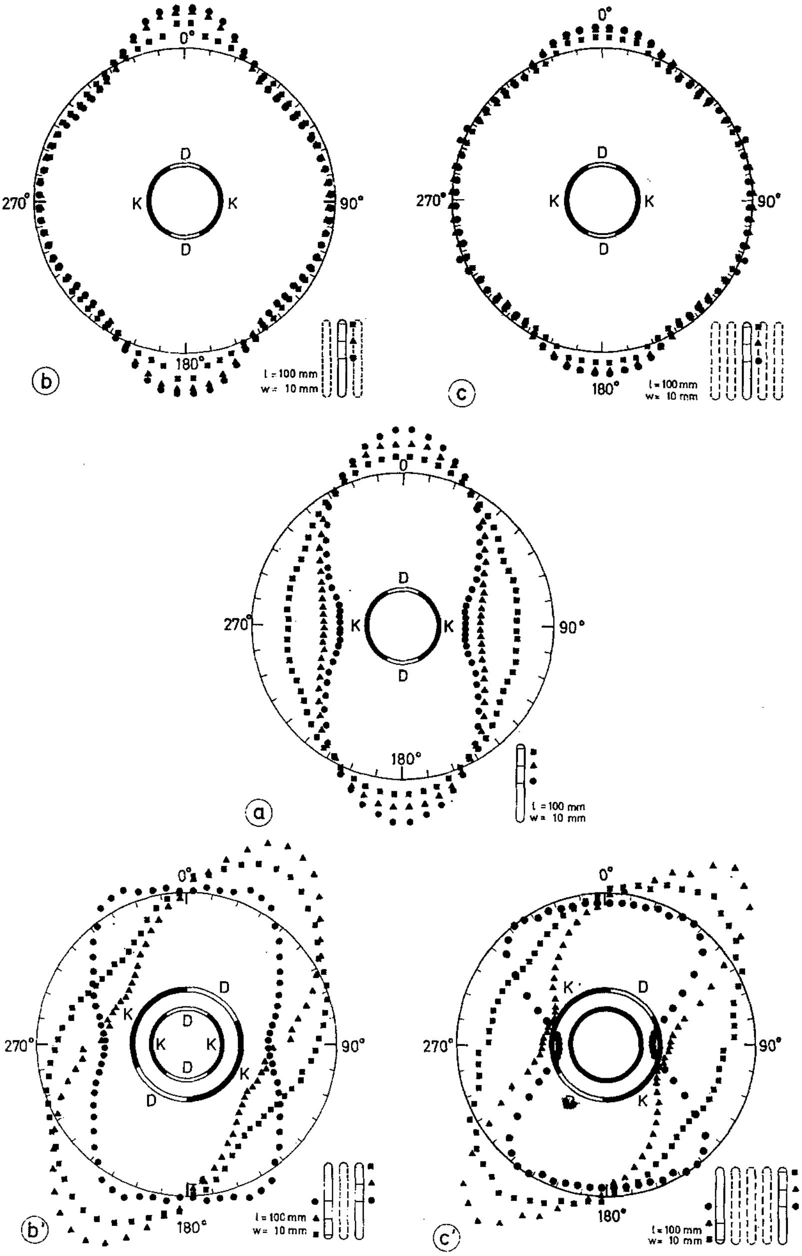

Fig. 5. Deformation of various models of the simple type (see Fig. 2a) under pressure load applied from varying directions. Angles are drawn on the large circles. a single slit; b,b′ and c,c′ median and peripheral slits of the three and five slit models, respectively. Zero deformation of the slit is given by the large circle itself. Compression and dilatation are drawn on its radii pertinent to the load direction under study. Whereas compression values are drawn inside the reference circle, dilatation values are drawn outside. ●, ▲, ■ different regions of the slits (see drawings of slits). Small circles concentric to the large ones show the spectrum of load directions resulting in compression (*K*) and dilatation (*D*) of the slits at their different regions

is shifted to about 45° (125°) and 135° (215°), respectively. Also, the differences between the different slit areas are very small compared to the isolated slit. Finally it should be noted that dilatation is reduced as well, although less than compression (Fig. 5a–c).

3. *The peripheral slits* of a group considerably add to the complexity of its deformation (Fig. 5b′, c′). Other than in case of the isolated and the median slits, deformation of the three slit areas differs both in degree and directional dependence (see inserts). Whereas the central areas (●) are still maximally compressed by loads applied perpendicularly to the slit axes the greatest values for the more distal ones (▲, ■) are found at about 125° (b′) and 140° (c′), respectively. It can be readily seen from the figures that the amount of deformation of a group's peripheral slits is in general much bigger than that of the median ones. It may even exceed that of the isolated slit (Fig. 5c′, ● and ▲; Fig. 5b′, ■). The central area of the peripheral slits in the five-slit group is remarkable for not showing any dilatation at all. It is compressed even by loads parallel to the slit axes. The maximum values found for dilatation in the peripheral slits of both the multi-slit models exceed those of the isolated slit. They occur in the more distal areas of the slits, however, and not in the central one as in the isolated slit.

II. Deformability of a Model Lyriform Organ

For the second experiment seven slits were modelled and arranged as found in the lyriform organ HS 8 on the posterior surface of the tibia (Fig. 2b). In accordance with the original organ the model slits had a troughlike shape. In addition to their specific position within the group they varied with respect to their length and the position of the deepest point of the trough, which marks the position of the dendrite within the slit (Fig. 2b)[3]. The differences found between the deformation of individual slits are thus the combined effect of these three parameters.

Fig. 6 summarizes the results.

1. There are considerable differences between the deformation of the seven slits. Maximum values of compression vary by a factor of 41 when comparing the most with the least deformed slit, *i.e.* slit 1 with slit 5.

2. The differences in deformation are roughly correlated to differences in slit length. The longest slit is the most labile one mechanically, whereas the shorter slits are much less so (Fig. 7).

This was to be expected from previous model experiments with isolated slits (Barth, 1972a) and is in principal agreement with simple beam theory as far as isolated slits are concerned. Deformation is not a sole function of slit length, however. On the contrary, the effect of the position of a slit within the group as outlined in the preceding chapter leads to marked deviations from it. Thus a minimum of deformation is found in slit 5 which has twice the length of slit 7, but

---

[3] The trough lies within the exocuticle and fully penetrates it only at its deepest part. Here the dendrite enters the slit and attaches to the covering membrane. For details see Barth (1971).

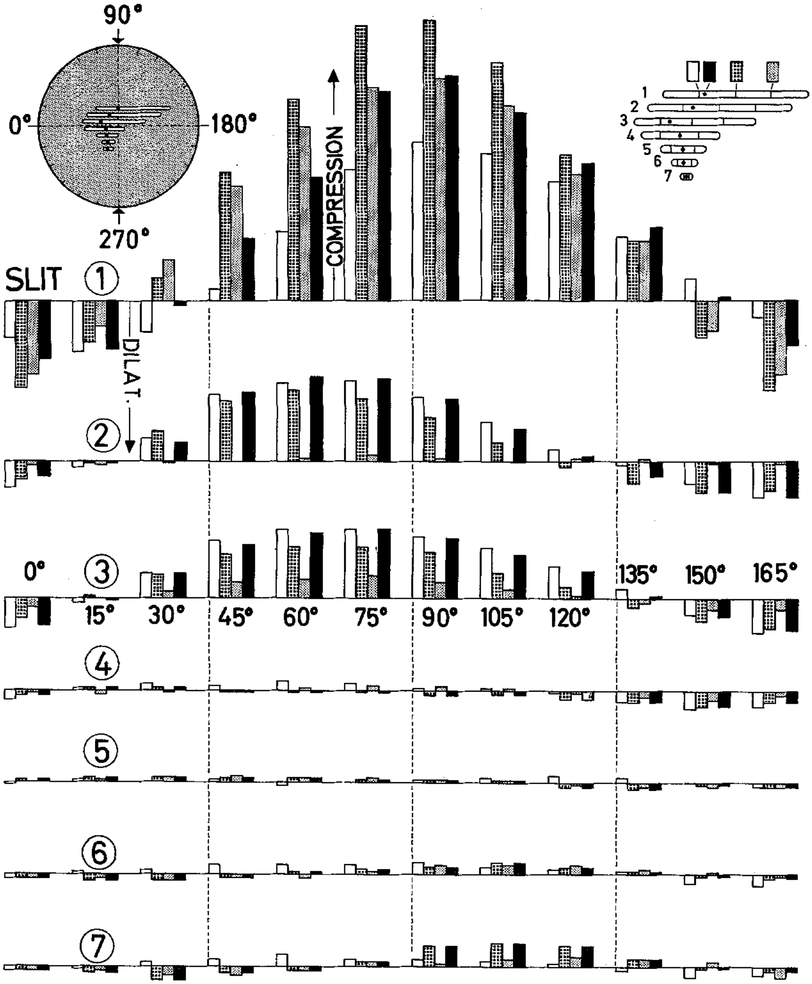

Fig. 6. Deformation of the more elaborate model (Fig. 2b). For each of the slits, which are numbered consecutively, compression (above zero line) and dilatation (below zero line) are shown in relative units as a function of load direction (see slit 3) and slit region. One of the four slit regions distinguished is the dendrite attachment site (black bar)

is compressed only one fourth as much. Both slit 1 and 7 are deformed more than would be expected from their length alone and in comparison with the rest of the slits. Evidently they take up the loads particularly well due to their most peripheral position in the group.

3. In slits 1, 2, and 3 of the tibial lyriform organ under study the dendrites do not attach to the mid-region of the slit, which is the most deformed one in isolated slits under load of any direction (Fig. 5a). Instead they attach to it more proxi-

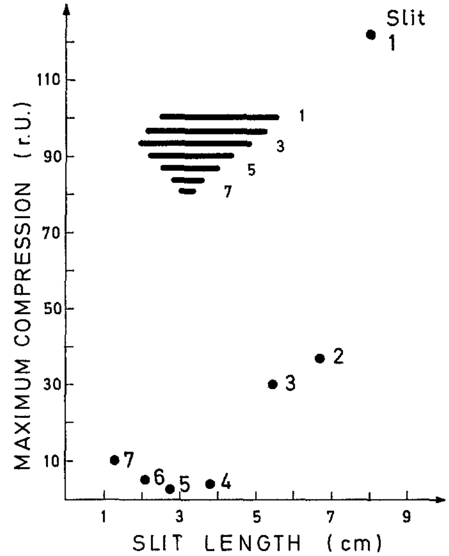

Fig. 7. Maximum compression of the different slits of the model lyriform organ (Fig. 2b) plotted against slit length. Numbers of slits identical with those on Fig. 6

mally (Fig. 1)[4]. When comparing the area most compressed in the model with that of the dendrite attachment site a coincidence is nevertheless found in slits 2 and 3. In slit 1, however, deformation of the mid-region is unsurpassed. The same is true for slits 6 and 7, whose dendrites attach to the mid-region of the slits.

Model slits 4 and 5 are more difficult to interpret due to the small degree of their deformation. In both cases the maximum values of compression are found slightly distal to the mid-region.

4. In general compression of the slits is greatest when the pressure load is applied roughly at a right angle (60–105°; angular resolution of measurement 15°) to the slits of the model. This is in agreement with the results obtained for the isolated slit (Fig. 5a) and the medium regions of the peripheral slits (Fig. 5b′, c′).

III. Lines of Principal Stresses in a Model Leg

Although differing in details the majority of the lyriform organs found on the spider leg has three topographical features in common: *1.* Their position on the lateral surfaces of the leg; *2.* their relative closeness to a joint; *3.* their orientation roughly parallel to the long leg axis. Features *1* and *3* also apply to the isolated slits (Vogel, 1923; Barth and Libera, 1970)[5].

Previous experiments have shown that excitation of the slit sense organs is elicited by compressional deformation and that this is most effectively achieved

---

[4] This feature is even more pronounced in the majority of the other lyriform organs on the spider leg (Barth and Libera, 1970).

[5] One of the exceptions to this rule is the metatarsal lyriform organ. It is located on the dorsal side of the leg and oriented perpendicularly to its long axis. The functional implications of these findings have been studied earlier (Barth, 1972b).

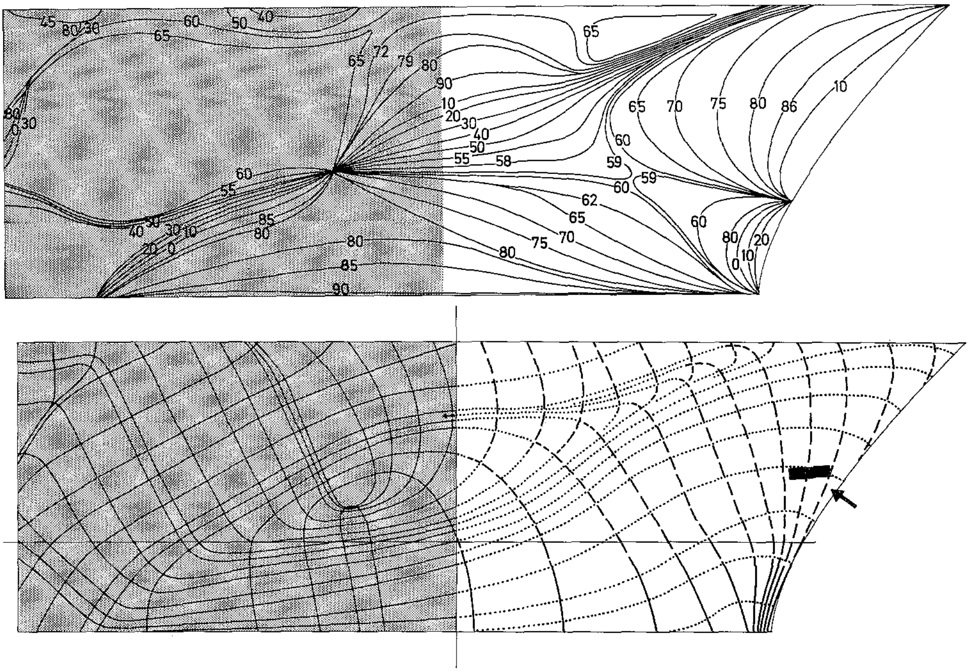

Fig. 8. Photoelastic experiment with a model leg. Both figures represent the ventrolateral parts of the model (see Fig. 4B). The *upper* drawing shows the isoclinics which are lines connecting all points where the principal stresses are oriented the same direction (or perpendicular to it, respectively) as the angle of linear polarization of the transmitted light. The reference angle (0°) is the long axis of the model. The lower figure shows the lines of principal stresses deduced from the isoclinics. The sign of the stresses was determined for the model surface: ---- pressure, —— tension, ... no stress. The shaded areas are doubtful in significance since the mechanics of the dorsal part of the model are modified by the attachment block for force P ("muscle attachment"). Force vector P formed an angle of 60° with the long axis of the model tibia in this experiment. Arrow points to lyriform organ (▬)

by pressure loads directed perpendicular to the slit's long axis (Barth, 1972a, b, 1973a).

In sections I. and II. of this paper it was shown that the same finding applies not only to the isolated slits but also to the slits of a lyriform organ.

It seems appropriate to conclude from these data that the lyriform organs are likely to lie in places where these stimulus conditions do indeed occur.

As in the model experiment described in section II. we took the tibial lyriform organ HS 8 as an example. An araldite model of the tibia was loaded as is explained by Fig. 4. It is important to realize that activity of the tibial muscles, which are all flexor muscles (Parry, 1957), will always result in pressure loads introduced to the tibia via its articular condyli (Fig. 3). Another load to be considered is bending of the cuticle due to tension forces exerted by muscular attachments onto the tibia. It is represented in the model as well.

Fig. 8 shows a perfect coincidence between the hypothesis and the results obtained for the model. The lines of principal stresses on the lateral surfaces run roughly perpendicular to the long axis of the model tibia. In addition they can be shown to be pressure (negative stress) lines at the niveau of the lyriform organs. On the other hand they were identified as tension (positive stress) lines on the ventral part of the model surface (see hatched area in Fig. 4b).

Changing the angle between the force vector P and the long axis of the model (which actually will occur in the spider leg during flexion and extension of the metatarsus) from 60° to 30° did not result in any noteworthy differences in stress distribution. Analysis of the dorsal surface of the model led to an unexpected result: There are pressure lines running roughly perpendicular to the model's long axis also.

Discussion

1. Stimulus Intensity Fractionation

The model experiments described in this paper were carried out to learn about the mechanical effects of loads on a close parallel arrangement of several slits, a feature pertinent to all lyriform organs.

The most obvious effect found is what we call in physiological wording "stimulus intensity fractionation". A close parallel arrangement produces enormous differences in deformation of the slits under load. This can be seen most readily by a comparison of the peripheral slits with the median slits of a group (Fig. 5). It should also be noted that the range of stimuli accessible to sensory analysis by lyriform organs can be expected to be considerably enlarged compared to both a single, isolated slit and—though to a much lesser degree—to an equivalent number of slits of corresponding lengths, but not closely lying side by side.

In addition all the model experiments point to significant differences in deformability among different regions of the same slit with respect both to its degree and directional properties. This was previously shown to apply to single isolated slits (Barth, 1972a). We now believe it to be the key for understanding the different patterns formed by the dendrite attachment sites in different lyriform organs (Fig. 1). It must be stressed in this context that in lyriform organs it is by no means always the mid portion of the slits which is maximally compressed. Instead it is suggested, on the grounds of the present as well as unpublished model studies, that the more peripheral location of the dendrite attachment sites found in many a lyriform organ (Fig. 1) indicates a shift of the site of maximum deformation towards the periphery of the respective slits.

The considerable effect of slit length on deformability must also be remembered in this context (Barth, 1972a; 1973a). It is clearly demonstrated by Figs. 6 and 7 of this paper. In case of a single, isolated slit the effect of slit length is roughly intelligible in terms of beam theory. Lyriform organs are much more complicated structures mechanically and with the data available there is no theory at hand for their proper quantitative theoretical interpretation.

Looking at the wealth of lyriform organs on the spider leg and considering the diversity of their outline shapes as well as differences in details of their topography we believe in a corresponding wealth of individual mechanical properties. It has become clear from the present study, however, that in all cases a broad range of sensitivities must be expected to be compiled in a lyriform organ.

It is concluded that lyriform organs are located at places where a broad spectrum of stimulus intensities does indeed occur. Unpublished electrophysiological data gave clear evidence that sensitivity varies considerably from slit to slit in one organ, indeed.

2. *Photoelastic Experiment*

We have chosen the tibia as an example for the photoelastic experiment because the lack of extensor muscles (see f. i. Parry, 1957) provides a relatively simple mechanical situation at the tibia/metatarsus joint. In addition the lyriform organs on the tibia were among those clearly involved in kinesthetic orientation behavior (Barth and Seyfarth, 1971; Seyfarth and Barth, 1972) and therefore are of particular interest in our present and future studies.

We do not believe to have solved all questions related to stress distribution and slit orientation with our photoelastic experiment. Instead, we consider it a first step in the analysis of stimuli occurring in the exoskeleton and adequate to the slit sense organs.

The results obtained are nevertheless considered applicable not to the tibia alone. It must be remembered that the femur/patella joint also has a dorsally located joint axis and lacks extensor muscles as well. In addition the activity of muscles always introduces loads to the respective leg segments via the articular condyli or hinges, be they flexors or extensors. The lines of principal stresses at joints where extensor muscles do occur should therefore take a similar course.

3. *Dynamic Loads*

In the model experiments reported here deformation of the slits was studied under static load. Natural stimulation such as occurs during locomotion will include dynamic forces as well.

The data collected under static load are considered a sufficiently accurate description of the dynamic situation as well, since elasticities are evaluated under static conditions. Viscosities may be expected to modify the type of deformation found only at very high frequencies (several KHz) unlikely to occur as natural stimuli for the majority of lyriform organs. A possible—if any— exception, however, may be the metatarsal lyriform organ already shown to be extremely sensitive to vibrations (Walcott and van der Kloot, 1959; Liesenfeld, 1961; Barth, 1972b). Click-like stimuli produced by an insect stepping onto the substrate or struggling in a spider web may contain such high frequencies.

The considerable differences in length found among the slit of many a lyriform organ (Fig. 1) might be interpreted as mechanical frequency range fractionation, *i.e.* tuning to different frequencies. The term "lyriform" would then ascribe a functional similarity to a lyra and not merely a morphological resemblance. Walcott and van der Kloot (1959) have indeed described such a tuning for the slits of the metatarsal organ of the house spider (*Achaearanea tepidariorum*)[6]. Their evidence came from a number of conflicting experimental results, however. Thus tuning was only found with airborne sound as stimulus. It could be abolished by vibrating the leg directly at different frequencies with a crystal phonograph cartridge. Such forced vibrations,

---

[6] Action potentials were recorded from the nerve of an amputated leg and classified by a five channel differential pulse height analyzer.

however, must be expected as natural stimuli when the spider leg rests either on a strand of the web or on the substrate.

Walcott and van der Kloot (1959) also report that the sharp tuning they found did not change by altering the "tension" on the slits. They finally attribute it to mechanical properties of the tarsus acting in conjunction with the slits rather than to the slits proper.

Clearly, the question of frequency range fractionation needs further study.

4. Stress Concentration at Multiple Notches

Notches are places of stress concentration and therefore of special interest in engineering (Peterson, 1960; Timoshenko and Goodier, 1970). The cuticular slit of a slit sense organ must be considered a notch (Barth, 1972a).

Stress concentration factors are highest for slits oriented perpendicular to the stress trajectories. Our photoelastic experiment suggests that this is the case with the majority of lyriform organs on the spider leg.

Closely spaced, multiple notches such as the slits of a lyriform organ represent a lesser degree of stress concentration, however, than single notches or holes do. Not only at the intermediate notches of a group is the stress concentration factor reduced but also—even though to a lesser degree—at the end notches where its maximum value is found[7]. As the distance between the notches increases this effect diminishes. Grouped slits (Barth and Libera, 1970; Barth and Wadepuhl, 1975) are therefore more similar to isolated ones than to true lyriform organs with respect to stress concentration.

5. Campaniform Sensilla of Insects

Our previous analysis of the functional morphology and adequate stimulation of the arachnid slit sensillum suggested a number of specific points concerning stimulus transformation and adequate stimulation in insect campaniform sensilla (Barth, 1972b) first studied by Pringle (1938). The postulated excitatory effect of compression *perpendicular* to the long axis of the sensillum cap has been verified experimentally in the meantime in two cases, namely for group 6 campaniform sensilla on the cockroach tibia (Spinola and Chapman, 1975) and for the densely packed campaniform sensilla on the fly haltere (Thurm, Stedtler and Foelix, 1975). In both cases the compressional forces are also directed perpendicular to the considerably elongated transverse axis of the dendritic end. This had been predicted too.

The present study points to another likely analogy between arachnid slit sensilla and insect campaniform sensilla. Both occur in three main types of configurations: isolated, loosely grouped, and lying closely side by side[8]. The

---

[7] In engineering stress concentration at an indispensable notch can be reduced by adding notches on both sides.

[8] Examples for isolated campaniform sensilla are those associated with the socket of hair sensilla on the cricket cercus (Gnatzy and Schmidt, 1971); for "loosely" grouped ones those found on the cockroach tibia (Pringle, 1938); for compound organs those on the fly haltere (Pflugstaedt, 1912). For slit sensilla see Vogel (1923), Barth and Libera (1970), and Barth and Wadepuhl (1975).

stimulus intensity fractionating property of a close arrangement of sensilla is predicted to apply in principal also to "compound" campaniform sensilla like those groups found on the fly haltere. Future study of these should consider a difference in deformation between the peripheral and the intermediate sensilla. Since the campaniform sensilla of the same group are all oriented alike on the haltere and thus will not differ in directional sensitivity (Pringle, 1948) stimulus intensity fractionation might well be important for an understanding of the great numbers found at such specific sites.

References

Barth, F. G.: Der sensorische Apparat der Spaltsinnesorgane (*Cupiennius salei* Keys., Araneae). Z. Zellforsch. **112**, 212–246 (1971)

Barth, F. G.: Die Physiologie der Spaltsinnesorgane. I. Modellversuche zur Rolle des cuticularen Spaltes beim Reiztransport. J. comp. Physiol. **78**, 315–336 (1972a)

Barth, F. G.: Die Physiologie der Spaltsinnesorgane. II. Funktionelle Morphologie eines Mechanoreceptors. J. comp. Physiol. **81**, 159–186 (1972b)

Barth, F. G.: Bauprinzipien und adäquater Reiz bei einem Mechanoreceptor. Verh. Dtsch. Zool. Ges. Mainz **66**, 25–30 (1973a)

Barth, F. G.: Microfiber reinforcement of an arthropod cuticle. Laminated composite material in biology. Z. Zellforsch. **144**, 409–433 (1973b)

Barth, F. G., Libera, W.: Ein Atlas der Spaltsinnesorgane von *Cupiennius salei* Keys. Chelicerata (Araneae). Z. Morph. Tiere **68**, 343–369 (1970)

Barth, F. G., Seyfarth, E.-A.: Slit sense organs and kinesthetic orientation. Z. vergl. Physiol. **74**, 326–328 (1971)

Barth, F. G., Wadepuhl, M.: Slit sense organs on the scorpion leg (*Androctonus australis* L., Buthidae). J. Morph. **145**, 209–228 (1975)

Föppl, L., Mönch, E.: Praktische Spannungsoptik. Berlin-Heidelberg-New York: Springer 1972

Gnatzy, W., Schmidt, K.: Die Feinstruktur der Sinneshaare auf den Cerci von *Gryllus bimaculatus* Deg. (Saltatoria, Gryllidae). I. Faden- und Keulenhaare. Z. Zellforsch. **122**, 190–209 (1971)

Liesenfeld, F. J.: Über Leistung und Sitz des Erschütterungssinnes von Netzspinnen. Biol. Zbl. **80**, 465–475 (1961)

Parry, D. A.: Spider leg-muscles and the autotomy mechanism. Quart. J. micr. Sci. **98**, 331–340 (1957)

Parry, D. A., Brown, R. H. J.: The hydraulic mechanism of the spider leg. J. exp. Biol. **36**, 423–433 (1959)

Peterson, R. E.: Stress concentration design factors. New York-London-Sydney: John Wiley & Sons, Inc. 1966

Pflugstaedt, H.: Die Halteren der Dipteren. Z. wiss. Zool. **100**, 1–59 (1912)

Pringle, J. W. S.: Proprioception in insects. II. The action of the campaniform sensilla on the legs. J. exp. Biol. **15**, 114–131 (1938)

Pringle, J. W. S.: The gyroscopic mechanism of the halteres of Diptera. Proc. roy. Soc. B **233**, 347–384 (1948)

Pringle, J. W. S.: The function of the lyriform organs of arachnids. J. exp. Biol. **32**, 270–278 (1955)

Seyfarth, E.-A., Barth, F. G.: Compound slit sense organs on thespider leg: mechanoreceptors involved in kinesthetic orientation. J. comp. Physiol. **78**, 176–191 (1972)

Spinola, S. M., Chapman, K. M.: Proprioceptive identation of the companiform sensilla of cockroach legs. J. comp. Physiol. **96**, 257–272 (1975)

Thurm, U., Stedtler, A., Foelix, R.: Reizwirksame Verformungen der Terminalstrukturen eines Mechanorezeptors. Verh. Dtsch. Zool. Ges. Bochum, 1974, 37–41. Stuttgart: Fischer Verlag 1975

Timoshenko, S. P., Goodier, J. N.: Theory of elasticity. Tokyo: McGraw-Hill Book Comp., Kogakusha Comp. Ltd. 1970

Vogel, H.: Über die Spaltsinnesorgane der Radnetzspinnen. Jena Z. Med. Naturw. **59**, 171–208 (1923)

Walcott, Ch., van der Kloot, W. G.: The physiology of the spider vibration receptor. J. exp. Zool. **141**, 191–244 (1959)

Prof. Dr. Friedrich G. Barth
Fachbereich Biologie
J. W. Goethe-Universität
D-6000 Frankfurt am Main
Siesmayerstraße 70
Federal Republic of Germany