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Spider mechanoreceptors

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Spiders have highly developed mechanosensory systems, some of which provide access to forms of stimulation alien to our own sensations. Studies of hair-shaped air movement detectors (trichobothria) and tactile sensors have uncovered an outstanding refinement of the processes of stimulus uptake and stimulus transformation, which reflect details of both stimulus physics and behavioral significance. They also emphasize the potential contained in the seemingly simple Bauplan of arthropod cuticular hairs. Embedded into the spider exoskeleton are several thousands of strain detectors (slit sensilla) measuring compressive exoskeletal strains induced by various forms of loads and forces. A compound slit sensillum (lyriform organ) on the leg has become an important model system for studies of mechanoreceptor primary processes at the cellular and membrane level.

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Current Opinion in Neurobiology 2004, **14**:415–422

This review comes from a themed issue on
Sensory systems
Edited by Catherine Dulac and Benedikt Grothe

Available online 22th July 2004

0959-4388/\$ – see front matter
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DOI 10.1016/j.conb.2004.07.005

Abbreviations

GABA γ -aminobutyric acid

Introduction

Sensory systems are not meant to provide organisms with a complete picture of physical reality. Instead, they inform the animal of the biologically relevant events in its outside and inside environments. Keeping data out of the nervous system is as important a function of sensory systems as providing the relevant information. Thus, sensory systems are an organism's windows to the world in a very limited sense only, their transparency being highly restricted. Sensory systems are 'designed' by evolutionary constraints in a way that ensures survival and reproduction by enabling the organism to behave in its species-specific manner in its species-specific environment.

Accordingly, important properties of sense organs reflect properties of the stimuli they are adapted to

monitor. Less obvious, however, is the degree of detail to which this is true. Typically, the details of the physics involved in stimulus transformation are far from trivial. They can be fully appreciated only by a combination of behavioral studies revealing the biologically relevant stimulus patterns and a corresponding analysis of the filter properties of the sensors. Recent studies on spider mechanoreceptors that bring together technical biology with electrophysiology and behavioral studies demonstrate the value of this approach. They also show that to a particularly high degree the selectivity and specificity of a sensor resides in the non-nervous structures of stimulus transformation, rather than in the transduction process proper.

The spider mechanoreceptors I discuss here are: first, hairs sensitive to medium flow, also called trichobothria and analogous to insect filiform hairs; second, hairs sensitive to touch; and third, slit sensilla, which are 'embedded sensors' measuring strains in the cuticular exoskeleton.

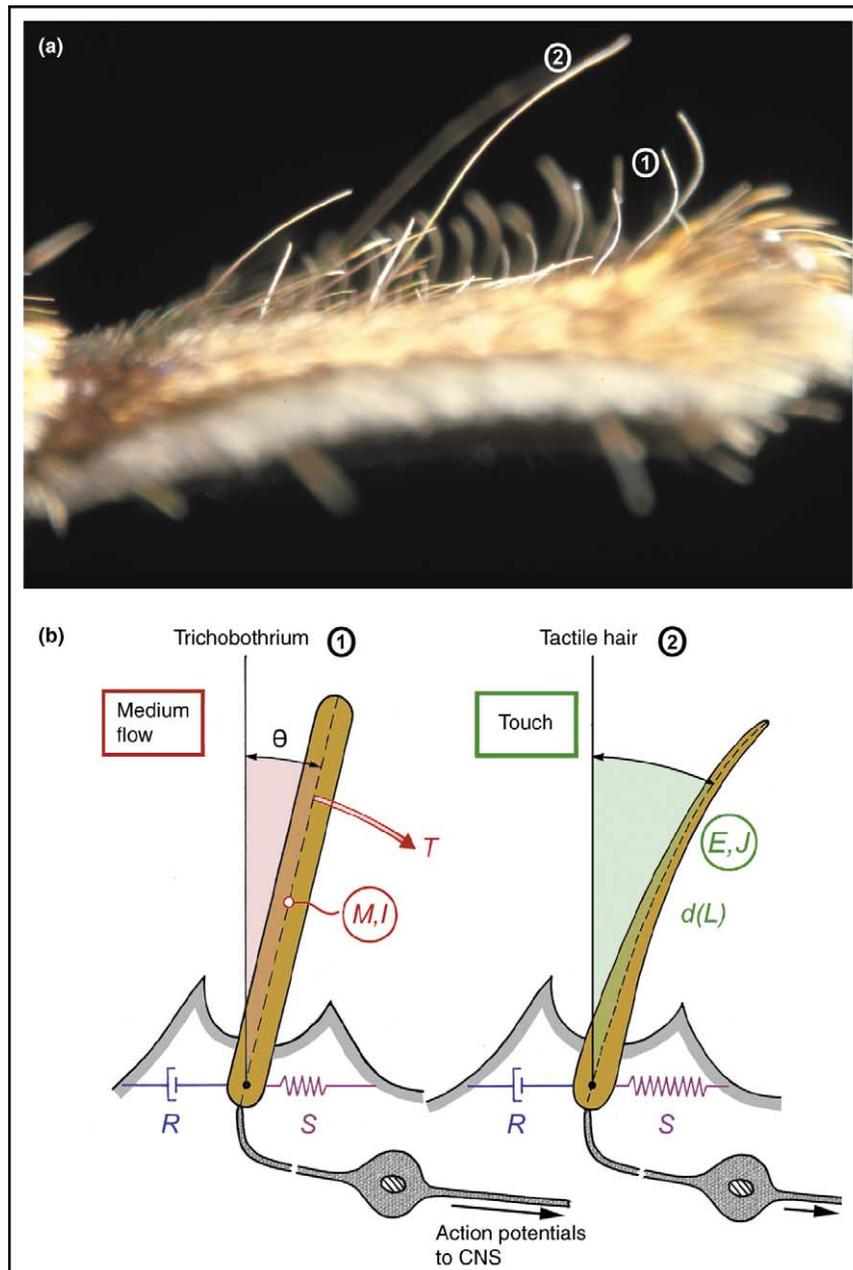
Medium flow sensors

Trichobothria are exquisitely fine hairs on spider legs (Figure 1a). They are 0.1 to 1.4 mm in length and around 10 μ m in diameter at their base [1–3,4**]. The flexibility of their anchorage in the exoskeleton exceeds that of all other hair sensilla. *Cupiennius salei*, a ctenid spider, has about 90 trichobothria on each of its legs that are driven by the frictional forces of airflow around them. Trichobothria have become model movement sensors. The outstanding sensitivity of the trichobothria suggests perfected interaction between the moving air and the hair. The underlying physics is to a large extent in the domain of fluid mechanics.

Absolute sensitivity

Recent studies of spider flow sensors (for a review please see Barth [4**]) have brought together mathematical modeling, numerical analysis [5,6,7**,8], both morphological and biomechanical work [3,9], and electrophysiological and behavioral experiments [10–12]. They have revealed an absolute sensitivity [7**] that is among the highest sensitivities known of a biological sensor and which was also found for analogous filiform hairs of a cricket [13**,14]. Using a mathematical model of hair motion, the work and the far field medium velocity required to attain an imposed threshold angular displacement could be calculated. It appears that far field velocity decreases and work increases with increasing hair length. Values for work are between 2.5×10^{-20} Joules and 1.5×10^{-19} J. They are slightly less for spider trichobothria than

Figure 1



Spider hair sensilla. **(a)** A spider leg tarsus (*Cupiennius salei*) showing several air flow sensors (trichobothria) (1) on its dorsal aspect and a long tactile hair (2). **(b)** Simplified diagram to illustrate some essential differences in the mechanical behavior of hairs adapted to sense medium flow and touch. See text for explanation. Abbreviations: d , diameter; E , Young's modulus; θ , deflection angle; I , inertia; J , second moment of area; L , length of hair shaft; M , mass; R , inertial resistance; S , elastic restoring force. Modified with permission from Barth and Dechant [18*].

for cricket filiform hairs [7**]. These are remarkable values, corresponding to fractions of the energy contained in a single quantum of green light [13**,14]. According to Shimozawa *et al.* [13**] in cricket filiform hairs the minimum amount of mechanical energy that can elicit an action potential in the sensory cell is in the order of

$k_B T$ (k_B , Boltzmann constant; T , temperature; 4×10^{-21} J at 300 °K). Thus, at threshold this sensillum works near the thermal noise of Brownian motion. It demonstrates signal enhancement by stochastic resonance [13**,15]. Clearly, these arthropod flow sensors operate at the limit of the physically possible, their sensitivity by

no means being inferior to that of the receptor cells of the human eye and at least equal to those of the ear, our own most sensitive sense organ [16,17].

'Design' principles

The equations given by Humphrey *et al.* [5,7**] calculate the behavior of a forced, damped, harmonic rod-like oscillator. They include the added or virtual mass, a factor much more important in water than in air (Table 1; [8]), and quantify the dependence of hair deflection angle, velocity, acceleration, and work on all the physical parameters that affect these parameters. In this respect, the 'design' principles of these sensors cannot only be described in a way that is meaningful for an engineer; they also tell the biologist how natural selective pressures might have affected the evolution of different hair parameters [6,7**,18*]. The elastic torsional restoring constant S at the base (joint) is in the order of only 10^{-12} Nm/rad

hair deflection. The inertial resistance R (damping constant of the articulation) is in the order of only 10^{-15} Nms/rad (Figure 1b). Values of S known for spider and fly tactile hairs are larger by three to four powers of ten [19,20].

Hair length and boundary layer

Spider trichobothria form groups of sensors that vary conspicuously in length [3]. In air, varying the length indeed turns out to be the most effective way of modifying the mechanical frequency response of a hair. The reasons for this are not simply changes in mass and elasticity of the hair suspension that accompany the variation in hair length. Rather, they are of fluid mechanical origin. The range of trichobothria lengths matches the actual size of the boundary layers at biologically relevant flow frequencies [3]. Boundary layer thickness limits the lower cut-off frequency of their mechanical response. Because boundary layer thickness decreases with increasing flow frequency, hair length in this way correlates with the mechanical frequency response [21]. On a spider leg, it varies roughly from 2600 μm to 600 μm within the frequency range of 10 Hz to 960 Hz. Short hairs increasingly remain in a zone of reduced flow velocity at low frequencies [3,5]. Interestingly, flow sensitive hairs of various terrestrial arthropods all show the same range of length, which probably reflects this relationship. The mathematical model also permits predictions regarding the geometry and mechanical properties of flow sensors in water (Table 1; [8]) and reasonable interpretations of the impact of different hair parameters on the evolution of flow sensitive hairs [6]. The detection of hydrodynamic stimuli by 'hairs' is widespread among aquatic animals, including crustaceans [22,23]. From the analysis of the spider case, media-dependent differences in stimulation physics can be predicted. These, in turn, must be expected to influence the mechanical and morphological properties of flow sensors in water (Table 1; [4**,8]).

Sensor arrays

What advantages do the conspicuous groups formed by spider trichobothria [3,4**] have over individual sensors? First, they cover a larger frequency range with high sensitivity. Second, theoretically, they can be used for a spectral analysis of a stimulus, provided that the central nervous connections permit such an operation. Interestingly, the physiological tuning of spider trichobothria seems to be the same, independent of hair length [10], which underlines the relevance of the differences in mechanical properties. In cricket filiform hairs, the torsional resistance within the hair base changes with hair length, therefore matching the frictional resistance at the air-hair contact. Such impedance matching maximizes energy transmission from the moving air to the sensory dendrite [13**]. It was recently found that there is no relevant viscous-mediated coupling among the grouped

Table 1

Hairs detecting water movement.

1. Boundary layer thickness, δ

$$\delta_{\text{water}} = 0.22 \times \delta_{\text{air}}$$

$$[\delta = 2.54(v/f)^{0.5}]$$

the reason:

$$v_{\text{water}} < v_{\text{air}}$$

$$[v = \frac{\text{dynamic viscosity} \mu}{\text{density} \nu}]$$

2. Drag per unit length, D

$$D_{\text{water}} = 43 \times D_{\text{air}}$$

$$D = \nu \times A V^2$$

$$\text{Drag} = \text{density} \times \text{area} \times \text{velocity}^2$$

3. Virtual (added) mass, VM

* I_{eff} in water $\gg I_{\text{eff}}$ in air

[$I_{\text{eff}} = f$ (fluid density, viscosity, oscillation frequency, hair diameter and length)]

* I_{VM} dominates I_{eff} in water mainly due to much larger dynamic viscosity μ .

* Resonance frequency in water \ll resonance frequency in air

The reason:

$$\text{Resonance frequency} \sim (S/I_{\text{eff}})^{0.5}$$

Medium flow sensors in water. From the theoretical and experimental analyses of the mechanical behavior of spider air flow sensors predictions can be derived regarding the behavior of hair-shaped sensors in water, which are common to many aquatic animals [4**,8,22]. The table raises three issues. First, boundary layer thickness δ is smaller in water than in air by a factor of 0.22 because kinematic viscosity ν in water is around 20 times less than it is in air. Second, drag D per unit length of the hair is 43 times greater in water than in air because of the greater density of water. Third, the virtual or added mass VM is much more important in water than in air. It dominates the effective inertia of the hair. From the first three points and theory explained in Devarakonda *et al.* [8] it follows that flow receptors in water might be considerably shorter than those in air and still be very sensitive. Contrary to the effect of hair length, hair diameter has hardly any effect in water and the values for S and R influence the frequency tuning of a hair to a lesser extent in water than in air. Morphologically and mechanically identical hairs are tuned to much lower frequencies in water than in air [4**,8].

trichobothria of *Cupiennius*, one of the main reasons being that there are relatively large spaces of 20 to 50 hair diameters between the hairs (Bathellier B, Barth FG, Albert JT, Humphrey JAC, unpublished).

Behavioral correlates

There are important correlates between the behavioral significance of air movement stimuli in spider prey capture behavior and the sensor properties [4**,9,10]. First, typically, an effective prey stimulus such as that produced by a flying insect is highly turbulent (r.m.s. [root mean square] values around 25% up to >50%). Velocities reach values up to around 1 m/s and frequencies higher than 100 Hz. Second, flow velocities of background air movement (related to *Cupiennius*) are typically <0.1 m/s with fluctuations <15% and dominated by frequencies <10 Hz in a very narrow frequency spectrum. Third, the prey signal dramatically changes with distance and equals the background flow at a distance of about 25 cm. At this distance prey capture behavior can no longer be elicited. Fourth, physiologically, the sensory cells are tuned to frequencies between 50 Hz and 120 Hz. Their response is strictly phasic, they never respond to static deflection, which also applies to all airflow sensitive interneurons that have been recorded so far [11]. Thus, trichobothria are adapted to pick up preferentially the highly turbulent prey signals.

Tactile hairs

Sensory hairs are the most common structures used for stimulus uptake in the animal kingdom. Spiders teach us how to turn an extremely sensitive medium flow sensor into a tactile sensor, which emphasizes the potential hidden in the seemingly simple Bauplan of a hair.

Bending of the hair shaft

Some spiders are covered by many thousands of inner-vented cuticular hairs. In *Cupiennius*, their density can reach 400 per mm². When a prominent tactile hair on the tarsus of *Cupiennius* is loaded from above (the usual way of being stimulated) its shaft is both deflected and bent (Figure 1a, b). Trichobothria do not bend when deflected by airflow, primarily because of the extremely low restoring force at their articulation (spring stiffness S in the order of 10^{-12} Nm/rad); its mechanical behavior is dominated by mass M and torsional inertia I . In the tactile hairs of the same species, S is greater by four powers of ten and has to be overcome by the stimulating forces. As a consequence the mechanically dominant parameters are Young's modulus E and the second moment of area J along hair length L (Figure 1b; [18*]). When touched by an object from above, the point of load introduction increasingly shifts towards the hair base with increasing load and hair deflection. Thereby, the effective lever arm and, thus, the stimulating moment decrease. This entails several 'clever' effects. First, the hair is protected against breaking; because of its bending the hair shaft is never deflected by more than around 12° at its base and

the bending moment is limited to around 4×10^{-9} Nm (Figure 2a). Second, the mechanical working range of the tactile hair is considerably extended as compared to a rigid hair. Third, sensitivity is higher for small stimuli than for large ones. Fourth, as shown by finite element analysis, the hair shaft is a structure of equal maximal strength: critical axial stresses caused by bending are avoided by an appropriate adjustment of the cross section of the hair, and thus J along its length (Figure 2b; [18*,24]).

Scaling down the stimulus

These touch detectors teach us how to combine protection against overloading with high sensitivity for small stimuli. When probing its surroundings with its front legs in darkness, *Cupiennius* hits obstacles with its tactile hairs at velocities of up to 11 cm/s [25]. The hair forms a lever. The movement of its tip is scaled down by a factor of around 750:1 (even without considering bending) close to the dendrite tips, with a corresponding amplification of force. The dendrites end close to the axis of rotation where movement is minimal. At spiking threshold the estimated dendrite sheath displacement is around 0.05 μm, and the force is in the order of 0.4 to 4×10^{-6} N [25,26], which is about two orders of magnitude more than estimated for cricket flow sensors (1 to 5×10^{-8} N) [13**,14]. There are no data yet on the molecular processes of stimulus transduction, such as those for *Drosophila* bristles [27]. Clearly, however, the mechanical scaling down of the stimulus is only possible because of the extreme mechanosensitivity of the dendritic membrane channels.

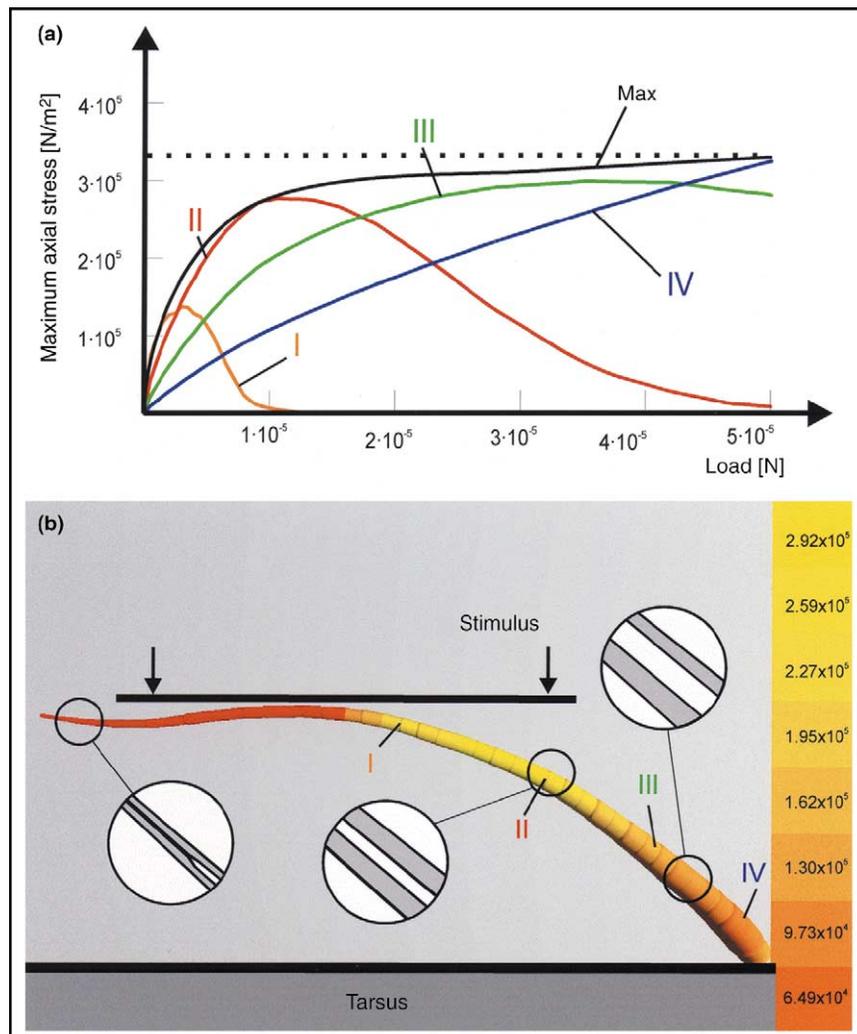
Information on the mere presence of stimulus

Electrophysiological experiments demonstrate that the sensory cells supplying the tactile hair are velocity detectors specialized to signal the mere presence of a stimulus, but not its time course and orientation in space [19]. Tactile sensing as a spatially and temporally distributed process still has not been studied in arthropods.

Strain detectors

Strain detection in arthropods is closely linked to the possession of an exoskeleton. It is a skeletal sense not found in other phyla. Spider slit sensilla represent a particularly well developed strain detecting system, which is involved in the detection of vibrations produced by mates, prey, and predators, and in the measurement of skeletal strains caused by muscular activity and hemolymph pressure [4**,28]. In recent years, one of the compound ('lyriform') slit sense organs on the spider leg has become a model case for studies of mechanoreceptor transduction and encoding at the cellular and membrane level (Figure 3a; [29,30**]). The application of intracellular recording techniques, including voltage-clamp, has revealed many details of the processes of mechanoreception and the control of their dynamic properties. The findings include the following.

Figure 2



Finite element simulation of spider tactile hair under load from above. **(a)** Maximum axial stresses due to bending of the hair shaft as a function of the tactile load. Roman numbers refer to sections of hair shaft indicated in (b). Note that the stress maxima are roughly the same along a wide stretch of hair length despite the differences in loads introduced at the different sections. **(b)** Maximum axial stress (Nm^{-2}) for each cross-section along the hair shaft. Hair diameter drawn too thick ($3\times$) relative to hair length (modified with permission from Dechant *et al.* [24]).

No standing potential and sodium driven receptor current

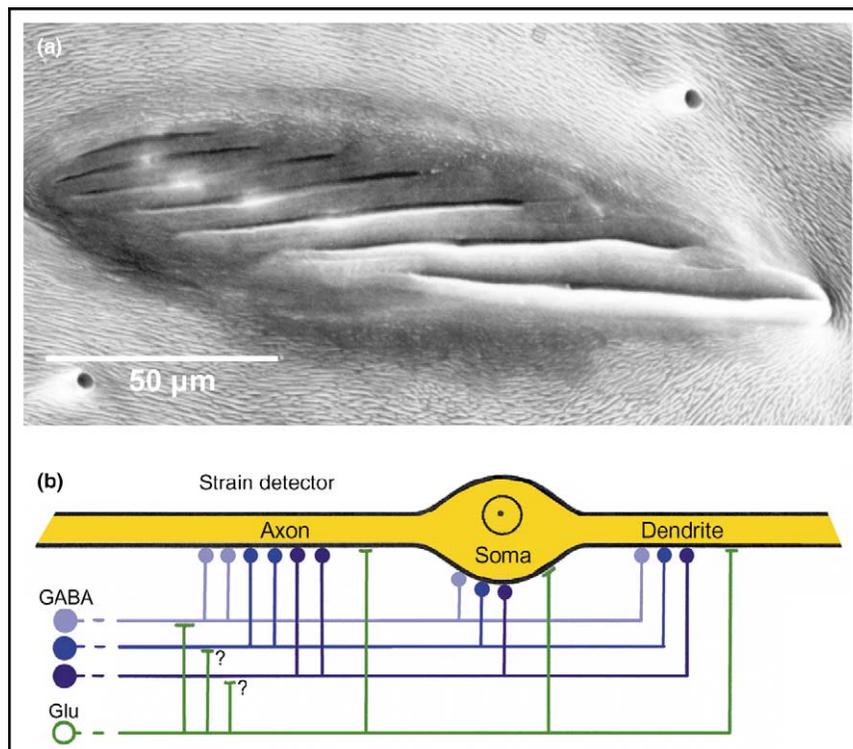
Previous studies [31,32] had already demonstrated a Na^+ -rich and K^+ -poor receptor lymph in spider cuticular sensilla, which differs from the insect case in which K^+ dominates [14,33]. Concomitantly, spider cuticular sensilla lack the standing potential typical of insects. In campaniform sensilla, the insect analog of spider slit sensilla, the receptor lymph is positively charged with respect to the hemolymph by up to 100 mV. This potential is largely caused by a K^+ -current of non-nervous origin (not unlike the situation in the human inner ear [34]) and substantially contributes to drive the receptor current. Voltage clamp experiments and the application of tetrodotoxin (TTX) and other agents have now clarified that in

slit sensilla the receptor current is indeed carried by Na^+ , and that the mechanosensitive channels are highly selective for Na^+ over K^+ . This not only contrasts with the situation in insect mechanoreceptors but also with that in inner ear hair cells and other mechanosensitive channels [35–37].

Site of mechanosensitivity

There is now experimental evidence that mechanosensitivity is restricted to the very tips of the dendrites in the spider slit sensilla [37]. Depleting the dendrites of microtubules did not abolish the receptor potential. Microtubules are therefore considered not crucial in regard to the gating of the mechanically activated membrane channels [37]. However, it is still difficult to ascertain what

Figure 3



Spider exoskeletal strain sensor. (a) Lyriform organ on the spider leg patella (*Cupiennius salei*) consisting of 7 slits. (b) Diagram showing the efferent fibers that surround two sensory cells supplying one of the 7 slits of the lyriform organ. Note numerous synapses formed along axons, somata, and dendrites of the receptor cells. Synapses are also found between these fibers and between them and glial cells. Different fibers show immunoreactivity to GABA and glutamate, respectively. (b) Modified from Fabian-Fine *et al.* [44*].

happened in this experiment at the very tip of the dendrites, where microtubules form tubular bodies typical of arthropod cuticular mechanoreceptors.

Initiation of action potentials

An older suggestion that action potentials initiate at the dendrite tips close to the site of mechanotransduction and propagate through the somata of the sensory cells [38] is now strongly supported by two sets of evidence. First, according to immunocytochemical analyses the density of voltage activated Na^+ -channels is similar in the axonal and dendritic membranes and lower by one-half at the soma [39]. Second, the passive properties of the dendritic membrane and its short length constant ($\ll 600 \mu\text{m}$) considerably attenuate the receptor potential on its way to a putative site of action potential initiation at the soma [40]. Action potential initiation in the dendrite was indeed suggested for several arthropod mechanoreceptors. It might also apply to the Pacinian corpuscle [41].

Efferent innervation

A most intriguing property of spider cuticular sensilla, including slit sense organs, is their profuse efferent

innervation. Foelix [42,43] was the first to note axo-dendritic, axo-somatic, axo-axonal and even axo-glial synapses at the receptor level in various arachnids. Recent studies in *Cupiennius* have confirmed and extended this notion (Figure 3b; for a review please see Fabian-Fine *et al.* [44*]). According to immunolabeling studies γ -aminobutyric acid (GABA), glutamate, and acetylcholine (ACh) are considered transmitter candidates at the efferent contacts received by the sensory cells of a compound slit sense organ [30*,44*,45]. The inhibitory function of GABA could be attributed to membrane shunting [46]. The exact roles taken by the many synapses in the periphery and the microcircuits potentially arising from them are largely unknown. The obvious hypothesis is efferent signal modulation. Recent evidence for the presence of metabotropic GABA_B receptors that might mediate long-term effects complicates the picture [47]. Peripheral nervous integration as indicated by the synaptic contacts might point to an ancient property linking the spiders to more primitive arthropods like *Limulus*, which are known to have peripheral nerve plexus [43]. However, the situation also appears to be similar to that in the crustacean muscle receptor organs [44*].

Conclusions and perspectives

The study of spider sensory systems has turned out to be highly rewarding. Apart from the visual systems, not treated here, this applies to various sensors dealing with different forms of mechanical input energy, which in many spiders dominate the guidance of behavior. The data reported in this review underline the fact that neurobiology starts way out in the sensory periphery, even before the stimulus reaches the sensory cell. The detailed studies of the processes of stimulus uptake and transformation in both medium-flow and tactile sensors not only reveal the match between the physical properties of the stimulus and the morphology and mechanics of the non-nervous auxiliary structures but they also to a large extent explain the behaviorally relevant selectivity and specificity of the sensors at this early stage of sensory processing. To be able to fully appreciate this, biology needs a close collaboration with the physical sciences. Physical scientists, in turn, gain access to the richness of biological solutions of technical problems that are potentially useful for developing novel bio-inspired synthetic sensors. Research into a spider strain detector (lyriform organ) has recently contributed fundamental insights into the cellular processes of mechanoreceptor transduction and encoding. A particular challenge for the future will be to understand adequately the functional role of the profuse efferent innervation found in the sensory periphery of spiders and other arachnids.

Acknowledgements

Research in the author's laboratories was supported by the Austrian Science Foundation (FWF: P-9336BIO, P-12192BIO, P-16348BIO). I am grateful to JAC Humphrey, Department of Mechanical and Aerospace Engineering, University of Virginia (Charlottesville) and FG Rammerstorfer, Institute of Lightweight Design and Structural Biomechanics, Vienna University of Technology, for their support of a truly transdisciplinary interaction between sensory biology and engineering.

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