

Cockroach Antennae

Jiro Okada

Cockroach antennae have been extensively used for studying the multifunctional sensory appendage that generates the olfactory, gustatory, tactile, thermal, and humidity senses. Of the variety of senses, the **tactile sense** is thought to play a key role for perceiving physical objects. Because most cockroach species are nocturnal, the tactile sense of the antenna would be essential to determine the position, shape, and texture of surrounding objects in the dark. Mechanoreceptors on the surface of the antenna are primarily responsible for the generation of tactile sense. In addition, the motor function of antenna also contributes to the **active tactile sense** (Staudacher et al. 2005; Comer and Baba 2011). The antennal movement is accompanied by the activation of **proprioceptors** at the antennal joints.

Cockroach Antenna as a Tactile Sense Organ

Cockroaches are insect species that are classified into the order Blattaria. Currently, over 4,000 species have been found in Blattaria, but of these, only a few are known to be pests. Because these species can tolerate the human environment, and are easily reared in laboratories, they are often used for various biological studies. *Periplaneta americana*, which is also known as the American cockroach, can be considered as the most representative species used for studying the antennal system.

Each antenna of adult *P. americana* is as long as its body length (≈ 40 mm), and consists of approximately 140 segments (Figures 1 and 2). The first and second proximal segments are called the **scape** and the **pedicel**, respectively, and the remaining distal segments are collectively referred to as the **flagellum**. Each segment is connected to the neighboring segments via flexible joints. However, only the head-scape and scape-pedicel joints can move actively with muscle contraction. The other joints connecting the flagellar segments are deflected only passively.

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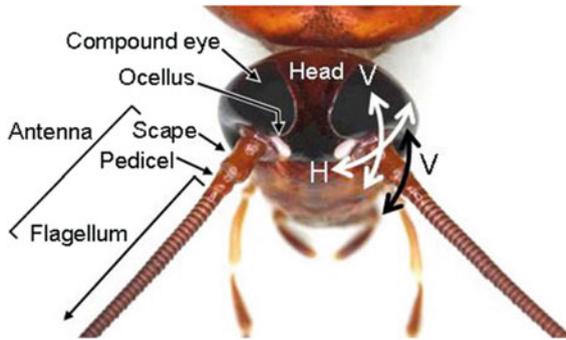


Figure 1 Head and antennae of the American cockroach *Periplaneta americana*. Antennae can move both horizontally (H) and vertically (V)

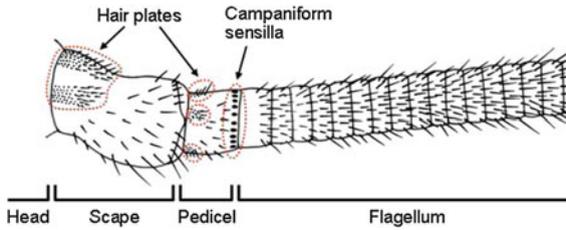


Figure 2 Lateral view of a cockroach's antenna

On the surface or beneath the cuticle of the antenna, there are numerous sensory units called **sensillum**. Some types of sensilla serve as mechanoreceptors that mediate the tactile sense.

Sensory System

Cockroach antennae have a variety of mechanoreceptors that differ in morphology, location, and function. Morphologically, the antennal mechanoreceptors are classified as follows: **hair sensillum** (or simply **hair**), **campaniform sensillum**, and **chordotonal sensillum**. The hair and campaniform sensilla are widely distributed on the surface of the antenna, whereas the chordotonal sensilla are located in the pedicel. Functionally, these receptors are classified as **exteroceptor** and **proprioceptor**, i.e. the external and internal mechanoreceptors, respectively. A recent histochemical study revealed that some mechanosensory neurons, including at least the cheatic (see below), chordotonal, and hair plate sensilla, are serotonergic (Watanabe et al. 2014).

Hair Sensillum

Hair sensilla are frequently found on the surface of the flagellum. Each of the mechanosensitive hairs in the flagellum contains a single mechanoreceptor and several chemoreceptor cells. Such multifunctional hairs with relatively thick and long shafts ($>50\ \mu\text{m}$ in length) are termed the sensilla cheatica or cheatic sensilla (the most prominent type of bristles, as shown in Figure 3). Each hair possesses a pore at the tip, which acts as a passage for molecules, and a flexible socket for passive deflection. The **cell body** (or perikaryon) of the mechanoreceptor beneath the socket is bipolar-shaped, and extends a **dendrite** distally to the base of the hair, and an **axon** proximally to the central nervous system. The dendrite contains longitudinally arranged sensory cilia (axoneme), and also a tightly packed microtubule structure (tubular body) at its tip. Deflection of the mechanosensory hair may deform the tubular body leading to the generation of electrical signals in the receptor cell via mechano-electric transduction. The **action potentials** appear only transiently upon the deflection of the hair, indicating the phasic (rapidly adapting) nature of the receptor (Hansen-Delkeskamp 1992).

Campaniform Sensillum

Campaniform sensilla are hairless mechanoreceptors located at each flagellar segment and the pedicel. They are characterized by an elliptical depression of the cuticles with a dome-like upheaval (Figure 4) or a pea-like protrusion (the latter is also called the marginal sensillum). Beneath the cuticle are a single mechanoreceptor cell and its accessory structures whose morphology is similar to the mechanosensitive hair. Each flagellar segment possesses several campaniform sensilla at both the distal and proximal margins. In *P. americana*, approximately 28 campaniform sensilla are arranged circularly around the distal margin of the pedicel (Toh 1981). The campaniform sensilla are presumably activated when the adjacent

Figure 3 Scanning electron micrograph showing the surface view of the flagellum. Courtesy: Dr. Y. Toh

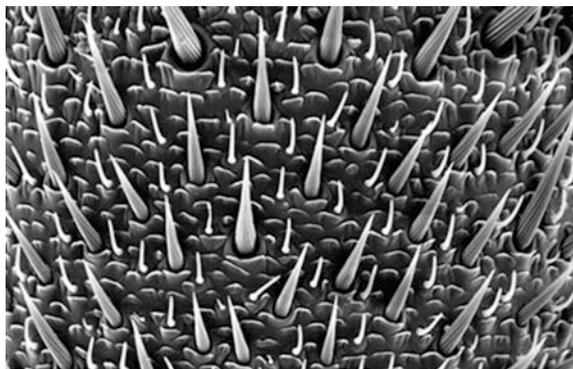
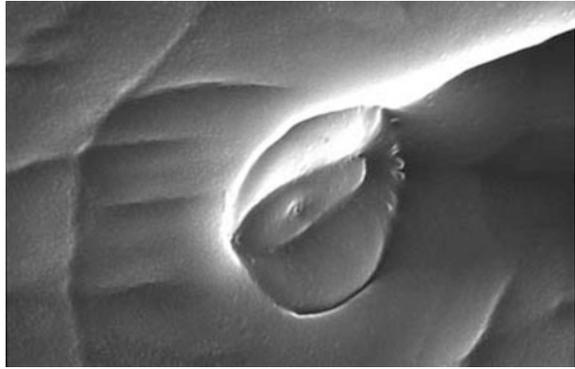


Figure 4 Magnified surface view of the campaniform sensillum. Courtesy: Dr. Y. Toh

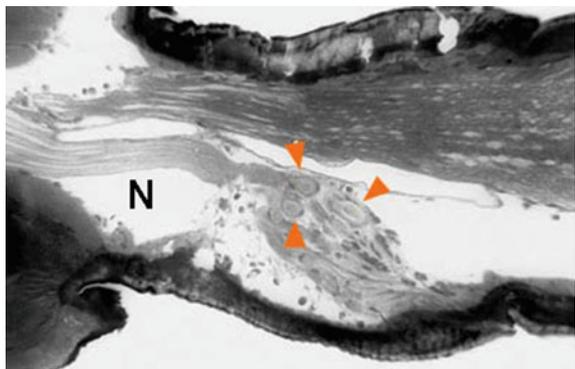


cuticular structures are under stress. Therefore, the extent and direction of flexion at the intersegmental joints are speculated to be monitored by the campaniform sensilla. In this regard, they may function as proprioceptors.

Chordotonal Sensillum

Chordotonal sensilla are internal mechanoreceptors that serve as exteroceptors or proprioceptors. There are two types of chordotonal sensilla inside the pedicel of *P. americana*: the **connective chordotonal organ** (or simply **chordotonal organ**) (Figure 5) and **Johnston's organ**, which consist of 50 and 150 sensory units designated as the **scolopidia**, respectively (Toh 1981). The morphology of a scolopidium is characterized by the presence of a scolopale cell and an attachment cell that surrounds the dendrites of the receptor cell. The tip of the dendrite is covered by a cap of secreted matter from the scolopale cells. The attachment cell connects the distal part of the scolopidium to the inner surface of the cuticle. Each scolopidium consists of two and three bipolar receptor cells in the chordotonal and

Figure 5 Internal morphology of the chordotonal organ. Arrowheads indicate cell bodies. N, afferent nerve. Courtesy: Dr. Y. Toh



Johnston's organs, respectively. The chordotonal organ may function as a proprioceptor for the scape-pedicel joint (Ikeda et al. 2004) or an exteroceptor for antennal contacts (Comer and Baba 2011). On the other hand, Johnston's organ is rather thought to be an exteroceptor for detecting sound or substrate vibration, considering its function in other insect species.

Hair Plate

Hair plates are clusters of the *pure* mechanosensory hair located at the base of an antenna. Several tens to over 100 hairs (15–60 μm in length) are arranged in the form of arrays adjacent to the head-scape and scape-pedicel joints (Okada and Toh 2000) (Figures 2 and 6). As the joint moves, a portion of the mechanosensory hairs is deflected by the joint membrane (Figure 6). At first, the hair plates seem to act as exteroceptors, but they actually function as proprioceptors for the active movements of the antennal basal joints. The receptor cells of the antennal hair plates in *P. americana* are known to be of a tonic-phasic type with a very slow adapting nature (Okada and Toh 2001).

Motor System

Antennal Muscles and Their Innervation

The cockroach antennae are controlled by five functionally different muscles located inside the head capsule and the scape (Figure 7, left side). The muscles in the head capsule span between the tentorium (an internal skeleton) and the proximal ends of the scape. The adductor muscle rotates the scape medially around the head-scape joint, while the abductor muscle rotates the scape laterally. The levator

Figure 6 Magnified surface view of the hair plate. Some sensilla (*arrowheads*) are deflected by the joint membrane (JM). Courtesy: Dr. Y. Toh

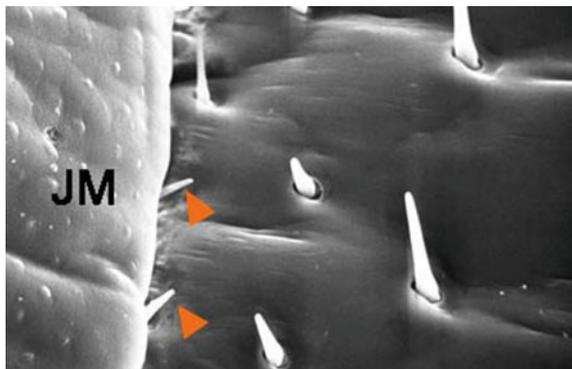
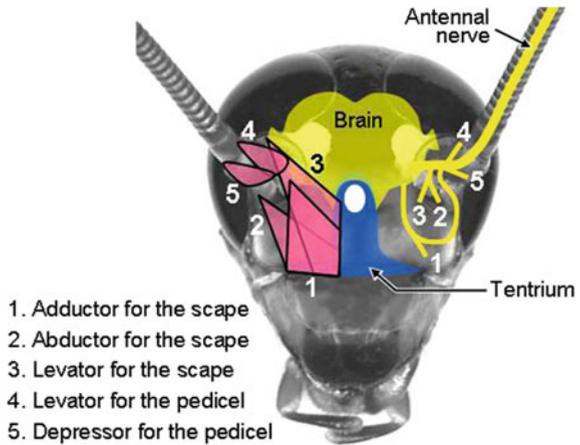


Figure 7 Frontal view of the five antennal muscles (*pink masses*) and the corresponding motor nerves (*yellow lines*)



muscle lifts the scape vertically. The other two muscles inside the scape span between the proximal ends of the scape and those of the pedicel: the levator and depressor muscles deflect the pedicel dorsally and ventrally, respectively, around the scape-pedicel joint. These five muscles are individually innervated by the antennal motor nerves arising from the brain (Figure 7, right side). Each antennal muscle may be innervated from 2–3 excitatory motor neurons (Baba and Comer 2008). It has also been suggested that some antennal motor nerves contain axons from a single “common” inhibitory motor neuron and dorsal unpaired median (DUM) neurons (Baba and Comer 2008). DUM neurons are considered responsible for releasing an excitatory modulator substance, possibly octopamine, to the antennal muscles.

Output Pattern

The output pattern of the antennal motor neurons has rarely been recorded for insect species probably because of the difficulty to generate their activities under the physiological experimental conditions. However, it has been reported in *P. americana* (Okada et al. 2009) that pilocarpine, a plant-derived muscarinic agonist, effectively induces the rhythmic bursting activities of antennal motor neurons even in isolated brain preparations. The drug-induced output pattern in cockroaches is well coordinated among the five antennal motor nerves. An agonistic pair of the motor nerves (3 vs. 4 in Figure 7) discharges bursting spikes with an in-phase relationship, whereas antagonistic pairs (1 vs. 2 and 4 vs. 5 in Figure 7) exhibit an anti-phase relationship with each other. These coordinated output patterns in an isolated brain preparation are comparable to the natural antennal movement.

Central System

Mechanosensory Center

The insect brain is composed of three distinct regions anteroposteriorly: the **protocerebrum**, **deutocerebrum**, and **tritocerebrum**. Sensory information received by the antennae is primarily conveyed to the deutocerebrum. Many anatomical studies clarified that the olfactory receptor afferents exclusively project to the primary olfactory center in the ventral deutocerebrum (**antennal lobe**), and non-olfactory (such as mechanosensory and gustatory) receptor afferents project to other regions from the deutocerebrum to the **subesophageal ganglion** (Figure 8). In contrast to the olfactory pathway, the mechanosensory pathways have not been adequately described in any insect species. An anatomical study in *P. americana* found that mechanoreceptor afferents in the basal segments project to the relatively dorsal part in the dorsal deutocerebrum (also known as the **dorsal lobe** or the antennal mechanosensory and motor center (AMMC)), while mechanoreceptor afferents in the flagellum project to the more ventroposterior areas in the dorsal lobe (Nishino et al. 2005). These antennal mechanosensory afferents also project up to the anterior region of the subesophageal ganglion. The central projections of the flagellar

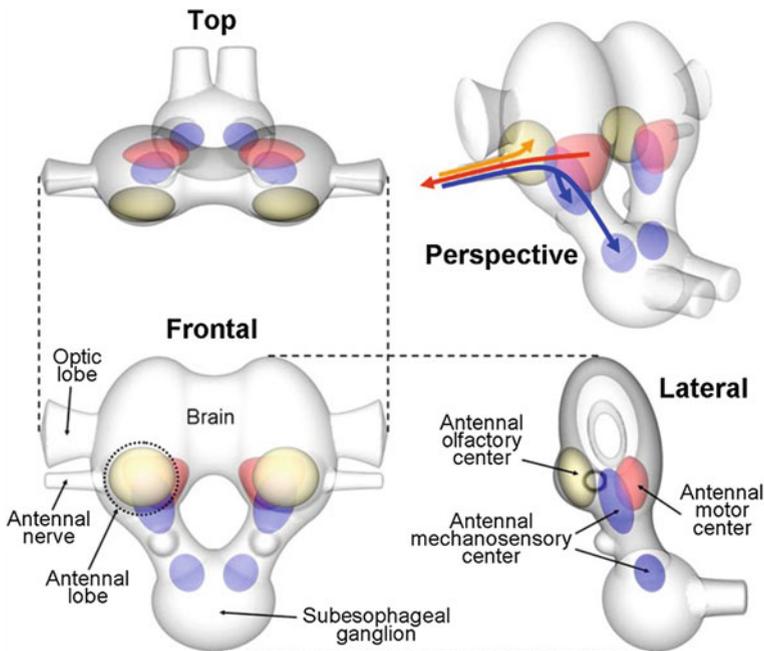


Figure 8 3-D cartoons showing antenna-related primary centers in the brain and the subesophageal ganglion. Arrows in the perspective view indicate the flow of chemosensory (yellow), mechanosensory (blue) and motor (red) information

mechanosensory afferents exhibit a topographical pattern, reflecting their peripheral locations, in the deutocerebrum (Nishino et al. 2005). Regarding the chordotonal sensilla, Comer and Baba (2011) showed that the central processes from the chordotonal organ are located from the deutocerebrum to the subesophageal ganglion. More recently, Watanabe et al. (2014) reported that serotonin-immunoreactive afferents from the chordotonal and Johnston's organs also project to the anteromedial region of the AMMC and subesophageal ganglion.

Motor Center

It is generally accepted that the primary motor center for the insect antenna is located in the dorsal lobe. Although the antennal motor center has been little known in the cockroach, an anatomical study elucidated its organization (Baba and Comer 2008). At least 17 antennal motor neurons were found in the deutocerebrum, and they were classified into five types according to their morphology. Although the positions of cell bodies differ according to their type, the dendritic processes from these neurons are colocalized at the dorsal area of the dorsal lobe (Figure 8). The dendritic zone is thought to be located dorsally to the antennal mechanosensory center. On the other hand, the central morphology of two dorsal unpaired median (DUM) neurons has been elucidated: both the cell bodies are located at the dorsomedial region of the subesophageal ganglion, and bilaterally symmetrical axons from the cell bodies run down to both sides of antennal muscles.

Interneurons

Tactile information from the antennal mechanoreceptors may be relayed to the following neurons for further sensory processing and/or expression of appropriate behavior. In this context, it would be essential to study individual antennal mechanosensory interneurons, particularly in the animals with a simpler central nervous system. Thus far, several physiological studies have identified such interneurons in cockroaches. Among the best known interneurons in *P. americana* are the "giant" descending mechanosensory interneurons (DMIs) (Burdohan and Comer 1996). Of the two DMIs identified, one (DMIa-1) has its cell body in the protocerebrum, and the other (DM Ib-1) has its cell body in the subesophageal ganglion (Figure 9). The DMIa-1 axon extends fine branches into the ipsilateral dorsal deutocerebrum where the antennal mechanosensory and motor centers are thought to be located, runs to the contralateral hemisphere of the brain, and descends to the abdominal ganglia while extending fine processes into the thoracic ganglia. The DM Ib-1 axon also descends in a similar morphological pattern. The DMIa-1 responds exclusively to the mechanical stimuli to the antenna. The DM Ib-1 is responsive to the stimuli to the head and mouthparts as well as the antenna.

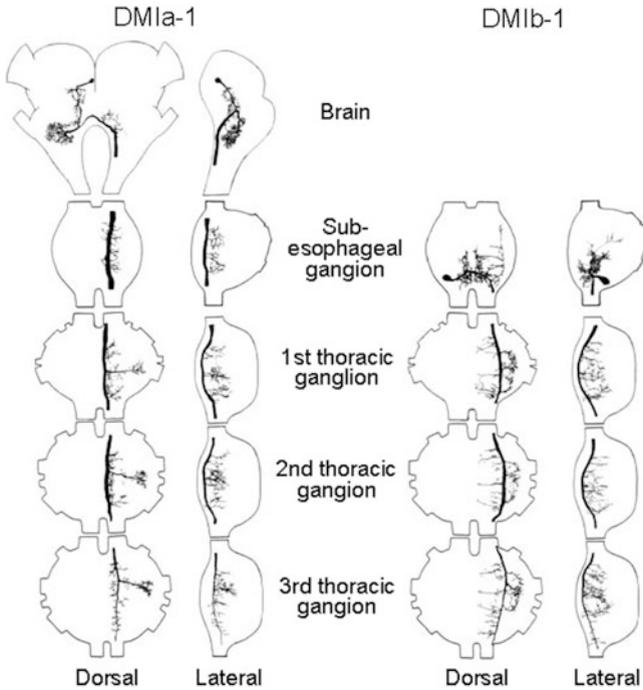


Figure 9 Central morphology of the antennal mechanosensory interneurons, DM1a-1 and DM1b-1. Modified from Burdohan and Comer (1996) with permission

The chordotonal organ is suspected to be a major mechanosensory input origin to the DMIs because its ablation leads to serious impairment in response to antennal mechanical stimulation, and the central processes of the chordotonal organ closely overlap the neurites of DMIs in the deutocerebrum (Comer and Baba 2011). The DMIs may be responsive for the control of an evasive locomotor behavior (see “Evasive behavior”).

Behavior

Anemotactic Behavior

Anemotaxis, a locomotor response to the wind, is thought to be a fundamental strategy to find odor sources located upwind. In three cockroach species (*Blattella germanica*, *Periplaneta americana*, and *Blaberus craniifer*), the anemotactic behavior in the absence of olfactory cues was found to have different patterns depending on both the species and wind velocity (Bell and Kramer 1979). *B. craniifer* directed and ran upwind in a wide range of wind velocities, while

B. germanica oriented downwind. *P. americana* oriented upwind in low-wind velocities, and downwind in high-wind velocities. When both the scape-pedicel and pedicel-flagellar joints of *B. craniifer* were fixed to prevent movement at the pedicel, positive anemotaxis was considerably impaired. This implies that the putative mechanoreceptors adjacent to the pedicel are crucial to detect wind direction and velocity.

Evasive Behavior

The insect antenna has been considered rather non-responsive to escape behavior. However, the responsiveness seems to depend on the tactile feature of the stimulants. For instance, if a cockroach (*P. americana*) comes in contact with a potential predator (spider), as sensed by the antenna, it would immediately turn away and escape from the spider (Comer et al. 1994). Similarly, cockroaches may discriminate tactile features (probably texture) between the spider and the cockroach by means of antennal probing (antennation) (Comer et al. 2003). The mechanoreceptors in the flagellum and the antennal basal segments are thought to be essential for acquiring tactile information and initiating an escape response, respectively (Comer et al. 2003; Comer and Baba 2011).

Wall-Following

Since cockroaches exhibit a positive thigmotaxis, they tend to walk or run along the wall. During such wall-following, both the antennae extend forward to remain in contact with the adjacent wall. A behavioral study revealed that *P. americana* is capable of turning at 25 Hz during a rapid wall-following (Camhi and Johnson 1999). This high-frequency turn helps avoid collisions while maintaining body at an appropriate distance from the wall. Tactile cues from the antennae would be essential for such a high-performance wall-following behavior. Baba et al. (2010) found that the response type of collision avoidance (stop, climb, reverse, redirect, and so on) depends on the configuration of obstacles detected by the antennae. In particular, the stop response may occur when both antennae simultaneously contact an obstacle. On the other hand, the mechanical interaction between the flagellum and wall affects the state of the antenna: the tip of the wall-side flagellum tends to project forward when following a relatively smooth wall and backward when following a rougher wall (Mongeau et al. 2013). The distance of the body from the wall is significantly influenced by the antennal state, i.e. nearer in the forward state and farther in the backward state.

Obstacle Negotiation Behavior

Cockroaches with non-escape walking also encounter external objects with a wide variety of shapes in their path and negotiate them in proper ways by using tactile information from the antennae. Harley et al. (2009) investigated the behavioral choice between climbing over and tunneling under when a cockroach encounters an appropriate size of “shelf”. They found that the choice depends on how the antenna hits the shelf. In the case of hitting from above the shelf, the cockroach may push up the body and try to climb, and in the case of hitting from below, it may tunnel. Furthermore, this behavioral choice is influenced by the ambient light conditions: under bright conditions, cockroaches prefer to tunnel. A line of studies has suggested that the central body complex (CC), a set of interconnected neuropils located along the midline of the protocerebrum, may play a key role in this behavioral choice because the focal lesioning of CC resulted in deficits in the relevant tactile behaviors (Ritzmann et al. 2012).

Tactile Orientation

When an antenna of a searching cockroach (*P. americana*) contacts a stable tactile object in an open space, the animal may stop and approach the object with antennation (see <http://www.scholarpedia.org/>). Similarly, a tethered cockroach mounted on a treadmill may attempt to approach a stable object presented to the antenna (Okada and Toh 2000). This antenna-derived tactile orientation behavior is probably due to the thigmotactic nature of cockroaches (see “Wall-following”). Because the extent of turn angle depends on the horizontal position of the presented object, cockroaches can discriminate the position of objects by antennation. The removal of hairs in the scapal hair plates resulted in significant deterioration in the performance of tactile orientation (Okada and Toh 2000), suggesting that the proprioceptors in the antennal joints are vital for the detection of an object’s position.

Electrostatic Field Detection

It has been reported that cockroaches appear to avoid an artificially generated electrostatic field (Hunt et al. 2005; Newland et al. 2008; Jackson et al. 2011). This evasive response may help them avoid, for instance, friction-charged objects and high-voltage power lines. Newland et al. (2008) proposed a possible unique mechanism for electrostatic field detection in *P. americana*. After the antennal joints between the head and scape were fixed, the treated animal could no longer avoid electrostatic field. They proposed the following working hypothesis. As a

cockroach approaches a charged field, it would produce biased charge distribution between the antennae and the cockroach's body. The antennae are then passively deflected by the Coulomb force in the electrostatic field. Finally, the antennal deflection may be detected by the hair plates at the head-scape joint.

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External Links

<http://blattodea-culture-group.org/> Blattodea Culture Group website.
<http://en.wikipedia.org/wiki/Cockroach> Cockroach in Wikipedia.



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Scholarpedia of Touch

Prescott, T.J.; Ahissar, E.; Izhikevich, E. (Eds.)

2016, XXII, 827 p. 266 illus., 188 illus. in color.,

Hardcover

ISBN: 978-94-6239-132-1

A product of Atlantis Press