

Chapter 14

Functional Morphology and Evolutionary Diversity of Vibration Receptors in Insects

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Abstract Vibratory signals of biotic and abiotic origin occur commonly in the environment of all living organisms. Many species deliberately produce such signals for communication purposes. Thus, it is not only useful but also advantageous and/or necessary to be able to detect and process vibratory signals with appropriate receptor organs. Mechanoreception is suggested to be evolutionarily ancient among animals (Kung 2005; Thurm 2001). Given the long evolutionary history, such receptors have very different anatomical structures and corresponding physiological properties. Responding to mechanical stress is a basic property of cells, even outside the nervous system. In the nervous system, specialized sensory cells and organs register mechanosensory signals and impart the information to higher centers. Structural and molecular adaptations in various mechanoreceptors can push these systems to a sensitivity at or near to the physical limits, e.g., with respect to the noise–stimuli relation. Here, we will deal with the vibratory receptor systems of insects, with a focus on the specialized scolopidial sensory organs from molecular mechanisms to systems analysis.

14.1 Anatomical Diversity of Sensilla

In insects, some vibration receptor types are located at the external surface or embedded in the cuticle, like campaniform sensilla, hair sensilla, or hairplates (Fig. 14.1). Other receptors are internal sensilla, like scolopidial sensilla or

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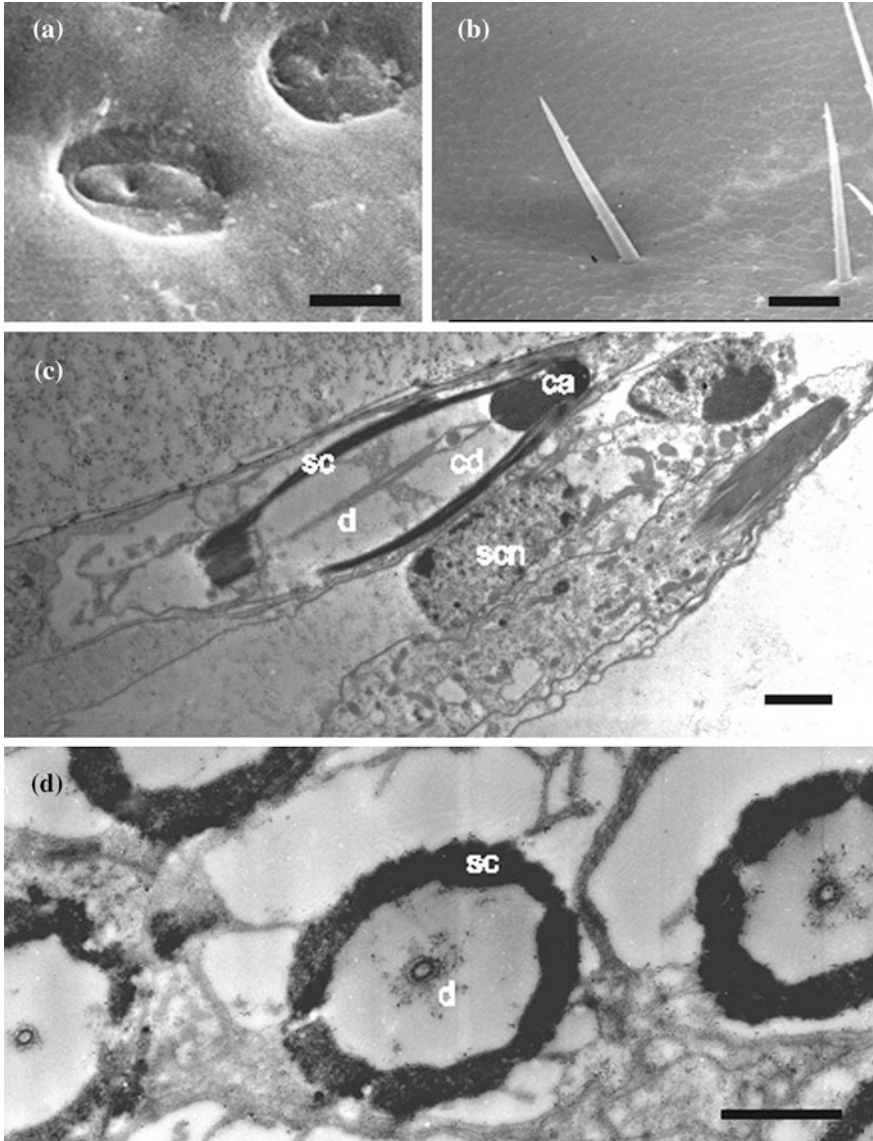


Fig. 14.1 Different mechanoreceptive sense organs of insects. **a, b** Scanning electron microscopic photos of campaniform sensilla **a** and hair sensilla, **b** of the appendages of *Decticus verrucivorus* (Orthoptera). **c, d** Transmission electron microscopic photos of scolopidial sensilla. **c** Longitudinal section of a scolopidium in the prosternal organ of *Homotrixa alleni* (Diptera). Note the dendrite (*d*) running in the lumen of the scolopale (*sc*). *ca* cap, *cd* ciliary dilation, *scn* nucleus of the scolopale cell. **d** Cross section of scolopidia in *Phormia regina* (Diptera). Scales **a** 10 μm , **b** 50 μm , **c** 2 μm , and **d** 1 μm (Unpublished data)

multipolar/multidendritic sensilla. Among these types, the scolopidial sensilla are particularly sensitive to vibrational stimuli. However, a classification and discrimination between the different mechanical processes, like cell expansion, stretching of organs, touch, substrate vibration, and airborne sound, is sometimes difficult, and adequate stimuli may overlap in a given type of sensilla. In the following, different types of sensilla are briefly reviewed with respect to their properties for mechanoreception of vibration.

14.1.1 Campaniform Sensilla

Campaniform sensilla (CS) are a type of external sensilla that is embedded in the cuticle. From the outside, the sensilla are characterized by a shallow dome (Fig. 14.1). Often, the anatomical structure is also indicative of the direction of stimulus perception. The campaniform sensilla react to mechanical stress in the cuticle—the stimuli can originate either from the animal's own movements (proprioception) or from external sources (substrate vibration). CS are located at different positions on the body segments and on appendages, such as the wings or halteres, where mechanical deformations can be detected (Keil 1997). CS can occur as single sensilla, or they can be arranged in groups. CS of the legs have been found to possess minimum acceleration thresholds at frequencies of 50 Hz and lower (Kühne 1982). Stimuli with such frequencies were responded to with a phase-lock of the action potentials. The upper cutoff frequency is some hundred hertz. The CS of legs typically have an axonal projection that is ramified in the lateral part of the corresponding ganglion (Schmitz et al. 1991; Merritt and Murphey 1992; Mücke and Lakes-Harlan 1995) (see also Fig. 14.6). CS occurring dorsally at the proximal tibia are involved in feedback loops of leg movement in many insects (Burrows and Pflüger 1988; Zill et al. 2011). The spatial location of the CS relative to vibration-receptive organs, like the subgenual organ, raises the question of whether CS responses might also be integrated in the neuronal vibratory network for filtering or modulation of information.

14.1.2 Hair Sensilla

Hair sensilla (HS) come in various anatomical shapes of the hair shaft (and were consequently differently named) and with different physiological functions (Fig. 14.1). Mechanosensory bristles can be found on all body parts. They are, just as CS, usually constructed by four cells during development: a sensory neuron, a sheath cell, a socket cell, and a hair shaft cell. The mechanosensory neuron has ultrastructural specializations in its dendrite, like the tubular body (Keil 1997). The tubular body is a massive complex of microtubules in the dendritic tip that is involved in mechanotransduction. Destruction of the tubular body leads to a

decrease in the receptor potential (Erler 1983). The interaction between stimuli, structural elements, and ion channels is the subject of an ongoing analysis of transduction mechanisms (Liang et al. 2011) (see also Sect. 14.2.2). Hair sensilla typically react to touch stimuli. However, filiform hairs might also react to vibrational stimuli, either direct or indirect. An example of indirect measurements is a vibrating leaf that moves air particles above its surface, which in turn deflect the filiform hairs of the insect. Parasitoid wasps might locate their vibration-producing prey within the leaves by such a mechanism (Meyhöfer and Casas 1999). Hair sensilla (trichobotria) of water striders also serve as vibration receptors (Goodwyn et al. 2009). Neuronal networks involving HS have been studied with respect to touch perception (Burrows and Newland 1993). The central projections of hair sensilla are somatotopically ordered in the lateral neuropile of the respective ganglion (Mücke and Lakes-Harlan 1995) (see also Fig. 14.6) and correlate with the receptive field of interneurons (Burrows and Newland 1993).

14.1.3 Multipolar Sensilla

In comparison with other sensilla in insects, least is known about function and physiology of multipolar sensilla. In contrast to bipolar neurons, these sensilla have multiple processes, which can cover much of the body surface (Grueber et al. 2002); in *Drosophila*, they are known as multidendritic (md) neurons. Multidendritic neurons might react to a variety of stimuli: Subsets of md neurons might be involved in proprioception (Grueber et al. 2002), whereas other subsets might respond to temperature or nociception (Tracey et al. 2003). Multipolar sensilla of locusts occur on different body positions and as joint receptors. They can react to vibrational stimuli, but are relatively insensitive (Kühne 1982).

14.1.4 Scolopidial Sensilla

Scolopidial sensilla or chordotonal organs in general have already been subject of a detailed treatise (Field and Matheson 1998). Therefore, their basic features are briefly summarized in the present review, and the focus here is on recent findings of the transduction mechanisms and a discussion of the complexity of sensory organs, their position, and evolution. Scolopidial sensilla are internal sensilla homologous to external sensilla and are characterized by an electron-dense structure, the “scolopale.” The scolopale is formed by actin filaments inside the scolopale cell and surrounds an extracellular space into which the dendrite of the sensory cells extends (Fig. 14.1). The dendrite terminates at an electron-dense cap that is formed by an attachment cell (Fig. 14.1). Further characters of the dendrite are a ciliary dilation and rootlets at its base in the cell body. The sensory cell is surrounded by a glial cell. Such a unit with basically a sensory cell, a glial

cell, a scolopale cell, and an attachment cell is termed a scolopidium. Based on ultrastructural data, two basic types are distinguished. Type 1 scolopidia have cilia with constant diameter and an extracellular cap. The proposed stimulus is an axial extension, and these sensilla are probably most important for vibration perception. Type 2 scolopidia have an enlarged distal segment in the cilium and an elongated tube. They occur often in crustaceans, but have also been shown in the Johnston's organ of insects (for review see Moulins 1976). The cellular composition of scolopidia varies between organs, as some scolopidia possess two sensory cells or additional ligament cells. Within the insect body, the scolopidia are arranged as single units, in small groups or in large, complex sensory organs. In the latter cases, distinct groups of scolopidia, named scoloparia, can occur within the organ complex and might have distinct physiological properties.

14.2 Scolopidial Organs

Scolopidial organs are located at different positions in the insect body. They are part of the sensory complement in the basic bauplan of an insect's segment (Fig. 14.2). For example, in *Drosophila* larvae, most segments contain three scolopidial organs, with a specific number of sensory units (Campos-Ortega and Hartenstein 1997; Hertweck 1931). Besides *Drosophila*, the scolopidial organs have been mapped in orthopteran body segments (Field and Matheson 1998; Meier et al. 1991), whereas in many other insects, only exemplary scolopidial organs have been described. The scolopidial organs are located within a specific segment or are connecting two segments. The position determines the physiological function and sensitivity, but the function may not be obvious on first sight. For example, it is possible that substrate vibrations are perceived with body scolopidial organs, although the body does not have direct contact with the substrate (see Sect. 14.2.3.4 on the prosternal organ). Among the head appendages, the Johnston's organ is well known as a receiver of antennal motion in many insects. Within the insect legs, scolopidial organs have typical positions (Fig. 14.2): in the proximal femur (femoral chordotonal organ), in the proximal tibia (subgenual organ, complex tibial organ), and in the distal tibia and tarsae (chordotonal organs with only a few scolopidia). In the following sections, the development, mechanisms of transduction, as well as functional morphology and physiology of chordotonal organs are reviewed in more detail, with a focus on the scolopidial organs in the proximal tibia.

14.2.1 Development

For different types of sensilla, an underlying developmental sequence has been identified for the cellular differentiation of chordotonal cells, CS, and HS (microchaetes) of *Drosophila* (Lai and Orgogozo 2004). During that sequence, a

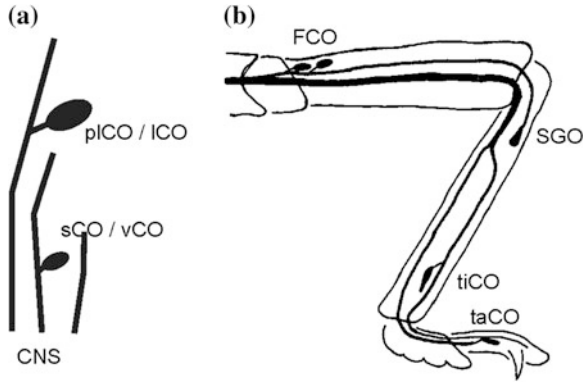


Fig. 14.2 Schematic overview of the location of scolopidial organs in the body segments and legs. **a** In a typical segment, two to three nerves innervate scolopidial organs at two positions (in Orthoptera, the pleural chordotonal organ (plCO) and the sternal chordotonal organ (sCO); in *Drosophila*, the lateral chordotonal organ (lCO) and the ventral chordotonal organ (vCO)). **b** In a typical insect leg, the femoral chordotonal organ (FCO) might have different subparts; the subgenual organ (SGO) is often accompanied by other scolopidial organs (see text), and chordotonal organs are located in the distal tibia (tiCO) and tarsae (taCO). (Modified from Campos-Ortega and Hartenstein 1997; Meier et al. 1991; Mücke 1991)

sensory mother cell divides asymmetrically, and after further cell divisions, four to five cells are generated. Thereby, two accessory cells (e.g., socket cell and shaft cell) differentiate and one sensory neuron with glial or sheath cells. By differential gene expression, the different types of receptor organs are generated. For example, mutations in the *cut* gene transform a hair sensillum into a scolopidial sensillum (Bodmer et al. 1987).

By contrast, the development of complex scolopidial organs is only partially understood. For formation of sensory units in the relatively large femoral chordotonal organ of *Drosophila*, the epidermal growth factor receptor promotes continuous generation of sensory mother cells (zur Lage and Jarman 1999). Complexity is not only a question of cell numbers, but also a question of distinct subparts of an organ, as these subparts might have different physiological properties. The complex tibial organ (CTO) of some Ensifera consists of three parts with different functions (see Sect. 14.2.3). The CTO develops during embryonic development (Klose 1996; Lakes-Harlan and Strauß 2006; Meier and Reichert 1990), but at least in some species of Tettigoniidae, the sensory cells of the parts of the CTO have different developmental origins (Fig. 14.3, unpublished results). The cells of the subgenual organ (SGO) and the *crista acustica* homolog (CAH) arise from sensory mother cells that proliferate at separate positions in the epidermal cell layer. Later, during embryogenesis, the cells form the CTO together and establish their specific central projections. Scolopidial sensory neurons grow their axons during embryogenesis or metamorphosis to the CNS (Lakes-Harlan and Pollack 1993; Lakes and Pollack 1990). These axons orientate along preformed

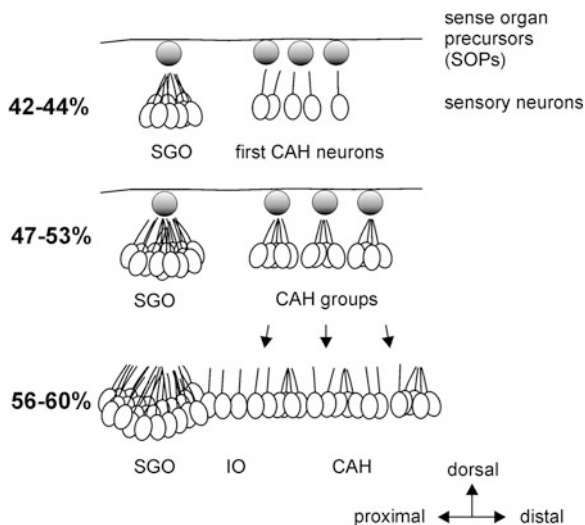


Fig. 14.3 Model of the developmental sequence of the complex tibial organ of *M. elongata* (Ensifera). The model is based on sequential preparations of embryonic stages (indicated by percentages of developmental time to larval hatching) with immunolabeling of the sensory cells. The cells of the subgenual organ (SGO) and the crista acustica homolog (CAH) have different developmental origins (sense organ precursor cells) and form together the complex sensory organ, including the intermediate organ (IO). (Based on unpublished data)

pathways in the embryo; in cases where the pathway is missing, the axons arrest their growth (Klose and Bentley 1989). For axonal guidance, the cell surface molecule Fasciclin I, which is expressed by the sensory cells and the target neuropiles in the CNS, could be important (Schäffer and Lakes-Harlan 2001). In the holometabolic Diptera, complex scolopidial organs like the femoral chordotonal organ (FCO) develop during metamorphosis. Interestingly, the axons of the FCO extend to the CNS, but after mid-metamorphosis, the organ is retracted within the femur and the axons are apparently shortened during this process (Lakes and Pollack 1990). By contrast, in the moth *Manduca sexta*, sensory units of the FCO are already present during larval stages (Kent et al. 1996). Vibration receptors are fully functional after hatching, and the sensitivity to vibration stimuli does not change during postembryonic development in tettigoniids and locusts (Rössler et al. 2006).

14.2.2 Mechanotransduction

Transduction of mechanical stimuli is a multistep process ranging from mechanical force acting on the receptors to neuronal activity of sensory neurons (French 1992). The first step is a mechanical coupling between the stimulus, e.g., a substrate

vibration, and the receptor structure. Such a structure could be the cuticle transmitting the external force. Consequently, embedded sensilla, the campaniform sensilla, can measure compression or strain of the cuticle that leads to activation of the receptor. In the case of the internal scolopidial sensilla, a longitudinal stretch of the dendrite is likely to be the adequate stimulus. The micromechanics of vibration inside a leg or other body parts are rarely investigated (see Sect. 14.2.3 for some discussion), although they might be decisive for the physiological function of the scolopidial organs. Subcellular structures in the scolopidial units, like a ciliary dilation in the dendrite of the sensory neuron, may also be important as suggested by mutant studies (reviewed in Field and Matheson 1998). The next steps in mechanotransduction are the opening of ion channels and changes in the membrane potential. In recent years, the molecular physiology of sensory transduction was pushed forward especially in the model system of the antennal Johnston's organ of *Drosophila* (Kernan 2007; Lu et al. 2009). The Johnston's organ consists of several hundred scolopidial units and is mainly an auditory and gravitation receptor.

Behavioral screens for flies defective in mechanotransduction identified candidate molecules for transduction gating, including ion channels of the transient receptor potential (TRP) ion channel family. TRP channels are cation channels with six transmembrane domains and cytoplasmic N- and C-terminals found in different sense organs; TRP channels can be classified into seven distinct groups based upon sequence similarities and structural characteristics (Christensen and Corey 2007; Matsuura et al. 2009).

Three TRP channels have been identified as candidates for the gating channel in mechanosensory cells: “No mechanoreceptor potential C” (NompC), “Inactive” (Iav), and “Nanchung” (Nan). These channels are specifically located in subcellular structures important for mechanotransduction: Iav and Nan are localized in the proximal cilia of chordotonal neurons (Gong et al. 2004); NompC is localized in the distal cilia of scolopidial neurons and the tubular body of campaniform sensilla (Lee et al. 2010; Liang et al. 2011; Keil 2012). Nan and Iav are expressed in most sensory neurons in the *Drosophila* Johnston's organ. These channels form heterodimers, and Nan is dependent on Iav for proper localization within the scolopidia (Gong et al. 2004). If Iav is deleted, the neuronal response to acoustic stimuli is abolished. It was discussed whether the Nan-Iav dimers may be mechanically activated by ciliary deflections or have a function in signal control downstream of the transducing channel, as disruption of Nan-Iav increases the active amplification in the hearing organ (Göpfert et al. 2006). While the majority of the Johnston's organ sensory neurons express NompC (Lee et al. 2010), only the neurons mediating hearing require it functionally for generating a regular neural response (Effertz et al. 2011). NompC includes an ankyrin spring of 29 ankyrin repeats (Howard and Bechstein 2004) and has been shown to be directly opened by mechanical stimuli (Yan et al. 2013). It may form the gating spring in campaniform sensilla (Liang et al. 2013) though not the gating channel in auditory neurons (Lehnert et al. 2013). The definite contribution of the respective molecules to mechanotransduction in *Drosophila* hearing is so far unresolved (Lehnert et al. 2013; Gong et al. 2013; Matsuo and Kamikouchi 2013). Given this functional

specialization between Johnston's organ neurons, the functional conservation or similarity of TRP channels in sensory organs for substrate vibrations like the subgenual organ or femoral chordotonal organ will be relevant to explore.

Related to the identity of the gating, channel is the question for the mechanism of channel opening ultimately causing mechanotransduction. According to a membrane force model, direct opening could result from transfer of forces on the neuron's cell membrane and a pull on the ion channel, opening the pore (Chalfie 2009; Christensen and Corey 2007). Indirect tether models in general assume that force is transferred to specific molecules/proteins which are linked to the ion channel and activate it by induction of a conformational change. Such molecules could be linked to the intracellular cytoskeleton or extracellular matrix molecules or a combination thereof (Chalfie 2009; Christensen and Corey 2007). In scolopidia of Johnston's organ of *Drosophila*, opening of the gating channel is supposedly direct and via gating springs (Albert et al. 2007). The short latencies in chordotonal organs in the submillisecond range support the hypothesis of a direct activation process (Albert et al. 2007).

In mechanoreceptors, the sheath cells produce a high concentration of potassium in the surrounding of the dendritic cilium compared to hemolymph (French 1988; McIver 1985). In scolopidial units, the scolopale space is filled by an endolymph with high potassium concentration, but low calcium concentration (Todi et al. 2004). The receptor potential of mechanoreceptors is proportionally graded to the stimulus intensity (French 1988). The primary sensory neurons are supposed to generate action potentials at the beginning of the axon. In the scolopidia of an orthopteran hearing organ, small non-propagating spikes are passively conducted back into the soma and the dendrites (Hill 1983).

14.2.3 Functional Morphology and Physiology

Scolopidial organs differ largely in their functional morphology. Here, we focus on those found within the legs, and especially in the proximal tibia, that have been investigated for several insect taxa, with another example of a vibration-sensitive organ in the thorax of an insect.

14.2.3.1 Femoral Chordotonal Organ

The femoral chordotonal organ (FCO) is probably present in all insects, and in many species, it is a large mechanosensory organ with up to hundreds of sensory units (Debaisieux 1938). It is located dorso-proximally in the femur and attaches via a cuticular apodeme at the femur-tibia joint (Fig. 14.2). While the FCO is in general a proprioceptive organ involved in sensory feedback loops required for limb coordination, it is also a vibration receptor in some insects. The functional specialization may be associated with structural subdivision. For example, in

orthoptera and stick insects, two distinct scoloparia are found, whereby the locust FCO and *Carausius* FCO contain heterodynal type I scolopidia with two sensory neurons each (Füller and Ernst 1973; Matheson and Field 1990). In the locust, the FCO of the middle leg contains 42 sensory neurons in the distal scoloparium and several hundred relatively small sensory neurons in the proximal scoloparium (Field and Pflüger 1989). Physiological investigations in the locust showed a functional distinction between the two groups: The distal scoloparium mediates the postural resistance reflex, while the proximal group does not affect this reflex (Field and Pflüger 1989). The latter group was suggested to be a functional receiver of vibrational stimuli between 50 and 300 Hz, as it responds to vibrations with displacements of 4- μm amplitude (Field and Pflüger 1989). Similarly, in the stick insect *Carausius morosus*, a proprioceptive function could be ascribed to the ventral scoloparium in the resistance reflex, leaving open the role of the larger dorsal scoloparium (Kittmann and Schmitz 1992). In the stick insect *Cuniculina impigra*, a high number of sensory neurons in the FCO were proven to be vibrosensitive (Sauer and Stein 1999; Stein and Sauer 1999), but a localization of the structural correlate was not given. A distinction into two scoloparia is also clearly present in crickets (Nishino 2000) and bush crickets (Theophilidis 1986), although in some species, the separation into two scoloparia may not be complete (Matheson and Field 1990).

In the green lacewing *Chrysoperla* (Neuroptera), the femoral chordotonal organ contains up to 26 scolopidia and it is vibroceptive with a maximum sensitivity at about 1 kHz with a threshold between 0.1 and 1 ms^{-2} (Devetak and Amon 1997). In some insects, the number of scolopidia can be as low as 12, e.g., in the stink bug, *Nezara viridula* (Michel et al. 1982). The number of sensory cells, however, is not size related, as in the small *Drosophila melanogaster*, the FCO has three subunits with 14–32 scolopidia each (Shanbhag et al. 1992). The FCO of *D. melanogaster* also reacts to low-frequency vibrational stimuli (Lakes-Harlan and Lefevre 2012). Together with a rather insensitive tibial scolopidial organ (Schneider 1950), the FCO might be an important source for vibration perception, as Diptera do not possess a subgenual organ (see below). The vibratory function of the FCO is further indicated by the central projection because parts of the dipteran FCO axons project in the mVAC (Merritt and Murphey 1992; see Sect. 14.2.4).

14.2.3.2 Scolopidial Organs in the Proximal Tibia

In many insect taxa, scolopidial organs are found in the proximal tibia; known exceptions are the Diptera and Coleoptera. The most widely distributed organ is the so-called subgenual organ (SGO), by which scolopidial sensilla are named according to their location just distally of the femur–tibia joint (Fig. 14.4). However, in a number of species, additional scolopidial organs in the proximal tibia are documented: a distal organ (in Caelifera and Blattodea: Friedrich 1929), an intermediate organ and a crista acustica or its atympanate homolog (in Ensifera), a Nebenorgan (Blattodea and Mantophasmatodea), and an accessory organ (in

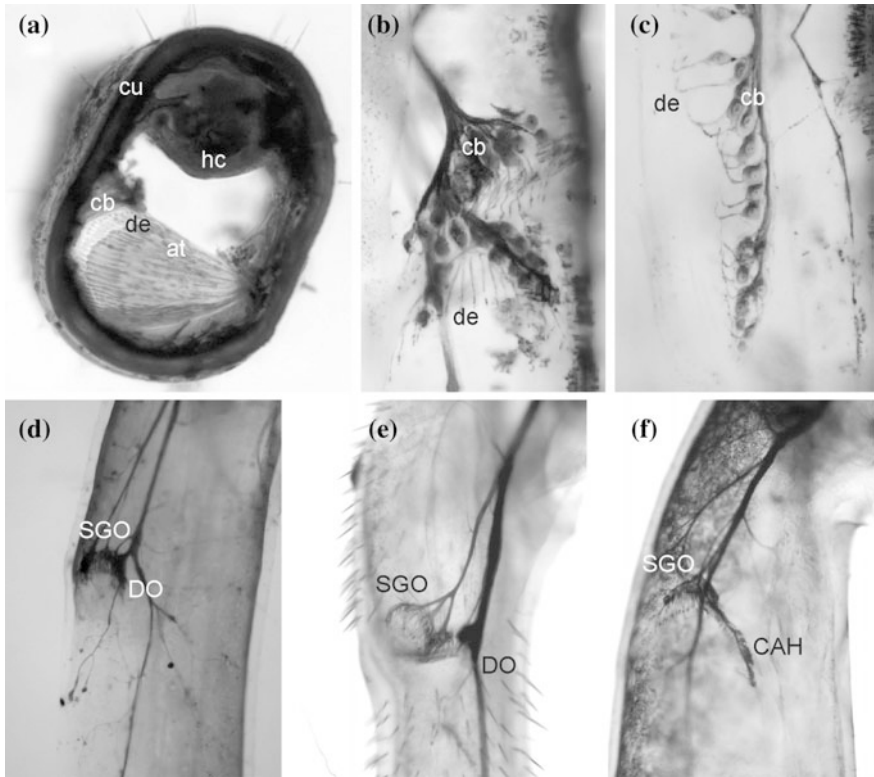


Fig. 14.4 Photoplate of scolopidial sense organs of in the proximal tibia of different insects. **a–c**, Midleg of *M. elongata* (Ensifera; photos courtesy of Jan Häusler, unpublished). **a** View from proximal end into an opened tibia to visualize the localization of the subgenual organ (SGO). Anterior is to the *left*; staining with Janus Green. **b** Frontal view of a nerve backfill of the SGO with distinguishable cell bodies and dendrites. **c** Frontal view of the crista acustica homolog (CAH). **d–f**, Lateral view of the SGO and further scolopidial sense organs in different orthopteran species (unpublished). **d** *Schistocerca gregaria* (Caelifera), **e** *Hierodula membranacea* (Mantodea), and **f** *Stenopelmatus spec.* (Ensifera). *at* attachment of the SGO; *cb* cell bodies of sensory neurons; *cu* cuticle; *de* dendrites; *DO* distal organ; *hc* hemolymph channel; *SGO* subgenual organ. Scale 100 μ m

Mantodea, Blattodea, and others: Strauß and Lakes-Harlan 2013). In contrast to the SGO, the specific functions and the evolutionary relations of the other organs are so far largely unknown.

The best-known vibration receiver is the subgenual organ, which has been studied in detail in a number of insect taxa and was documented in most Pterygota. It is not connected to leg joints and detects external stimuli transferred to the leg. The SGO is considered to be the most sensitive vibration receptor in insects (Cokl and Virant-Doberlet 2003). All subgenual organs contain type 1 scolopidia with a single sensory neuron per scolopidium (Field and Matheson 1998), but the

organization of the subgenual organ is of notable diversity (Fig. 14.5): it is club shaped in some Hymenoptera species and in termites (Howse 1964), whereas in other Hymenoptera, the organ hangs in the hemolymph cavity (Vilhelmsen et al. 2001, 2008). In orthopteroid insects, the SGO is often sail shaped and suspended in the hemolymph (Lin et al. 1995; Schnorbus 1971). In this case, the cap and accessory cells span the hemolymph channel (Fig. 14.4); in other cases, the SGO is more like a “mass” of cells (Nishino and Field 2003). In Lepidoptera, it is diffusely organized and apparently the scolopidia are distally unattached (Howse 1968). In Hemiptera, like *N. viridula* or a species of Membracidae, *Stictocephala bisonia*, scolopidial cells are attached to a ligament stretching along the tibia from proximal to distal (Michel et al. 1982, Roze unpublished). This anatomy of scolopidial cells might even raise the question of whether those cells in Hemiptera and Neuroptera should actually be named subgenual cells. In other insects, scolopidial units adjacent to the SGO that extend into the longitudinal axis of the tibia are named intermediate organ or distal organ (see below). Further anatomical, physiological, and developmental studies are needed to clarify whether the differences are purely nomenclatorial or based on the possibly convergent evolution of tibial sense organs. The subgenual organ can be innervated by two different leg nerves. In orthopteroid insects, the sensory nerve 5B1 innervates one part of the subgenual organ and another part is innervated by a branch of the mixed leg nerve 5B2. In the tettigoniid *Mecopoda elongata*, the nerve 5B2 innervates the posterior portion of the subgenual organ and contains more axons of the subgenual scolopidia than the sensory nerve innervating the complex tibial organ.

The numbers of scolopidia in the SGO vary largely between species. In the stink bug *N. viridula* (Heteroptera), it consists of just two scolopidia (Michel et al. 1982), and in the neuropteran *Chrysoperla carnea*, it consists of three scolopidia (Devetak and Amon 1997), and many orthopteroid species have 20–80 scolopidia (Rössler 1992; Schnorbus 1971). For adult tobacco hornworm moths, *M. sexta*, about 30 neurons are found in the SGO (Kent and Griffin 1990). A large variance occurs within Hymenoptera: The SGO of ants contains 10–40 scolopidia (Howse 1964; Menzel and Tautz 1994), that of the honeybee *Apis mellifera* around 40 scolopidia (Kilpinen and Storm 1997), and in parasitoid wasps, females of certain species can have 300–400 SGO scolopidia (Vilhelmsen et al. 2008). The functional relevance of the SGO structure and cell numbers has only been discussed for the parasitoid wasps (see Sect. 14.2.4).

The subgenual organ reacts to substrate vibration, but in cockroaches is so sensitive to mechanical stimuli that it might react to airborne stimuli despite lack of tympana (Shaw 1994). For physiological characterization of substrate vibration, an important parameter is the threshold: the lowest displacement or acceleration stimulus that elicits a neuronal response. For the cockroach *Periplaneta americana*, displacements of 0.22–5 nm at a frequency of 1.57 kHz can be detected by subgenual receptors (Shaw 1994). Similar values have been found in the green lacewing, which corresponds to an acceleration threshold of 0.02 m/s² (Devetak and Amon 1997). The vibroreceptors in *N. viridula* are tuned to different frequencies but share minimal thresholds around 0.01 m/s² (Cokl 1983). The cricket *Gryllus*

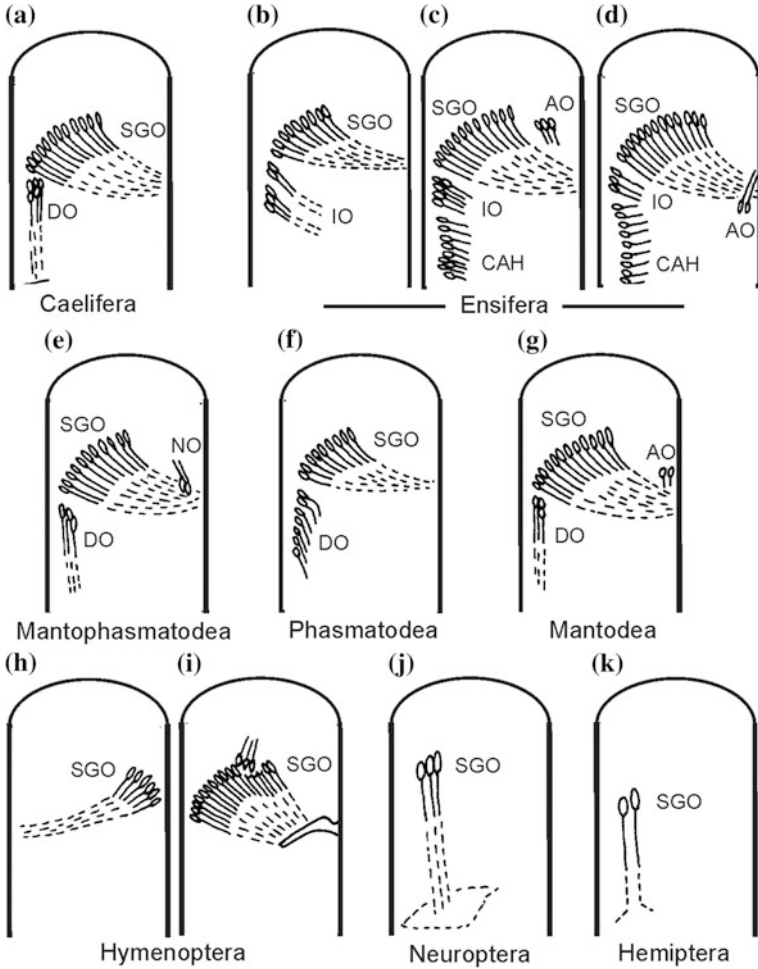


Fig. 14.5 Schematic overview of the sensory arrangement of scolopidial organs in the proximal tibia of different taxa. Drawn are sensory cell bodies with their dendrites and their attachment (stippled). Compare the overall similarities in Orthoptera (**a–d**), and in orthoptera-related groups (**e–f**), to more distantly related taxa (**h–k**). Note the large differences within the Hymenoptera (**h**: ant, **i**: parasitic wasp) that are probably caused by specialized functional adaptations. Drawings are based on the following: **a** *Schistocerca gregaria* (Lin et al. 1995), **b** *Troglophilus neglectus* (Jeram et al. 1995), **c** *Comicus calcaris* (Strauß and Lakes-Harlan 2010), **d** *Hemideina femorata* (Nishino and Field 2003), **e** *Karoophasma biedouwense* (Eberhard et al. 2010), **f** *Sipyloidea sipylyus* (Strauß and Lakes-Harlan 2013), **g** *Hierodula membranacea* (unpublished), **h** *Camponotus ligniperda* (Menzel and Tautz 1994) and *Apis mellifica* (Schön 1911), **i** *Orussus abietinus* (Vilhelmsen et al. 2001), **j** *C. carnea* (Devetak and Pabst 1994), and **k** *N. viridula* (Michel et al. 1982) and *S. bisonia* (Roye, unpublished). AO accessory organ, CAH crista acustica homolog, DO distal organ, IO intermediate organ, NO Nebenorgan, and SGO subgenual organ. Anterior is to the left, proximal to the top. Drawn not to scale; cell numbers are represented, but not exactly depicted

bimaculatus has been found to be highly sensitive: The threshold of midleg subgenual receptors was at only 0.0018 m/s^2 at frequencies from 700 to 1,000 Hz (Dambach 1972). This sensitivity is not seen throughout the Ensifera, as the tree weta has a threshold of 0.015 m/s^2 for vibrational signals at 1 kHz (McVean and Field 1996). Subgenual thresholds in both locusts and bush crickets range between 0.01 and 1 m/s^2 with little species-specific variation (Kühne 1982). Whereas in crickets, the midleg reacts most sensitively to vibrational stimuli (Dambach 1972), in *C. carnea*, the metathoracic hindlegs were most sensitive (Devetak and Amon 1997). In Mantodea, the vibration sensitivity has been tested with respect to functional adaptations of the leg pairs. The foreleg is adapted for prey capture and typically held in the position known for mantis without contact to the substrate; the other legs are used for standing and foraging and are in contact with the substrate. However, no major functional adaptation could be found: The sensory organs in the three legs are highly similar, and furthermore, the legs do not have different physiological sensitivities (unpublished results). The characteristic frequency (CF), defined as the frequency with the lowest threshold, is in crickets around 700–1,000 Hz in the midlegs and 400–500 Hz in the hindlegs (Dambach 1972). In the midlegs of various species of bush crickets, the CFs range from 500 to 1,500 Hz (Kühne 1982). Tuning curves as well as intensity response curves vary between recorded neurons, suggesting that vibratory stimuli can be precisely fractionated and coded in the SGO. Even the few SGO neurons in *Nezara* may discriminate different frequencies (Cokl 1983). A major difficulty with the interpretation of some physiological data is that they cannot be unequivocally ascribed to the subgenual organ. Extracellular recordings could contain responses from unidentified elements; in intracellular recordings, SGO neurons were identified via (an assumed) physiology and by their probable central projection. Only in a very few cases has the peripheral cell body been labeled and its position unequivocally identified (see Fig. 14.6, recording and labeling by A. Stumpner, Göttingen).

An important, but rarely addressed question is what are the mechanical forces and parameters driving the physiological reaction of the vibration receptors. It has been suggested that the SGO acts like an accelerometer (Schnorbus 1971). In the honeybee, it has been possible to document the vibrations of the SGO itself. Substrate vibrations are transferred to the hemolymph, and the sensory organ is actually oscillating with the hemolymph rather than in the hemolymph (Kilpinen and Storm 1997). Thus, the subgenual organ's oscillations are matched with the hemolymph oscillations and model calculations show that it behaves as an overdamped system (Storm and Kilpinen 1998). The model suggests that the sensory cells of the SGO are displacement sensitive. Velocity threshold curves of SGO neurons from *Nezara* run in parallel with equal acceleration values below best frequency and in parallel with equal displacement lines above the best frequency (Cokl 1983). In addition, the SGO of honeybees was shown to have stimulus-direction-specific responses (Rohrseitz and Kilpinen 1997). These results indicate that careful control of the stimulus application is important and that further research is needed to understand the micromechanics of vibration perception in the SGO and other scolopidial sense organs. Interestingly, the structure of the SGO of

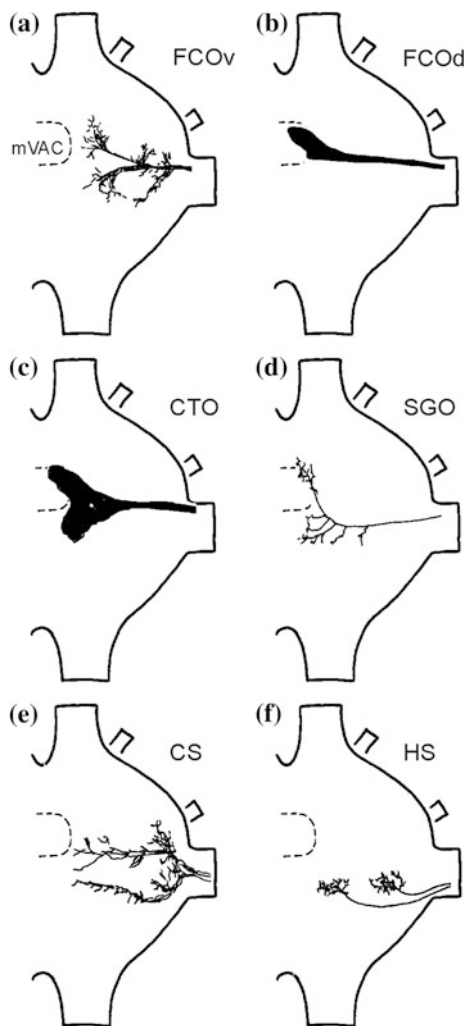


Fig. 14.6 Schematic overview of typical central axonal projections of mechanoreceptive sensory fibers. The projections are outlined in a generalized segmental hemiganglion. The median ventral association center (mVAC) is outlined, to indicate which fibers project into this internal neuropile. **a, b** The femoral chordotonal (FCO) can have different central projections: **a** Fibers of the dorsal scoloparium of crickets (Nishino 2000) or the proximal part in locusts (Field and Pflüger 1989) project into the mVAC; **b** Other fibers of the FCO have a more lateral projection. **c** Projection of the midleg CTO of *Stenopelmatus* (Strauß and Lakes-Harlan 2008b). **d** Projection of single fiber originating in the SGO. This neuron has been recorded from and it has been stained completely with neurobiotin, thereby confirming unequivocally its origin in the SGO of *Ancistrura nigrovittata*, Ensifera (courtesy of Dr. Stumpner, Göttingen, unpublished). **e** Central projection of campaniform sensilla from the leg of locusts. **f** Central projection of hair sensilla on leg parts, which are somatotopically ordered within the neuropile (two positions are indicated by the two arborization areas). Drawings generalized after (Pflüger et al. 1988 for the ganglion outline) [**a, b** after (Nishino 2000), **c** after (Strauß and Lakes-Harlan 2008b), **e** after (Hustert et al. 1981) and **f** after (Mücke and Lakes-Harlan 1995)]

aqueous larvae and land-living adults of Plecoptera is rather similar (Wittig 1955), although different mechanical forces might act on the legs.

In many taxa, the subgenual organ is not the only scolopidial organ in the proximal tibia, although vibration perception can obviously be well achieved with the SGO alone (Fig. 14.5). Thus, questions arise about the function and the evolution of the other sensory organs. As an example, this can be studied in the Ensifera, which possess the so-called complex tibial organ (CTO). Within the foreleg of Tettigoniidae, this organ complex is associated with sound-propagating structures and can perceive vibratory stimuli as well as acoustic stimuli. The CTO comprises the subgenual organ, an intermediate organ, and a crista acustica (in tympanate legs). The *crista acustica* is a conspicuous feature of the CTO due to its more or less linear arrangement of sensory cells, which correlates with physiological response properties of the auditory receptors (review: Stumpner and von Helversen 2001). Recently, such a tripartite CTO has also been described in atympanate Ensifera (Strauß and Lakes-Harlan 2008a, b), including a structure homologous to the *crista acustica*. The distinct parts of the CTO have commonalities, but also differences: The parts have different attachments, partly different adequate stimuli and different developmental origin. The scolopidia of the SGO are orientated circularly within the leg and clearly separated from the other two parts. The scolopidia of the intermediate organ point toward an attachment fixed at the dorsal tibia. The scolopidia of the *crista acustica* homolog (CAH) point toward a supporting structure that extends in the longitudinal axis of the leg. The intermediate organ and the CAH are probably vibration receivers, but physiological details are so far unknown. The different dendritic attachment in comparison with that of the SGO might indicate perception of other physiological parameter. For example, the CAH might not vibrate with the hemolymph as the SGO (see above). Thereby, other parameters, like different waveforms or different oscillation planes, might be perceived by the CAH. Biophysical measurements of the oscillations of the CAH will hopefully resolve the physiological properties. Interestingly, the CAH is present not only in deaf ensiferans, but also in the atympanate legs of hearing Tettigoniidae. Thus, it is likely that the organ complex has an important function in the sensory world of Ensifera. Generally, it might be more than a coincidence that the CTO has been formed in the proximal tibia. The position just distally of the femur–tibial joint seems to be well suited for perception of vibratory signals, due to filter properties of the leg (Cokl personal communication). Consequently, also other taxa have distinct scolopidial organs in the proximal tibia besides the SGO (Fig. 14.5): In Caelifera and Mantophasmatodea, a distal organ has been described (Eberhard et al. 2010; Lin et al. 1995). The Mantophasmatodea have a pronounced vibrational communication with species-specific signals (Eberhard and Picker 2008). The vibrational sensitivity of the leg nerves reaches thresholds of 0.01–0.001 m/s² within a frequency range from 600 to 1,200 Hz (Eberhard et al. 2010). The precise origin of this physiological response is not known, although the SGO is likely to be the most sensitive vibration receptor. Phasmatodea possess an elaborated distal organ besides the SGO (Strauß and Lakes-Harlan 2013).

Another organ in the proximal tibia is the accessory organ, which has only a few sensory units attached to the dorsal cuticle. It is present in mantids as well as in some orthopterans in close association with the other parts of the sensory complex. The function of the organ is unknown; it might contribute to the information processing of relevant vibratory signals.

14.2.3.3 Tarsal Chordotonal Organs

Scolopidial organs can be found in different parts of tarsi of many insects (Mücke 1991; Goodwyn et al. 2009; Wiese 1972). The function of these scolopidial organs has been addressed in water striders, which detect water surface waves for prey location. The respective sensors of water vibrations are located in the tarsi, as cutting of the entire tarsi abolished the orientation of the animal (Murphey 1971). In *Aquarius paludum*, three scoloparia occur in the tarsi. Each scoloparium contains 2–3 scolopidia and is orientated in different directions, which might be seen as sensory adaptation to perception of complex water wave vibrations (Goodwyn et al. 2009). In the backswimmer *Notonecta glauca*, the tarsal chordotonal organ enables localization of the wave-producing prey (Wiese 1972). The tarsal chordotonal organ is located in the distal tarsomere and consists of two scoloparia (proximal and distal) with three and five sensory neurons, respectively. The sensory units respond in the behaviorally relevant frequency intensity range (Wiese 1972). However, not all tarsal chordotonal organs might serve as vibration receivers: In *C. carnea*, a sensitive vibration response was lacking (Devetak and Amon 1997), and in Mantophasmatodea, the destruction of the tarsal chordotonal organ did not change the vibration sensitivity (Eberhard et al. 2010).

14.2.3.4 Prosternal Chordotonal Organ

The prosternal chordotonal organ of Diptera is interesting for several aspects. This organ presents an example of a sense organ that is *not* immediately obvious for substrate vibration perception. The prosternal chordotonal organ is located in the prothorax, directly behind the head. It attaches to a neck membrane and has therefore been proposed to monitor head movements (Preuss and Hengstenberg 1992). However, it could be shown that the organ reacts sensitively to high-frequency vibrations not found in movements of the head or during flight (Lakes-Harlan et al. 1999; Stölting et al. 2007). The organ might therefore be able to pick up substrate vibrations. This finding is furthermore in accordance with the hypothesis that the prosternal organ was modified during evolution into a hearing organ (Lakes-Harlan and Heller 1992; Lakes-Harlan et al. 1999; Robert et al. 1992). The evolutionary scenario implicates that the animals first perceived vibratory signals and that modifications in the sound-propagating structures (enlargement of a tracheal chamber and thinning of tympanal membranes) resulted in the capacity to perceive airborne sound.

The physiology of the prosternal organ is also interesting with respect to unknown vibratory sense organs in other insects. For example, Membracidae have been shown to communicate with vibratory signals and to react very sensitively to vibratory stimuli (Cocroft 1996; Cocroft and McNett 2006). The vibratory stimuli might be sensed by the SGO, but perhaps also with scolopidial organs at other body locations. Many Membracidae have a spectacular morphology with protuberances and extensions of the body surface. These structures have been shown to vibrate in response to substrate vibration, whereby the maxima and minima of vibrations follow a complex system (Cocroft et al. 2000). If an internal scolopidial organ were located near the maximum of such vibrations, this organ could pick up the substrate vibrations, similar to the prosternal organ. Future experiments will certainly unravel the behaviorally relevant sensory organs.

14.2.4 Neural Networks and Neuroethology

The central projections of the sensory fibers are the first level in the neural networks processing vibrational information. Probably in order to facilitate efficient neuronal processing, these central projections are usually ordered within the central nervous system by type of the sensory neuron and/or by position of the sensory cell body (Fig. 14.6). Consequently, the central projection of the sensory neuron may be indicative of its function. In each segmental ganglion of insects, a neuropile area, the median ventral association center (mVAC), is known for processing of vibratory, auditory, and proprioceptive information (Pflüger et al. 1988). The projection into this neuropile may also be indicative of a vibration-receptive function of its sensory cells.

As described above, the FCO often contains two distinct parts (scoloparia) and these parts also have different projections in the corresponding ganglion. In locusts, the proximal part has a dense projection close to the midline within the mVAC and the distal part has a rather loose projection, not merging with that of the proximal scoloparium (Field and Pflüger 1989; Mücke and Lakes-Harlan 1995). In crickets and in wetas, neurons of dorsal parts of the FCO project into the mVAC (Fig. 14.6; Nishino 2000, 2003). In these species, even a more detailed order in the central projection of small groups of neurons could be shown. Furthermore, distinct central projections also correlate with different physiological properties (Matheson 1992). In the Diptera, the FCO projects into the mVAC as well (Merritt and Murphey 1992). Given that the mVAC is often the first-order neuropile involved in vibration processing, the projection in Diptera could indicate that at least parts of the FCO play a role in sensing vibrations. The sensory neurons of the prosternal chordotonal organ of Diptera project among other areas into the mVAC of all three thoracic neuromeres, in both atympanate and tympanate Diptera (Stölting et al. 2007; Stumpner et al. 2006).

On the other hand, the sensory cells of the vibrosensitive SGO do not project completely in the mVAC. The central projection of the SGO has unequivocally

been documented in orthopterans either by labeling a complete single cell during recording (Stumpner 1996) or by careful anterograde backfills (Nishino and Field 2003). The fibers of the tettigoniid SGO might project into the mVAC, but not close to the midline (Fig. 14.6; Stumpner 1996). Axons with a bifurcating morphology project anteriorly in the mVAC, whereas subparts of the SGO also have posterior projecting fibers that do not reach the mVAC, but establish an ordered projection outside the mVAC (Nishino and Field 2003). The complex tibial organs of the atympanate Ensifera also have a projection within the mVAC, but so far it has not been unequivocally resolved whether the cells of the CAH project into the neuropile (Fig. 14.6; Strauß and Lakes-Harlan 2008a, b). Nevertheless, in the different atympanate Ensifera analyzed so far, the distinct overall projections in the taxon-specific anatomies of the mVAC are likely to originate at least partly in the CAH (Strauß and Lakes-Harlan 2008a, b, 2010). The accessory chordotonal organ in wetas also projects into the mVAC (Nishino and Field 2003). A CO that does not project in the mVAC is the proprioceptive tarsal CO in locusts (Mücke and Lakes-Harlan 1995). It will be interesting to study the central projection of the tarsal CO in the water strider, which is supposed to register water vibrations (Goodwyn et al. 2009).

In contrast to the scolopidial sensilla, mechanosensitive hair sensilla have somatotopically ordered, often tufted-like projections mainly in the lateral neuropiles of the respective ganglion (Fig. 14.6; Burrows and Newland 1993; Mücke and Lakes-Harlan 1995). Campaniform sensilla often have a widely arborized projection in lateral neuropiles, as shown in locusts and flies (Fig. 14.6; Hustert et al. 1981; Merritt and Murphey 1992). Some of the CS may reach the median ventral association center with single axonal branches. As mentioned above, external sense organs (es) like sensory hairs can be transformed into chordotonal sensilla in *Drosophila* embryos. Such transformed sensilla exhibit a variety of central projection anatomies ranging from those of es neurons to those of chordotonal neurons (Merritt et al. 1993). Thus, the formation of a central projection is probably controlled by a number of genes.

The mechanosensory neurons synapse onto vibratory interneurons that distribute and compute the information in the CNS (Rössler et al. 2006). One of the first features of such networks is probably the localization of the source of the stimuli. Such directional discrimination is possible by calculation of the input from the receptors of different legs (Virant-Doberlet et al. 2006). However, it has to be kept in mind that the sensitivity of the different legs can be different (see above) and that additional input from scolopidial organs in various parts of the body could contribute to the networks. Biologically relevant answers of discrimination are given by the behavior of the animal: ant lions that locate their prey in sandy pits (Devetak 1998); toktok beetles in the Namib Desert tap on the sand surface with their abdomen and attract each other (unpublished observations). In other species, vibrotaxis might supplement phonotaxis. In crickets or tettigoniid, species-specific vibratory signals can facilitate orientation in a complex 3D habitat, like bushes, toward conspecifics (Latimer and Schatral 1983; Stiedl and Kalmring 1989; Weidemann and Keuper 1987). Holometabolous caterpillars can detect and

discriminate vibratory signals occurring on leaves with so far unidentified sense organs (Guedes et al. 2012). These exemplary observations show the ability of various species to locate vibrational stimuli.

14.2.5 Evolution

Vibration receptor organs have evolved in relation to selective pressures on vibration perception, and some organs have later been further modified for perception of airborne sound. The receptor organs have to match the distinct parameters of vibratory signals relevant for reproduction and offspring. But can receptor organ complexity be related to vibratory signaling or parameters of vibratory signals, like frequency, displacement, and others?

Insects that possess a subgenual organ as a sensitive vibration receiver have between two and several hundred sensory units. Orthoptera with elaborated acoustic and vibratory communication signals have about 20–80 scolopidia in each of the subgenual organs of their legs. So far, no correlation between cell number and signal has been worked out for Orthoptera. However, it has been shown that subgenual organs with few neurons are apparently sufficient to serve vibration communication and may even discriminate different frequencies (Cokl 1983). The subgenual organs of the neuropteran *Chrysoperla* contain only three scolopidia (Devetak and Pabst 1994), and only two scolopidia are in the SGO of the bug *Nezara* (Michel et al. 1982). Thus, from a strictly numerical perspective, a low number of receptor units might be functionally sufficient. It can be asked what the receptors in insects with more sensory neurons are used for, or whether they are functionally redundant.

On the other hand, an example for sensory adaptation has been proposed in some groups of parasitoid wasps. These female wasps tap on the substrate with their antenna to evoke “echoes” of vibration by which they locate their hosts. This behavior is termed vibrational sounding. Apparently, the receptor organ for the echoes is the subgenual organ, which contains 300–400 scolopidia in 55 species of Orussidae (Vilhelmsen et al. 2001) and five of 39 subfamilies of Ichneumonidae (Broad and Quicke 2000). This enlargement of the subgenual organ correlates with the vibrational behavior and ecological factors, like host size and substrate (Broad and Quicke 2000). The co-organization of sounding and signal detection indicates a coevolution between signal evocation and signal detection. The increase in number of receptors may functionally improve the ability to detect the hidden hosts. For specific taxa, phylogeny is helpful to infer the ancestral situation of a sensory system. However, the Orussidae are a basal group (Vilhelmsen et al. 2001), and therefore, the enlarged subgenual organ may not be apomorphic in this lineage.

The evolution of the tibial scolopidial organ in relation to vibrational signals has also been discussed for Ensifera. While crickets and bush crickets mainly use acoustic signaling (Bailey 1990), several taxa lack hearing organs but instead use

vibrational signals by substrate drumming with hindlegs or abdomen (Field and Bailey 1997; Gwynne 2004; Weissman 2001). In the ensiferan phylogeny, the plesiomorphic situation seems to be the possession of a subgenual organ together with an intermediate organ (which might be related to the distal organ or Nebenorgan in other taxa). Such neuroanatomical organization is present in a cave cricket (Raphidophoridae: Jeram et al. 1995). Other taxa of atympanate Ensifera (Stenopelmatidae, Schizodactylidae, and Gryllacrididae) possess a tripartite CTO (Strauß and Lakes-Harlan 2008a, b, 2009, 2010) with receptor structures homologous to that in tettigoniids, but without adaptations to sound reception. Since the serial organization in all three leg pairs is similar (e.g., the numbers of scolopidia), it was presumed that the sensory organ structure represents the ancestral organization of hearing organs and therefore might have a vibroceptive function (Strauß and Lakes-Harlan 2009). In this case, it can be argued that the detection of vibration was the ancestral function of the subgenual organ, to which further receptor structures were added with a presumptive function in analyzing intraspecific signaling by substrate vibration. The additional receptor structures might be necessary for detecting vibration parameters independent from hemolymph oscillations that can be perceived by the SGO (see above for details).

The question of evolution of vibration receptors has rarely been analyzed in detail. Hopefully, future studies will show which selective pressures acted on the formation of scolopidial organs and what constraints influence the evolution of these interesting sense organs.

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