A Spider's Sense of Touch: What to Do with Myriads of Tactile Hairs?

2

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Contents

Abstract

Some spiders are densely covered by an intriguingly large number of mechanoreceptive hairs on their exoskeleton, the wandering spider *Cupiennius salei* being the main example examined here. All of these hairs represent first-order lever arms, whose deflection triggers nervous impulses in the sensory cells ending at their base. Their sensitivities differ greatly. By far the most sensitive hairs are the trichobothria. They respond to the frictional forces contained in the slightest movement of air. The large majority of the hairs, however, are much less sensitive. They represent touch receptors, including proprioreceptive hairs, which monitor the movements of joints. The mechanical properties of the hairs such as their resistance to deflection and their directional properties vary as do

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details of their morphology (like structure of socket and outer hair shaft, length, angle of hair insertion). Although such differences are graduated, the distributions of some main morphological types form stereotyped patterns on the spider exoskeleton. The functional significance of these patterns in regard to particular behaviors is largely unknown. The enormous versatility of the tactile sense nevertheless clearly emerges from the analysis of prominent examples of hairs and their relation to behavior. Like in other senses, stimulus transformation turns out to be a most important evolutionary playground for biologically applied physics and to a large extent to be responsible for the fine-tuned match between the sensor and the adequate stimulus patterns which it is meant to receive for different behavioral tasks.

2.1 Introduction

The diversity and ingenuity of animal sensors have evolved to enable organisms to behave in favor of their fitness. Animal sensors absorb energy of different form in tiny quantities and generate electrical signals which carry the relevant information about their inside and outside world to the central nervous system. To a large extent the picture the central nervous system creates of an animal's environment and *in*vironment is based on this information. However, this information is by no means comprehensive in a physical sense but instead a highly filtered, limited, distorted, and species-specific image of what can be measured objectively. Like art (according to a saying by Pablo Picasso, Wilson 1984), sensory images are lies that help the animal to recognize the biologically relevant truth. Once we know these images, they also help us to recognize the role a specific sense organ plays as a mediator between the environment and behavior. We therefore expect to find important aspects of an animal's habitat to be reflected in the properties of sense organs and in the way the information provided by them is handled. This is what sensory ecology and this book mainly is about (see also Dusenbery 1992; Barth and Schmid 2001; Barth 2002a).

Sensory ecology has old roots, dating back at least to the early twentieth century, when Jacob von Uexküll (1909, 1920) stressed the subjectivity and predetermination of an organism's relations to its environment and their species-specific uniqueness. Thus, a sensor's technical refinement is only one side of this coin. The other side, brilliantly demonstrated by the work of Karl von Frisch (1965) and his many followers, is its match to specific features of the biologically relevant stimulus patterns and the performance of the entire organism in its habitat (Barth 2002a). As pointed out by Wehner (1987) in his seminal paper on "matched filters" in spatial orientation, animals often use surprisingly simple information to solve a complex behavioral task. They then largely rely on a highly specialized sensory periphery while dealing with natural stimulus patterns of sometimes frightening complexity.

For many if not most spiders, the mechanical senses are particularly important for the guidance of their behavior. Their mechanical senses are very well developed (Barth 1997, 2002a, b, 2004, 2012b, 2014; Fratzl and Barth 2009). Computational biomechanics and mathematical modeling not only revealed many of the physical constraints underlying their operation but also helped to understand tendencies of adaptation and to predict optimizing tendencies of natural selection (Dechant et al. 2001; Bathellier et al. 2005, 2012; Hößl et al. 2006, 2007, 2009, 2014; Humphrey and Barth 2008). Spider mechanosensors respond to a wide range of stimuli. These include the energy contained in minute substrate vibrations down to displacement values of 10^{-7} m (Barth and Geethabali 1982), the slightest whiff of air down to velocities as small as 0.15 mm/s (Barth and Höller 1999; Barth 2014), micro-strains in their exoskeleton, and deformations resulting from them on the order of nanometers (Hössl et al. 2009; Schaber et al. 2012).

Even when considering all senses including vision, a spider's sensory space is small. There are no long distance senses like our hearing and vision. However, despite its limitation to a few meters at most (vibration sense), the sensory world of spiders is rich, not the least due to a remarkable technical refinement of its mechanoreceptors. Combining research into the behavior, ecology and physical properties of natural stimuli have given us some idea about the evolutionary selection pressures that must have led to the adaptedness of slit sensilla, trichobothria, and tactile hairs (Lit. see above) (for chemoreceptive hairs, see Tichy and Barth 1992; Barth 2002a).

This chapter deals with the tactile sense of *Cupiennius salei*, a wandering spider mainly at home in Mexico and Central America (Barth 2002a; Barth and Cordes 1998, 2008), which has served our research for more than half a century now and found its way into many international laboratories. Research into the tactile sense of arthropods has been much neglected as compared to vision, hearing, and chemoreception, the senses appealing much more to many because of their dominant presence in our own human perceptions and consciousness (Barth 2012a). The tactile sense is a close-range sense par excellence. It seems to be particularly well developed in wandering spiders and prominently contrasts their lack of true long distance sensing. Although still far from a full understanding of the spider tactile sense, there are some interesting facets known already. These may justify the attempt of a review not meant to be exhaustive but pointing to the importance and refinement of the spider tactile sense, as well as to the gaps in our understanding and the challenges and promises of future research.

2.2 Numbers and Morphological Types

The sensilla of interest here are cuticular hairlike sensilla protruding from the exoskeleton, which respond to forces deflecting their hair shaft by direct contact. The exoskeleton of *Cupiennius* and many other spiders is densely covered by hairs. Their huge number amounts to several hundreds of thousands in an adult *Cupiennius* (Fig. 2.1a). Hair density is up to $400/\mathrm{mm}^2$ (Eckweiler 1983; Friedrich

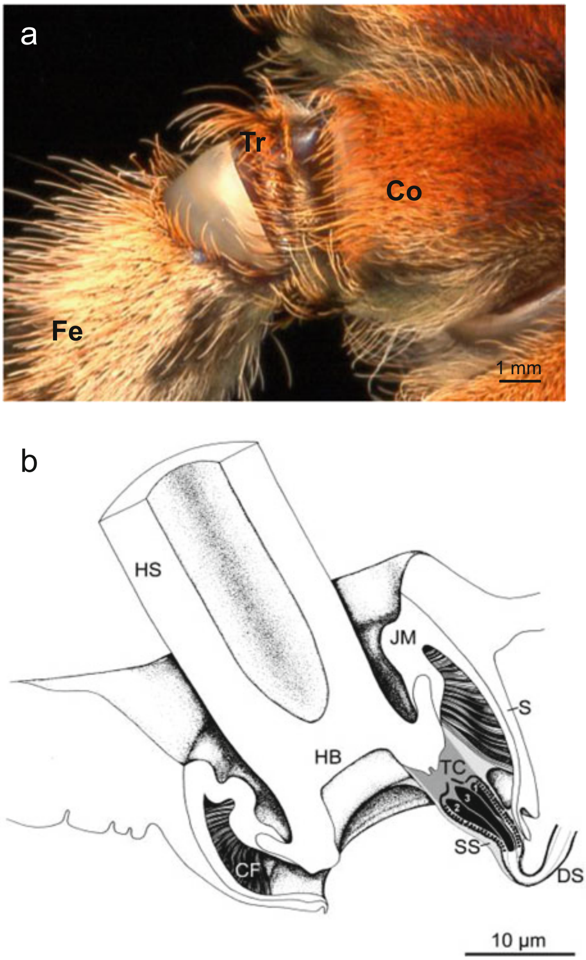

Fig. 2.1 (**a**) Ventral view of the proximal part of a walking leg of *Cupiennius salei*, showing the intriguingly large number of tactile hairs. *Fe* femur, *Tr* trochanter, *Co* coxa. (**b**) Reconstruction of fine structure of the basal part of a tactile hair (see TaD1 in Fig. 2.4a). CF connecting fibrils, *DS* dendrite sheath, *HB* hair base, *JM* joint membrane, *S* cuticular socket, *SS* socket septum, *TC* terminal connecting material, *1–3* tubular bodies of the three sensory cells innervating the hair (**b** from Barth et al. 2004)

1998), a number which exceeds that of the mechanoreceptors in the human glabrous skin by far (e.g., Meissner afferents on human fingertip ca. 150/cm^2; Johnson et al. 2000). The large majority of the hairs are innervated (Foelix 1985; Friedrich 1998) and show a pronounced cuticular socket structure and a tubular body in their dendrites, indicating their mechanoreceptive function (Foelix 1985). The major exception is the short yellowish plume hairs of adult spiders; they are not innervated (Eckweiler 1983). Even the contact chemoreceptive hairs are supplied by two mechanoreceptive dendrites (in addition to 19 chemoreceptive ones), and some of the scopula hairs ventrally on the tarsus and metatarsus are innervated by one or two sensory cells as well (Foelix 1985; Friedrich 1998).

A pressing question posed by this richness in hair sensilla is whether we can safely distinguish morphological types and how these are distributed over the skeletal surface.

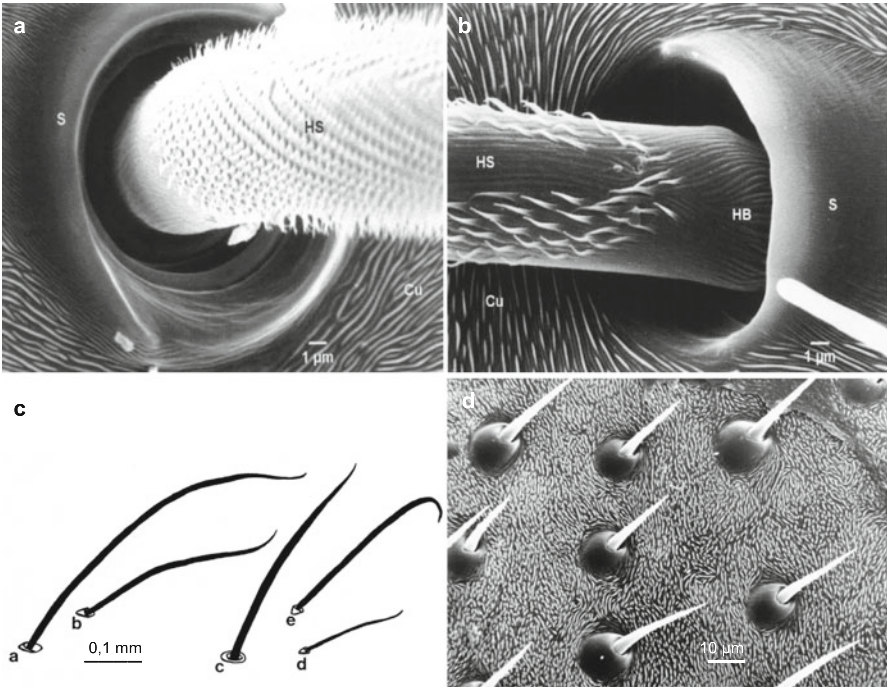

Fig. 2.2 Examples of mechanosensitive hair sensilla of *C. salei* differing morphologically. (**a**) "Open" round socket of a long tactile hair (1.5 mm) dorsally on the prosoma and forming a steep angle (ca. 82°) with the exoskeletal surface and showing largely isotropic directional properties; for abbreviations, see below. (**b**) Partly closed, slipper-like socket of tactile hair on the walking leg femur with a much smaller insertion angle and freedom of movement restricted in the direction toward the leg tip; *Cu* cuticle, *HB* hair base, *HS* hair shaft, *S* socket. (**c**) Variability of the shape of the hair shaft taking tactile hairs on the walking leg (*a*, *b*, *c*) and pedipalpal (*d*, *e*) tarsus as examples; note also differences in socket structure relevant for the mechanical directionality of the hairs and the angle they form with the cuticular surface. (**d**) Hair plate sensilla on the cheliceral basal segment (posterior side facing the labium) (**a**, **b** from Ullrich 2000, **c**, **d** from Friedrich 1998)

I do not consider the airflow-sensitive trichobothria here. They have received a lot of attention already (Humphrey and Barth 2008; Barth 2014). Nor the scopula hairs of which only a few are innervated and not the contact chemoreceptors. The tactile hairs treated here make up for the majority of all hair sensilla and, depending on their location, serve either exteroreceptive or proprioreceptive (e.g., hairs at a joint) functions. Like in other spiders, they are innervated by three sensory cells in *Cupiennius* (Foelix 1985; Friedrich 1998), the exception being the single sensory cell innervating the short and stout hairs of the coxal hair plates (Schaxel 1919; Seyfarth et al. 1990) and most likely also the more recently found hair plates on the chelicerae (about 100 sensilla proximally on the basal segment and facing the rostrum and about 45 sensilla in a group facing the midline of the body; Friedrich 1998) (Fig. 2.2d). The so-called long smooth hairs described by Eckweiler et al. (1989) and serving to measure the distance between neighboring coxae are supplied by one neuron only as well. For details on both the hair plate sensilla and the long smooth hairs, the reader is also referred to the literature.

Assuming that the morphological diversity of tactile hairs is functionally significant, we may hypothesize that their respective patterns of distribution are constant but different on different body areas exposed to different stimulus patterns. To see what the variability is actually like and whether a classification into distinct hair types is possible at all, the following parameters were analyzed (Friedrich 1998): the shape of the hair socket, the hair length, the shape of the hair shaft, and the microtrichs found along its length. As it turns out the distribution pattern of hair types characterized by a certain combination of these parameters indeed is very conservative. However, intermediate forms of hair types are found as well. They render the distinction of clearly separable types more difficult or even doubtful. But what is the variation like?

Hair socket Its diameter varies between 3 and 15 μm, and there are big differences regarding its degree of openness, which affects the directional characteristics of hair shaft deflection (Fig. 2.2a, b). The socket of hairs with a steep insertion angle of 80–90° is round and "open," whereas it is sunk into the exoskeleton in the direction of the hair shaft's orientation in hairs with small insertion angles like 30°. As seen from above, this latter type is the "closed," slipper-like socket type. There are intermediates between these two forms of sockets. Typically, the inner socket rim is smooth, but on the chelicerae, some sockets were found to bulge in a distinct way which strongly affects the hairs' mechanical directionality.

Hair shaft length and shape The length of the hair shaft varies between ca. 60 μm for hairs with a diameter of ca. 3 μm at their base and ca. 500 μm for hairs with a diameter of ca. 10 μm at their base (measured right above the socket). Hair shaft shape varies greatly (Fig. 2.2c), affecting both a hair's deflection and deformation under tactile load and its responsiveness for particular load directions. Some hairs are uniformly bent toward the exoskeletal surface, whereas others show s-shaped bends or a strong bend distally only. Another characteristic of *Cupiennius* tactile hairs is the variability of their surface structure (Friedrich 1998). With very few exceptions only, all these hairs are covered by some form of protuberances or microtrichs, which come as scales, may be thorn-like, or form fine pili (branchlets), reminding of the surface of trichobothria, where a fine coat of 'branchlets' is increasing the sensitivity to airflow (Barth et al. 1993; Humphrey and Barth 2008). The functional consequences of the surface structures of spider tactile hairs were not studied yet but are expected to affect the friction between the hair and the object touching it and thus the introduction of the tactile force into the hair. A pair of hairs opposing and deflecting each other in this way at the tibia-metatarsus joint is described below (Sect. 2.6.2.3).

Taking all kinds of tactile hairs together, one finds a linear correlation between the socket diameter and hair shaft diameter as well as between shaft diameter and the logarithm of hair length (Fig. 2.3a). Taking the socket diameter and the degree

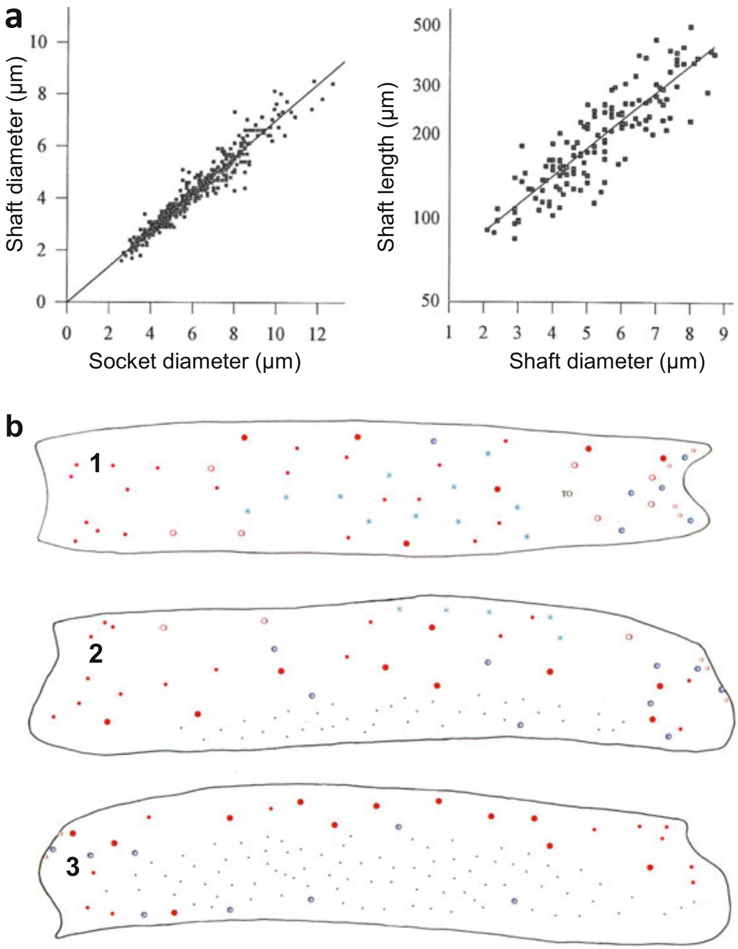

Fig. 2.3 Structural properties common to different tactile hairs on the sternum and the tarsi of walking legs and pedipalps of animals representing the seventh developmental stage. (**a**) Linear relationship between the diameters of the socket and the hair shaft (*left*; $n=640$, $r^2=0.93$, data from three animals) and the diameter of the hair shaft and the logarithm of its length (*right*; $n=143$, $r^2=0.77$, five animals). (**b**) Constant and stereotyped patterns of hair arrangement on different body parts, examples taken from the walking leg tarsus (seventh developmental stage). *1* dorsal, *2* anterior, and *3* posterior aspect. ○ long tactile hairs with open socket (>250 µm); ◦ short hairs with open socket (<250 µm); ● long hairs (>250 µm) with closed socket; • short hairs (<250 µm) with closed socket; ∗ trichobothria; © contact chemoreceptors; • scopula hairs; *TO* tarsal organ (**a**, **b** modified from Friedrich 1998)

of socket openness as the relevant parameters helps to compare the sensory inventory at different parts of the spider body (see below). Since socket diameter correlates with hair diameter and hair diameter with hair length, it also is a measure for the hair shaft's aspect ratio.

2.3 Distribution

According to careful mapping (using a scanning electron microscope, Jeol JSM-35SF, and light microscopical measurements aided by electronic image analysis, Lucia M/Comet 3.52; video camera Sony 3CCD), each of the body parts studied (walking leg tarsus, pedipalpal tarsus, sternum) had its own characteristic pattern of arrangement of the various types of hairs. Figure 2.3b exemplifies this finding for a juvenile spider (developmental stage 7). Presumably, the specificity and constancy of the patterns in different areas of the exoskeleton are functionally relevant, indicating an adaptation to different tactile stimulus patterns and potentially representing simplified templates of them (for arthropod visual orientation, see Wehner 1987). Unfortunately, we are still far from a sufficiently quantitative understanding of these stimulus patterns, although some of them seem to be simple (see Sect. 2.6 below).

Höger and Seyfarth (1995) studied the *development* of tactile hairs and tactile behavior during the entire lifetime of *Cupiennius salei*. The first tactile hairs appear before hatching (stage 2), when the spiderlings are still protected in their egg sac and a hair's stimulation only causes seemingly uncoordinated movements. After hatching from the egg sac, the next molt (stage 3), profound changes have occurred. The number of hairs has increased immensely. Höger and Seyfarth (1995) report an increase from ten hairs at stage 2 to >3000 tactile hairs per leg at stage 3, only counting those present in what they call the "tactile reflexive field" for body-raising behavior (see under Sect. 2.6.2.2). This receptive field comprises the ventrolateral coxa, the trochanter and proximal femur of the leg. The dramatic changes in hair number go along with a fivefold increase in hair density, which then remains roughly constant from stage 5 to adulthood. The hairs seem to occur just at the right time. At stage 3 (first complete stage; age ca. 30 days), the spiderlings do not rely on their yolk sac anymore but have to move around for prey now. Their reflective body raising (see Sect. 2.6.2.2), elicited by tactile stimulation of any and even a single hair in the "tactile reflexive field" (and mainly due to the activity of the hair's slowly adapting sensory cell), is now fully developed.

2.4 Coping with the Stimulus by Well-Matched Micromechanics

2.4.1 The "Clever" Hair Shaft

Computational biomechanics has helped a lot to reveal the refinement of tactile hair structure and its relevance for stimulus uptake and transmission and thus also to reveal the nature of the evolutionarily relevant fundamental physical constraints that must have contributed to shape the sensors (Dechant et al. 2001; Barth and Dechant 2003; Barth 2004; Fratzl and Barth 2009). The hairs examined in detail are found dorsally on the walking leg tarsus and metatarsus. They are conspicuously long (e.g., hair TaD1: 2.6 ± 0.2 mm, $N = 7$, steep insertion angle of 58° ± 4°; Barth et al. 2004) and stick out of the carpet of other hairs, thus forming the outer boundary of the spider's tactile range (Fig. 2.4a). Only a few points will be raised here to highlight the biomechanical "cleverness" for dealing with the adequate stimulus. More details are found in the literature (see above).

The *stiffness of the articulation* of these hairs is larger by up to four powers of ten than that of the trichobothria, which are exquisitely sensitive to airflow (Humphrey and Barth 2008; McConney et al. 2009; Barth 2014). Like in fly macrochaetae (Theiß 1979), spring stiffness S is in the range between 10^{-8} and 10^{-9} Nm/rad. As a consequence the forces needed to overcome joint stiffness S, which are in the range of micronewtons, bend the hair shaft in addition to deflecting it. This fundamentally distinguishes them from the trichobothria, which respond to the frictional forces contained in airflows implying that they are much more sensitive. Different from the trichobothria case, the forces due to the inertia of the tactile hair shaft's mass may be neglected, not so Young's modulus E and the second moment of area J along the bending hair shaft. These parameters dominate the hair's mechanical behavior when loaded by a tactile force from above (as it happens when the spider is wandering around at night, see below). Due to its bending, the hair shaft's angle with the cuticular surface is never smaller than ca. 12°. This is seen by direct microscopical observation and numerical modeling based on finite element analysis, taking the cross-sectional heterogeneity of the hair shaft (diameter, curvature, wall thickness) along its length (with J, the axial moment of inertia, assuming values varying by almost four powers of ten) into account. With increasing load the point of contact of the stimulus from above is steadily moving toward the hair base. Thereby, the effective lever arm decreases and the bending moment increases. This increase slows down with increasing stimulus forces until it saturates at ca. 4×10^{-9} Nm (Dechant et al. 2001).

What does this mean in more general terms? The hair's micromechanical behavior implies both protection against breaking and a considerable enlargement of the working range as compared to that of a stiff, non-bending rod. It also tells us that the mechanical sensitivity of the hair is higher for small deflections than for large ones (forces needed to deflect the hair, ca. 5×10^{-5} N/° and ca. 1×10^{-4} N/°, respectively). This in turn implies a particular responsiveness to the initial phase of a stimulus. Like the majority of biological senses, the tactile hairs are more "interested" in changing than in static stimulus conditions.

The *axial stresses* in the hair shaft due to its bending measured up to about 3.2×10^5 N/m^2. Importantly, the hair shaft was found to be a structure of equal maximal strength, again pointing to its mechanical robustness and a nonnervous sensory periphery surprisingly well matched to and coping with the adequate stimulus. This conclusion is supported by the observation that joint restoring torques vary in individual hairs, whereas maximum stresses and bending do not. We conclude that Young's modulus varies in a way finely tuned to the stiffness of the joint (Dechant 2001; Dechant et al. 2001).

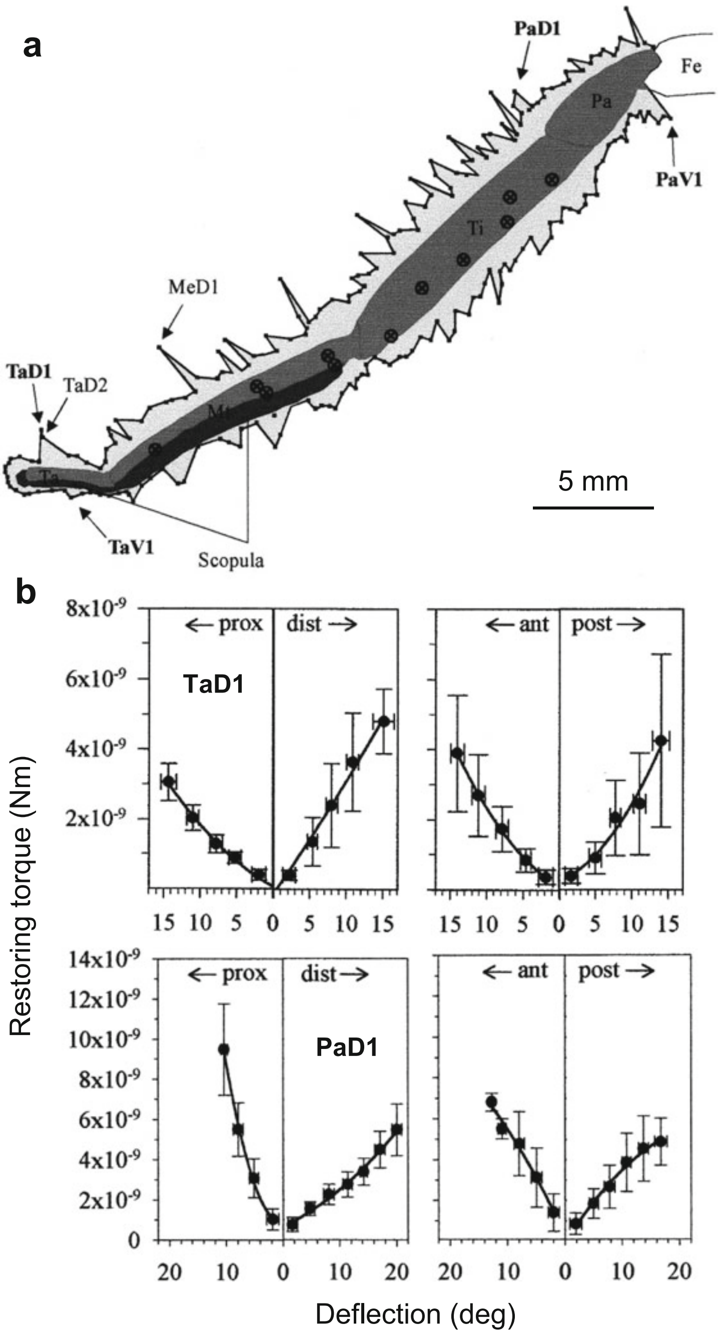

Fig. 2.4 (**a**) Tactile space of *C. salei*, taking its distal leg segments as example (*Fe* femur, *Pa* patella, *Ti* tibia, *Mt* metatarsus, *Ta* tarsus). ● indicate tips of tactile hairs forming outer border of tactile space. *TaD1*, *TaD2*, *TaV1*, *MeD1*, *PaD1*, and *PaV1* indicate particularly long or steeply inserting well-studied tactile hairs. (**b**) Force (restoring torque) resisting hair deflection in different

An additional clever match of the tactile hair with the stimuli it is exposed to is that it also bends within the socket, even before the hair shaft touches it (Fig. 2.5). A quantitative description of this "*second joint*," which can be directly seen in slice preparations of intact hairs and again increases the hair's mechanical robustness, is found in Barth et al. (2004).

The micromechanical analyses now available may serve as a point of reference when studying other tactile hairs in search of overarching rules and big patterns of understanding their diversity.

2.4.2 The Coupling of the Sensory Dendrites

Like the hair shaft, the hair base proper appears to be "designed" for a combination of mechanical sensitivity and mechanical protection of the *dendritic endings*. The proximal part of the long tactile hair found dorsally on the tarsus has an anchor-like shape and connects to the joint membrane (Fig. 2.1b) (Foelix 1985; Barth et al. 2004).

As judged from transmission electron micrographs, the dendritic sheath is *not directly coupled* to the hair base as is the case in insect mechanoreceptive hairs (Keil 1997). Instead, there is a broad strand of material (looking homogeneous in the TEM) between the hair shaft and the dendritic sheath and the same material (according to TEM) within the distally open dendritic sheath and between the tubular bodies of the three dendrites (Fig. 2.1b) (Barth et al. 2004). A challenging question for future research concerns the mechanical properties of this material. Presumably these properties strongly affect stimulus transmission to the dendrites proper. The same structural phenomenon seems to be typical in spider tactile hairs in general. It was also found in tactile hairs on the prosoma and femur and at the femur/patella joint (Ullrich 2000) and similarly in tactile hairs on the legs of *Ciniflo*, a cribellate spider (Harris and Mill 1977). The fine structural details of the dendrite attachment sites look remarkably similar in the different tactile hairs of *Cupiennius*, as if they clearly were not a main source of hair diversity.

In slice preparations of intact hairs, the hair shaft's *axis of rotation* can be pinpointed by identifying the area of no translational movement. It has a highly acentric position, lying on the proximal side of the shaft's anchor-like base and right above the apical end of the dendritic sheath. From this the length of the inner lever arm of the hair shaft could be determined. It measures ca. 3.5 μm only, implying a length ratio of the outer versus the inner lever arm of 750 and more. This ratio in turn implies that the displacement of the hair tip is scaled down considerably and the force close to the dendrites amplified correspondingly. Deflection of the hair by

◄

Fig. 2.4 (continued) directions. *Upper* row refers to hair *TaD1*, *lower* row to hair *PaD1* (for both hairs: $N=6$, $n=1$, $r > 0.95$). Note pronounced un-isotropic behavior of the resisting force for distal and proximal deflection of hair PaD1 (**a**, **b** modified from Friedrich 2001)

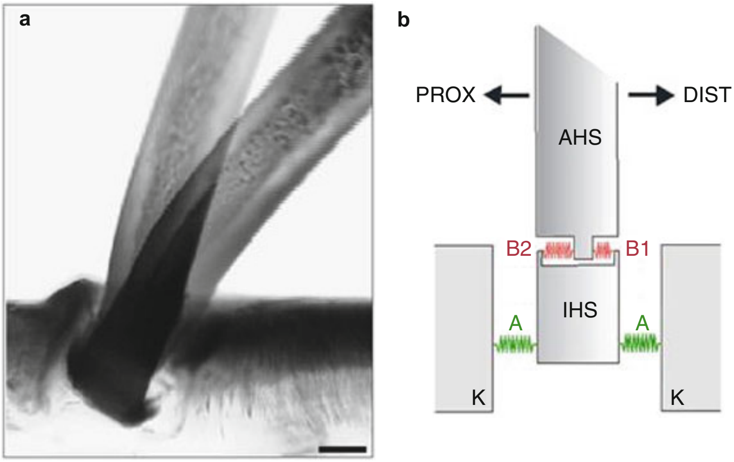

Fig. 2.5 (**a**) The second joint within the socket as seen in hair TaD1 (see Fig. 2.4a) when superimposing pictures of the hair shaft in resting and deflected (20°) position, respectively; note bending close to base of hair shaft. (**b**) Schematic representation of hair base of tarsal hair TaD1. Whereas *A* represents the elasticity of the hair suspension in the socket, *B1* and *B2* represent the hair's ability to bend close to its suspension. According to measurements of the restoring torques for proximal and distal hair deflection, *A* is equal in both directions, whereas the stiffness of *B* in proximal direction is larger than in distal direction. *AHS* outer hair shaft, *HIS* inner hair shaft, *K* cuticle (**a**, **b** from Barth et al. 2004)

10° is close to the maximum occurring under natural conditions (the hair then just does not touch the socket yet). The restoring torques counteracting such a stimulus are in the order of 10^{-8}–10^{-9} Nm. They only moderately depend on the direction of the hair's deflection in the given case (see also below). The hair base closest to the dendrites is displaced by about 0.5 μm (toward the side opposing that of the outer lever arm movement). At the hair's physiologically determined threshold deflection of 1° (slow cell, see below), this value decreases to 0.05 μm (Albert et al. 2001). Considering (i) the shortness of the hair's inner lever arm, (ii) the presumed absorption of at least a fraction of its force and displacement by the deformation of the terminal connecting material, and (iii) the close proximity of the dendrite terminals to the axis of rotation again leaves us with the idea that the hair base, like the outer hair shaft and its "second joint" within the socket, is "designed" to protect the sensillum from being overloaded and damaged (Barth et al. 2004).

2.4.3 Forces, Torques, and Directionality

Taking both the diversity of the tactile sensilla of *Cupiennius* and the unfailing presence of identical modifications of the common Bauplan at the same location on its exoskeleton into account, it seems justified to assume that the hairs are adapted to different functions. One way to get a first idea about the differences implied in regard to the relevant stimulus patterns is the analysis of the sensors' mechanical properties. These might well reflect important aspects of stimulation under natural conditions.

The *restoring moments* opposing the deflection of a hair can be measured with high resolution (in the order of 1 μN) by deflecting it with a glass capillary whose own deflection is proportional to the restoring torque and calibrated with a microbalance (Wiese 1976; Albert et al. 2001; Dechant et al. 2001). Such measurements are another way to characterize the diversity of the tactile hair sensilla. So far we have data on (i) four hairs located on the tarsus and patella of the walking legs known to be involved in active tactile behavior (see Sect. 2.6.1; Friedrich 2001) and tactile hairs (ii) on the prosoma, (iii) dorsally on the femur, (iv) at the femur/patella joint, (v) dorsally on the patella, and (vi) ventrally on the tarsus (Fuchs unpublished). All these hairs form the outer limit of the tactile space as shown in Fig. 2.4 a, standing out of the carpet of surrounding cuticular hairs. Interestingly, the tactile hair ventrally on the tarsus (length ca. 0.8 mm, insertion angle 70°) amidst a wealth of scopulate hairs was the most easily deflected, with elastic restoring constants S measuring 5.9×10^{-11} Nm/° and 9.1×10^{-11} Nm/° for distal and proximal deflection, respectively. We speculate that it may play a role not only during locomotion, providing sensory feedback, but also for prey capture (Melchers 1967; Klopsch et al. 2013; Barth 2014), the fine control of spinning the egg sac and holding it, and the highly refined copulatory behavior (see below under Sect. 2.6.2.4). The equivalent values for the long tactile hair dorsally on the tarsus (length ca. 2.6 mm, insertion angle ca. 60°) were 2.5×10^{-10} Nm/° and 1.7×10^{-10} Nm/°. Apart from this, all other hairs behave similarly, sometimes with a moderately anisotropic mechanical behavior of their articulation. Examples are given in Fig. 2.4b. The most pronounced mechanical directionality is that of joint hairs, where easy deflectability coincides with the direction of the relevant stimulus load.

A strong *dependence on direction* of the torque resisting deflection is well documented for tactile hairs at the joint between tibia and metatarsus (see below under Sect. 2.6.2.3). The values of the torsional restoring constant S (elastic restoring force opposing hair deflection) for the natural direction of stimulation were smaller by one to two powers of ten compared to those for all other directions (between ca. 5×10^{-12} and 2×10^{-11} Nm/deg; Schaber and Barth 2014). Similar differences, well matched to their behavioral role, were found for the hairs at the femur/patella joint (Barth and Fuchs unpublished). A quantitative mathematical description of the mechanical directional behavior of arthropod cuticular hair articulations in general is shown in Fig. 2.6 and detailed in Dechant et al. (2006).

In this study, a simple mathematical model is described which is applicable to any anisotropic articulation reacting with different joint stiffnesses to loads from different directions. Only a few parameters are needed to quantitatively describe the mechanical directionality. These parameters are S_p and S_t, the joint stiffnesses in the preferred direction of deflection and in a plane transversal to it and the stiffnesses for opposite directions. The equation derived in Dechant et al. (2006) well describes the directionality of a large range of structurally different arthropod hairs (with directionality curves ranging from isotropic to figure eight shaped) in good

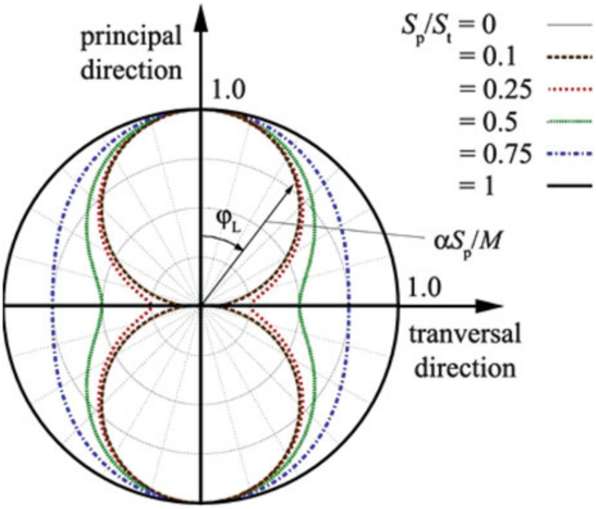

Fig. 2.6 Directional characteristics of the joints of arthropod hair sensilla; polar plot derived from mathematical model for different ratios of joint stiffnesses in preferred direction (S_p) and the direction transversal to it (S_t). φ_L load direction, α actual deflection angle of hair under load; φ_α actual direction of deflection; M moment introduced to the joint (Modified from Dechant et al. 2006)

$$\alpha = \sqrt{\alpha_p^2 + \alpha_t^2} = M\sqrt{\frac{\cos^2(\varphi_L)}{S_p^2} + \frac{\sin^2(\varphi_L)}{S_t^2}}$$

agreement with experimental data. It also takes into account the discrepancy between the direction of the stimulus force and that of hair deflection.

As expected, the S values of the tactile hairs examined are all considerably higher (by up to ca. four powers of ten) than those determined for the airflow-sensitive trichobothria (Barth et al. 1993).

The most rewarding outcome of our studies aiming at a better understanding of the diversity of the seemingly innumerable mechanosensitive hairs on the exoskeleton may have been the appreciation of biomechanical details. These details to a large extent tell us how the basically simple Bauplan of a cuticular sensory hair can be adjusted to a variety of functions by the modification of only a few physical parameters. At the same time, the quantitative assessment of these details sheds light on the selection pressures contributing to the evolution of different hairs. We now more clearly see the keys of the piano evolution plays with. Similar to the complex visual systems involved in spatial orientation and highlighted as "matched filters" by Wehner (1987) as examples of sensory systems in general, individual mechanoreceptive hairs are highly selective and tuned to different types of stimulation, even way out in the sensory periphery by way of their nonnervous stimulus-transmitting structures.

2.5 Types of Physiological Responses and Information Encoding

The tactile hairs TaD1 and MeD1 of *Cupiennius* (s. Fig. 2.4a) were extensively studied electrophysiologically as well. They are the longest tactile hairs dorsally on the tarsus and metatarsus of the leg, respectively, protruding from the exoskeletal cuticle at an angle of $58 \pm 4°$ (TaD1) and 73° (MeD1). They are 2.6 ± 0.2 mm (TaD1) and 3.2 ± 0.1 mm (MeD1) long (mean ± SD; $N = 6$) (Albert et al. 2001). Like most other tactile hairs, they are supplied by three bipolar sensory cells (Foelix and Chu-Wang 1973; Harris and Mill 1977), one of these being substantially larger (53 ± 8 μm) than the others (23 ± 8 μm). For unknown reasons but in agreement with older studies (Harris and Mill 1977), only two of the three cells could be demonstrated unequivocally in extracellular electrophysiological recordings (Albert et al. 2001; but see Eckweiler and Seyfarth 1988 for hairs ventrally on the proximal leg). Notwithstanding this problem, which needs intracellular recordings to be solved, all studies available classify the nerve impulse response of the tactile hair sensory cells as phasic, with different rates of adaptation to maintained stimuli. The tactile hairs studied are all movement detectors. They respond to the dynamic phase of a stimulus, that is, to the hair deflection velocity. For the tactile hairs dorsally on the distal leg of *Cupiennius*, angular deflection thresholds are about 1°. When deflected with behaviorally relevant stimulus velocities (up to 11 cm/s; see Sect. 2.6.1), the maximum action potential frequency occurs already 1.2 ms after stimulus onset and is followed by a rapid decline. Both the fast cells (responding to the dynamic phase of the stimulus exclusively) and the slow cells do not provide detailed information on the time course of the stimulus or on the deflection angle but merely on its presence and onset (Albert et al. 2001). Note that this is in good agreement with the conclusions drawn from the analysis of the hair's micromechanical properties (see under Sect. 2.4.1).

Interestingly, the deflection velocity threshold is much lower for the "slow" than for the "fast" cell. To give an example for TaD1, whereas it is $30 \pm 9°$/s for the "fast" cell (response saturation at $\geq 650°$/s), it is $<0.1°$/s for the "slow" cell (saturation at ca. 250°/s) (Albert et al. 2001).

2.6 Matched to Specific Behaviors?

With the knowledge on the mechanical and physiological properties of individual tactile hairs at hand, one may proceed and ask for the behavioral significance of the spider tactile sense and the sensors' context-dependent adaptations. The task is difficult, in particular because the answers rely on a quantitative knowledge of the relevant pattern of tactile stimulation. The few pixels we have of a complex and multifaceted picture nevertheless reflect the refinement of a seemingly unspectacular sense and deepen the impression that arthropod tactile behavior needs much more attention than it so far received. We will first discuss (a) the tactile analysis of surfaces by active touch, then turn to (b) simple reflexes elicited by passive touch and (c) to the measurement of joint movements by tactile hairs (proprioreception), and finally summarize findings regarding (d) body raising initiated by tactile stimulation. This last behavior is a particularly well-studied tactile "simple behavior" of *Cupiennius* and other spiders. To conclude, a short paragraph (e) will point to the complexity of the tactile guidance of copulation behavior.

2.6.1 Actively Gained Contact Information for the Adaptive Control of Locomotion

In search of the functional logic of tactile hairs, one finds that, typically, tactile sensors in general show phasic response characteristics. The tactile analysis of surface structures therefore depends on active movement which largely determines the contribution of individual receptors. On the level of a single receptor hair, the texture of a surface (its profile) is represented as a sequence of hair shaft deflections. Thus, the mechanical limits of spatial resolution lie in the dynamics of the deflected hair shaft's return to its resting position.

In complete darkness, *Cupiennius* uses its first pair of legs like antennae to intentionally probe its immediate surroundings while walking around on its dwelling or another plant during its nocturnal activity period. This near-range exploration behavior and tactile orientation first described by Schmid (1997) is referred to as "guide stick walk." Upon the first contact with an object, the spider switches the mode of leg movements and starts to scan the surface with the dorsal aspects of the tarsi and/or metatarsi of its first two pairs of legs. According to video analyses (Friedrich 2001), the individual scanning movements are very regular with a velocity between 4 and 10 cm/s (6.4 ± 1.4 cm/s; $N = 12$). They differ from the pattern seen during locomotion. At a mean duration of 230 ± 82 ms ($N = 12$), the distance covered by the movement was 1.5 ± 0.8 cm ($N = 12$). The first contact with the substrate is mainly by the dorsal aspect of the tarsi. While scanning, the tarsi move at an average velocity of 10 cm/s (Fig. 2.5a).

This implies that it will take some 15 ms only until the hair touches the tarsal surface (provided movement is not slowed down). The action potential conduction velocity of tactile hair afferent fibers was estimated to be between 0.45 and 0.63 m/s (Eckweiler 1987). The distance of the tactile hair to the central nervous system (CNS) is about 6 cm in adult spiders, which implies a total conduction time of 95–133 ms. Obviously then the collision of the tarsal hair with the substrate is indeed not slowed down by efferent control, and a number of neighboring hairs will be stimulated together with the largest ones (Friedrich 2001).

Different from stereotyped tactile reflexes elicited by the stimulation of single hairs (see below Sect. 2.6.2.2), the motor pattern of active touch is variable and presumably depends on the activity of many hairs on correspondingly larger areas of the legs. For a nocturnal animal like *Cupiennius*, to probe its immediate environment using its tactile sense must be highly relevant.

When plotting the maximum impulse rate of the fast cell's response against velocity of hair deflection (movement of cover glass from above), saturation is reached between 100 and 200°/s for TaD1 and MeD1. Leg movement velocities during active touch are all within the saturation range of both impulse rate and threshold. Therefore, the fast cell functions like a quasi-digital indicator of a tactile event without providing any details about stimulus intensity and direction (Albert et al. 2001).

For an estimate of the *spatial resolution* possible with these movements, the distances between the tactile hairs located dorsally on the tarsus were determined. The average distance between one sensillum and its six nearest neighbors is remarkably constant for spiders of different age (measured from 2-month-old spiders to 1-year-old female adults). It measures 52 ± 18 μm ($N = 4$; $n = 12$), corresponding to an average *density* of $370 \pm 90/\text{mm}^2$ (Höger and Seyfarth 1995; Albert 2001). This is a remarkably high density. It is hard not to assume that it reflects high spatial resolution and its corresponding behavioral importance.

An additional parameter to be considered is the velocity with which deflected hairs return to their resting position when released. When deflecting prominent tactile hairs dorsally on the tarsus and metatarsus (TaD1, TaD2, MeD1) in the distal direction, which is the biologically most relevant one, stroboscopic analyses showed that the velocity of the restoring movement amounts to some unexpected 25.000°/s for the tarsal hairs (TaD1 28.000°/s; TaD2 23.000°/s) and to even 130.000°/s for the metatarsal hair. A deflection of the hair shaft up to touching the socket was fully restored in only 1–2 ms. Such time periods are sufficiently short at the biologically relevant velocities of leg movements to resolve the surface structure in fine detail. The following experiment demonstrated this directly.

The movement of the spider's leg, when it probes and hits a surface, can be imitated by moving a plane object oriented in parallel to the exoskeletal surface toward the hair base (or leg surface). From the nonlinear increase of hair deflection (well represented by a hyperbolic function) with decreasing distance of the stimulating object (Dechant et al. 2001), it follows that a surface texture of constant depth will increasingly deflect the hair the closer it comes to the hair base. The threshold depth of a surface structure still detected by the hair will therefore decrease in the same way. Taking a threshold deflection of 1° needed to elicit an action potential and a distance of the hair tip to the cuticle surface of 1850 μm, threshold depth will be about 275 μm when touching the tip but only ca. 75 μm at a distance of 1000 μm. When mounting a surface profile of 340 μm height on a planar surface and drawing it over tarsal hair TaD1 in the distal direction (imitating the spider's scanning behavior) (Fig. 2.7a), the nervous response of the slow cell considerably increases when the distance between stimulus and tarsal surface is reduced. Spatial resolution therefore decreases dramatically with decreasing distance of the moving stimulus to the hair base or increasing pre-deflection of the hair (Albert 2001). To effectively probe a surface, the tarsi should just slightly touch it (Fig. 2.7b).

Whereas the *fast cell* innervating a spider tactile hair is interpreted as a quasi-digital indicator of touch as such (similar to a yes or no response), the *slow cell* is thought to be most relevant when the spider starts to scan the surface (Friedrich 2001) and to learn about its texture/structure with well-coordinated brushing

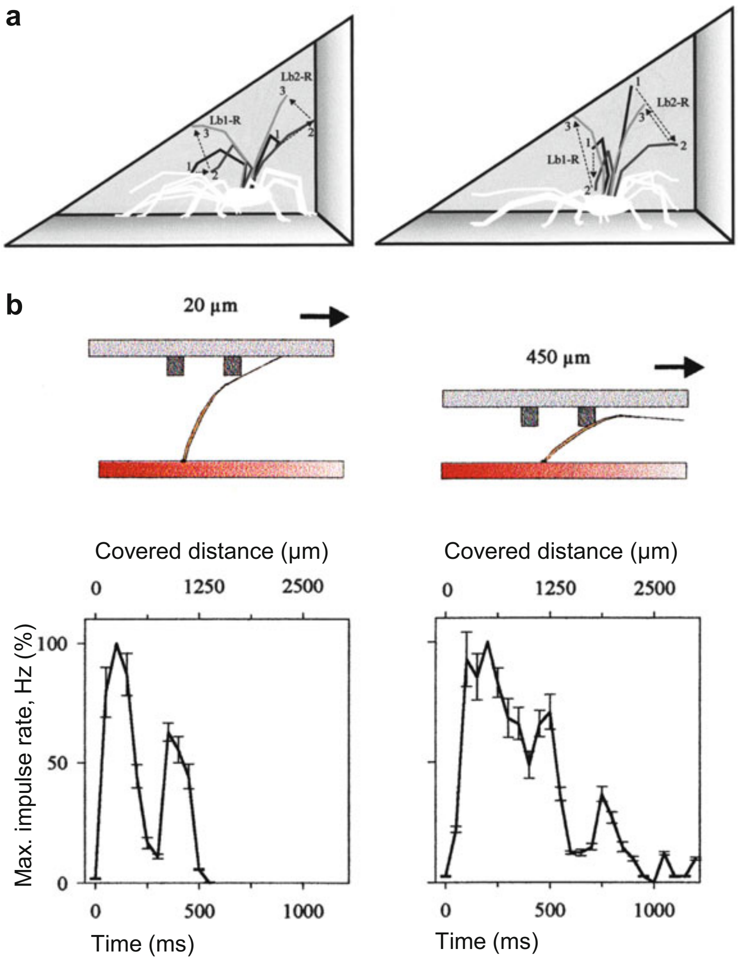

Fig. 2.7 (**a**) Active tactile behavior of *C. salei* under *red* light (λ >630 nm) or blindfolded in a corridor with triangular cross section. Superposition of individual video frames shows movement of the first two pairs of legs (*Lb1* and *Lb2*; R *right*). Movement starts with the leg in position 1 in the direction indicated by *arrow*. Time span covered by drawings ca. 500 ms each. (**b**) Pre-deflection reduces the tactile contrast and spatial resolution. Electrophysiologically recorded response of slow sensory cell innervating hair TaD1 (see Fig. 2.4a) to a test stimulus consisting of two bars protruding 340 µm from a planar surface and separated by a gap of 750 µm; *left* and *right*: pre-deflection 20 µm downward and 450 µm from hair tip, respectively. ($N = 2$, $n = 6$) (**a** from Friedrich 2001, **b** from Albert 2001)

movements (Albert et al. 2001; see also Sect. 2.6.2.4). The profile of a surface is then translated into a spatiotemporal pattern of hair shaft deflections and the nervous activity caused by them. Due to the leg's scanning movements, the surface profile is not only reflected by the simultaneous excitation of different receptors but additionally by the temporal sequence of activity of the individual receptor. The "slow cell" seems to be better suited for this job than the "fast cell" for the following reasons: (i) no absolute velocity threshold, (ii) independence of its angular threshold deflection from the velocity of hair shaft deflection and thus constant spatial sensitivity for the entire range of leg movement velocities, and (iii) the potential of stronger modulation of the response due to its slower decrease (adaptation), which does not represent fatigue but goes along with unchanged excitability and sensitivity (Albert 2001). Remarkably, a similar role is attributed to the slowly adapting SAI tactile units in vertebrate glabrous skin (Johnson 2001).

2.6.2 Simple Stereotyped Behavior

The locomotion of spiders differs from that of other arthropods. Not only is hydraulic force used to extend the more distal joints of the legs but there are also many more muscles in the leg of a spider than in that of other arthropods. In addition the muscles are poly-neurally innervated by many more motor neurons (Sherman 1985). Possibly then spider leg movements are particularly subtle, and their fine control may rely on a particularly well-developed sensory periphery (Seyfarth 1985). And indeed three main types of sensors are found near the leg joints: slit sense organs, internal joint receptors, and large numbers of mechanosensitive hairs bridging the joints (see Sect. 2.6.2.3).

2.6.2.1 Synergic Withdrawal

As far as we know, resistance reflexes opposing an imposed joint movement are elicited by the internal joint receptors (Seyfarth and Pflüger 1984), whereas synergic reflexes acting in synergy with the imposed movement are due to the stimulation of strain-sensitive lyriform organs (Seyfarth 1985). The deflection of tactile hairs has been known to passively trigger withdrawal activity or turning away of the entire spider, moving the leg away from the stimulus (Seyfarth and Pflüger 1984). Apart from the (i) *withdrawal of a leg*, several other stereotyped reflex behaviors have been known in *Cupiennius* to be elicited by the stimulation of a single hair (Friedrich 1998). One of these is (ii) *raising the opisthosoma* elicited by the stimulation of long tactile hairs ventrally on the opisthosoma. If stimulated several times, the opisthosoma moves upward stepwise in an evasive way until it reaches the anatomical limit for that movement. The spider then continues to raise its opisthosoma by a tilting movement of the entire body, extending the hind legs only. Another reflex reaction following the stimulation of single hairs in their vicinity is the (iii) *withdrawal of the spinnerets* (Fig. 2.8a). Again, the reaction is stepwise and additive upon repeated stimulation. When stimulating long tactile hairs on the prosoma behind the eyes, *Cupiennius* shows (iv) *body lowering*, again in a stepwise additive manner upon repeated stimulation. This behavior is kind of the opposite of the (*v*) *body-raising reflex* (Eckweiler and Seyfarth 1988) described in more detail below (Fig. 2.8b). Presumably, all these reflexes serve a protective purpose and the avoidance of potential injuries by obstacles during the spiders' nightly activity. However, *raising the opisthosoma* may also play a role in

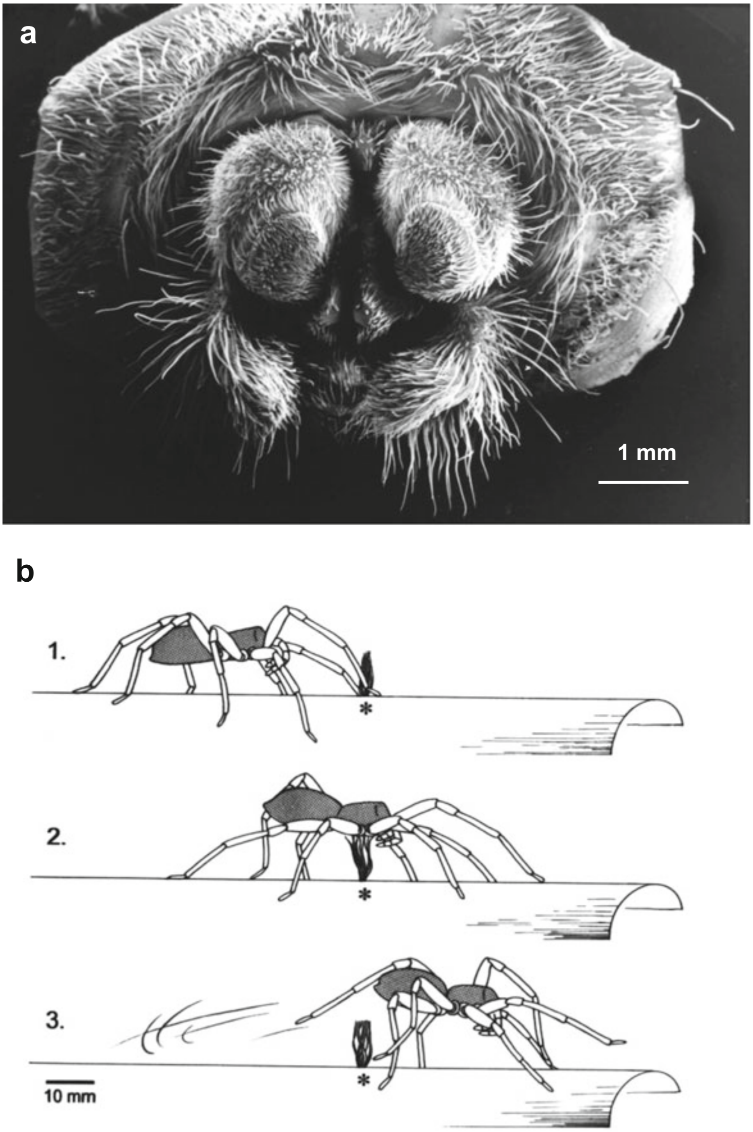

Fig. 2.8 (**a**) Spinnerets of *C. salei*; note large number of sensory hairs. (**b**) Tactile body raising: *C. salei* as it approaches (*1*) and walks across (*2*, *3*) a 10 mm high wire obstacle (*). Neuronal correlates, including central nervous pathways, of this behavior are particularly well studied (see text) (**b** from Seyfarth 2000)

copulation behavior when the female has to raise its opisthosoma to permit the introduction of the male palpal embolus into the epigyne (see under Sect. 2.6.2.4). Likewise, the *withdrawal of the spinnerets* may serve the fine adjustment of the spinning movements, e.g., when spinning the egg sac, attaching the safety thread on the plant, or properly carrying the egg sac (Melchers 1963; Barth 2002a).

2.6.2.2 Body Raising and a Spider's Mechanosensory Neuronal Circuit

Owing to the excellent neuroethological analysis by E.-A. Seyfarth and his associates, the "*body-raising*" behavior of *Cupiennius salei* (also found in four other species of *Cupiennius*, in the salticid *Phidippus regius* and the theraphosid *Brachypelma* sp.) now is the best understood tactile behavior in any spider. In addition to the behavior, neuronal mechanisms and the components responsible for the flow of sensory information could be identified at many levels, ranging from the sensory periphery to the central nervous system (Eckweiler and Seyfarth 1988; Milde and Seyfarth 1988; Seyfarth 2000). Although stereotyped and easy to elicit, the behavior is not a "simple reflex."

The tactile stimulation (deflection) of long tactile hairs on the ventral aspect of the proximal leg segments and sternum first induces a local response only, activating the *coxa levator* muscle of the stimulated leg. This muscle pulls the coxa against the prosoma, while more distal leg joints are extended hydraulically by hemolymph pressure (Blickhan and Barth 1985). As a consequence, internal joint receptors located in the tergo-coxal joint are stimulated which in turn initiate a pluri-segmental response. Now the muscles in all remaining legs are contracting almost simultaneously and the legs are extended. Whereas the local reaction is seen ca. 30 ms after the onset of stimulation, the final body raising is observed after ca. 120 ms only. These delay times are very consistent indicating a rather stereotyped reflex pathway (Seyfarth 2000). Intracellular recordings from neurons in the central nervous system revealed the following neuronal correlates of the local and pluri-segmental response to tactile stimulation. (i) The primary afferent fibers of the tactile hairs project ventrally into the fused spider subesophageal ganglion (Babu and Barth 1984; Anton and Barth 1993; Ullrich 2000; Seyfarth 2000). Their many "local" branches mainly remain in the ipsilateral leg neuromer. (ii) The somata of the motor neurons, which activate the coxal muscles, are found in the dorsally located "motor area" of the neuromer, ca. 200 μm away from the hair afferents. Like the 30 ms delay time between stimulus onset and motor response, this is taken as an argument against rapid monosynaptic connections. (iii) Seyfarth and his associates identified both mono- (local) and pluri-segmental interneurons. In addition to spiking (short bursts) local interneurons, there were also interneurons responding to a tactile stimulus with a longer-lasting graded potential. These interneurons modulate the strength of muscle contraction as shown by experimental current injection. The pluri-segmental spiking interneurons extend into several leg neuromers. They respond to a tactile stimulus and their activity is instantly followed by body raising. Remarkably, the activity of such neurons can also be elicited by the experimental displacement of the coxo-trochanteral joint, which leads to a pluri-segmental motor response as well. Since these neurons are confined to the ventral part of the subesophageal ganglionic mass, they may well be connected to the motor neurons by the premotor non-spiking local interneurons, the only interneurons known to have the corresponding arborizations. Most likely, the afferent activity of internal joint receptors is distributed to all legs by the spiking pluri-segmental neurons (which are assumed to be part of a "command system"; Seyfarth 2000), and the local circuitries are then activated as described.

2.6.2.3 Proprioreception at a Leg Joint

Considering the diligent and well-controlled movements seen in spiders, an important role of sensory feedback is likely. As mentioned before, there are long tactile hairs not only dorsally on the tarsus and metatarsus but also ventrally. These hairs might well play such a role during normal locomotion providing information about the contact with the substrate (Fig. 2.4a). Remember that among all tactile hairs tested so far (see Sect. 2.4.3), they are the most easily deflected. In a recent study, mechanosensitive hair sensilla ventrally at the tibia-metatarsus joint (Fig. 2.9a) were examined asking for their potential adaptedness to their presumed proprioreceptive function in monitoring joint movement (Schaber and Barth 2014). Are these hairs indeed suited to this function as their specific location suggests?

Yes, they are. The changes of the joint angle during locomotion go along with their *deflection* in the distal (metatarsal hair) and proximal (tibial hair) direction, respectively. The hair shafts are covered by thousands of microtrichs arranged in regular rows, which reversibly interlock at their tips with the microtrichs of the hairs on the opposing leg segment. Thus, the opposing hairs deflect each other during joint flexion at each step by roughly the same amount (up to 60°). Note the similarity of their S values. Assisting the hairs' deflection in the relevant direction, the force resisting it, is smaller by one to two orders of magnitude in the direction of natural stimulation (torsional restoring constant S ca. 10^{-10} Nm rad^{-1}) as compared to the other directions (Fig. 2.9b) (where the hairs behave similar to the tactile hairs dorsally on tarsus and metatarsus; see Sect. 2.4.3). The torques for deflections in the proprioreceptive direction measured less than 1 nNm for angles $\leq 30°$ and up to 9 nNm at 70°, when the hair shaft already touched the socket wall. During normal locomotion, this does not happen even at maximum flexion of the joint (Fig. 2.9b).

Electrophysiological recordings from the sensory neurons supplying the joint hairs (neurons of the tibial and the metatarsal hairs) during quasi-natural stimulation corresponding to the pattern of joint flexion during locomotion revealed the following: (i) The hairs are pure movement detectors, and only deflection away from the resting position elicits a short burst of action potentials, whereas the return to it remains unanswered. (ii) The angular deflection threshold eliciting one action potential varied between 0.7 and 15°, depending on the frequency of the simulated stepping rate (0.1–5 Hz). The velocity of joint flexion was well resolved by the rate of action potentials, which saturates only at stepping rates higher than those occurring during walking.

All available evidence supports the idea of a role played by the hairs at the tibia-metatarsus joint and other joints in the fine control of joint movement during walking and other activities like spinning the egg sac. Ventrally at the most distal of the leg joints between metatarsus and tarsus, about 16 long hairs (up to 3 mm) bridging the joint were found to respond to dorsoventral displacement of the tarsus due to substrate vibration (Speck-Hergenröder and Barth 1988). These joint hairs

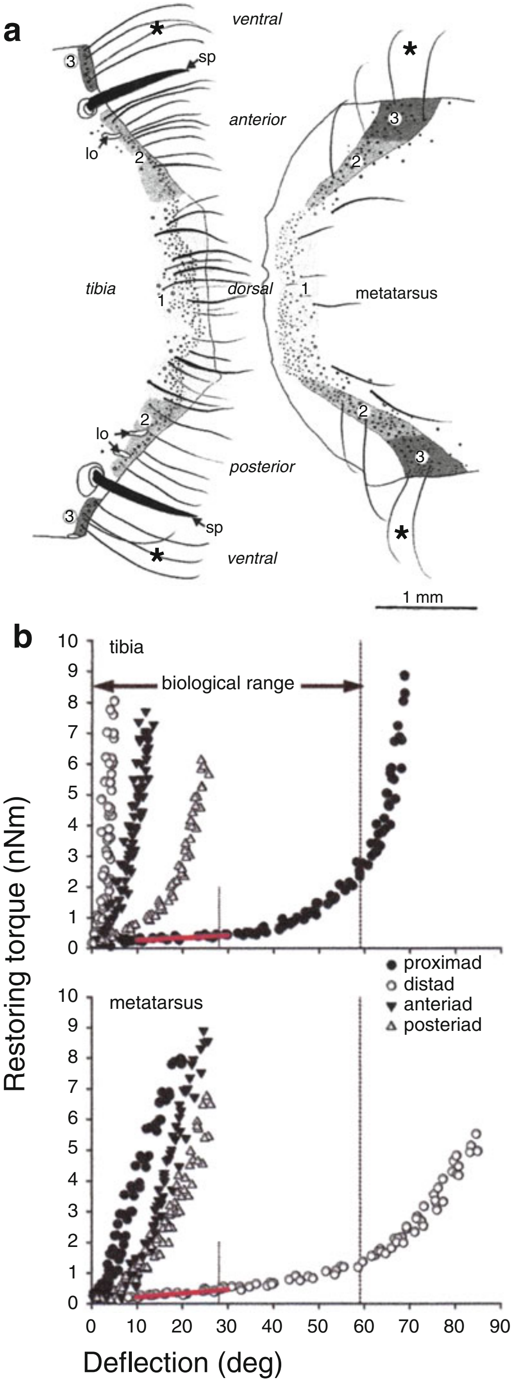

Fig. 2.9 Proprioreceptive joint hairs of *C. salei*. (**a**) Distribution of hairs of different morphologies at the tibia-metatarsus joint of a walking leg in a flattened cuticle preparation. *Asterisks mark* hairs studied in some detail in regard to their presumed proprioreceptive function. *sp* spine, *lo* lyriform organ. (**b**) Mechanical directionality seen from the restoring torques of hairs opposing each other on the tibia (Ti3 hair) and the metatarsus (NMe3 hair). *Dotted line* at 59° marks maximum hair deflection by joint flexion during moderate locomotion, and line at 28° gives the corresponding mean value. *Red* regression line used to determine torsional restoring constant *S*. Note opposite mechanical behavior of the two hairs in the proximal/distal plane of deflection (**a**, **b** modified from Schaber and Barth 2014)

are slightly bent with their tips touching the tarsus. According to recordings from interneurons in the leg ganglia onto which the hairs of the same joint converge, their absolute sensitivity is highest between 70 and 150 Hz and lower by at least two powers of ten than that of the spider's main vibration sensor, the metatarsal lyriform organ (Barth and Geethabali 1982; Barth 2002a).

2.6.2.4 Tactile Stimuli Guiding Copulation or Touching the Complexity of Haptic Perception

It is the courtship and copulatory behavior of *Cupiennius* and many other spiders with its intensive informational interaction which demonstrates both the subtleties and the limits of our knowledge of the sense of touch in spiders particularly well. After a chemical and a vibratory phase, courtship ends in a tactile phase where the mates are in direct contact and chemical communication is likely to play a role as well (Barth 1997, 2002a). As is typical for animals with internal fertilization, in general the sense of touch then becomes very important for mate selection and actual copulation. Although a lot is known about the sensors per se, our understanding of the sensory perception of entire tactile patterns still is in the dark. Analyses of input integration in the central nervous system and in-depth behavioral studies with a focus on sensory aspects are still badly needed.

In *Cupiennius*, copulation follows an elaborate sequence of courtship behaviors (Melchers 1963; Barth 1993; Hrncir et al. unpublished). It is of the lycosid type (Rovner 1971; von Helversen 1976) where the male approaches the female from in front, touches her legs and the dorsal pro- and opisthosoma, and then climbs over her prosoma until he reaches her opisthosoma (Fig. 2.10).

The male then gently strokes over the female's prosoma and opisthosoma with his pedipalps and legs. To insert his pedipalpal embolus into the female epigyne, the male glides down laterally on the female, strongly touching the female opisthosoma laterally and ventrally mainly with his first (72 % of touches) but also its second legs (21 %) and pedipalps (7 %). He either exhibits simple touches or brushing. The female then raises its opisthosoma by an average of 44° and, importantly, rotates it along its long axis by an average of 29° ($N = 19$). She thereby exposes her opisthosomal underside and epigyne to the male. The male again brushes/scrapes over the female's underside with his pedipalps in search of and toward the copulatory pore of the duct leading to the receptaculum seminis (Fig. 2.10). Then its sperm is transferred which takes between 25 and 45 min. After finishing the sperm transfer with one of his pedipalps, the male assumes its initial position on the female prosoma again and, following the same sequence of events, inserts his other pedipalp into the second copulatory pore on the other side of the female's opisthosoma.

Whereas the duration of the different components of the copulation's tactile phase differs widely between individuals, their sequence is stereotyped and the tactile sense strongly involved in this complex sequence of events. Two questions may illustrate this. (i) Does the male need tactile cues to properly orient on the female and (ii) can the raising and swiveling of the female opisthosoma be related to tactile stimulation of the female by the male at particular areas (see also Rovner

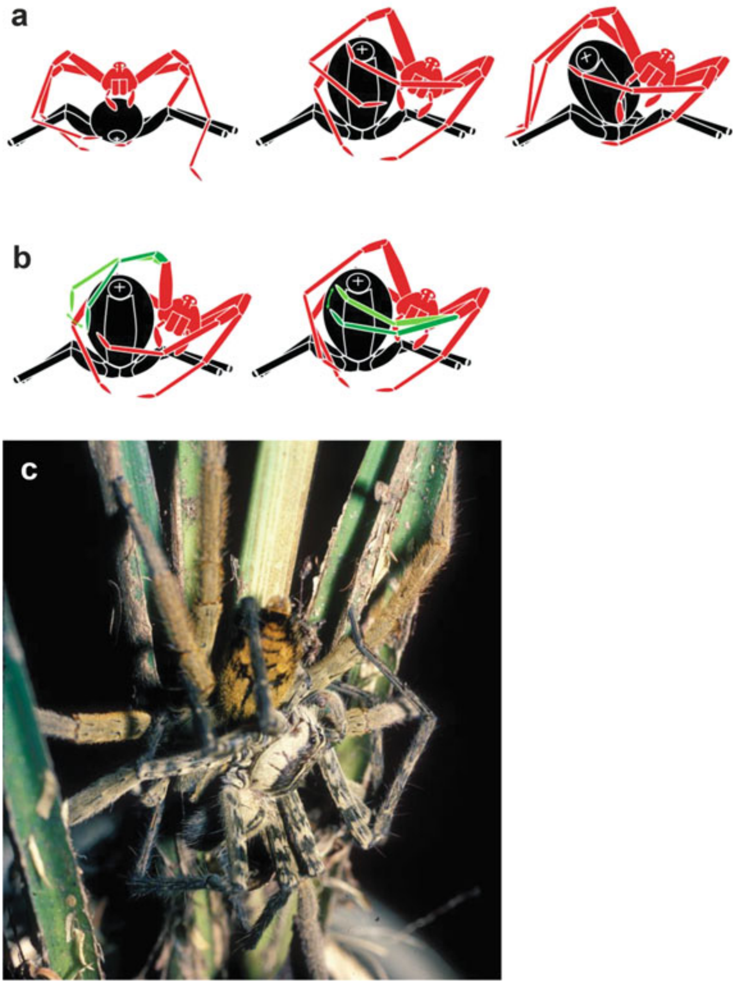

Fig. 2.10 Tactile stimulation during pre-copulatory behavior (*Cupiennius*). (**a**) Male (*red*) mounting a female (*black*) from in front (typical of the "lycosid type") after having touched her legs and dorsal pro- and opisthosoma. He continues touching the female in typical ways until he finds the female copulatory pore (see text). (**b**) Two different ways of the male to touch the female: *left*, simple touch with the tarsus touching the female opisthosoma for some 50 ms only; *right*, brushing movement of tarsus without interrupting contact. (**c**) shows *C*. *coccineus* copulation (Hrncir et al. unpublished data)

1971 for *Lycosa rabida*)? To answer such questions, first a quantitative description of the behavior is needed. Using video cameras we analyzed the raising and swiveling of the female opisthosoma in 55 pairs of *Cupiennius salei* (Hrncir et al. unpublished).

The frequency of male tactile activity strongly increases toward the time of the female's raising of the opisthosoma and then declines again toward its rotation and the sperm transfer. Before the raising of the female opisthosoma, the male tactile stimuli focus on the ventro-anterior area of the opisthosoma close (posterior) to the epigyne and on the spinnerets. After shaving the tactile hairs ventrally and ventrolaterally in the posterior region of her opisthosoma (posterior to epigyne), the female never raised her opisthosoma, despite normal male behavior. Presumably then *she needs tactile stimulation of this region*. The rotation of her opisthosoma, however, was as usual. When stimulating artificially, it is just these areas where large raising angles are achieved. Rotation of the opisthosoma could be eliminated by shaving it ventrolaterally, anterior to the epigyne, which implies that *the male needs tactile sensory input to start his active rotation of the female opisthosoma*. The rotation could never be elicited by artificial tactile stimulation of the female opisthosoma. It is actively achieved by the male using his first pair of legs (as can also be shown in copulations with dead females). As seen from the many male touches, the presence of the female spinnerets is important for his correct orientation on his partner. Following the experimental removal of the spinnerets, the number of touches further increases significantly (Hrncir et al. unpublished).

Clearly, we are still a long way from recognizing the potential "template" of such complex stimulation in the arrangement and properties of the receiver's arrays of tactile hairs.

In engineering, a "matched filter" is used to detect a particular known signal in the presence of noise and to maximize the signal to noise ratio. A commonly known application is for the detection of the reflected echo signal of a radar sender emitting electromagnetic pulses. The task is to detect the known signal or template in the unknown signal. As we have seen, particular mechanoreceptive hairs are tuned to different types of mechanical stimulation, and their properties may be considered kind of templates of the relevant stimulus patterns. Thinking in terms of evolution, this is trivial, the nontrivial part being the rigorous quantitative analysis of the details and the synthesis of the parts to form a whole. We have come some way along this path in regard to individual hairs. However, there is still an enormous lack of knowledge of potential "templates" to be applied to the many different behavioral situations a spider finds itself in and involving hundreds or thousands of sensory hairs exposed to complex spatiotemporal stimulus patterns. As a corollary of this, there is hardly any but a most superficial understanding of the spatial design of the tactile surface of spiders and other arthropods. It will not be an easy task to change this situation to the better, but certainly a lot can be achieved with the technologies now available.

2.7 Concluding Remarks

Impressed by the sheer number and density of the tactile hairs covering the exoskeleton of *Cupiennius* and other spiders, one is tempted to look for some simplifying overarching rules governing their role in touch reception. In the end, an organismal biologist would like to understand how all these sensory hairs interact to construct the spider's subjective tactile reality. To this end we need careful quantitative analyses at many levels of organization.

A first general rule might be hidden in the morphology of the hairs. But are there clearly distinguishable modifications of the general Bauplan of the sensory hair? The detailed comparative analysis of hair morphology revealed the nonexistence of strictly separate types of tactile hairs (Friedrich 1998: Ullrich 2000). Instead there are graduations and intermediates between them. It is nevertheless possible, however, to distinguish large classes of hairs such as "long (>250 μm) and with open socket" and "short (<250 μm) and with closed socket." Thus, classified hairs form different stereotyped patterns typical of particular areas of the exoskeleton (Fig. 2.3). We therefore hypothesize that these patterns at least to some extent reflect features of the various tactile stimulus patterns relevant at different specific locations. A detailed analysis of such stimuli is still largely lacking. And it is demanding on a quantitative basis taking into account all relevant mechanical aspects (like contact forces, adhesion, friction, restoring torques, and hair deflections) for areas densely equipped with many tactile hairs.

Another prime focus of future interest must be the central nervous system. So far the study of "body raising" (Fig. 2.8b) (review by Seyfarth 2000) is the only one fully detailing a tactile behavior at different levels, from the touch receptors and primary afferents to interneurons, motor neurons, and behavior, thus revealing the entire information flow necessary. This study may well serve as an excellent example for similar studies which might also include data on the effects of the sense organs' efferent control. Whereas the fine structural and chemical basis of efferent control is well established in spiders, its functional implications are still far from being sufficiently understood (Foelix 1975; Albert and Barth 1999; Fabian-Fine et al. 2000; Panek et al. 2002). According to neuroanatomical studies (reviewed in Barth 2002a), the primary afferents of tactile hairs are organized in a somatotopic way, the terminal arborizations of sensilla situated proximally or more distally on the leg being represented in the dorsal and more ventral sensory longitudinal tracts (SLTs), respectively. The afferent fibers reach the subesophageal ganglionic mass along the main leg nerves. Their fine branches ramify in the corresponding leg neuromer, contacting interneurons and sending branches to the SLTs (which also are neuropils in addition to tracts). There a lot of convergence of the projections from different tactile hairs and other sensors is seen. Some branches of the primary afferents were also shown to reach the supraesophageal ganglion.

The examples of tactile hairs so far studied in detail amply demonstrate the fine-tuning of their micromechanical properties to particular tasks. For particularly long tactile hairs forming the outer borderline of the spider's tactile space (Fig. 2.4a) (not considering active touch), the structure and mechanical properties of the hair shaft together with the mechanics of its suspension were shown to be exquisitely adapted to both sufficient mechanical sensitivity and protection from breakage by overloads (Dechant et al. 2001; Fratzl and Barth 2009). Together with the phasic electrophysiological properties of the sensory cells, this also makes a perfect event detector particularly sensitive to the initial dynamic phase of a stimulus deflecting the hair

(Albert et al. 2001). Proprioreceptive hairs opposing and deflecting each other, thereby monitoring joint movement, exhibit opposite mechanical directionality (Fig. 2.9). Apart from interactions with its abiotic environment, where the importance of small spaces serving the spider as retreats during the day may have strongly contributed to the evolution of a highly performing tactile sense, the tactile communication with the sexual partner during pre- and copulatory behavior (Fig. 2.10) deserves particular attention.

Sensory ecology has wide boundaries which should include principles of behavior and evolution in addition to studies mainly driven by the question of how a sensory system works. Nevertheless it may well be that the search for the overarching rules and general principles of organization is not the most adequate approach of research. As our knowledge presently stands, it may be more promising to search for the ways how the spider deals with different "tactile problems" inherent in its particular lifestyle. Such an approach also reflects the opportunistic character of natural selection, with no one designing "the" optimal system. In regard to the sense of touch, the comparison of spiders differing in lifestyle like wandering and web-building spiders, or nocturnal and diurnal spiders, might be particularly rewarding. As already pointed out, the same applies to a future focus on the quantitative analysis of complex mechanical stimulus patterns. Although the sensory periphery promises many more discoveries underlining its role in simplifying the flow of information by selecting, filtering, and preprocessing it, the central nervous integration of tactile input needs much more attention than it so far received. Using the tactile capabilities of their antennae, honeybees discriminate between different surface structures, forms, sizes, and locations of objects (Erber 2012). Regarding spiders, experimental data may eventually enable us to comment on questions like "Does the spider use information on form and surface structure (texture)? How is this information gained and which potential role do different modes of active touch, like tapping or brushing, and the timing of tactile sampling play?"

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