8

TOUCH

Touch sensitivity in *C. elegans*: mec mutations - touch receptor neurons - genetic analysis - MEC proteins - resemblance to mammalian ENaCs - other mec genes and their protein products - possible molecular structure of *C. elegans* tactile receptor – TRP channels on nose rays. **Touch sensitivity in spiders**: tactile hairs – trichobothria – slit sensilla – lyriform organs. **Touch sensitivity in insects**: tactile sensilla – TRP channels - subgenual organs - detection of water ripples by pond skaters and water-boatmen - acoustic sensilla – Drosphila: Aristae - Johnston's organ - sensitivity to wing-beat frequencies - tympanal organs (ears): stucture and function - communication - prey detection - detection of insectivorous bats by lacewings and moths - structure of Noctuid ear - Noctuid countermeasures against bats. **Touch sensitivity in mammalian skin**: fast adapting receptors: Pacinian corpuscles, Meissner's corpuscles, Krause's end bulbs, hair follicle receptors; slow adapting receptors: Merkel cells, Ruffini organs, C-mechanoreceptors. **Central pathways in mammals**: tracts in spinal cord - somaesthetic cortices - columnar structure - receptive fields - somaesthetic homunculus. **Plasticity of the cortex**: mice whisker barrels - monkey fingers - cello players - Braille readers. **Concluding rremarks**: a universal sense - social grooming - communication and bonding.

It can be argued, as we noted in the introduction to Part Two, that touch is the indispensable sense. It is difficult to imagine what it would be like without this sense modality. Indeed, it is difficult to imagine how the world would appear to a being lacking the sense of touch. Our very notions of solidity, resistance, of objectivity itself, would hardly have developed in the absence of this all-pervading sense. Yet, compared with our intimate knowledge of the molecular biology of olfactory and visual receptors, our understanding of the precise mechanisms by which our tactile receptors work is as yet sparse and unsatisfying. This, however, is slowly beginning to change with advances in molecular biology and the use of simple 'model organisms', such as the tiny soil-dwelling roundworm, *Caenorhabditis elegans*.

8.1 MECHANORECEPTION IN *CAENORHABDITIS ELEGANS*

We noted in Chapter 5 that *C. elegans* has been intensively studied by molecular biologists. In essence, when geneticists felt that the major outlines of prokaryocyte biology had been established with work on *E. coli* and that protistan biology was well advanced in the type–example of yeast, *Saccharomyces cervisiae*, the next and final frontier

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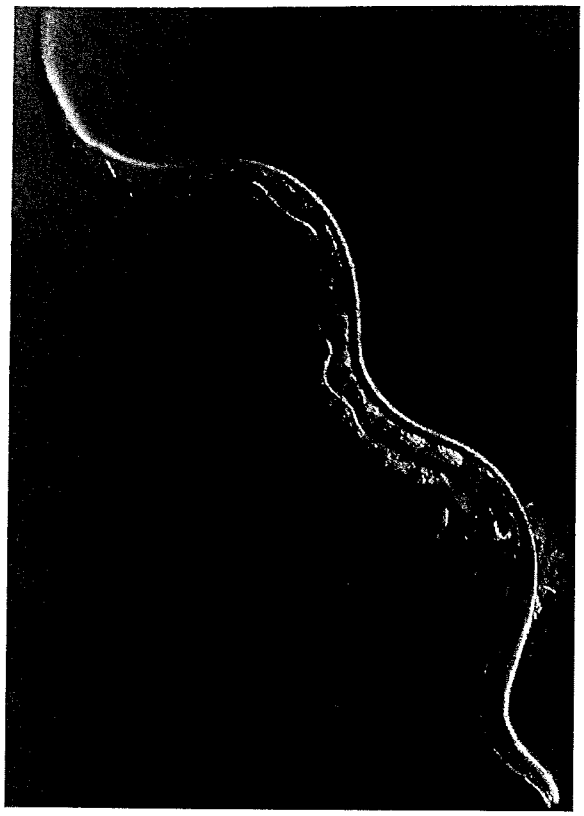

Figure 8.1 *Caenorhabditis elegans*. This worm is about 200 mm in length. *C. elegans* consists of 959 somatic cells of which 302 constitute the nervous system. The body is translucent and many of its cells can be distinguished in the living animal. From White, J. G. (1985), Neuronal connectivity in Caenorhabditis elegans, *Trends In Neurosciences*, **8**, 277–283, © 1985 with permission from Elsevier Science.

beckoned in the Metazoa. Geneticists consequently looked for an animal that was easily cultured and had a rapid generation time, so that the powerful methods used in microbial genetics could be adapted and applied. The organism chosen was the small (circa 0.5 mm long) free-living soil nematode *Caenorhabditis elegans* (Figure 8.1). Over some forty years of intensive investigation this organism has yielded up the secrets of its genetics, its physiology, its anatomy and its behaviour. The precise number of nerve cells in its central nervous system is known (302), the synaptic structure of the nervous system and each of its neurons has been totally elucidated in the electron microscope and its genome was determined in 1998.

Like all animals *C. elegans* is sensitive to touch. There are two systems. Touch to the body wall is detected by a group of six neurons, whilst that to the nose is detected by three neurons in the mechanosensitive rays, or 'cilia'. Let us consider each in turn.

Mechanosensitivity of the lateral body wall has been investigated using two touch stimuli: a gentle touch on the body with an eyelash glued to a cocktail stick and a more vigorous prod with a thin wire. The most interesting results have come from investigations of the response to the gentle stimulation.

When *C. elegans* is placed in a petri dish it moves forward with a sinusoidal motion until it encounters a tactile stimulus. If it is given a gentle touch on the anterior part of its body the movement reverses and the worm squirms backward across the dish; if the gentle touch is applied to the posterior it will move forward. A large number of mutations (over 440) affecting 15 genes have been shown to interfere with these responses. That the worms were still capable of movement was confirmed by using the vigorous wire prod. Most of these mutations were classified as *mec* mutants because the phenotype they generate is described as mechanosensitive abnormal (mec). In consequence, the genes are called *mec* genes and the proteins which they designate MEC proteins.

It can be shown that touch is detected by six touch detector neurons. There are: two anterior lateral microtubule cells (left and right) – ALML and ALMR; two posterior lateral microtubule cells (left and right) – PLML and PLMR; one anterior ventral microtubule cell – AVM. One further neuron seems to be involved although, unlike the others, it is unable to mediate touch avoidance on its own. This is the posterior ventral microtubule cell – PVM. The anatomical location of these touch detector neurons is shown in Figure 8.2.

The touch receptor neurons, as their names indicate, are filled with a bundle of extra large microtubules. Electron microscopy suggests that the individual microtubules in the bundle are linked together and they all have the peculiarity of consisting of 15 protofilaments (rather than the 11 protofilament ultrastructure of other *C. elegans* microtubules or the 13 protofilaments found in microtubules elsewhere in the animal kingdom). These extra-large and ultrastructurally rather odd microtubules are much shorter than the neuron (no more than about 5% of the latter's length) and seem to run obliquely to the

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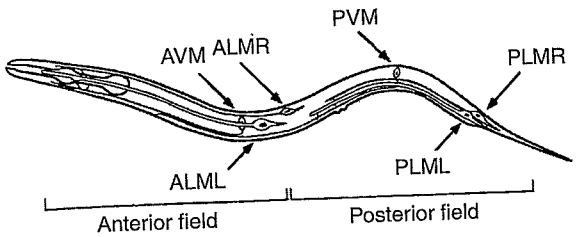


Figure 8.2 *C. elegans* touch receptor neurons. Note that there are two fields of touch sensitivity determined by the disposition of the neurons in the nematode's body. ALML = anterior lateral microtubule cell left; ALMR = anterior lateral microtubule cell right; PLML = posterior lateral microtubule cell left; PLMR = posterior lateral microtubule cell right; AVM = anterior ventral microtubule cell. From Tavernarakis and Driscoll, 1997: with permission, from the *Annual Review of Physiology*, Volume 59, by Annual Reviews, http://www.Annual Reviews.org.

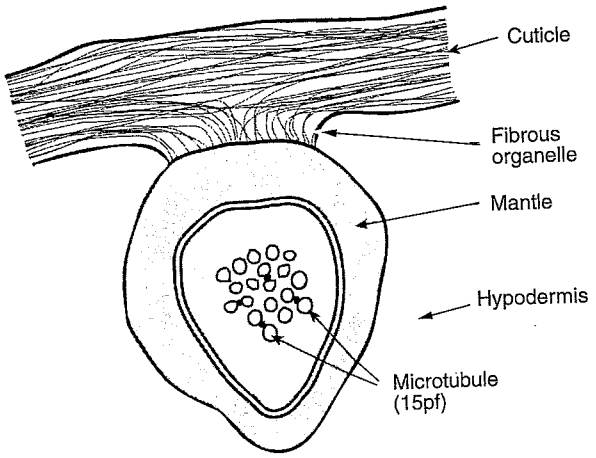


Figure 8.3 Ultrastructure of *C. elegans* touch receptor neuron in transverse section. The neuron is surrounded by a connective tissue mantle and is attached to the cuticle by a 'fibrous organelle'. It contains a bundle of microtubles (each composed of 15 protofilaments (pf)). Adapted from Tavernarakis, N. and Driscoll, M. (1997).

latter's longitudinal axis. Their distal ends are embedded in the boundary membrane of the neuron, suggesting some mechanical linkage. The microtubules are essential to the functioning of the neuron. If they are disrupted by colchicine or by mutation, touch sensitivity is lost.

The touch receptor neurons themselves run just beneath the cuticle ('skin') of the worm to which they are attached by an extracellular 'mantle' of fibrous material (Figure 8.3). The ultrastructure suggests that there is mechanical continuity between the cuticle and the microtubules within the touch neurons. It is worth recalling that the tubular body of insect mechanosensitive hairs is also composed of close-packed microtubules, in this case bridging the neurosensory cell and the cuticle (Sections 7.1.2 and 8.2.1).

Genetic analysis proceeded by generating mutations in the worm and examining their progeny for loss of response to gentle touch. When such a loss was detected, molecular biological techniques were employed to determine what structure the mutated gene normally designated. In some cases the genes were found to be responsible for factors necessary for the development of the touch cells themselves, in other cases for controlling the action of other *mec* genes. In more interesting cases genes were discovered which designated channel proteins and accessory elements connecting the channels to the cuticle on the one hand and to the neuronal microtubules on the other.

Mec-4 and *mec-10* are the two genes which designate the channel proteins – MEC-4 and MEC-10. These genes have also been called 'degenerins' because mutations in them, leading to defective MEC-4 and MEC-10, cause the cells in which they are expressed to swell and die. Both MEC-4 and MEC-10 belong to a superfamily of proteins which includes the three subunits of the mammalian epithelial Na^+-channel protein (ENaC). There are two transmembrane segments; both C-terminal and N-terminal are intracellular and there is a large extracellular loop (Figure 8.4). Although the precise structure of the MEC channel has yet to be determined, analogy with other channels, especially the mammalian ENaC channel, suggests an assembly of six subunits, possibly a mixture of MEC-4s and MEC-10s. There is some evidence that *mec-6* encodes another channel subunit, MEC-6, in which case the channel would consist of a heteromultimer of MEC-4, MEC-6 and MEC-10 subunits.

As mentioned above, far more than merely two *mec* genes are known. The roles played by the proteins these other *mec* genes encode has in many cases been elucidated. Mutations in *mec-7* and *mec-12*

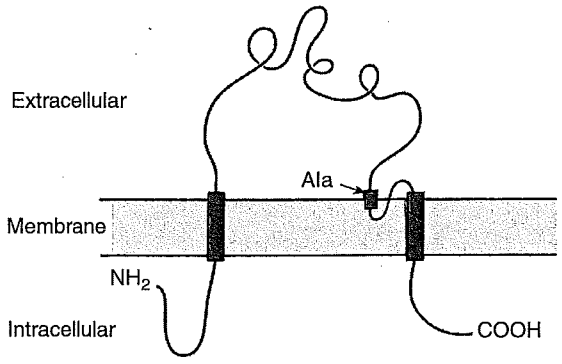


Figure 8.4 Transmembrane topology of the MEC-4 protein. There are two transmembrane domains and a small membrane insertion just before the second transmembrane helix. The bulk of the 768 residue protein is, as indicated, in the extracellular space . When $Alanine_{713}$ (Ala) is replaced by a bulkier amino acid cell death ensues. Adapted from Tavernarakis, N. and Driscoll, M. (1997).

disrupt the 15 protofilament microtubules which are so characteristic of the touch receptor neurons. Another gene, *mec-2*, has been shown to designate a 481 amino acid protein (similar to the stomatin of mammalian red blood cell cytoskeleton) that is believed to act as a link between the MEC channel and the microtubules (Figure 8.5). Yet other genes, *mec-1, mec-5, mec-9* code for proteins (MEC-1, MEC-5, MEC-9) which are found outside the plasma membrane in the mantle.

An interesting, though so far somewhat speculative, model has been proposed to link all these elements together into a functioning tactile receptor. This model is shown diagrammatically in Figure 8.6. MEC-1, MEC-5 and MEC-9 are organized to transmit pressure on the cuticle to the MEC-4 subunit and open the channel. When the channel opens, Na^+ ions flow down their concentration gradients and the neuron is depolarized. This mechanical transmission works if the channel is stabilized by attachment to an internal microtubule. This attachment, as we have seen, is provided by MEC-2. Alternatively, the mechanical deformation might displace the microtubule network which, as it is attached to the membrane (see above), might increase the tension on the plasma membrane and thus open the channel. The number of 'mights' in the preceding sentence shows that here we are at the frontier of research. Only further careful experiment will eliminate false hypotheses where they exist.

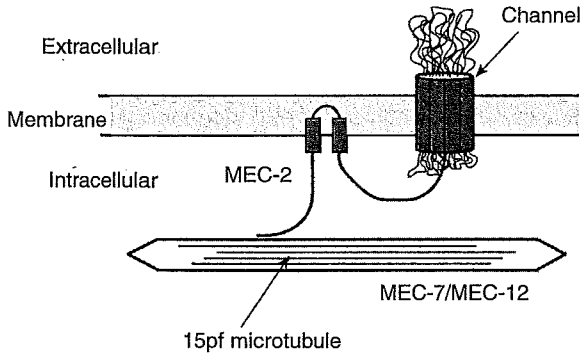
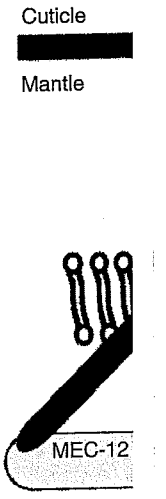


Figure 8.5 Proposed linkage provided by MEC-2 to one of the 15 pf microtubules of a touch receptor neuron. It is suggested that the N-terminal of MEC-2 interacts with a microtubule and the C-terminal with the channel. Adapted from Tavernarakis, N. and Driscoll, M. (1997).

Although, as indicated, much remains speculative, the *C. elegans* body-wall touch receptor is much the best known animal mechanoreceptor at the molecular level. Before moving on, it is worth looking forward to Chapter 9, where we shall be concerned with vertebrate hair cells. It has been suggested that the molecular mechanism worked out for the *C. elegans* mechanoreceptor may help elucidate the operation of these very different sense organs. We shall consider this interesting comparison in more detail in Section 9.3.2 and Box 9.1.

The second type of touch receptor in *C. elegans* is much less well known. These receptors are located on three sensory neurons in the nose 'rays' of the worm. A member of the TRPV family, OSM-9, is expressed at the tip of each neuron. Loss of function mutations of the OSM-9 gene (*osm-9*) leads not only to loss of sensitivity to nose touch but also to hyperosmolar solutions and the normally attractive odorant, diacetyl. The finding that OSM-9 is involved in several other sense modalities suggests that, although it may form a crucial link in the detection of mechanical distortion of the anterior rays, it may not itself be involved in the gating mechanism. It is interesting and perhaps significant to note that the mammalian homologue of OSM-9 known as TPRV4 (or OTRPC4) is a selective Ca^{2+}-channel. Quite recently it has been discovered that another TRP channel, TRPA1, is involved in nose touch and foraging responses. Mutations of *trpa-1* lead to defects in nose touch responses and this, and other evidence, points to the presence of this cation channel which, in this case, can be



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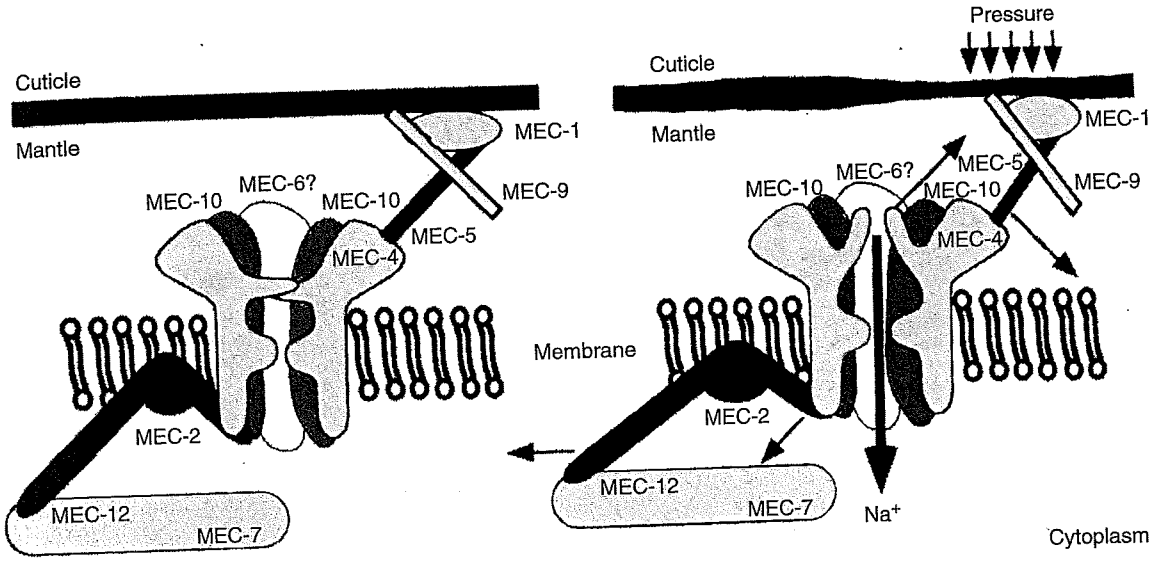


Figure 8.6 Conceptual model of *C. elegans* touch receptor. Explanation and nomenclature in text. From the *Annual Review of Physiology*, Volume 59, © 1997, with permission from Annual Reviews, http://www.Annual Reviews.org.

activated by mechanical pressure. These findings are of considerable interest, as members of the TRPA subfamily have not only been implicated in *Drosophila* thermosensitivity but also in mammalian cold sensitivity and mechanoreception.

8.2 SPIDERS

We looked at the cuticular sensilla of insects in Section 7.1.2, and we shall discuss them in more detail in the next section. In this section we shall examine the mechanoreceptors of those insect predators – the spiders. Spiders resemble insects and other arthropods in the possession of a hard exoskeleton, so their mechanoreceptors bear many resemblances to those found in insects although the common insect–arachnid ancestor is many hundred million years in the past. These resemblances thus show a remarkable evolutionary parallelism and indicate that the sensory problems presented to terrestrial animals living within a hard exoskeleton have only a few optimal solutions. Because of their age-old warfare with the insects, evolutionary forces have tuned spider sensory systems to respond to tiny changes in the environment with extreme rapidity. In order to catch their prey, their eyes and mechanoreceptors have achieved remarkable levels of sensitivity. The most important external mechanoreceptors are tactile hairs, thrichobothria and slit sensilla.

8.2.1 Tactile Hairs

Spiders are notoriously hairy. Indeed, this may account for some of the distaste they engender. But the hairs are not merely for decoration or defence: most of them are innervated and respond to tactile stimuli. Careful examination shows that they consist of a lengthy cuticular shaft springing from a shallow socket in which it can move (Figure 8.7). Three dendritic nerve endings are attached to the bottom of the shaft and electrophysiological recording shows that, when the shaft moves, action potentials are generated in the sensory fibres. The response is very rapid (less than 10 ms) and also rapidly adapting.

8.2.2 Trichobothria

Trichobothria are extremely slender hairs which spring from highly specialized sockets (Figure 8.8). They are some 0.1–1.4 mm in length and no more than about 10 μm in diameter. They are far less common than tactile hairs and are often arranged in regular rows. Indeed the arrangement of trichobothria is often used by systematists to classify spider species, a

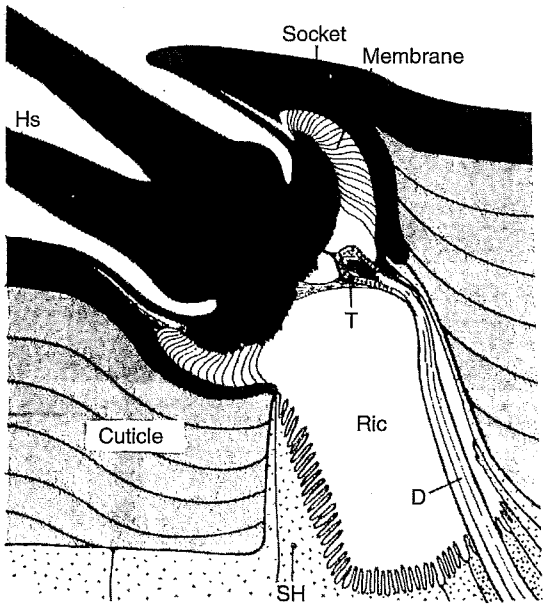


Figure 8.7 Arachnid tactile hair. The hair is inserted into a socket in the cuticle and three dendritic terminals attach to its base. D = dendtrites; Hs = hair shaft; Rlc = receptor lymph cavity; SH = sheath cell; T = terminals of dendrites. From Harris, D. J. P. and Mill, P. J. (1977) *J Comp Physiol A Sens Neural Beh*, **119**, 37, with kind permission of Springer Science and Business Media.

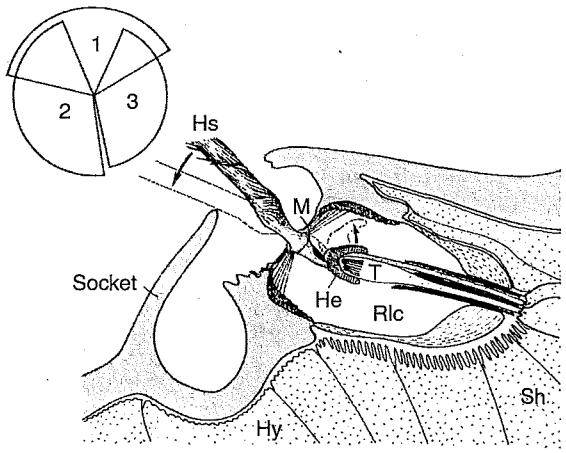


Figure 8.8 Trichobothrium. The long slender hair shaft (Hs) is inserted through a very thin cuticle (M) into a helmet shaped structure (He). The potential movement of this structure is shown by the arrow. The terminals (T) of four sensory neurons make contact with this helmet and three of the four have directional selectivity (see inset figure). Hy = hypodermis; Rlc = receptor lymph cavity; Sh = sheath cells. From Foelix (1982) *Biology of Spiders*, Copyright © 1982, Harvard University Press.

procedure known as trichobothriotaxy. Trichobothria are extraordinarily sensitive. The base of the hair is embedded in an extremely thin (0.5 μm) cuticular membrane and is continued as a 'helmet' into the socket (Figure 8.8). The dendrites of four sensory nerves are inserted in the helmet and three of these have been shown to have a directional sensitivity. The normal stimuli are changing air currents and low frequency pressure changes in the atmosphere. Trichobothria never respond to continuous static deflection.

Biophysical investigations have shown that spider thrichobothria are among the most sensitive of all mechanoeceptors, only rivalled by the rather similar filiform hairs of crickets. It has been calculated that the energy required to reach response threshold is between 2.5×10^{-20} J and 1.5×10^{-19} J, a fraction of the energy present in a single photon of green light and very near the limit imposed by Brownian motion. This extreme sensitivity is believed to be the outcome of a phenomenon called stochastic resonance (SR). In this process, interestingly enough first applied on a global scale to account for the periodicity of the ice ages, an oscillating subthreshold stimulus is assisted at random (stochastic) intervals to reach threshold by an unrelated underlying set of fluctuations. In the trichobothrian case, the principal stimuli are fluctuating air flows, perhaps due to the beat of nearby insect wings and the random underlying fluctuations are provided by Brownian motion.

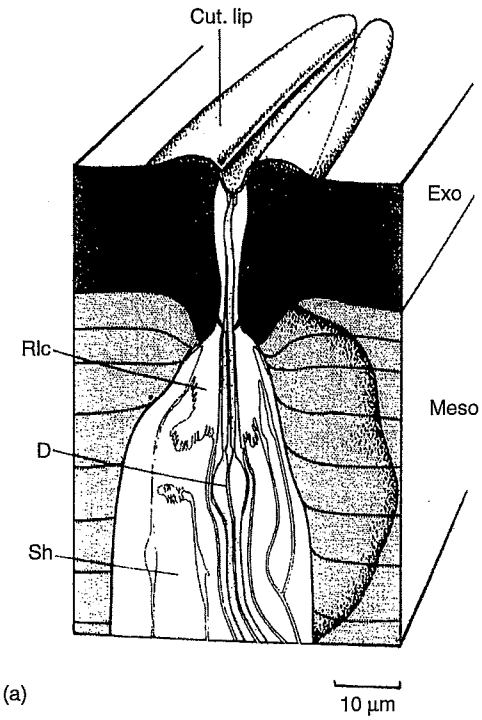
It can be shown that the optimal frequency response of the trichobothrium hair is related to its length. Short hairs are most sensitive to low frequencies and long hairs to higher frequencies. Thus the regular rows of trichobothria mentioned above contain hairs of many different lengths and thus cover a whole range of frequencies. They are, in consequence, well adapted to detecting air turbulence created by nearby insects, especially flying insects, at distances up to 25 cm.

8.2.3 Slit Sensilla and Lyriform Organs

We have already noted (Chapter 7) that insects develop a number of mechanoreceptors to detect stress and strain on the exoskeleton. This is also the case

with spiders. The best known of these are the so-called 'slit' sensilla. These sensilla detect not only movement of the body but also vibrations produced by mates, prey and predators and haemolymph pressure. These receptors are embedded in the exoskeleton and distributed over the entire body surface, although the greatest density is found in the legs. In many cases slit sensilla line up to form parallel rows which, because of their resemblance to the musical instrument, are called **lyriform organs**.

Each slit sensillum, as Figure 8.9a shows, consists of a trench some 8 to 200 μm long and 1–2 μm wide



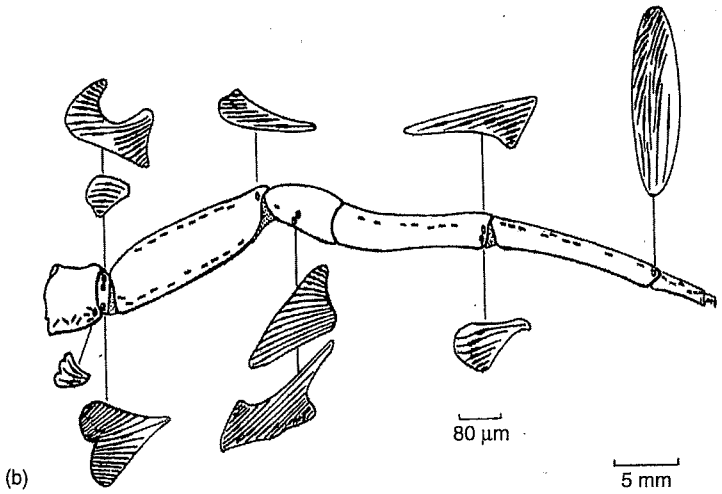


Figure 8.9 (a) Slit sensillum. The slit runs through the exocuticle into the mesocuticle where a large receptor lymph cavity holds the dendrites (D) of two sensory neurons. One of these dendrites reaches up to the very delicate cuticle covering the slit and the other reaches the bottom of the slit. Rlc = receptor lympn cavity; Sh = sheath cells. (b) Lyriform organs on the posterior side of the first leg of the wolf spider *Cupenius salei* of Central America. The black dots indicate the positions of the lyriform organs on the legs and the enlargements show the direction of the slit sensilla in the organs. From Foelix (1982) *Biology of Spiders*, Copyright © 1982, Harvard University Press.

bordered by prominent lips and covered by a thin cuticular membrane. Beneath this membrane the slit reaches down through the exocuticle to an underlying chamber where two sensory dendrites are located, one of which attaches to the covering cuticular membrane. In the tip of this dendrite is found a typical 'tubular body', such as is found in insect mechanoreceptor sensilla (Section 7.1.2). Stimulation of slit sensilla is by mechanical deformation. Downward pressure on the slit pushes the lips together and the cuticle connecting them bows inwards. This stimulates the underlying dendrite. It has been found that only compression not dilation elicits impulses in the sensory fibre. Groups of slit sensilla arranged parallel to each other (Figure 8.6b) are known as lyriform organs. It is found that the peripheral slits of lyriform organs are deformed more easily than those at the centre, so this may provide some information about the degree of exoskeletal stress.

What role do slit sensilla and lyriform organs play in a spider's life? It is clear that they provide feedback on the spider's own movements, but they also have a significant role to play in detecting pressure waves in the atmosphere – sound – and other external stimuli. The tarsal slit sensilla of a number of spiders show maximum sensitivity to atmospheric pressure waves in the frequency range between 300 and 700 Hz. It can be no coincidence that the wing beats of many insects fall within this range. The metatarsal lyriform organs of web spiders belonging to the order Aranaidae act as highly sensitive vibration detectors. A displacement of the leg tip by as little as 1–2.5 nm at 2–5 kHz is sufficient to elicit a response in these spiders. Any vibration of the web is thus instantly sensed. Tibial and femoral lyriform organs provide kinaesthetic orientation in wandering spiders (order Lycosidae). When these organs are intact, these spiders can retrace an earlier run without the aid of external cues by 'replaying' their earlier motility pattern. If the lyrifom organs are destroyed, this ability is also destroyed.

8.3 INSECTS

We looked at the role of sensilla in insect kinaesthesia in Chapter 7 (campaniform sensilla and chordotonal organs). Here we shall look in more detail at tactile

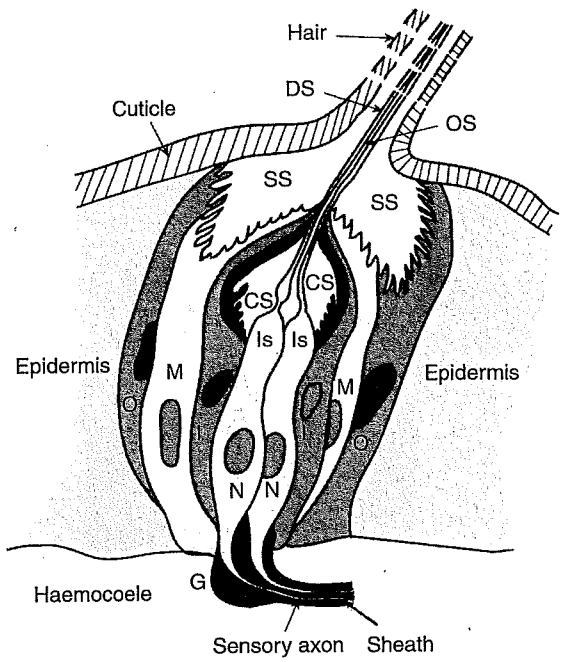
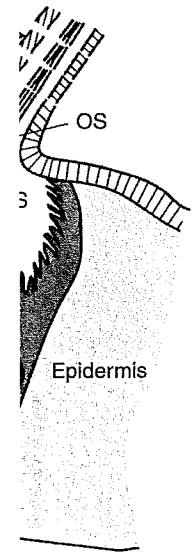


Figure 8.10 Typical insect sensillum. CS = ciliary sinus; DS = dendritic sheath; G = basal glial sheath cell; M = intermediate or trichogen cell; N = neurosensory cell; IS = inner segment; O = outer or tormogen cell; OS = outer segment (cilium); SS = sensillar sinus After Gilbert, L. L. & Kerkut, G. A. (1985).

sensilla. Figure 8.10 shows a typical hair sensillum. It consists of a cuticular projection enclosing one or more neurosensory cells and several sheath cells. The neurosensory cells have large nuclei and send a lengthy dendrite into the cuticular projection. This dendrite is differentiated into two distinct regions, often at about the middle of its length. The proximal segment (**inner segment**) resembles the rest of the perikaryon; the distal segment (**outer segment**) is, however, a modified cilium. It is often referred to simply as the cilium and possesses the characteristic internal 9 × 2 ultrastructure of microtubules. This ultrastructure is continued to the tip, unless the dendrite branches. In these latter cases the microtubules become distributed among the branches. The sensory axon springing from the base of the cell travels directly back to the CNS in a sensory nerve.

The number of sheath cells varies greatly from one sensilla to another but typically there are three types: **inner sheath cell** (= **thecogen cell**) which are homologous to the scolopale cell of scolopidia (see Section



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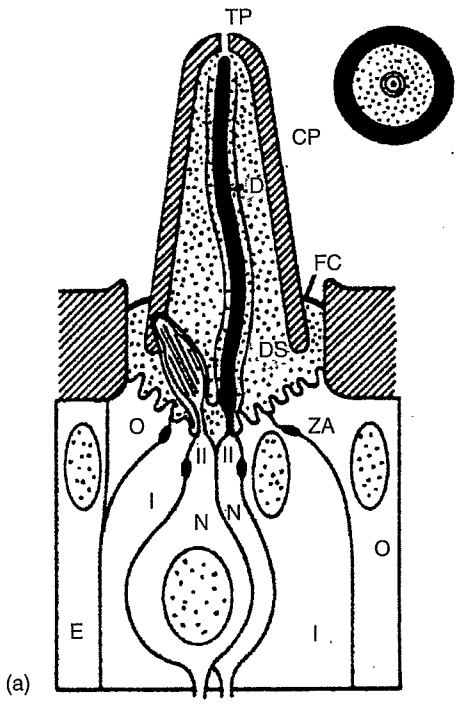

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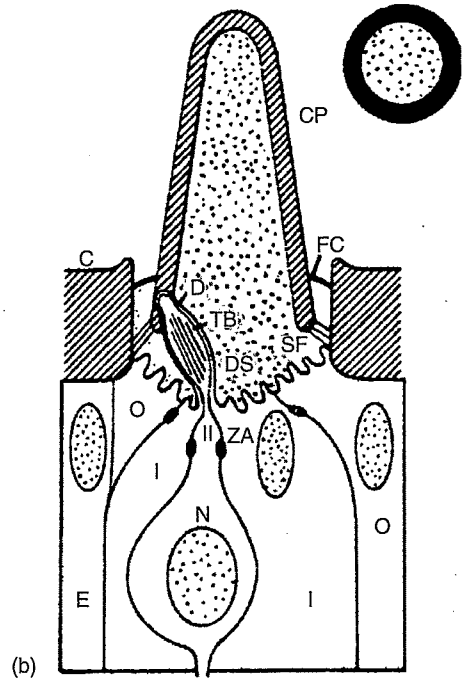


(b)

7.1.2), the **intermediate** or **trichogen cell** and outermost of all, the **outer** or **tormogen cell**. The inner sheath cells secrete the dendritic sheath. Proximally they enclose a small fluid-filled sinus, the **ciliary sinus** (Figure 8.10). The intermediate and outer cells form the **sensilla sinus** beneath the cuticle and around the dendritic sheath. The proximal ends of the intermediate and outer cells abut the haemolymph in the haemocoele and their distal ends send large numbers of microvilli into the sensillar sinus. They are thought to have an important function in both nutrition and in the formation of the fluid in the sensillar sinus. Their strategic position between the haemocoele and the latter sinus makes them well adapted to this function. In addition to the sheath cells, intermediate and basal cells are often present. The latter are sometimes referred to as glial cells as they wrap around the sensory axons, insulating them from each other and from the haemolymph.

Far from all sensilla are mechanosensory. In other parts of this book we shall meet gustatory, olfactory, hygroscopic and thermal sensilla. The sense modality is determined by the dendrite of the neurosensory cell contained within the sensillum. In many cases, where there is more than one neurosensory cell, there may be dual or even more modalities. For instance, mechanosensitive and chemosensitive neurosensory cells may inhabit the same sensillum. Partly for this reason, the classification and terminology applied to insect sensilla has been complicated and confusing. Whereas olfactory and gustatory sensilla (for obvious reasons) develop terminal pores (Figure 8.11a), many mechanosensitive sensilla are without pores (aporous) (Figure 8.11b).

Mechanosensitive hair sensilla sometimes spring directly from the cuticle but more often are attached

Figure 8.11 (a) Uniporous bimodal sensillum. In addition to the mechanosensory neuron with its tubular body there are one or more other neurosensory cells whose dendritres extend up towards the terminal pore. CP = cuticular process; D = dendrite outersegment; DS = dendritic sheath; E = epidermal cell; FC = flexible cuticle; I = inner sheath cell; N = neurosensory cell; O = outer sheath cell; OS = outersegment of dendrite; TP = terminal pore; ZA = zonula adherens intercellular junction. (b) Mechanosensory sensillum in a flexible socket. The dendrite is attached to a tubular body which is inserted into the cuticle of the hair. D = attachment of tubular body to cuticle of hair; SF = suspensory filaments. Other labels as in (a). (After Blum, 1985: with permission).

by flexible sockets to the exoskeleton. Movement of the sensory hair provides the adequate stimulus to depolarize dendrite. Movement in one direction causes depolarization, movement in the other hyperpolarization. In many cases the sensillary hairs are, constrained by their points of insertion into the exoskeleton to move most freely in one plane: they are, in other words, strongly direction selective.

In Figure 8.11b the hair sensillum is represented as containing a single neurosensory cell whose dendrite is attached to the interior of the hair by a **tubular body**. Electron microscopy shows that this body consists of from 50 to 100 closely packed microtubules. These microtubules are exquisitely sensitive to distortion induced by movement of the sensillum. It can be shown that their lower threshold is a distortion of 3–5 nm. Can we make a connection with the microtubules which pack the neurosensory cells of *C. elegans*? Deflection of the sensillary hair in one direction causes a depolarization; deflection in the other direction leads to a hyperpolarization. These voltage changes across the membrane occur within 100 μs of the onset of the deflecting stimulus. This implies that they are due to opening and shutting of ion gates in the membrane. We shall see, in Chapter 9, that vertebrate hair cells have a similar biophysics. On this analogy it is concluded that the opening and closing of ion gates is stretch activated. Suspensory filaments which attach the base of the sensillary hair to the cuticle, together with the cuticular embedment and the attachment of the tubular body, ensure that there is an optimal plane through which the sensillum can move. This directional sensitivity is obviously of considerable importance in detecting in which way body parts, air or substrate are moving.

Is anything known about the 'ion gates' underlying the voltage changes across the membrane of the tubular body ? In fairly recent times there has been a great deal of evidence that members of the ubiquitous TRP superfamily of cation channels are involved. A gene encoding a *Drosophila* hair cell mechanotransduction channel has been identified. When this gene, *nompC* (*no m*echanoreceptor *p*otential C), mutates, the fly loses its mechanosensitivity. It is left with practically no sense of balance and often almost falls over itself when it attempts to walk. Analysis of the gene shows it to be a member of the TRPN family of TRP channels. It is thus suggested that, when the sensillary hair moves in a specific direction, it stretches the tubular and/or dendritic membrane, opening TRP channels and the consequent influx of cations depolarizes the membrane. The response to stretch may be by a bilayer mechanism similar to that we discussed for the MscL channel in *E. coli* (Chapter 6). Movement of the hair in the opposite direction has an opposite effect: the channels are closed and the membranes hyperpolarize. It may be that the hair cells in the mammalian (including human) inner ear also use members of this superfamily of channels in their rather similar microphysiology. We shall look at this microphysiology in the next chapter.

Not all insect sensilla, as we have already noted, are mechanosensory. Thus in many cases, as Figure 8.11a shows, the tip of the sensillum is penetrated by a pore and contains at least two neurosensory cells only one of which is mechanosensitive. The sensillum is thus bimodal. The other sensory cells may be olfactory or gustatory. The dendrite of the mechanosensitive neurosensory cell is, as in the previous case, attached to the interior of the sensillary hair by a tubular body. The other neurosensory cells develop single long, often branched, 'dendrites' extending the full length of the sensillum, terminating just beneath the pore. These 'dendrite(s)' are in fact modified cilia and are often called 'outersegments'. We shall meet well studied examples of chemosensitive cilia when we come to examine vertebrate gustatory cells (Chapter 13) and olfactory cells (Chapter 14), where we shall also discuss insect chemoreception.

Returning, however, to mechanosensory sensilla, it will be remembered from Chapter 7 that extensive brushworks of mechanosensitive sensilla develop at the joints between insect segments and appendages, thus providing the animal with a wealth of kinaesthetic information. Mechanosensitive sensilla are also, of course, employed as tactile hairs all over the body, particularly the head, and are richly developed in the antennae, especially the antennae of nocturnal, crepuscular and cave dwelling and/or underground forms. The cerci of cockroaches, for instance, have an abundance of lengthy filiform sensilla.

Mechanosensitive sensilla also play important roles in the detection of vibration. The subgenual organ of many insects is particularly significant in detecting vibrations in the 10–50 Hz range. In the American cockroach, *Periplaneta*, the range is much higher (as we saw in Section 7.1.2) and encroaches

on that which we would define as the acoustic domain. In addition to vibration detection by the subgenual organ, a number of insects develop vibration detecting scolopidia in their tarsi. Several species of aquatic Hemiptera and Coleoptera make use of these vibration sensors to detect the radiating ripple engendered by prey which has just dropped into their pond. The hemipteran pond-skater, *Gerris*, touches the water surface with its tarsi from above, whilst the water-boatman, *Notonecta*, swims on its back with its tarsi palpating the surface film of the water from below. A wave amplitude of no more than 0.5–4 μm provides an adequate threshold and the optimal frequency ranges from 20–200 Hz. Time differences of 1–4 ms combined with amplitude differences between the outspread tarsi are used to determine the direction of the source of disturbance. In these cases the sense organs involved consist of a small number, less than ten, scolopidia in the tarsi. It is no great step from these vibration detectors to mechanoreceptors which, like those of the vertebrates (Chapter 9), have evolved to detect the gentle atmospheric vibrations that we subjectively know as sound. Indeed it is not easy to separate insect vibration detectors from acoustic detectors for, unlike vertebrates, the same receptors are often activated by oscillations in the ground, in water and in air.

8.3.1 Acoustic Sensilla and Tympanic Organs

Insects develop two basic types of specialized sound detector: hairs and tympanic organs. Hairs are only significant sound detectors very near the sound source. They depend on distortion by the lateral movement of the air. Thus sensory hairs on the cercae of cockroaches and orthopteran insects, such as the locust, are able to detect acoustic stimuli emitted at a distance of a few centimeters, whilst sensory hairs on the bodies of some moth caterpillars respond to the wing beat frequencies of approaching predatory wasps. The fruit fly, *Drosophila*, develops feathery 'aristae' on the third antennal segment (Figure 8.12b); these are tuned to detect at close range the wing vibration which acts as the mating call of the species. In many insects **Johnston's organ** also acts as a vibration detector. This organ is, in fact, found in the second antennal segment, or pedicel, of nearly all insects. It consists of a large number of closely packed scolopidia. In different insects it has different functions, ranging from flight speed indicator (bees) to gravity detector (*Dytiscus*, the water beetle). In the mosquitoes and chironomid midges it is greatly developed and consists of many thousands of scolopidia attached to an intricate internal structure. In these insects it functions to detect the wing beat frequencies (a few hundred Hz) of conspecifics, especially prospective mating partners, at distances of up to a meter.

The other type of sound detector evolved in the insects – tympanic organs, or ears – respond not so much to lateral movement of the surrounding air (as is produced by the flapping of wings) but to pressure waves. Like the ears of vertebrates, they are thus able to detect sound sources at considerable distances and are sensitive to frequencies ranging up to and beyond 100 kHz. Tympanal organs are developed in at least seven insect orders including Neuroptera, Lepidoptera, Coleoptera, Hemiptera, Orthoptera, Diptera and so on. They are used in communication, attack and defense.

In essence, the insect tympanal organ consists of three elements (Figure 8.12e): a much thinned area of cuticle which often has a silvery appearance known as the **tympanum** or **tympanic membrane**; beneath the tympanum is an **air filled cavity** derived from the tracheal spaces; connected to the tympanum are the **chordotonal organs** which sense any vibration. This basic design is elaborated into a wide variety of different structures so that insects have a great diversity of auditory mechanisms. Tympanal organs are, moreover, found in many different parts of the insect's anatomy. The locations where tympanal organs have been found in different insects are shown in Figure 8.13. Insect 'ears' are by no means as anatomically restricted as those of vertebrates.

Acoustic communication is well developed in the Orthoptera (grasshoppers, crickets) and Hemiptera (suborder Homoptera: cicadas). Usually it is the male which emits a loud calling song and the female is induced to fly or walk towards him. Cicada calls are often of high intensity; indeed, they are audible to the human ear at distances of over a mile in the tropical forest. Selection pressure has also ensured that they are very distinctively different from one species to the next. Mole crickets (Gryllotalpidae) are also highly vociferous. The male constructs

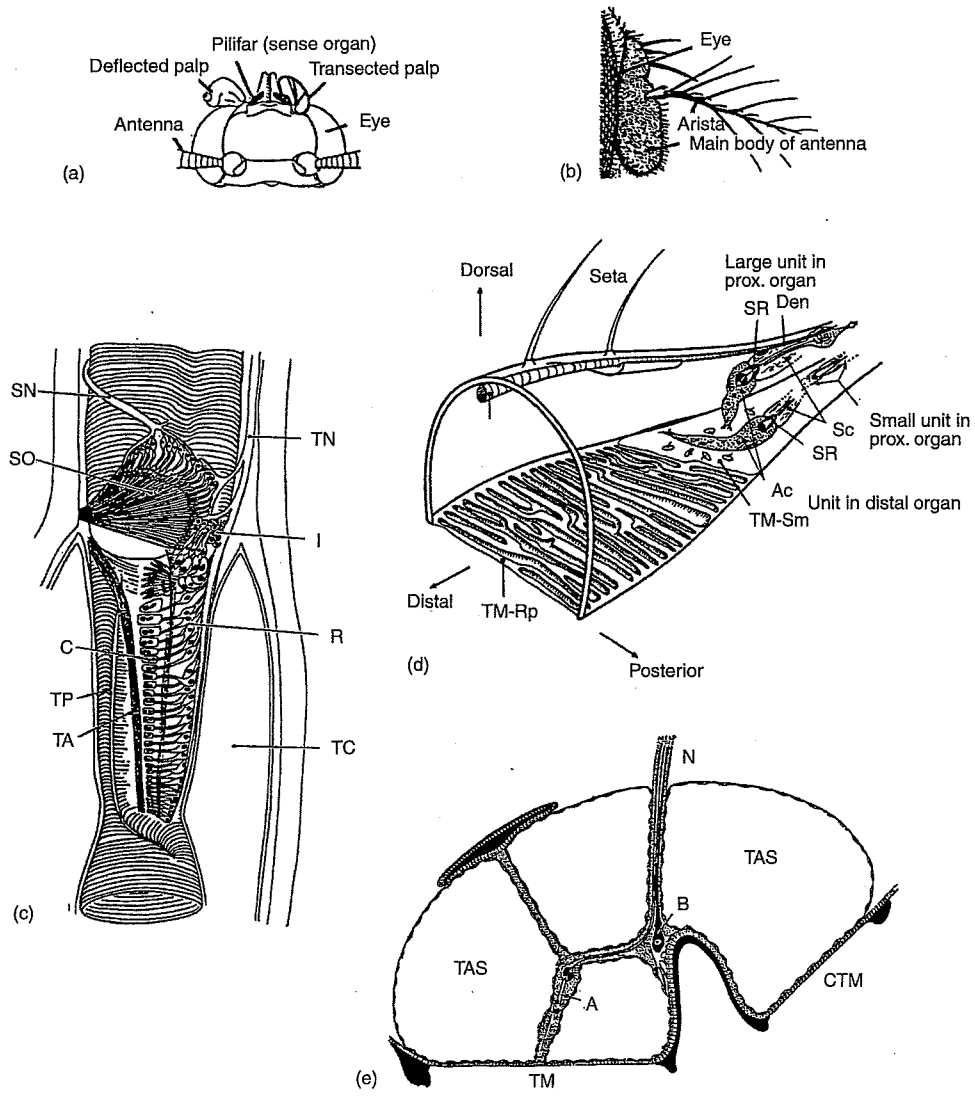


Figure 8.12 Various types of insect acoustic sensilla. (a) The *Hawkmoth* has two major types of acoustic sensilla: tympanal organs in the palps and pilifer organs. The tympanal organs in the palps are filled with air sacs crossed by delicate membranes (right hand palp transected). They act as pressure detectors and in combination with the pilifer organs can detect the ultrasonic emissions of insectivorous bats. (b) The *Fruit fly* (*Drosophila*) arista springs sideways from the third antennal segment. It is tuned to respond to viscous movement amongst the gases making up air in response to the wing beat of conspecifics. B from Frazier, J.L. (1985) with permission from John Wiley & Sons. (c) Tibial ear of the *long-horned* (*Tettigoniid*) *grasshopper*. These insects (also crickets) develop ears in the tibia of their forelegs (C = cap cell; I = intermediate organ; R = receptor cell; SO = subgenual organs; SN = subgenual nerve; TA = anterior trachea; TC = tracheal cavity; TN = tympanic nerve, TP = posterior trachea). (d) *Lacewings* develop acoustic receptors in the form of swellings in the veins of the anterior pair of wings. The swelling is bounded laterally and dorsally by a thick cuticle but ventrally by a thin rippled cuticle. Two chordotonal organs consisting of altogether about 25 scolopidia (only two shown in figure) are attached to this thin tympanal cuticle. The organ responds to high frequency bat echolocation calls (Ac = attachment cell; Den = dendrite; Sc = scolopale cells; SR = scolopale rod; TM-Rp and TM-Sm = rippled and smooth parts of tympanic membrane; Tr = trachea). (e) *Noctuid moth* ear. This is found in the metathoracic segment and consists of extensive segments of tympanal membrane covering an air-filled space. Two receptor cells (A) respond to vibration of the tympanic membrane (B = nonauditory neuron; CTM = counter-tympanic membrane; N = tympanic nerve; TAS = tympanic air sac; TM = tympanic membrane. A, C, D and E from Michelsen A. (1974) *Handbook of Sensory Physiology, Vol V/1* p.395, fig 5; p. 396, fig 6, © 1974, by permission of Springer-Verlag.

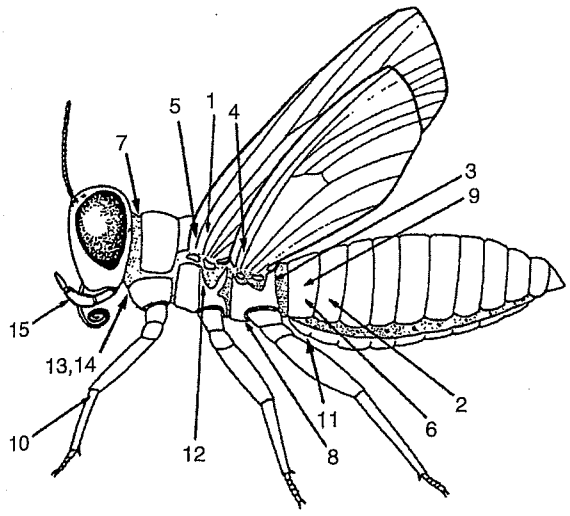


Figure 8.13 Distribution of tympanal organs on insects. The figure shows a 'generalized' insect giving the position of tympanal organs. *Lepidoptera*: 1 = wingbase (*Chrysopa*), 2 = abdomen (noctuid moths, etc.), 3 = metathorax (noctuids) 4 = base of fore or hind wing (Papilionoidea); 5 = forewing base (Hedyloidea), 15 = pilifer organ (hawk moths); *Coleoptera*: 6 = abdomen (Cicindelidae (beetle)), 7 = cervical membranes (Scarabaeidae (beetle); *Dictyoptera*: 8 = ventral metathorax (Mantodea (*Mantis*) and Blattoidea (cockroaches)); *Orthoptera*: 9 = first abdomenal segment (Acridida (locusts)), 10 = prothoracic leg (Gryllidae (Gryllus)); *Hemiptera*: 11 = abdomen (Cicadidae (*Cystosoma*), 12 = mesothorax (Corixidae (*Corixa*); *Diptera*: 13 = ventral prosternum (Tachinidae (*Ormia*)), 14 = ventral prosternum (Sarcophagidae (*Colcondamyia*). From Hoy and Robert, 1996: with permission, from the Annual review of Entomology, Vol 41, © 1996, by Annual reviews (http://www.Annual Reviews.org).

a horn-shaped burrow which acts as a megaphone. The male's great cry attracts females flying high in the air. In some grasshoppers the male's song elicits a replying call from the female so that a duet is set up between them.

Detection of prey by acoustic means is practiced by some tachinid flies. *Ormia ochracea*, for instance, listens for the mating call of male field crickets, *Gryllus integer*, and homes in to deposit its parasitic larvae. The ears of these flies can be shown to have adapted so that they are most sensitive to the dominant frequency (4.8 kHz) of the male cricket's song. But, perhaps the most interesting use of insect tympanal organs is that developed by nocturnal and crespuscular lacewings and moths to detect and avoid predatory bats. Green lacewings (*Chrysopa carnea*) possess a tympanal organ near the base of each anterior pair of wings (Figures 8.12d and 8.13). They comprise two chordotonal organs consisting of a total of about twenty five scolopidia. These tympanal organs are able to detect bat cries in the range 13–120 kHz. Bats, as we shall see in the next chapter, emit from 7 to 30 search pulses per second. When prey is located and the bat homes in for the kill, the pulses increase in frequency. The lacewing tympanal organs detect the search pulses and the insects reflexly fold their wings and nosedive out of the sky before the bat sonar locks on.

In most moths tympanal organs develop bilaterally in the metathorax. In some cases they are also to be found in first, second and seventh abdominal segments and, in the case of hawk moths, in balloon-shaped palps on the head (Figure 8.12a). Their anatomy varies very little from one moth species to another (Figure 8.12e). They consist of a tympanum (about 1 μm thick) behind which is a tracheal air sac connected to the exterior via a spiracle. Vibration of the tympanum is detected by one, two or four neurosensory cells supended in a connective tissue strand that runs between the centre of the tympanum and a cuticular support.

In moths of the very large superfamily Noctuoidea each tympanic organ has two neurosensory cells, A1 and A2, whilst four are present in the abdominal ears of members of the superfamily Geometridae. Noctuid moths are sensitive to airborne sound over the range 3–150 kHz. It is interesting to note that both the range and peak sensitivities vary in island faunae that are exposed to particular populations of bat predators. In other words, noctuid hearing is tuned to the intensities and frequencies of indigenous bats. The two neurosensory cells of the noctuid ear respond to different intensity ranges. The A1 cell responds to a lower intensity range (peak sensitivity, in some species, at 40 dB) and the A2 is tuned to respond at a higher intensity (e.g. 60 dB). There is no evidence at present that frequency can be discriminated and, indeed, it is difficult to imagine a physiological mechanism (with a two cell system) that could achieve this function. Direction of the sound source can, however, be detected. This depends on the presence of bilateral ears. If one ear is inactivated, experimentally or by infestation with the ear mite, *Dirocheles phalenodectes*, the ability to locate

the sound source is lost. Another mite, *D. scedastes*, infests both of the noctuid's ears but does not destroy the tympanum or acoustic nerve. In this case the ability to localize a sound source remains and the moth is better able to avoid marauding bats. In this particular 'arms race' with the three players, mite, moth and bat, *D. scalestes* is better adapted to survive than *D. phalenodectes*.

The A1 cell of noctuid moths can normally detect the ultrasonic search pulses of an insectivorous bat at a distance of 30–40m. If the bat is flying at about 8m/s this gives the moth four or five seconds to take defensive action. Because of its ability to detect the direction of the sound source, the moth normally turns and flies directly away from the bat. The bat, in turn, will probably not be aware of the moth until it is within 5 m or so. Its call will then increase in intensity and pulse repetition rate and will consequently activate the A2 cell. The moth has now less than a second to avoid capture. It undertakes a series of desperate avoidance manoeuvres. These consist of zig-zags, loops, spirals, power dives or passive falls into cluttering foliage. Some moths are also able, during these last desperate fractions of a second, to emit sound in a final attempt to escape the sharp, oncoming teeth.

There remains some controversy over the exact function of these moth sound emissions. It may be that it is to warn the attacking bat that the moth is obnoxious or poisonous. In this sense the warning sound may be analogous to the bright warning colouration that warns birds off distasteful daytime insects. If this is the case, it would be interesting to determine whether moth acoustics show instances of Batesian mimicry. Other investigations have, however, suggested that moth clicks are attempts to jam the bat's echolocation. It has been shown that they are almost identical to the echoes which bats would expect to pick up from their own emissions. It may be, therefore, that these sounds confuse the bat's analysis (Chapter 10) making it 'see' an obstruction where there is none and, in veering to avoid it, miss its mark on the moth.

Let us turn now from the remarkable sophistications of insect mechanoreceptors to the seemingly more prosaic topic of the sense of touch in the mammalian skin. We shall see that it too can be regarded as a sensory surface. It is responsive not only to mechanical stimuli but also to thermal stimuli and to those which cause pain. These latter stimuli we shall consider in Chapters 20 and 22. In the next section of this chapter only sensitivity to mechanical stimulation will be considered. In Chapter 9, where we consider vertebrate 'hair cells', we shall return to the extraordinary sensitivities of devices evolved to detect the gentle touch of acoustic vibrations and the huge opportunities thereby opened for communication across distance. We shall also return to the continuing crepuscular contest between moth and microchiropteran.

8.4 TACTILE RECEPTORS IN MAMMALIAN SKIN

The mammalian skin is home to a great array of mechanoreceptors. In this chapter we only consider those found in the skin of the eutheria, in particular in the skin of *Homo sapiens*. In Chapter 21 we discuss all-too-briefly the remarkable push-rod mechanoreceptors found in prototherian mammals, the platypus and spiny anteater.

There are several ways to classify the sensory endings in the skin of euthrian mammals. One commonly used classification is into fast and slow adapting receptors. The first respond only during initial indentation of the skin and remain silent during steady pressure; the latter respond both during onset of the stimulus and during constant displacement.

8.4.1 Fast Adapting Receptors

Fast adapting receptors include **Pacinian corpuscles**, **Meissner's corpuscles**, **Krause's end bulbs** and **hair follicle sense endings**. Pacinian corpuscles are found in both glabrous (i.e. non-hairy, such as the palms of the hand and the soles of the feet) and in hairy skin; hair follicle endings (by definition) only in hairy skin; Meissner's corpuscles only in primate glabrous skin; and Krause's end bulbs only in non-primate glabrous skin.

8.4.1.1 Pacinian Corpuscles

These are oval structures ranging from 0.5–2 mm in length. They are to be found in the deeper layers of the dermis of the skin. In section, an onion-like structure is revealed. They consist of layers of connective

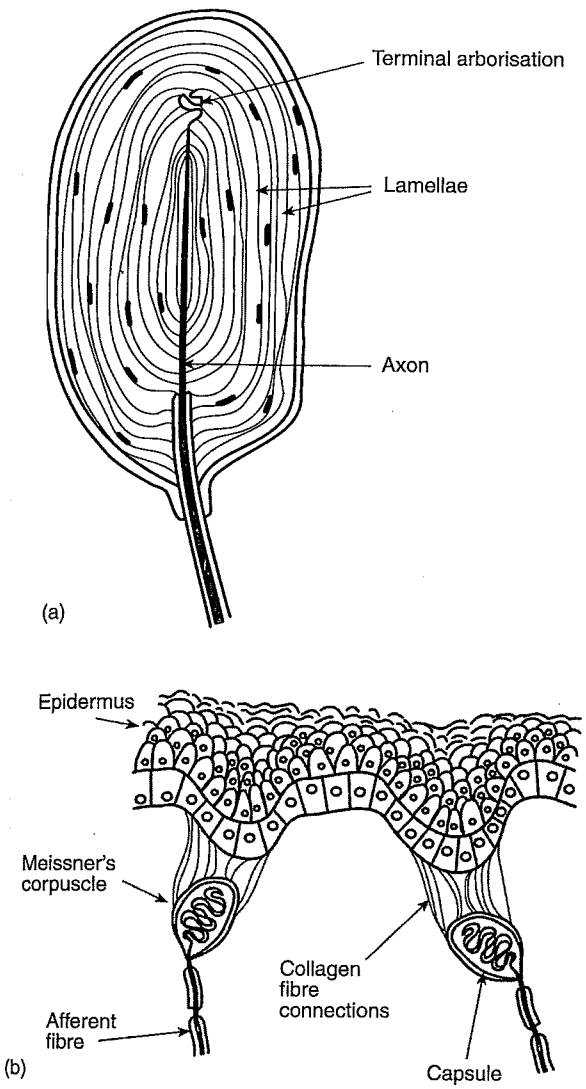


Figure 8.14 (a) Pacinian corpuscle. (b) Meissner's corpuscle.

tissue surrounding an unmyelinated nerve fibre (Figure 8.14a). It is believed that the layered structure has the function of transforming a steady indentation of the skin into a transient stimulus. This is accomplished by the indentation causing a momentary slippage of the layers over each other until, rapidly, a new equilibrium is reached, when the pressure on the sensory nerve ending is relieved. Hence Pacinian corpuscles are able to detect vibration even when subjected to steady pressure.

A generator potential (depolarization) can be detected in the unmyelinated ending, when the corpuscle is compressed. This results in a short burst of impulses in the sensory fibre, which adapts in one or two seconds to zero or a very low frequency. As their physiology suggests, the principle function of Pacinian corpuscles in the skin is to detect vibration. The frequency to which they respond ranges from as low as 70 Hz to as high as 1000 Hz. They are, however, most sensitive in the middle of the range (200–400 Hz), where a deformation of no more than 1 μm is a sufficient stimulus.

8.4.1.2 Meissner's Corpuscles

These are also found in the dermis of glabrous skin. The nerve endings are surrounded by a connective tissue capsule that is connected to the overlying stratified epithelium by collagen fibres (Figure 8.14b). This provides an effective mechanical linkage between the surface of the skin and the sense organ. The nerve endings themselves form a spiral within the capsule, the helices of which are separated by sheets of Schwann cells. The endings are stimulated by movement of the skin and, in particular, by vibration. The frequency range of the vibratory stimuli is lower than that characteristic of Pacinian corpuscles, ranging from 10–200 Hz.

8.4.1.3 Krause's End Bulbs

These are rather similar to Meissner's corpuscles. They are, however, mainly restricted to non-primate mammals where they are, once again, found in glabrous skin. They have a lamellated capsule surrounding either a rod-like or a spiral nerve ending. Like Meissner's corpuscles they respond to vibrations in the low frequency range, 10–100 Hz.

8.4.1.4 Hair Follicle Receptors

Sensory nerve endings form a complex meshwork around a hair follicle just beneath the sebaceous glands (Figure 8.15). Each ending forms an enlargement filled with mitochondria and tightly enclosed by Schwann cells. The endings are distributed around the follicle, some in the outer vascular layer, others penetrating to a position between the outer and inner root sheath cells. Some branches run vertically up along the hair follicle, others circle around it. Yet

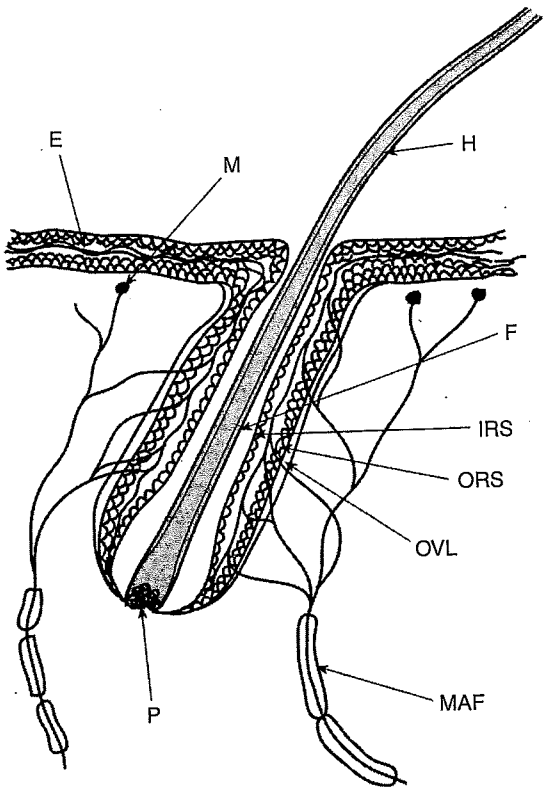


Figure 8.15 Sensory innervation of hair follicle. E = epidermins, F = follicle; H = hair; IRS = inner root sheath; M = Merkel disc; MAF = myelinated afferent fibre; ORS = outer root sheath; OVL = outer vascular layer; P = papilla.

other branches terminate in Merkel discs beneath the epidermis. The hair follicle receptors are classified into at least three different types (D,G,T) according to their sensitivity and rate of discharge. They respond to any movement of the hair. In many mammalian species the hairs in the vicinity of the mouth are extended to form elongated whiskers (vibrissae) and tactile hairs. The receptors associated with these hairs include both fast and slow adapting types. We shall give further consideration to vibrissae when we come to consider the central analysis of tactile information later in this chapter.

8.4.2 Slow Adapting Receptors

In contrast to the fast adapting receptors of the previous section, these receptors respond to the displacement of the skin but sustain their discharge when the skin is held in its new position. There are three types: **Merkel cells**, **Ruffini endings** and **C-mechanoreceptors**. It is conventional to group these slowly adapting receptors into two categories. Type I receptors respond if the skin is stroked rapidly, type II receptors respond to a constant displacement of the skin, particularly when it is stretched.

8.4.2.1 Merkel Cells

These fall into the type I category. They lie just beneath the epidermis and possess large, irregularly formed nuclei and microvilli which project into the epidermal cells (Figure 8.16a). At their bases are disc-like expansions of the ends of sensory axons (Merkel discs). A group of ten to twenty Merkel cells make synaptic contact with the ending of a single sensory axon. They respond to sudden displacements of the skin, as in stroking.

8.4.2.2 Ruffini Endings

This is a type II ending and responds to steady displacement of the skin. They are found in the deep layers of the dermis. As shown in Figure 8.16b, the termination of the sensory axon breaks up into a network of fine processes which ramify in the interior of the connective tissue capsule.

8.4.2.3 C-mechanoreceptors

Large numbers of unmyelinated C-fibres take their origin in the dermis of the skin, many of them starting close to the dermo–epidermal junction. There are no differentiated sense endings associated with these fibres. They respond with a slowly adapting discharge to steady indentation of the skin. C-fibres also respond to other sensory modalities: temperature (Chapter 20), tissue damage (pain) (Chapter 22).

8.5 CEREBRAL ANALYSIS OF TOUCH

The vast majority of sensory fibres from the skin's sensory receptors enter the spinal cord via the dorsal (= posterior) roots and terminate in the dorsal horn of the grey matter. The mechanoreceptive afferents, which are generally large diameter fibres (except, of

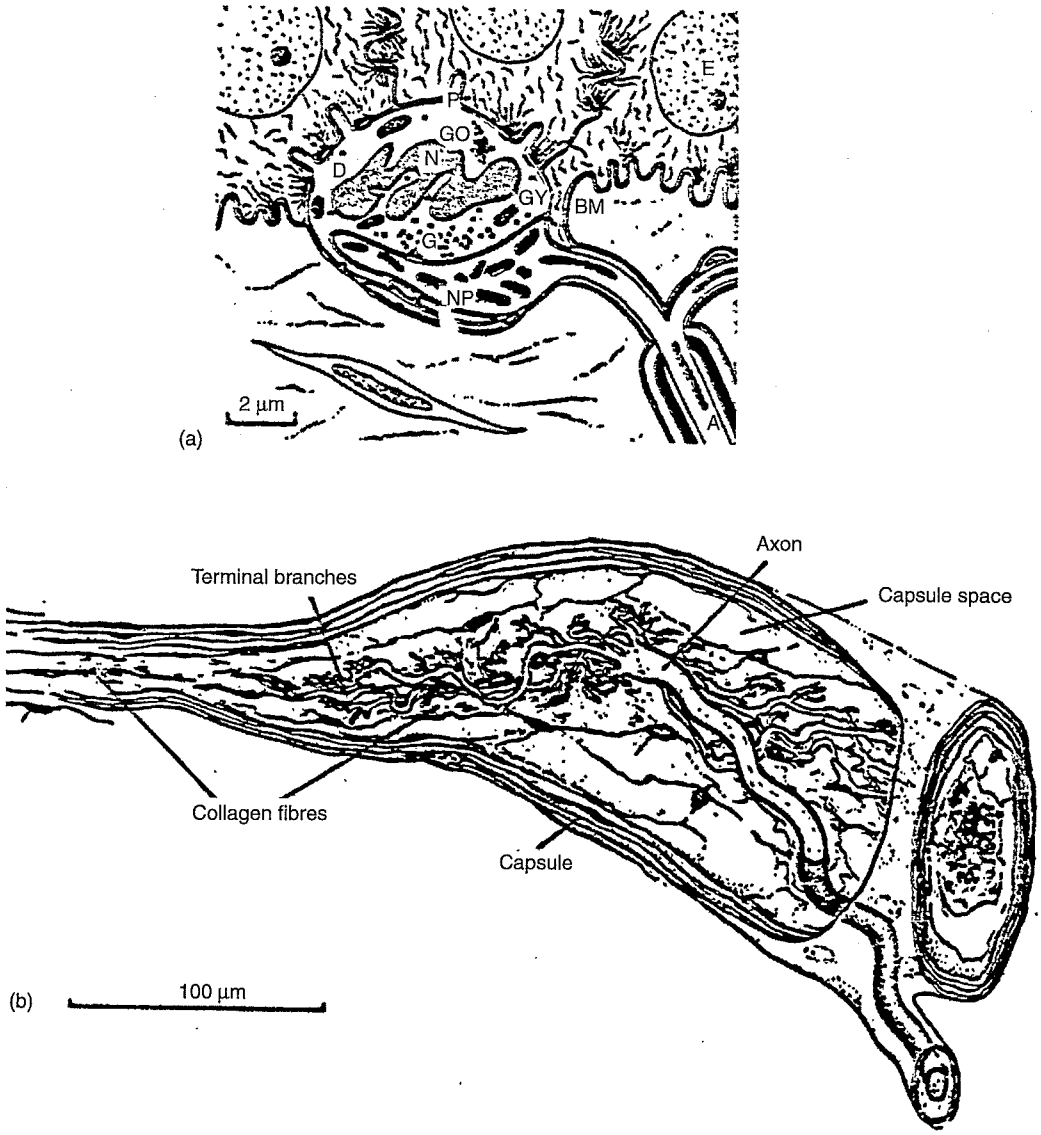


Figure 8.16 (a) Merkel cell. The myelinated axon branches to innervate ten to twenty Merkel cells. The termination of each branch is expanded to form a disc (Merkel disc). A = afferent axon; BM = basement membrane of epidermal cells; D = desmosomes; E = epidermal cell; GO = Golgi bodies; N = nucleus of Merkel cell; NP = Merkel disc. (b) Ruffini ending. The sensory axon breaks up within the connective tissue capsule to form an interweaving complex of terminals. A and B from Iggo, 1982: by permission of Cambridge University Press.

course, the C-fibre mechanoreceptors), usually take a central position in the dorsal root, surrounded by finer fibres from pain and thermoreceptor endings. The cytons of all the fibres are located in the dorsal root ganglia. A fair proportion of the small diameter unmyelinated fibres (about 30%) travel back down a portion of the dorsal root and then turn into the ventral roots to terminate in the ventral horn of the grey matter (Figure 8.17). Most of these fibres originate in the viscera. The area of skin sending input into each dorsal root is termed a dermatome (Figure 22.5). Adjacent dermatomes overlap.

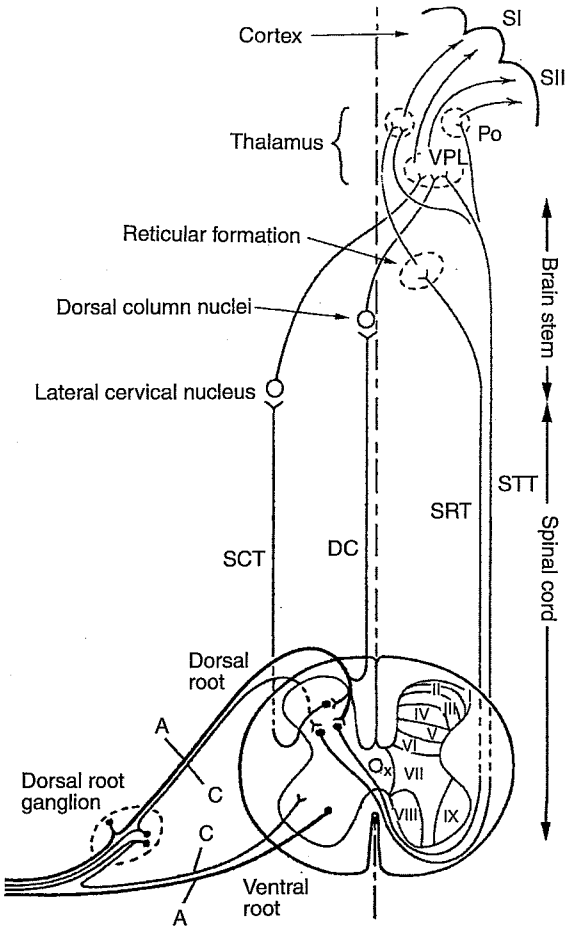


Figure 8.17 Afferent pathways in spinal cord. The A and C fibres are shown entering the spinal cord through the dorsal (= posterior) root. A proportion (circa 30%) of the C-fibres turn back and find their way to the ventral horn of the grey matter via the ventral (= anterior) root. All the sensory fibres have their cell bodies in the dorsal root ganglia. The pathways in the CNS to the somatosensory cortices are shown. Further explanation in text. DC = dorsal column fibres; IL = Intralaminar nucleus; Po = posterior thalamic nucleus; S1 = primary somaesthetic area; SII = secondary somaesthetic area; SCT = spinocervical tract; SRT = spinoreticular tract; STT = spinothalamic tract; VPL = ventroposterior thalamic nucleus. From Iggo, 1982: by permission of Cambridge University Press.

Once in the spinal cord, the fibres take a number of routes to the cerebral cortex. Four major routes are recognized (Figure 8.17) although they do not form anatomically distinct tracts. The spinocervical tract (SCT) and dorsal column fibres (DC) travel up the ipsilateral side of the spinal cord to end in the lateral cervical and dorsal column nuclei, respectively. From there a further relay crosses over, in the region of the medulla, to terminate in the ventro-posterior nucleus of the thalamus. A final neuron then runs on to terminate in the primary or secondary somaesthetic areas of the cerebral cortex. The other two routes, as shown in Figure 8.17, involve a cross-over at the level of the spinal cord (within two segments of the point of entry) to form the spino-reticular tract (SRT) and spino-thalamic tract (STT). Fibres in the SRT run up in the ventro-lateral quadrant of the spinal cord to nuclei in the midbrain and thalamus. From there the input is directed to the cortical somaesthetic areas. Finally, the STT consists of fibres in the antero-lateral quadrant of the spinal cord, ending in three thalamic nuclei (Figure 8.17). A significant number of nociceptive fibres track towards the cerebrum in this tract. Once again a final fibre leads upwards into the cerebral somaesthetic areas.

These pathways and nuclei ensure that a certain amount of information processing occurs before the somaesthetic input reaches the cortex. Although it is believed that individual dorsal horn neurons have a one-to-one relationship with their input fibres, there is little doubt that interneurons within the dorsal horn are also influential. We shall meet a significant instance of this synaptic interaction when we come to consider nociceptive fibres and the sensation of pain in Chapter 22. More extensive interaction between different types of mechanosensory input occurs in the thalamic nuclei.

The first destination of the somaesthetic fibres in the cerebral cortes are the two somaesthetic (or somatosensory) cortices. The primary somaesthetic cortex is located in the postcentral gyrus, just behind the Rolandic fissure, and the secondary cortex is located (in primates) on the superior wall of the Sylvian fissure.

The primary somaesthetic cortex is subdivided into three cytoarchitectonic areas: Brodmann areas 1, 2, 3a and 3b (Figure 8.18). Somaesthetic fibres from the thalamic nuclei terminate in areas 3a and 3b and the cells in those areas then project to areas 1 and 2. The thalamic nuclei also send a sparse projection to the secondary somaesthetic cortex but most fibres to this region originate from all four subdivisions of the primary somaesthetic cortex. Indeed, this cortex is very dependent on the primary cortex.

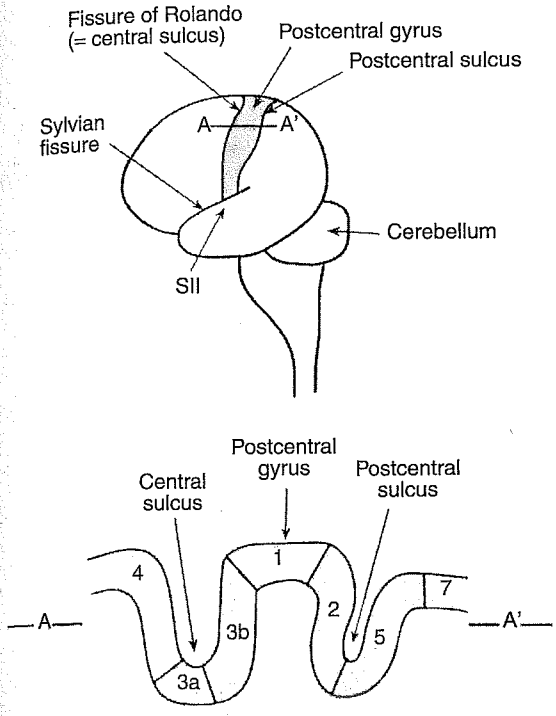


Figure 8.18 Upper part of figure shows lateral view of cerebrum to show the position of the somaesthetic cortices. SII = secondary somaesthetic cortex. The bottom part of the figure shows a section through the cortex (labelled AA′ in upper figure). The Brodmann cytoarchitectonic areas (BA areas) are labelled.

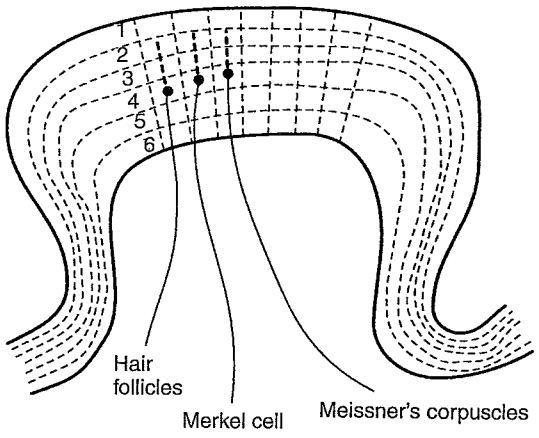


Figure 8.19 Schematic section through somaesthetic cortex to show its horizontal stratification into six layers and its vertical subdivision into columns. As indicated in the text each column is dedicated to one submodality. Although each BA receives a full set of somaesthetic input there is some specialization. BA3a is dominated by input from muscle spindles; BA3b by cutaneous receptors; BA2 by deep pressure receptors and BA1 by rapidly adapting cutaneous receptors.

If the connections from the primary cortex are severed, the neurons in the secondary cortex fall silent. In contrast, removal of parts of the secondary cortex has no effect on the primary cortex.

If we turn to the histological structure of the primary somaesthetic cortex, we find that it, like all other regions of the mammalian neocortex, displays a six-layered stratification (Figure 8.19). The input fibres from the thalamic nuclei terminate in layer 4. The other layers contain cells whose axons run out of the cortex to other parts of the brain. Layers 2 and 3 project to other cortical regions, especially Brodmann areas 5 and 7. Layer 5 projects to subcortical nuclei and Layer 6 projects back to the thalamus.

Less obvious to the microscopist is a columnar structure running orthogonal to this stratification (Figure 8.19). These columns were first discovered during microelectrode analysis by Vernon Mountcastle. Although special staining techniques reveal them to have histological reality, they are perhaps best regarded as units or modules of physiological activity. The columns are 300–500 μm in diameter and run vertically through the cortex and thus include cells from all six histologically distinguishable layers. Microelectrode recording has shown that all the cells in a given column respond to the same type or subtype of stimulus. Indeed, Mountcastle found that the specificity was even greater: all the cells in a given column respond to the same type of receptor. For example, all the cells in one column may respond to movement of the hairs on a particular part of the body's surface; all the cells in another may respond to rapidly adapting Meissner corpuscles in the same or different part; in yet another column the cells will respond only to slowly adapting Merkel receptors and so on. A cortical column is thus a very specific computing module. It receives precise information about one sense submodality from one small area of the body's surface. It will also receive input information from other columns in the somaesthetic cortex and (via the corpus callosum) from equivalent columns on the other side of the brain.

Microelectrode recording shows, furthermore, that not only does each columnar cell respond to a very particular sense modality but it is also very specific about where the stimulus is coming from. Cells in the primary somaesthetic cortex can thus be said to have 'receptive fields (RFs)' (Chapter 3). The receptive fields of neighbouring cells will often overlap and there is a certain dynamic shifting of boundaries. The size of the RFs in different parts of the anatomy varies widely. RFs for cells receiving input from the finger tips are about 3–4 mm in diameter. In contrast, RFs for cortical cells receiving input from the trunk are over one hundred times larger. In other words the system is arranged so that it makes biological sense. Those parts of the body from which fine discrimination is demanded are 'scrutinized' in minute detail by cells in the somaesthetic cortex. Parts that do not normally need such attention have correspondingly few cells devoted to them.

Cortical cells whose receptive fields are located in the same part of the body's surface are grouped together in the cortex. This leads to a representation of the contralateral body surface developing in the primary somaesthetic cortex that can be mapped by the physiologist's microelectrode. This is sometimes called the **somaesthetic homunculus** (Figure 8.20). It was, in fact, first detected by the Canadian neurosurgeon, Wilder Penfield, during brain operations carried out under local anaesthetic. To be sure that any excisions did not lead to disastrous outcomes, Penfield would stimulate the cortex at various points and ask the patients to report what they felt. Because the magnitude of the RFs of the cortical cells varies so widely, the resulting map is strikingly non-isomorphous. It should be noted, moreover, that the somaesthetic cortex contains not just one homunculus but four: one in each subregion, that is Brodmann areas 1, 2, 3a and 3b. These maps are all in rough alignment with each other. Finally, it can be shown that the homunculus varies in a biologically appropriate manner from one mammal to another.

We noted above that the RF areas of cells in the somaesthetic cortex were not fixed and rigid but able to expand and contract in response to different circumstances. Similarly the quantity of cortex devoted to particular parts of the body can also change in response to experience. Perhaps the best known experimental examination of this lability was carried out on the vibrissae of mice.

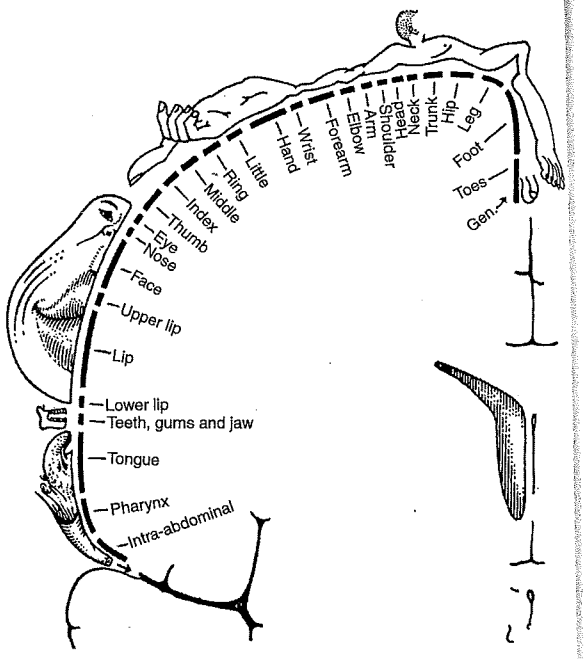
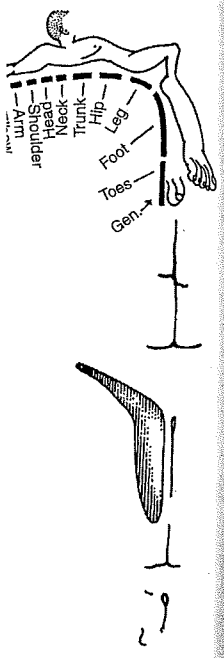


Figure 8.20 Somaesthetic homunculus. The figure shows a coronal section through the postcentral gyrus. Note the large areas devoted to the hand and to the face and lips.

8.6 PLASTICITY OF THE SOMAESTHETIC CORTEX

We saw above that rapidly adapting mechanosensory fibres invest the lower parts of hair follicles and detect any movement of the hair. In many mammals this sense is greatly enhanced by the development of vibrissae (whiskers) in the region surrounding the mouth. In the mouse the quantity of cortex devoted to the whiskers is greater than that devoted to the paws. Each whisker sends about 100 myelinated fibres via the trigeminal nerve ultimately to the primary somaesthetic cortex. The fibres terminate in layer IV of the cortex in specialized structures called 'barrels' (Figure 8.21). Each barrel consists of between 1500 and 2500 neurons and is from 100 to 300 μm in diameter. The number of barrels corresponds exactly to the number of vibrissae on the contralateral side of the face and, furthermore, they are arranged in the same way as the whiskers are arranged.



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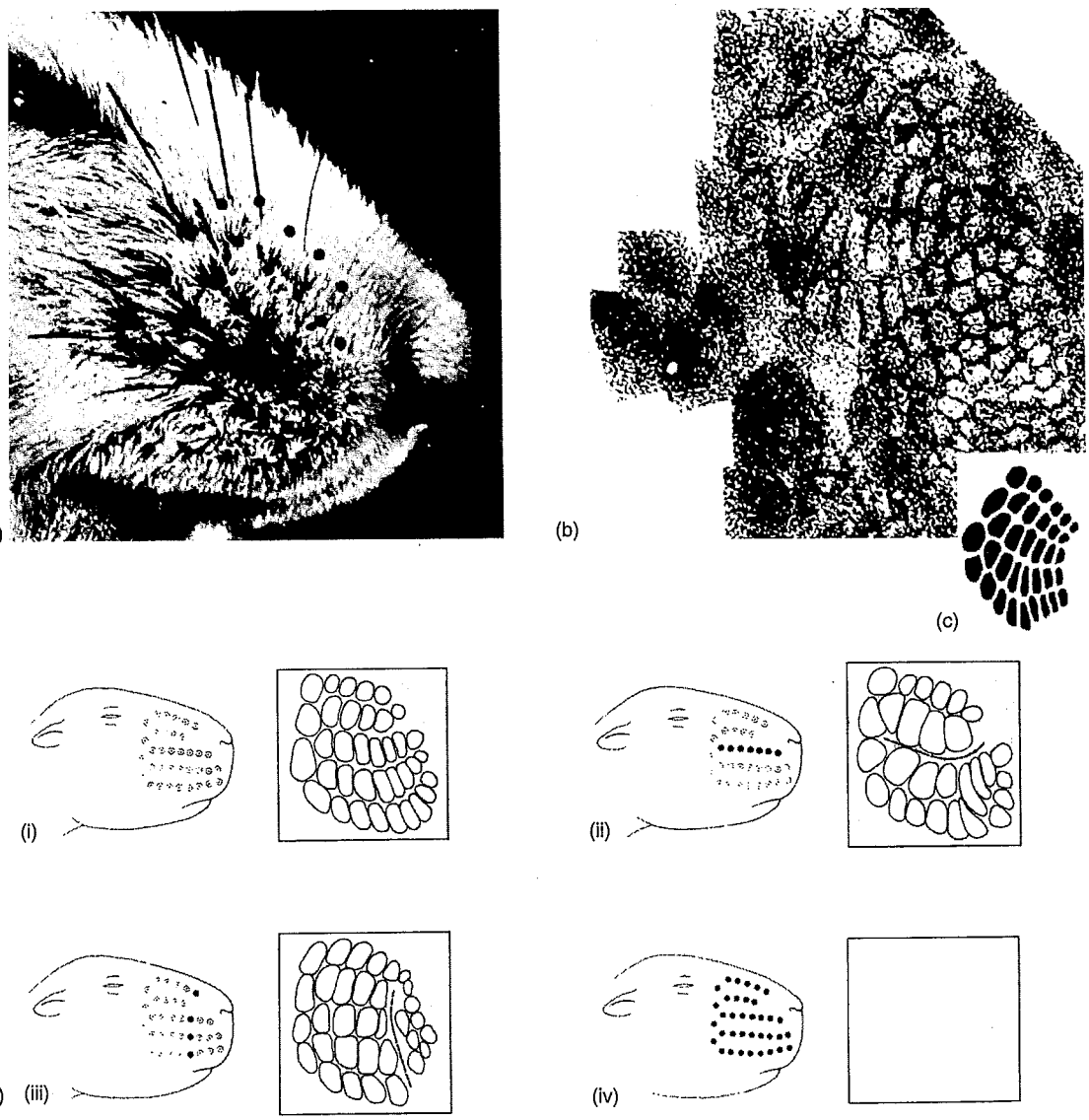

Figure 8.21 Mouse whisker barrels. (a) Head showing five rows of vibrissae. (b) Section of cortex showing 'barrels', each corresponding to one whisker. (c) Diagram to show the organization of the whisker barrels. (d) Diagrams to show the effect of removing whiskers. (i) Full set of whiskers, full set of barrels; (ii) one row of whiskers removed, unaffected barrels grow into territory of unused barrels; (iii) one column of whiskers removed; again unaffected barrels colonize space left by missing barrels; (iv) total removal of whiskers; loss of all barrels. From Woolsey and Van Der Loos, 1970, *Brain Research*, **17**, 205–42, Copyright © 1970, Elsevier.

Woolsey and Van Der Loos carried out some very instructive experiments on this well characterized system. If mice were bred with extra whiskers, extra barrels appeared in the somaesthetic cortex. However, the entire barrel field did not increase in extent but the extra barrels were squeezed in between the usual array. It is as if the vibrissal input is competing for limited cortical space. Similarly, if vibrissae were removed, the corresponding barrels atrophied and their space was taken over by the remaining barrels.

The exact biochemical mechanisms by which this remarkable lability of the cortex in response to peripheral input is achieved is still the subject of much research. We shall see a similar plasticity when we come to consider the primary visual cortex.

Experiments with monkeys trained to carry out a task involving two finger tips touching a revolving wheel revealed a similar plasticity in the somatosensory cortex. Maps of the finger area (obtained by microelectrode recording) before and after the training showed a several-fold increase in the cortical representation. Furthermore, although the total area of finger representation in the somaesthetic cortex increased, the areas of the receptive field of the cells penetrated by the microelectrode were significantly smaller than in the untrained cortex. Similar results have been shown in monkeys that have lost digits, although in these cases, of course, the cortical representation of the missing digit shrinks whilst that of the remaining digits increases.

The advent of sophisticated techniques of neuroimaging, especially functional magnetic resonance imaging (fMRI) and magnetoencephalography (MEG), has enabled analogous investigations to be carried out on humans. MEG studies have shown that the somatosensory representation of the fingers of the left hand is significantly expanded in string players (violin, viola, cello, double base, etc.) when compared with the representation of the digits of the right hand or with the representation of the left hand digits of non-string orchestral players.

Another interesting investigation has been carried out with patients adjusting to blindness by acquiring Braille reading skills. The use of fMRI and the location of somatosensory evoked potentials (SEPs) by EEG techniques have shown that there is an enlargement of the area of somatosensory cortex dedicated to the Braille-reading finger. It appears that there is at first an 'unmasking' of pre-existing neural connections and later these are made permanent by structural changes. In those afflicted with blindness early in life, the occipital cortex is also drawn into the response to the Braille-reading finger. This is interesting as it is well known (Chapter 18) that the occipital cortex is normally concerned with vision. fMRI and SEP scans again show that in these individuals cortico-cortical connections are established (or confirmed) between the somatosensory/motor cortices, which normally process inform tion relating to touch and movement of the Brai reading finger, and visual cortices 1 and 2. Th connections seem to be important for reading ac racy. We shall see when we come to Chapter 18 tl the primary visual cortex also (at least in the se sitive period) adapts to sensory (in this case visu input. The maps in the sensory cortices are by means fixed and unchangeable: like other parts the anatomy, they respond to use and disuse.

8.7 CONCLUDING REMARKS

Aristotle, as we noted in the introductory quotatic to Part Two, believed that 'touch' was the definit characteristic of an animal. He also believed it w the most fundamental of all the senses. We can s what he meant. In this chapter we have gone, whe the Stagirite had no means of going, beneath the ski and looked at the various sense organs and ending responsible for the sense of touch. We have seen ho right the philosopher was in his estimate of its un versality and antiquity. We have remarked how touc sensitivity in the tiny nematode, *C. elegans*, promise to throw light on mechanisms at work even in our selves. We noted also how touch receptors had bee developed by the insects to detect ripples on the sur face of water and the atmospheric pressure change we know as sound. We shall look at analogous devel opments in the vertebrates in the next chapter, where we consider the vertebrate ear.

But our examination of the sense of touch took us further into the life of animals than 'mere' detection of atmospheric vibration. We saw how insect 'ears' are used (amongst other things) for interindividual communication. We noted how moths and lacewings are able to detect the onrush of predatory bats. But, more than this, touch has become deeply enmeshed in the social life of many animals. Anyone who has watched the interaction of social insects, such as ants and bees, will know that the sense of touch is vital: they continuously subject each other to sessions of intense palpation. This use of the sense of touch is also of crucial importance in some of the social mammals, particularly some primates. The processes of mutual grooming, although originally evolved to clear monkey pelts of ectoparasites, has transferred

to social bonding. Some monkey troops (depending on size) spend up to 20% of their time in this activity. Such tactile interaction has profound effects on the neuroendocrine system, enabling often exciteable and aggressive animals to live calmly in close proximity to each other. Some have said that humans have substituted vocal gossip to generate the same effect as this tactile bonding. But touch remains profoundly significant in our own species. From shaking hands to more intimate contact, the touch of two skins plays an indispensable role in communication between human individuals.