ZOOLOGY

DZG LECTURE

Spider senses – technical perfection and biology**

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Summary

This essay deals with sensory biology in a broad sense. It takes mechanosensory systems of spiders to illustrate a few basic issues. Particular attention is given to two aspects. *1*. There is a remarkable "ingenuity" in the uptake and transformation of the adequate stimuli way out in the sensory periphery, which is reflected by an intimate relationship between the physical properties of the stimuli and the characteristics of the structures receiving and transforming them. We need to understand the details of this relationship in order to understand the relationship of an organism to its environment. *2*. Sensory systems represent interfaces between the environment and behavior. As highly selective filters they have not evolved to provide abstract knowledge but to guide a particular behavior. The signals sent to the central nervous system are meaningful only in regard to their behavioral significance. – Some details of stimulus transformation in biological strain gauges (slit sensilla), airflow detectors (trichobothria) and touch receptors (tactile hairs) are described. Some of the refinement in the periphery is then meshed with the behavior of the whole organism. In this way the value shall be underlined of trying to understand reductionist details as building blocks of the complexity which enables an organism to behave in its own particular way in its species specific environment.

Key words: Sensory biology, neuroethology, biotechnology, mechanoreception, arthropods

No life without sensing

Sensors and sensing are fundamental properties of all living beings, from protists and indeed bacteria to man. Life without them is hardly possible because behavior needs guidance by them. Neither reactions to changes in the environment outside the organism nor to changes in its inside would be possible. Without them, life would not "make sense" anymore and the lost capability of homeostasis would have fatal consequences. Survival and securing the genes for the next generation could no longer be the fundamental achievements of living beings. Accordingly, one finds a fascinating richness and diversity of sensory systems throughout the animal kingdom. This of course also applies to spiders, a large group of about 40,000 described species with remarkable ecological success. A considerable part of this success must be attributed to highly developed sensory systems which are the result of about 400 million years of evolution. The complex behavioral patterns shown by spiders are unthinkable without the spiders' armament of sensors.

Compared to such a long evolutionary history, the roughly 35 years of my own preoccupation with spiders of the genus *Cupiennius* are just a nano-flash in time. Yet this flash has brought to light fascinating details of spider sensory systems and their behavioral roles and has at the same time taught us a lot about more general

issues in biology. It enabled us to have at least a glimpse at the order which meshes elemental principles of some sensory systems with the whole organism at different levels of function, and it helped us to understand at least a few reductionist details as building blocks of the complexity which is the core of neuroethology.

Cupiennius, the priceless spider

Spiders of the genus *Cupiennius* mainly live in Central America. Eugène Simon (1848–1924), the famous French arachnologist, established the genus in 1891. *Cupiennius salei* (Fig. 1), the most popular in our research among the nine described species (Lachmuth et al., 1984; Barth and Cordes, 1998), was first collected by Monsieur Salé near Cordoba and Veracruz in Mexico. Graf Eugen Wilhelm Theodor von Keyserling (1832–1889) described the now lost holotype as *Ctenus salei* in 1877 (Keyserling, 1877). Today, *C. salei* still can be found near Cordoba. Actually, we did much of our field work in this area. It seems like a nice coincidence of history that now, 125 years after its first description in the Proceedings of the Zoologisch-Botanische Gesellschaft in Vienna, it is at Vienna University that *C. salei* (and other species of the genus) has been bred by the hundreds since 1987, when we brought our colony with us from Frankfurt. Among the prominent features of *C. salei* is its close association with plants (mainly monocots) on which it hides during the day in retreats in between the leaves and preys and courts at night. *Cupiennius* forms a genus of hunting or wandering spiders which do not live in a spider web or build a web to catch prey like the familiar orb weavers or funnel web spiders. *C. salei* is a large night active spider with a leg span of about 10 cm, as are its close relatives *C. getazi* and *C. coccineus* (Barth, 2001). All of these species can be bred in large numbers and all year round in the laboratory far away from their homeland, which is one of the keys to their "success" as priceless research animals.

It remains unclear why Eugène Simon chose *Cupiennius* as the name for the genus to which the spider collected by Mr. Salé in Mexico now belongs. Most likely he was a highly educated researcher who knew the satires (called sermones by its author) of Quintus Horatius Flaccus, the famous Roman writer (65–8 BC). In sermon I 2, 36 Horatius mentions Cupiennius Libo from Cumae who is said to have been a good friend of Emperor Augustus. From Pomponius Porphysio, the antique commentator of Horatius, we learn: Gaius Cupiennius Libo Cumanus Augusti familiaritate clarus corporis sui diligentissimus fuit sectator matronarum concubitus. The relation between the reputation of Cupiennius of being a voluptuous adulterer and "Matronenjäger" and our spider remains enigmatic.

Using only a few selected examples, the following essay strives to shortly illustrate two aspects related to the "sense of senses". One is about the sensory periphery, the other about behavior.

(1) The uptake of the adequate stimuli very often shows a remarkable ingenuity and efficiency and again and again demonstrates how many clever ways nature has found to solve "technically" difficult problems. There

Fig. 1. *Cupiennius salei* (Keyserling, 1877), adult female (leg span about 10 cm). **(A)** Ventral view with typical black annular patterns on the femora, broad black median stripe on the opisthosoma and terra-cotta red hairs on the coxae (photograph kindly provided by Raphael Barth). **(B)** Spider injecting venom into a grasshopper caught on a bromeliad only seconds before the photograph was taken (near Cordoba, Mexico; from Barth, 2001).

is a wealth of biologically applied physics and engineering seen in the intimate relationship between the properties of the stimulus and the properties of the structures receiving and transforming it. In many cases, knowledge of this relationship way out in the sensory periphery substantially contributes to our understanding of the relationship between an entire organism and its species specific environment.

(2) The second aspect to be illustrated here is as trivial as it is important. Sensory systems and the sense they make remain inconceivable without considering behavior. On the contrary: the senses are the interfaces between the environment and behavior. The signals provided for the central nervous system by the sensors only become information by their ethological meaning. Sensory systems have evolved to permit particular behaviors. These have to be taken into account if we strive for a full understanding of what the sensors have to tell the brain.

The well "engineered" sensory periphery

Slit sensilla – biological strain gauges

Slit sensilla (Fig. 2A) may be called biological strain gauges. They are "embedded sensors" in engineering terminology and closely related to a particular sensory function of the spider exoskeleton. When the exoskeleton is subjected to mechanical loads from internal sources like muscular activity or hemolymph pressure (Fig. 2B), or from external sources like substrate vibration, the forces entail strains in the cuticle. In other words, the cuticular material will be slightly deformed. There are roughly 3,500 slit sensors embedded into the exoskeleton of *Cupiennius salei*, mainly on the legs, which are capable of measuring such deformations (review: Barth, 2001).

These deformations are minute. This is easily understood in case of fully sclerotized exocuticular material whose modulus of elasticity (Young's modulus; in the order of 18 GPa, spider leg tibia) resembles that of bone. In more practical terms that means that on the tibia, to take an example, strains in the order of 20 μm (ppm; under load the original length l_o of a piece of material changes by a factor of 20×10^{-6}) occur during locomotion and effectively stimulate spider slit sensilla, provided they are compressional strains (negative tension) (Blickhan and Barth, 1985). The tiny slits in the exoskeleton (width less than 2 μm, length from about 8 to 200 μm) send off action potentials, when compressed by a few Ångström units (10^{-8} cm) only. This remarkable sensitivity tells us that the relationship between the properties of the stimulus and the morphology and position of the slits in the exoskeleton must be a very

close one. For its deeper understanding, knowledge is needed of the size, the sign, and the course taken by the lines (trajectories) of principal stresses under natural stimulus conditions at the site of the sense organs. The organs examined in this way are indeed found in areas of compressional forces and are oriented roughly at a right angle to them, which implies maximum mechanical sensitivity (Fig. 2C; Barth and Pickelmann, 1975; Blickhan and Barth, 1985). Considering the directional properties of slit sensilla, the logic can be turned around and the sign and orientation of strain trajectories predicted at a particular site from the orientation of the slits.

A characteristic feature of slit sensilla is their occurrence as compound organs, forming arrays of up to 29 slits in close parallel arrangement. The advantages gained by such arrays over single slits seem to hide the most advanced features of "mechanical engineering" exhibited by the slit sensilla. This is at least partly paralleled by physiological refinement and differentiation among the slits. We do not know enough yet about this, but the exemplary examination of lyriform organs already demonstrated differences in threshold compression, a considerable enlargement of the working range, in particular the range of high differential sensitivity, and a remarkable influence of the detailed pattern formed by the parallel slits on their mechanical properties (deformability by cuticular strains under load), including their directional sensitivity (Barth and Bohnenberger, 1978; Bohnenberger, 1981; Barth et al., 1984; review: Barth, 2001). One of the lyriform organs is exceptional with regard to its orientation perpendicular to the leg's long axis and its dorsal arrangement, bridging a furrow in the exoskeletal cuticle distally on the metatarsus. This nicely shows us how crucial details of arrangement may be in a strain measuring sensory system. The features mentioned above make this organ a very sensitive vibration detector responding to substrate vibrations down to 10^{-6} to 10^{-7} cm. This is the same order of magnitude as found for the vibration detectors of cockroaches (so far considered the champions), crickets, and other insects and indeed also in the range of the "hair" deflection in the hair cells of the vertebrate inner ear. The spider metatarsal vibration receptor also nicely reveals, how successfully evolution dealt with the mechanics offered by the exoskeleton for a sensory system representing biological strain gauges.

Trichobothria – hairs that catch the wind

A close look at the surface of a spider such as *Cupiennius salei* brings to light an astonishing finding. There are several hundred thousands of innervated cuticular hairs and up to about 400 such hairs per mm^2 (Fig. 3A). Almost all of them are mechanically sensitive. Sensory
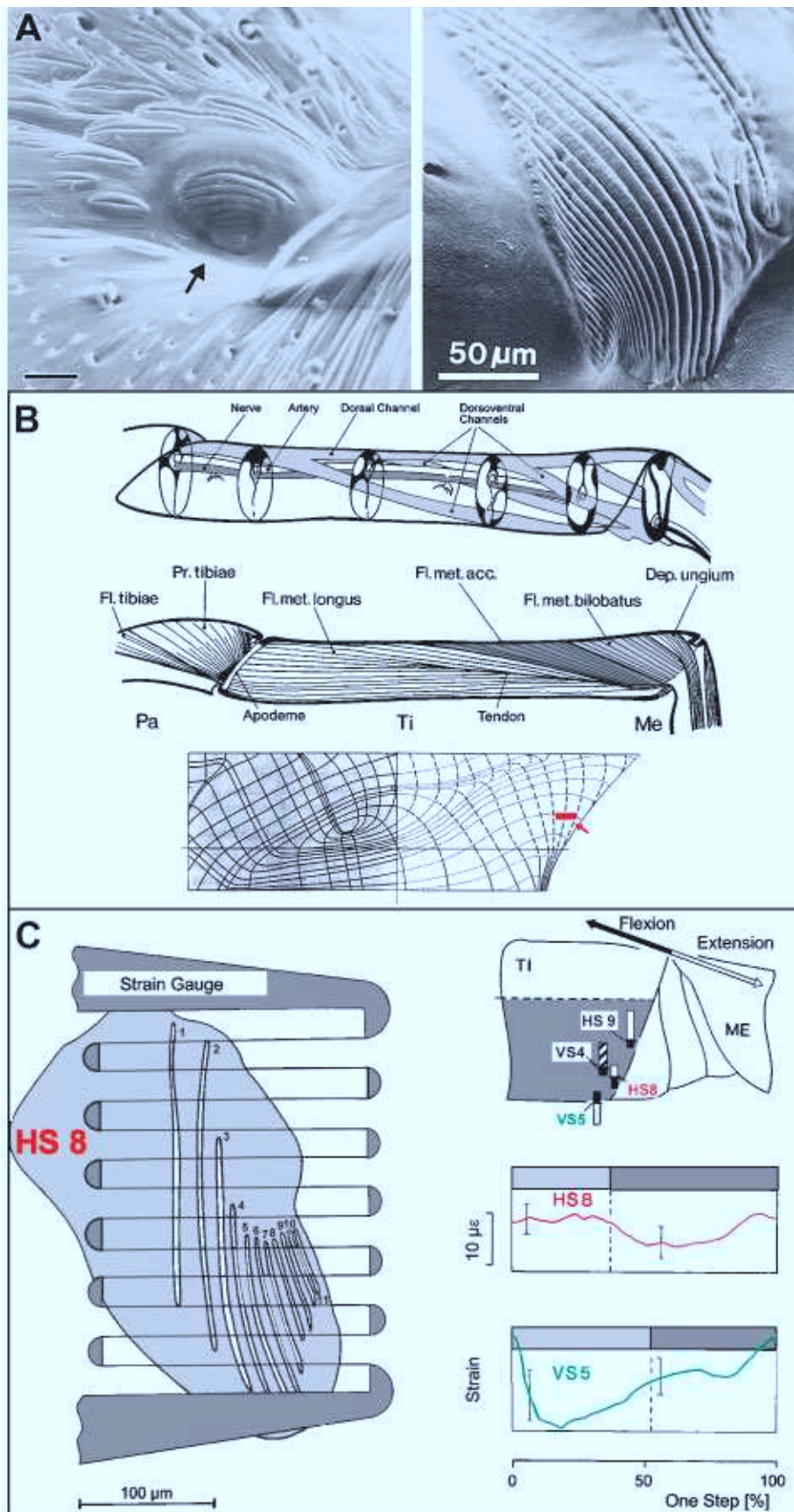
Fig. 2. *Slit sensilla.* **(A)** *Left:* Loosely arranged group of slit sensilla and lyriform organ (arrow) on the trochanter of a walking leg. *Right:* Lyriform or compound organ on trochanter (after Barth 2001). **(B)** The main sources of the strains in the exoskeleton measured by the slit sensilla are hemolymph pressure and muscular forces. *Top:* Lacunae in the tibia forming well defined channels for the fast transport of hemolymph during joint movements. *Middle:* Arrangement of flexor muscles in the spider leg tibia (*Ti*); *Pa* patella, *Me* Metatarsus; *Fl* flexor, *Pr* promotor. *Bottom:* Tension and pressure lines in a model tibia under quasi-natural load (simulating muscular forces introduced through the condyli during flexion of the joint). Arrow points to lyriform organ HS-8 laterally on the tibia in an area of pressure (negative tension, broken lines). Ventral part of distal tibia characterized by tension (continuous lines). **(C)** *Left:* Strains at the site of lyriform organs can be measured in vivo by attaching miniature strain gauges onto the cuticle. *Right:* Top, during flexion of the metatarsus (ME) negative strains at the lateral sites of organs HS-8, HS-9 and VS-4 compress and thus effectively stimulate, whereas the ventral organ VS-5 is in an area of positive strain and not stimulated. During leg extension the situation reverses. Middle and bottom, strains at organs HS-8 and VS-5 during one step in a freely walking spider. Dark shading of bar above graphs indicates stance phase (stimulation of HS-8), light shading indicates swing phase (stimulation of VS-5; after Barth and Pickelmann, 1975; Blickhan and Barth, 1985).

cells ending at their respective base are adequately stimulated by the deflection of the hair shaft.

The so-called trichobothria (analogous to insect filiform hairs) of spiders are medium flow sensors (Fig. 3B). They respond to the slightest movement of the surrounding air, as for instance produced by a potential prey animal flying by (reviews: Barth, 2000, 2001). Considering their mechanical sensitivity, trichobothria represent an extreme case within the spectrum of mechanosensitive hair sensilla. Their hair shaft is taken along by the frictional forces exerted by the slightest air flow. According to recent analyses, both cricket filiform hairs (Shimozawa et al., 2002) and spider trichobothria (Humphrey et al., 2002) are the champions among all known bio-sensors in regard to absolute sensitivity. Physically exact calculations of the work driving a trichobothrium over one oscillation cycle yielded values down to 2.5×10^{-20} Ws (Joules). This value corresponds to a fraction of the energy contained in one quantum of green light. For cricket filiform hairs even

Fig. 3. Hair sensilla (*C. salei* female). **(A)** Ventral view of proximal leg segments; note dense cover of cuticular hairs mainly serving mechanosensory functions. **(B)** Tarsus of a walking leg; note trichobothria (length up to 1.4mm) dorsally on the tarsus with bend of distal part of their hairshaft (from Barth, 2001).

values in the order of 10^{-21} Ws have been determined (Thurm, 1982; Shimozawa et al., 2002) for an oscillation cycle at 5 Hz and maximum deflection at sensory threshold roughly corresponding to 1/100 of the energy of a single photon. The obvious conclusion is the same as in case of the slit sensilla: Such an exquisite sensitivity rests on an intimate interaction and coupling between the moving air and hair.

Again, much of the extremely "well engineered" processes of stimulus uptake and transformation can be understood by interpreting them as reflections of the physics of the stimulus. In the given case this means that one has to consider fluid mechanics. A trichobothrium can be represented by an inverted pendulum and much of its quantitative understanding rests on Stokes' now classical analysis of "the effect of the internal friction of fluids on the motion of pendulums" dating back to 1851. Figure 4 left and center shows some of the key parameters to be taken into account. Whereas the hair is deflected by torque T (Nm), which is due to the viscous forces of the medium flow, both S (Nm/rad) and R (Nms/rad) oppose deflection, S representing the elastic restoring force and R the viscous damping. Among other things, the mathematical modeling informs us about the significance of the mass of the hair shaft, its length, diameter and surface structure as determinants of mechanical sensitivity. Thus, it turns out that the sensitivity of the range of best frequencies is particularly large with regard to hair length L. In other words: If one was to modify or adjust the tuning in a corresponding artificial sensor, one would primarily do this by changing L, and only secondarily by adjusting R and S (Barth et al., 1993; Humphrey et al., 1993, 2001). Interestingly, this is what we find in the trichobothria. Typically, these form groups of hairs with lengths between about 0.1 mm and 1.5 mm and with corresponding best frequency ranges between about 40 Hz and 600 Hz. Compared to an individual hair, a group of hairs just slightly differing in length represents a set of bandpass filters which enlarges the range of high sensitivity considerably. Mathematical modeling also permits predictions regarding adaptive evolution, that is to say it helps us to understand how evolution can play the keyboard of parameters at its disposal (Humphrey et al., 2001).

The main reason for the dependence of frequency tuning on hair length is not primarily due to the implicit differences in mass (long hairs being more sensitive to low frequencies and short hairs to higher ones) or in the elastic restoring force. Instead, there is a special relationship between the *lower* end of the bandpass characteristics of a trichobothrium and the boundary layer. This is a zone of reduced medium flow velocity in the immediate vicinity of surfaces within the flow, like the body surface of the spider. Boundary layer thickness increases
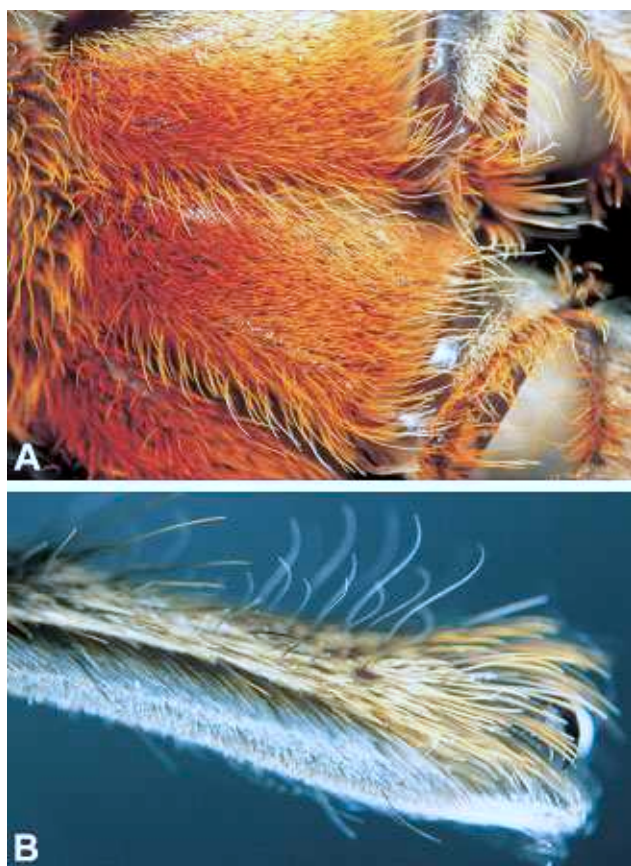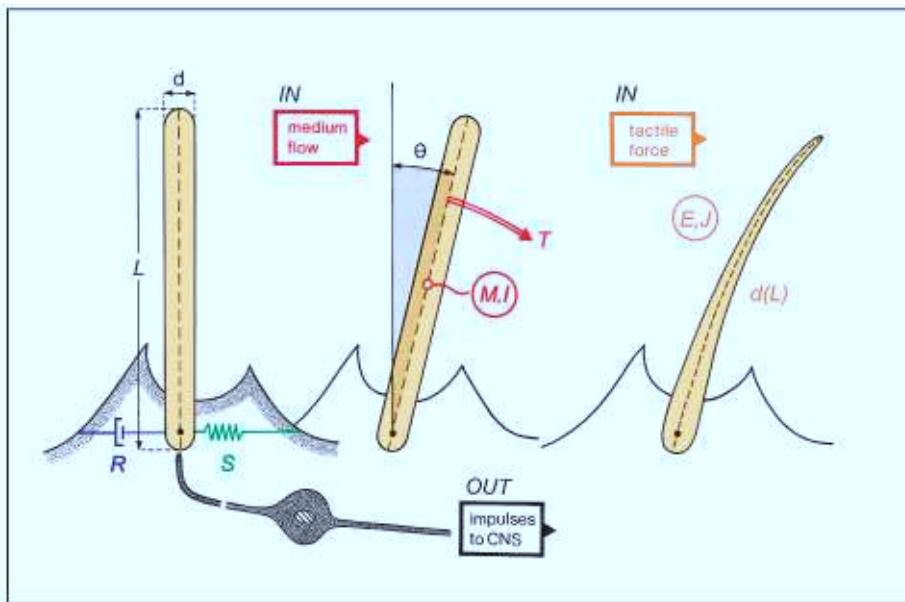
Fig. 4. *Arthropod mechanosensory hair sensilla. Left:* Schematic representation of parameters to be considered; *L* length and *d* diameter of hairshaft, *R* frictional resistance and *S* torsional restoring constant or spring stiffness of articulation. *Center:* Hair sensitive to airflow like trichobothrium or insect filiform hair. Deflection (Θ) is by viscous forces (*T*, torque). *S* is very small and as a consequence the hairshaft is not bent by the stimulus. *Right:* In spider tactile hairs the articulation is much stiffer than in trichobothria, with values of *S* larger by about four powers of ten. Thus a tactile hair is both deflected and bent by the stimulus (from above). The hair parameters mainly to be considered in order to understand hair mechanics are mass *M* and its torsional inertia *I* in case of the flow sensors and Young's modulus *E* and the second moment of area *J* along the length *L* of the hairshaft in case of tactile hairs (after Barth and Dechant, 2002).

with decreasing flow frequency. According to direct measurements with the laser anemometer, the length of the trichobothria is in the range of boundary layer thickness. Using an oscillating airflow, the thickness of the boundary layer above the spider leg varied roughly from 2.600 µm to 600 µm over the range of 10 Hz to 959 Hz (Barth et al., 1993). The consequence is the following: At low frequencies short hairs "get stuck" in the zone of reduced particle velocity, whereas long hairs are exposed to the higher velocities found at a larger distance from the surface. The *upper* frequency end of the bandpass properties of a trichobothrium is due to the inertia of the hair shaft and of the virtual mass moved along with it. The moment of inertia increases by a factor of 10^3 with hair length and the hair becomes increasingly immobile with increasing frequency.

Tactile hairs – not just rigid pencils

The large majority of the numerous cuticular hairs covering the spider exoskeleton does not serve the detection of air movement. Instead, most of the hairs are tactile hairs, contrasting the trichobothria and nicely illustrating the potential contained in the seemingly simple "Bauplan" of an arthropod sensory hair.

When deflected by the viscous forces of the air flow around them, trichobothria do not bend. The main rea-

son for this is the extremely low elastic restoring force at their articulation. In trichobothria spring stiffness *S* is of the order of 10^{-12} Nm/rad. As a result, the forces acting on flow sensors are too small to bend the hair shaft to any relevant degree. The hair parameters dominating the mechanical behavior are mass *M* and torsional inertia *I* (Fig. 4 center). In the tactile hairs examined by us, the situation is radically different due to a difference in a few parameters only. In tactile hairs spring stiffness *S* measures about 10^{-8} Nm/rad. It is larger by about four powers of ten than in case of the flow sensors. Due to the forces needed to overcome this stiffness, the hair is not only deflected but also bent by the stimulus (Fig. 4 right). As a consequence, Young's modulus *E* and the second moment of area *J* along length *L* of the hair shaft are the mechanically dominant features (whereas *M* and *I* may be neglected due to the relative size of the stimulating force; Barth and Dechant, 2002).

In most cases of the touch receptors we examined stimulation will be from above. When touched by an object from above, the hair shaft is pushed down and bent. It turns out that the hair shaft is a surprisingly "clever" stimulus transmitting structure. The point of load introduction increasingly shifts towards the hair base with increasing load and deflection. Accordingly, the effective lever arm and the stimulating moment decrease
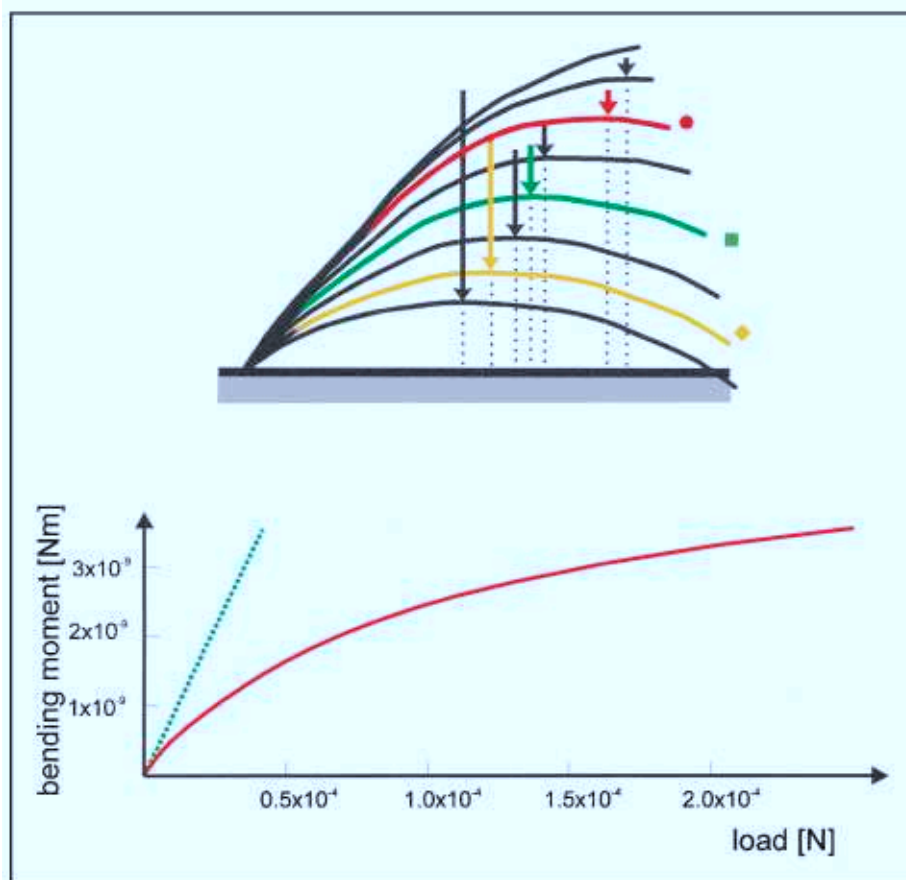
Fig. 5. Bending of a spider tactile hair by mechanical stimulation from above. *Above:* With increasing load (see force vectors, which are not drawn to scale) and hair deflection the effective lever arm represented by the hairshaft shortens. *Below:* According to finite element simulation and following microscopical observation of the hair's bending behavior the bending moment increases more slowly with increasing load (see red curve). The dotted green line shows how much faster the moment would increase in case of a hair not bending under load (constant lever arm; after Dechant et al., 2001).

with increasing loading force. The largest bending moment equals only about 20% of that to be expected for a rigid hair (Fig. 5). Remarkably, due to its bending, the hair shaft never is deflected by more than about 12° at its base. Similarly, the bending moment increases much more slowly with large loading forces than with small ones and reaches saturation at about 4×10^{-9} Nm. What does that mean in more practical terms? *First*, the hair is protected against breaking. S*econd*, the hair's mechanical working range is considerably extended as compared to a rigid hair. *Third*, the mechanical sensitivity is higher for small deflections than for large ones (ca. 5×10^{-5} N/° as compared to ca. 1×10^{-4} N/°), which goes along with a corresponding relative decrease of the moment at the hair base with increasing stimulus load.

Finite element analysis (Dechant et al., 2001) brought to light even more evidence of "clever engineering". Axial stresses (the major stress component) in the hair due to its bending reach values of up to ca. 3×10^5 N/m². Maximum stress values remain largely same although the loads introduced at the different contact points differ considerably during a loading cycle. In other words, the hair shaft is a structure of equal maximal strength which implies that critical stress values are successfully avoided by a corresponding adjustment of the hair's cross section (and thus *J*) along its length. Several regions of the hair shaft with differing mechanical properties can indeed be distinguished (Dechant et al., 2001). Micromechanical refinement in the smallest detail!

No sense in senses without behavior

When trying to understand sensory systems, one must never forget that for the animal the "goal" is not abstract knowledge but survival and reproduction. The sense of senses is not in their technical perfection per se, as fascinating as their "design" may be. In the last instance the sense of senses is in the biological meaning of the nervous signals which result from highly selected and filtered stimuli. It is the relation to a particular behavior which qualifies these signals as information.

In the following this shall be illustrated with a few examples not taken from the brain but from the sensory cells far out in the periphery.

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Prey capture

Cupiennius is a nocturnal sit and wait predator. Shortly after sundown, when the light intensity has fallen to about 15 lux, it turns around and leaves its retreat, typically staying nearby for about half an hour until, to the human eye, it has become completely dark. Then, at a light intensity below 0.1 lux, *Cupiennius* walks onto a leaf where it sits fully exposed in wait for prey. By this time the wind has died down and insects start emerging from their hiding places. When *Cupiennius* slightly raises its body the experienced observer knows that it has noticed potential prey like a cockroach or a grasshopper, crawling around on the plant at a distance of half a meter or more. When the victim is within reach, it is overwhelmed within a few hundred milliseconds (Fig. 1B). Evidently, this behavior is based on a substantial amount of sensory information. The most important clues telling the spider about the presence and location of prey are transmitted through the plant and air, respectively: (1) *Substrate vibrations* like those produced by a cockroach while walking around on the plant; (2) *air movements* like those produced by an insect while passing by in flight (reviews: Barth, 1998, 2001). How does *Cupiennius* recognize the biologically meaningful prey signal and distinguish it from background noise?

Substrate vibrations

According to the measurement of vibrations on their dwelling plants in the field, the spiders are exposed to three types of vibrations which differ in regard to the spectrum of the frequencies the vibrations contain (Fig. 6). (*a*) "Abiotic" vibrations caused by *wind* are characterized by very low frequencies, usually with a peak well below 10 Hz. The spectrum is very narrow. Often there are no components above 10 Hz, and if present they are smaller by 40 to 60 dB than the main peak. (*b*) Quite in contrast to the wind induced vibratory background, *prey* signals such as those produced by a cockroach are "noisy", that is to say that they are broad-band and contain higher frequency components. Their dominant peaks are between 400 Hz and 900 Hz and the –20 dB frequency bands extend from a few Hz to ca. 900 Hz. (*c*) The male vibratory *courtship* signals, which will be considered more extensively below, are characterized by their regular temporal structure with syllables produced in sequences of up to 50 at intervals of about 350 ms. The most prominent frequency components are close to 100 Hz, roughly between "wind" and "prey". The female courtship vibrations lack the syllable structure and are temporally more irregular than the male signal, with a broader frequency spectrum and the main components between 20 Hz and 50 Hz.

According to numerous experiments, the spiders do indeed distinguish between vibrations caused by wind, prey, and the sexual partner, respectively. There is also good evidence that they actually use the above-mentioned characteristics to accomplish this. In the present context, this implies that prey-catching behavior can be elicited significantly more often with broad-band signals than with sine wave vibrations. The results of neurophysiological experiments are consistent with this. The sensory cells of the metatarsal vibration receptor
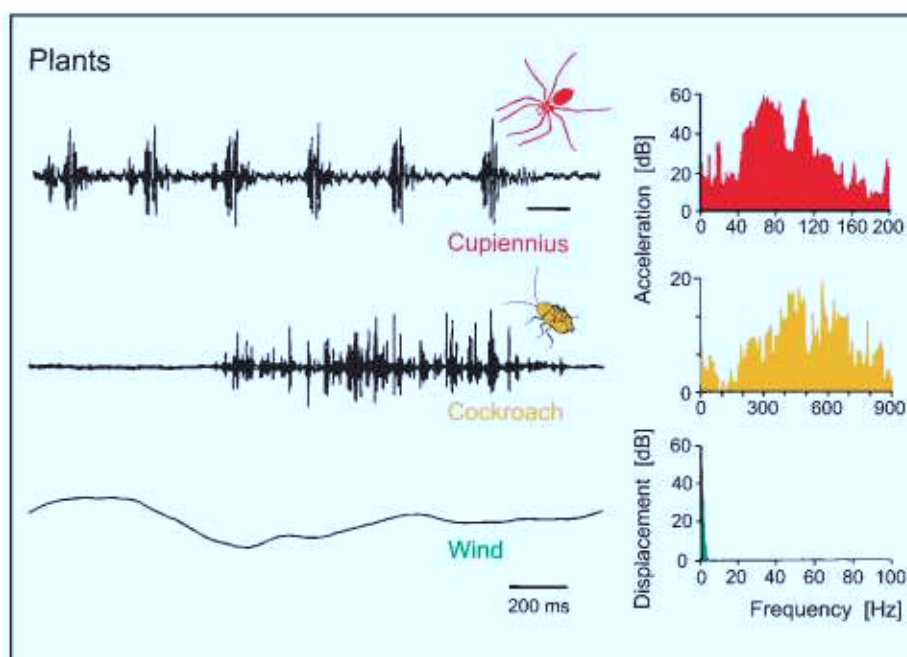

Fig. 6. The vibrational environment of *Cupiennius* in its natural habitat when sitting on its dwelling plant. *Left:* oscillograms, *right:* frequency spectra of typical signals. From top to bottom: male courtship vibration, prey (cockroach) crawling on the plant, and vibrations due to wind (after Barth, 1986).

are significantly more sensitive (by as much as about 10 dB) to narrow-band vibrations (bandwidth 1/3 octave, Q = 0.35) than to pure sinusoidal stimulation. The same applies to vibration sensitive interneurons in the CNS, where the difference can be as great as 20 dB (Speck-Hergenröder and Barth 1987). Another argument supporting the idea that peripheral sensory filtering reflects behavioral needs, is provided by the shape of the threshold curves of the slits of the metatarsal organ. The slits all behave like high-pass filters. Whereas they are relatively insensitive up to about 40 Hz (in some slits only 1 Hz or 20 Hz), their sensitivity increases rapidly towards higher frequencies. In more practical terms this means that at low frequencies the tarsus must be displaced by 10^{-2} to 10^{-3} cm in order to elicit a response, while at higher frequencies this value falls by up to 40 dB per decade, reaching 10^{-6} to 10^{-7} cm (10 Å) at 1 kHz (Barth and Geethabali 1982). All available information suggests that the primary sensory cells block the low frequencies typical of background vibrations. They seem to be the first part of a neuronal two-stage filter and followed by vibration sensitive interneurons which in all our experiments invariably showed threshold curves with a well pronounced optimum in the low (ca. 100 Hz), middle or high frequency range, picking out the biologically relevant signals from the mixture of frequencies contained in a vibratory stimulus (Barth, 1998).

The remarkable absolute sensitivity of the spider vibration receptor as such is of course not only of academic interest, but highly relevant in regard to the range of a sensory system. Here is another parameter in the sensory periphery relevant for our understanding of behavior. When knowing (*a*) the intensity and frequency components of the natural signals originally emitted and (*b*) the transmission properties of typical "*Cupiennius* plants" in addition to the threshold curves of the primary sensory cells, the range of vibratory signals can be determined. This was done in some detail with regard to the vibratory signals used by *Cupiennius* to communicate during courtship (reviews: Barth, 1997, 2001). The distance record for courtship communication in the field so far is 3.8 m. It was measured in Costa Rica with a male and female *C. coccineus* sitting on a banana plant. Such remarkable distances to a large degree rely on the fact that the metatarsal organs of spiders are among the most sensitive vibration receptors in the animal kingdom.

Air movements

In *Cupiennius* (unlike in orb weavers which need web vibrations as indicators of an insect caught in the web and thus approachable) prey-catching behavior can be easily elicited by air movements alone. A hungry spider jumps towards a buzzing fly held by the experimenter nearby (Fig. 7). In the wild, why doesn't the spider ever jump into the air and try to catch the ever present wind? To answer this question one first needs to know in more detail the kind of airflow fields *Cupiennius* encounters in its habitat. It will then turn out that properties of the sensory periphery again reflect properties of biologically relevant stimuli.

When darkness has fallen and *Cupiennius* has left its retreat to prey, typically the air is still warm and damp

Fig. 7. Airflow stimuli and prey capture behavior. *Left:* Sequence of video frames showing the spider's reaction to the airflow produced by a fly flying on a leash (modified from Brittinger 1998). *Middle:* Spectra of the airflow signal behind a tethered flying fly at increasing distance from the fly (modified from Barth and Höller, 1999). *Above right:* Characteristic spectrum of airflow measured above the spider sitting on its dwelling plant after sundown (after Barth et al., 1995).
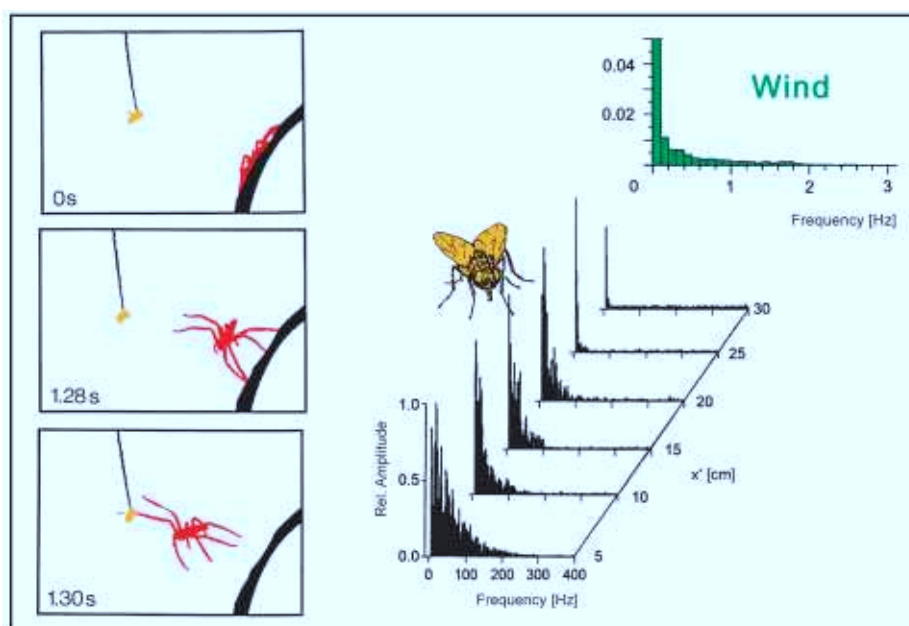
but the air movement is much slower than during daylight and also much steadier with a prominent reduction of the likelihood of gusts (Fig. 7). Measurements of the wind above spiders waiting for prey on their customary plants in Costa Rica during their nighttime activity period revealed the following. Flow velocities typically are below 0.1 m/s and r.m.s. values (as a measure of fluctuations) below 15%. Velocities of up to 0.4 m/s were only observed rarely. The background flow is dominated by frequencies below 10 Hz and characterized by a remarkably narrow frequency spectrum (Barth et al., 1995), strongly reminding of the abiotic plant vibrations (Fig. 6). One important advantage that *Cupiennius* obtains by being active at night becomes obvious when the characteristics of the background flow are compared to those of a typical prey signal.

Taking the fly signal as an example, which so promptly elicits prey capture behavior, the following properties are likely to be typical features of airborne prey signals in general. The downward directed airstream representing the fly signal reaches velocities of up to about 1 m/s, 4 to 7.5 cm behind and below the fly. The fluctuations in local mean velocity are of the order of 25%, but sometimes up to 56%, as compared to 2 to 3% of the undisturbed background. The frequencies produced by the fly are in the region of 100 Hz. However, the proportion of high frequencies in the spectrum rapidly changes with distance. At a distance of 25 to 30 cm from the fly the spectrum of the airflow very much resembles that of the background flow (Fig. 7; Barth and Höller, 1999).

Remarkably, this is also the distance at which *Cupiennius* does not react with approach behavior to the airflow signal of a fly anymore. The maximal distances from which a reaction can be elicited depend on the exact position and orientation of the signal source and vary between about 17 and 27 cm. The spider "sees" with its trichobothria equally well in all horizontal directions (Brittinger, 1998; Barth 2001). This nicely corresponds to the distributed arrangement of the flow sensors on the legs and pedipalps all around the spider's body. After ablation of the trichobothria *Cupiennius* does not react anymore.

The "mechanical" range of a single trichobothrium (taking the deflection of its shaft as a measure) when stimulated with the fly signal also used in the behavioral experiments, is 50 to 70 cm. Its "physiological" range (indicated by the discharge of action potentials) agrees with this finding. Why then is it that the spider does not jump towards a fly more than about 25 cm away? We assume that the spider recognizes the changes in the signal which occur with increasing distance from the signal source. At a distance of 25 cm the airflow resembles background flow and thus has lost its behavioral significance. In addition, a signal from that

far away has taken several seconds to arrive at the spider, so that an attempted prey capture hardly has a chance of success. It would probably also take the spider too long to approach the prey.

Physiologically, the receptor cells of single trichobothria are tuned to a frequency range between 50 and 120 Hz (in the coresponding experiment the hair is directly coupled to a vibrator) which agrees with important components of the air currents produced by flying insects (Barth and Höller, 1999). Remarkably, this is independent of trichobothrium length. The differences in frequency tuning of hairs of different length found under natural stimulus conditions (ranges between 40 and 600 Hz) are mainly due to reasons of fluid mechanics (see above).

Apart from their frequency tuning and absolute sensitivity, it is the strictly phasic response behavior of the trichobothria which seems to reflect properties of the biologically relevant stimuli. Trichobothria are velocity (and acceleration) sensitive, which is no surprise when considering that it is the frictional forces in the airflow which drive them. The receptor cells exclusively respond to the movement of the hairs, not however to static deflection. Likewise, interneurons in the spider CNS were found to predominantly respond to the sudden increases of flow velocity (Friedel and Barth, 1997). Remembering the properties of the prey signal, we conclude that the trichobothrial system is excellently suited to encode its characteristic highly fluctuating time course. According to the responses of primary sensory cells like that shown in Figure 8, this is indeed the case.

Courtship

In *Cupiennius* the time the male and the female spend together is less than one hour. After this period the sexual partners go their separate ways as before. Their brief meeting, however, is full of ingenious mechanisms which together ensure reproduction. On the way to copulation it is again the vibration sense which plays a prominent role because there is a highly developed vibratory communication between the sexes (review: Barth, 1997, 2001).

Communication is initiated by the female. Her dragline contains a sexual pheromone identified as the S-dimethyl ester of citric acid (Tichy et al., 2000; Schulz et al., 2000). When the male encounters a female dragline on his nocturnal wanderings, he examines it carefully with the chemoreceptive hairs on his pedipalps, assumes the courtship posture (slightly raising his body), and finally starts to produce vibrations by oscillatory up-and-down movements of the opisthosoma. The substrate vibrations thus induced in the plant through the legs are propagated through the plant as

bending waves. Their mean attenuation of about 0.3 dB/cm is comparatively small, an important reason being that they are of low frequency. As a consequence, the male vibrations reach the female at surprisingly long distances. The maximum so far observed by us on a banana plant in Costa Rica was 3.8 m. The female responds to the male with her own vibrations within a narrow time window of about 1 s (Fig. 9). After having received the presumptive partner's signal, the male starts approaching the female while their reciprocal vibratory "flirting" continues.

As mentioned earlier, the male opisthosomal vibratory signals are characterized by a distinct temporal pattern which not only sets it apart from background and prey vibrations but also plays a crucial role in species identification by the female and thus in reproductive isolation. Accordingly, the temporal (not so much the spectral) patterns of the male vibratory signals are species specific. In *C. salei*, individual packets of up to 50 syllables are separated by silent pauses lasting up to 10 s. On average, syllable duration is 100 ms and pause duration in between successive syllables is 250 ms. In species living sympatrically like *C. getazi* and *C. coccineus* the relevance of reproductive isolation is obvious. Hence, courtship signals of the spider's own species must be distinguished not only from prey and

background vibrations, but also from the courtship vibrations of other *Cupiennius* species.

After having demonstrated behaviorally that *Cupiennius* can indeed do this and after having identified various properties of the female releasing mechanism, the question was, how the female vibration receptor responds to the male signal and, more precisely, how well the temporal patterns are encoded by it. As it turns out, the metatarsal organ is well tuned to certain parameters of the male signal and there is considerable filtering which in some importants respects closely matches the results of behavioral experiments (Baurecht and Barth, 1992, 1993).

Amplitude

The stimuli reaching the metatarsal organ vary greatly in amplitude. This is not only due to the varying vigor of the signal sender, but also to varying geometric and other conditions of stimulus transmission to the female receiver through the plant. As was to be expected from this, signal amplitude is among the less influential signal parameters in behavior. Likewise, individual slits of the metatarsal vibration receptor can cover the entire natural range of acceleration amplitudes of about 3–1000 mm/s^2. They accomplish this by a logarithmic relationship between syllable acceleration amplitude

Fig. 8. Response of trichobothrium to airflow stimulus produced by flying fly (see Fig. 7). *Top:* Arrangement of trichobothria on walking leg of *Cupiennius salei*. The examined trichobothrium belongs to group D1. *Middle:* The fly signal given as airflow velocity. *Bottom:* Response (original recording of action potentials and discharge frequency) of one of the sensory cells associated with the trichobothrium (after Barth and Höller, 1999).
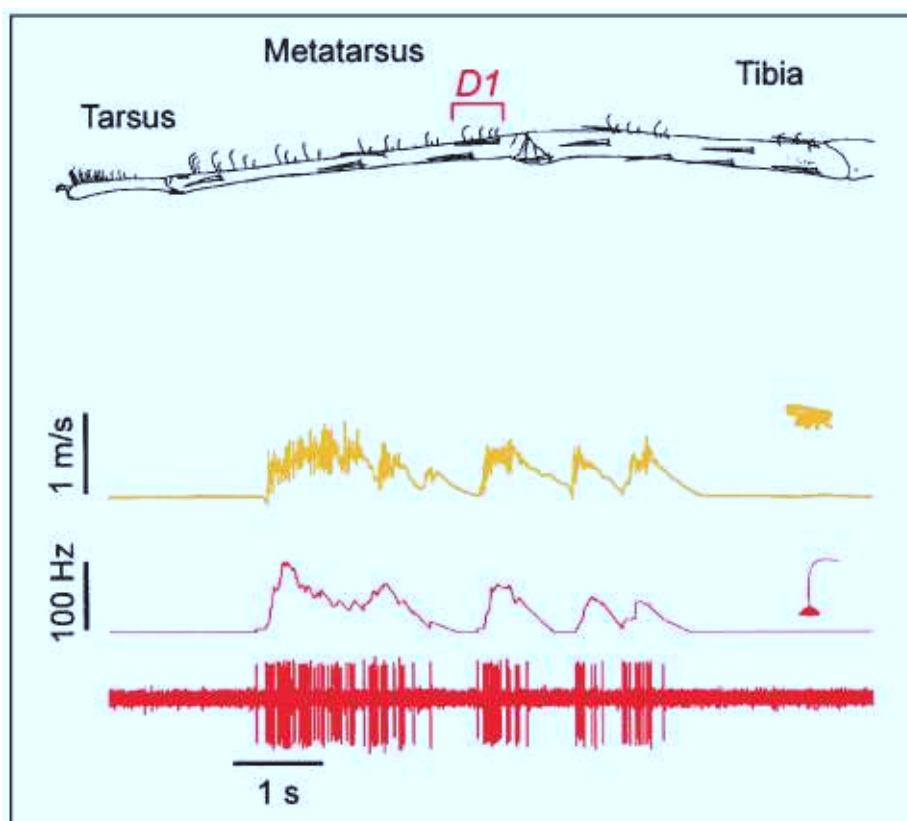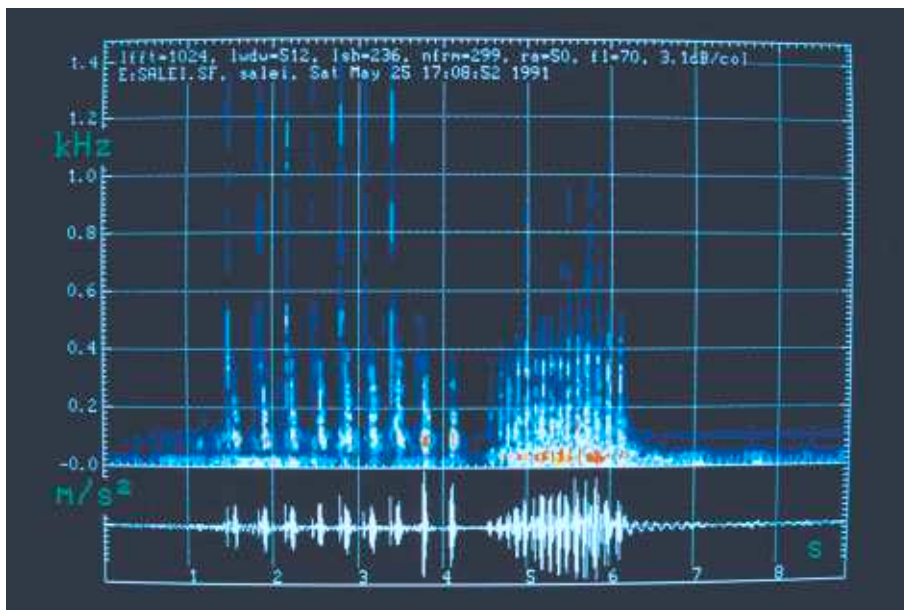
Fig. 9. Vibratory signals used by *Cupiennius salei* to communicate with its sexual partner during courtship. Oscillogram (lower trace, acceleration of plant leaf) and "sonagram" (vibrogam) of a series of 9 male syllables followed by a female vibratory response. Note the energy maxima (red areas) at very low frequencies (male: around 100 Hz; female: around 40 Hz; data from D. Baurecht; Barth, 2001).

and discharge rate. Remarkably, the response threshold both for the female spider's behavior and the individual slit is about 8 mm/s². At the other end of the scale, that is at stimulus amplitudes greater than about 1.000 mm/s² (and thus exceeding the highest naturally occurring amplitudes), the synchronization between the receptor response and the male signal rapidly decreases. This implies that the receptor doesn't precisely copy the signal's temporal structure anymore (Fig. 10). The reason is an increasing number of action potentials *between* the syllables, that is during the silent period of the vibratory signal. We assume that the sensory misinterpretation at too-high amplitudes is an important reason for the marked decline in female behavioral responses in the same amplitude range. The argument is strengthened by the finding that the vibration signals produced by scratching and drumming with the pedipalps which contain higher frequency components than the opisthosoma signals and have differing ethological significance, are to a great extent processed separately from the opisthosoma signals by the female's metatarsal organ. Remarkably, the response curves of the corresponding small slits of the metatarsal organ are not logarithmic but linear between 10 and 10,000 mm/s² (Fig. 11; Baurecht and Barth, 1992, 1993).

Temporal pattern

Important filter properties of a sensory organ may not at all be obvious from its responses to "clean" laboratory stimuli such as simple sinusoidal vibration in the given case. The special behavioral significance of the temporal pattern of the male courtship signal has already been mentioned. Is there a particular match between the response characteristics of the metatarsal organ and this pattern?

Stimulation of the female vibration receptor with entire natural male courtship series consisting of many syllables indicates that this is indeed the case (Baurecht and Barth, 1993). (1) As the series proceeds, the number of action potentials per syllable decreases. The quality of the representation of the temporal pattern (syllables, pauses), however, is maintained. (2) When using series with increasing numbers of syllables, it turns out that the signal-to-noise ratio becomes larger, because the synchronization of stimulus and excitation improves progressively and the number of nerve impulses between syllables decreases. (3) The end of the series of syllables is especially marked by a poststimulatory depression of the receptor response which falls below the spontaneous discharge rate. Remarkably, behavioral experiments had shown that a series must consist of at least three syllables to cause a female response in 50% of cases (with the response rate increasing until the series contains 12 syllables), and also that only syllables grouped to form series, that is packets of syllables, effectively elicit a female response (Schüch and Barth, 1990).

What do we learn from this?

1. The sensory world of *Cupiennius* and of many other spiders (though not all) is to a high degree dominated by mechanical stimuli. The ability to detect cuticular strains, tactile stimuli, air movements, and substrate vibrations is exquisite. It provides the spider with highly resolved pictures of a multitude of mechanical events.
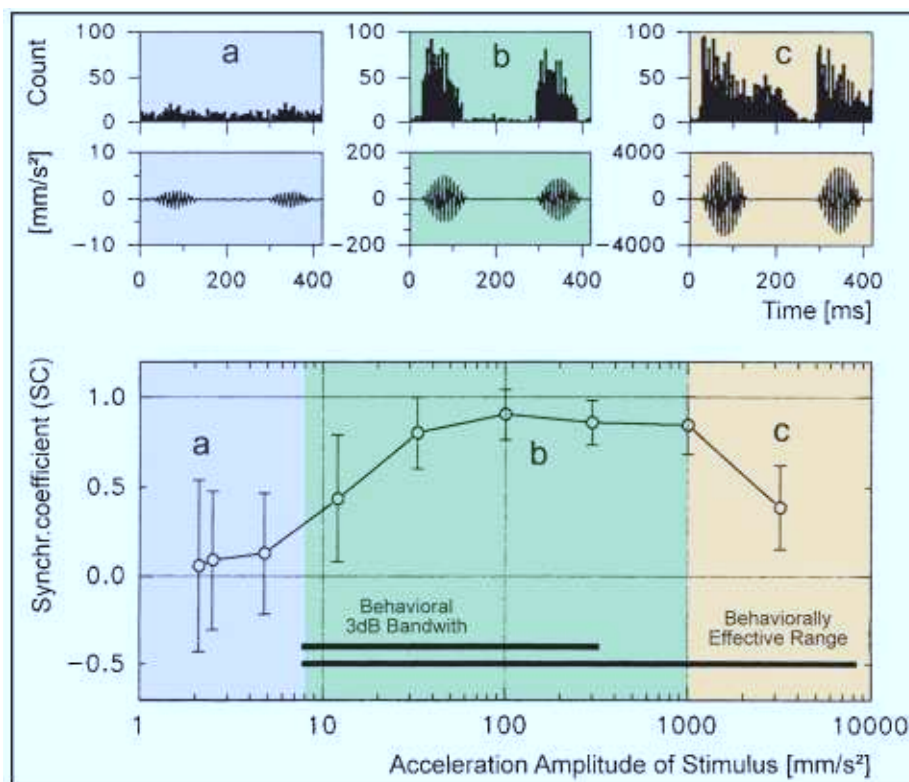
Fig. 10. *Top:* Response of one of the long slits (slit 2, PST histograms) of a female metatarsal lyriform organ of *Cupiennius salei* to synthetic male courtship vibrations to show dependence of copying properties on signal (acceleration) amplitude. *Bottom:* Synchronization coefficient *SC* as a measure of the copying quality. *SC* = 1 indicates perfect copying of syllable and pause duration, *SC* = 0 indicates no copying. Note relationship between receptor response and behavioral response (after Baurecht and Barth, 1993).
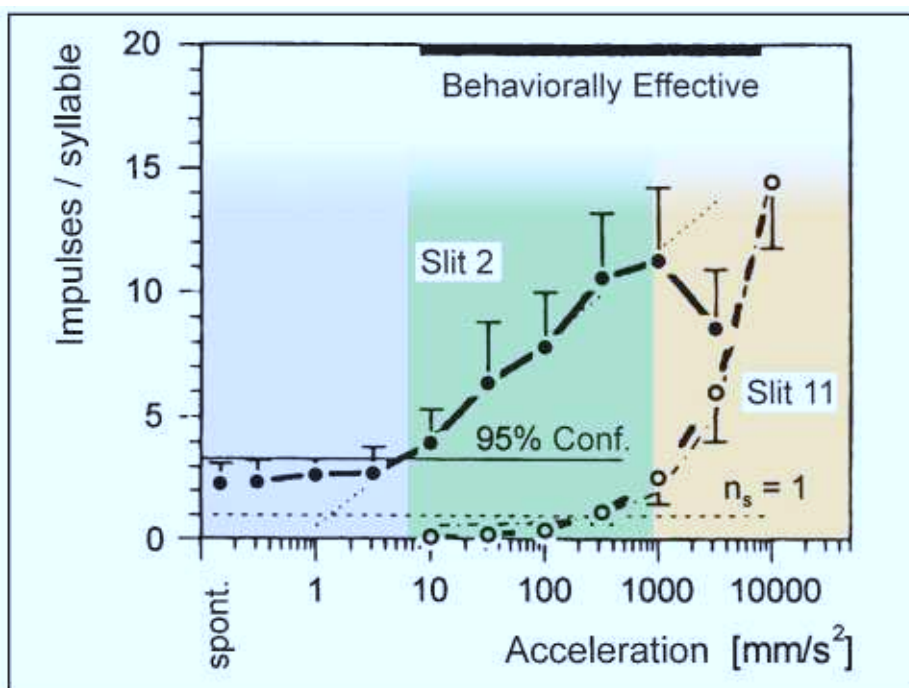

Fig. 11. Difference in response characteristics of long slit 2 and short slit 11 of female metatarsal organ to vibrational stimuli (male syllables) of increasing intensity (acceleration amplitude). 95% confidence interval of spontaneous discharge frequency denotes threshold of slit 2. Note logarithmic relationship between stimulus and response of slit 2 between 3 and 1000 mm/s^2 and linearity of same relationship in case of slit 11 over the whole range tested (after Baurecht and Barth, 1993).

The corresponding sensors are all widely distributed over the body surface allowing for adequate spatial resolution.

2. Neurobiology starts way out in the periphery. By their well developed filter properties, the sensors already considerably influence behavior. It seems that this is one of the reasons why arthropods perform so well behaviorally despite the small size of their brain. The spider's sensory periphery not only is "clever", but also has at its disposal an enormous number of sensory

cells, which by far exceeds that of the neurons in the central nervous system (CNS).

3. Sensors are not the transparent windows to the world as we tend to consider them. They rather inform the CNS only or very preferentially about the biologically (behaviorally) relevant stimulus patterns.

4. Evolutionary processes are remarkably creative. Permanent "quality control" through natural selective pressures over millions of years often led to masterpieces of "engineering". Spider senses exemplify this nicely. This is fascinating in its own right, but also stresses the potential lying in a close cooperation between biologists and engineers. Artificial micro- and nanosensors have gained enormous importance in industry, bioengineering, medicine, robotics, manufacturing and intra- and extraterrestrial exploration. What the biologists can offer here are not ready-made instructions of how to build and manufacture a sensor, but their familiarity with a treasure house of inspiring solutions to a wide spectrum of sensory problems. The most valuable input from engineering to sensory biology, on the other hand, is the application of computational skills and mathematical quantification (Barth et al., 2002).

5. Obviously, biology is also fascinating in areas where its questions are not primarily derived from a molecular, but from an organismic point of view. Karl von Frisch was an unrivalled master of this kind of approach. His discoveries inspired many fields of zoological research now flourishing. Comparative sensory biology is the most prominent among them and still offers endless opportunities to celebrate the ingenuity of life.

Acknowledgements

References

Barth, F. G. 1986. Vibrationssinn und vibratorische Umwelt von Spinnen. Naturwissenschaften 73 (9): 519–530.

Barth, F. G. 1997. Vibratory communication in spiders: Adaptation and compromise at many levels. In: M. Lehrer (ed.) Orientation and Communication in Arthropods. Birkhäuser, Basel: 247–272.

Barth, F. G. 1998. The vibrational sense of spiders. In: Hoy RR, AN Popper, RR Fay (eds.) Springer Handbook of Auditory Research. Comparative Hearing: Insects. Springer, New York: 228–278.

Barth, F. G. 2000. How to catch the wind: spider hairs specialized for sensing the movement of air. Naturwissenschaften 83: 51–58.

Barth, F. G. 2001. Sinne und Verhalten: aus dem Leben einer Spinne. Springer Verlag, Berlin. English edition 2002. A Spider's World: Senses and Behavior. Springer Verlag, Berlin.

Barth, F. G. and J. Bohnenberger. 1978. Lyriform slit sense organ: threshold and stimulus amplitude ranges in a multi-unit mechanoreceptor. J. Comp. Physiol. 125: 37–43.

Barth, F. G. and D. Cordes. 1998. *Cupiennius remedius* (Araneae, Ctenidae), a new species in Central America, and a key for the genus *Cupiennius*. J. Arachnol. 26: 133–141.

Barth, F. G. and H.-E. Dechant. 2002. Arthropod cuticular hairs: tactile sensors and the refinement of stimulus transformation. In: Barth F.G., J.A.C. Humphrey, T.W. Secomb (eds.) Sensors and Sensing in Biology and Engineering. Springer Verlag, Wien: 159–171.

Barth, F. G. and Geethabali. 1982. Spider vibration receptors. Threshold curves of individual slits in the metatarsal lyriform organ. J. Comp. Physiol. A 148: 175–185.

Barth, F. G. and A. Höller. 1999. Dynamics of arthropod filiform hairs. V. The response of spider trichobothria to natural stimuli. Phil. Trans R. Soc. Lond. B 354: 183–192.

Barth, F. G. and H.-P. Pickelmann. 1975. Lyriform slit sense organs. Modelling an arthropod mechanoreceptor. J. Comp. Physiol. 103: 39–54.

Barth, F. G., E. Ficker and H.-U. Federle. 1984. Model studies on the mechanical significance of grouping in compound spider slit sensilla. Zoomorphology 104: 204–215.

Barth, F. G., U. Wastl, J. A. C. Humphrey and R. Devarakonda. 1993. Dynamics of arthropod filiform hairs. II. Mechanical properties of spider trichobothria (*Cupiennius salei* KEYS.) Phil. Trans. R. Soc. Lond. B 340: 445–461.

Barth, F. G., J. A. C. Humphrey, U. Wastl, J. Halbritter and W. Brittinger. 1995. Dynamics of arthropod filiform hairs. III. Flow patterns related to air movement detection in a spider (*Cupiennius salei* KEYS.). Phil. Trans. R. Soc. Lond. B 347: 397–412.

Barth, F. G., J. A. C. Humphrey and T. W. Secomb (eds.). 2002. Sensors and Sensing in Biology and Engineering. Springer Verlag, Wien (in print).

Baurecht, D. and F. G. Barth. 1992. Vibratory communication in spiders. I. Representation of male courtship signals by female vibration receptor. J. Comp. Physiol. A 171: 231–243.

Baurecht, D. and F. G. Barth. 1993. Vibratory communication in spiders. II. Representation of parameters contained in synthetic male courtship signals by female vibration receptor. J. Comp. Physiol. A 173: 309–319.

Bohnenberger, J. 1981. Matched transfer characteristics of single units in a compound slit sense organ. J. Comp. Physiol. A 142: 391–401.

Blickhan, R. and F. G. Barth. 1985. Strains in the exoskeleton of spiders. J. Comp. Physiol. A 157: 115–147.

Brittinger, W. 1998. Trichobothrien, Medienströmungen und das Orientierungsverhalten von Jagdspinnen (*Cupiennius salei* Keys). Dissertation, University Vienna.

Dechant, H.-E., F. G. Rammerstorfer and F. G. Barth. 2001. Arthropod touch reception: stimulus transformation and finite element model of spider tactile hairs. J. Comp. Physiol. A 187: 313–322; see also erratum p. 851.

Friedel, T. and F. G. Barth. 1997. Wind-sensitive interneurones in the spider CNS *(Cupiennius salei)*. Directional information processing of sensory inputs from trichobothria on the walking legs. J. Comp. Physiol. A 180: 223–233.

Humphrey, J. A. C., R. Devarakonda, J. Iglesias and F. G. Barth. 1993. Dynamics of arthropod filiform hairs. I. Mathematical modelling of the hair and air motions. Phil. Trans. R. Soc. Lond. B 340: 423–444.

Humphrey, J. A. C., F. G. Barth and K. Voss. 2001. The motion-sensing hairs of arthropods: using physics to understand sensory ecology and adaptive evolution. In: Barth F.G., A. Schmid (eds.). The Ecology of Sensing. Springer Verlag, Berlin: 105–125.

Humphrey, J. A. C., F. G. Barth, M. Reed and A. Spak. 2002. Arthropod motion sensing hairs: biological models for micro-electromechanical sensors. In: Barth F.G, J.A.C. Humphrey, T.W Secomb (eds.). Sensors and Sensing in Biology and Engineering. Springer Verlag, Wien: 129–144.

Keyserling, E. 1877. Über amerikanische Spinnenarten der Unterordnung Citigradae. Verh. zool-bot. Ges. Wien 26: 609–708.

Lachmuth, U., M. Grasshoff and F. G. Barth. 1984. Taxonomische Revision der Gattung *Cupiennius* SIMON 1891 (Arachnida, Araneae, Ctenidae). Senck. biol. 65: 329–372.

Schüch, W. and F. G. Barth. 1990. Vibratory communication in a spider: female responses to synthetic male vibrations. J. Comp. Physiol. A 166: 817–826.

Schulz, S., M. Papke, H. Tichy, E. Gingl and R. Ehn. 2000. Identification of a new sex pheromone from silk dragline of the tropical hunting spider *Cupiennius salei*. Angew. Chem. 39: 4339–4341.

Shimozawa, T., J. Murakami and T. Kumagai. 2002. Cricket wind receptors: Thermal noise for the highest sensitivity known. In: Barth F. G., J. A. C. Humphrey, T. W. Secomb (eds.). Sensors and Sensing in Biology and Engineering. Springer Verlag, Wien: 145–157.

Speck-Hergenröder, J. and F. G. Barth.1987. Tuning of vibration sensitive neurons in the central nervous system of a wandering spider, *Cupiennius salei* Keys. J. Comp. Physiol. A 160: 467–475.

Stokes, G. G. 1851. On the effect of the internal friction of fluids on the motion of pendulums. Trans. Camb. Phil. Soc. 9: 8ff (reprinted in: Mathematical and Physical Papers, Vol III, pp. 1–141. Cambridge Univ. Press 1901).

Thurm, U. 1982. Grundzüge der Transduktionsmechanismen in Sinneszellen. Mechano-elektrische Transduktion. In: Hoppe W., W. Lohmann, H. Markl, H. Ziegler (eds.). Biophysik. Springer Verlag, Berlin: 681–696.

Tichy, H., E. Gingl, R. Ehn, M. Papke and S. Schulz. 2000. Female sex pheromone of a wandering spider (*Cupiennius salei*). Identification and sensory reception. J. Comp. Physiol. A 187: 75–78.