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The role of antennal hair plates in object-guided tactile orientation of the cockroach (*Periplaneta americana*)

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**Abstract** The searching behavior of blinded cockroaches was examined under unrestrained conditions, in an arena, and on a treadmill. When cockroaches searching in a circular arena touched a stationary object (metal pole) with their antennae, they frequently approached the object more closely, and then climbed up it. Similar orientation behavior was observed in tethered animals in open loop conditions, walking on a Styrofoam ball. In these restrained cockroaches, a single antenna sufficed to distinguish the angular positions of an object, in the horizontal plane (0°, 45°, and 90°). A group of mechanosensitive hairs on the basal segment of the antenna (scapal hair plate) appears to play a major role in antennal object detection in the horizontal plane, as gauged by shaving off these scapal hair plates. In unrestrained cockroaches, shoving the scapal hair plate increased the time needed to approach an object. Under tethered conditions, the ability to turn towards and to establish antennal contact with a test object was significantly impaired.

**Keywords** Cockroach · Antenna · Tactile orientation · Hair plate · Mechanoreceptor

**Abbreviations** *HP* hair plate · *ICI* inter-contact interval · *S-HP* scapal hair plate

**Introduction**

In many animals, perception of objects in space largely depends on vision, but nocturnal animals usually use other cues for environmental searching, such as auditory or tactile cues. Many nocturnal insects have a pair of well-developed antennae. These vary widely, but many cases are known where chemore-, mechano-, thermo- and hygro-sensitive hairs are found on the same antennae, which thus function as multimodal sensors (reviewed by Schneider 1964; Homberg et al. 1989). Of these, mechanosensitive hairs may play an important role for the perception of the local physical environment.

The cockroach *Periplaneta americana* used in the present study is a nocturnal insect, and its antenna consists of 150–170 segments (Seelinger and Tobin 1981). The first and second proximal segments are called the scape and the pedicel, respectively, while the remaining distal segments are referred to collectively as the flagellum. The flagellum is particularly long (about 5 cm) in *P. americana*. In addition to carrying the olfactory sense organs, it is equipped with mechanosensilla and is used as a feeler to probe the mechanical characteristics of objects. In contrast, most sensilla on and inside the pedicel and scape supposedly act as proprioceptors, assessing the position and movement of the antenna (Schafer and Sanchez 1973; Toh 1981). The major sensory structures found in insect antennae are hair plates, campaniform sensilla and chordotonal organs (Janet’s organ and Johnston’s organ; reviewed by Schneider 1964; Homberg et al. 1989). When a cockroach contacts a local object with its antennae, the distance to the object might be encoded by the positions of the respective sensilla along the flagellum that are mechanically stimulated. The direction of the object might be detected by the angle at which the antennae are held, as encoded by the proprioceptors in the two basal antennal segments. Tactile information from the flagellum and directional information from the basal segments then would be integrated in the CNS to generate a tactile picture of local space. Most sensory afferents from the flagellum project to the two antennal lobes, the primary afferent centers for chemical and mechanical information in the deutocerebrum. Mechanosensory afferents from the basal segments project primarily to the dorsal deutocerebrum (also called the dorsal lobe), but also to the subesophageal ganglion in locusts (Gewecke 1979; Bräunig et al. 1983), in honeybees (Maronde 1991), and
even to the thoracic ganglion in moths (Hildebrand et al. 1980), flies (Nässel et al. 1984), and ants (Ehmer and Gronenberg 1997). Despite the many anatomical descriptions, behavioral and functional studies of mechanosensory information from the antennal basal segments have been limited.

In this article, tactile perception in the cockroach *P. americana* is examined. We describe a stereotyped orientation behavior in searching cockroaches, an object-guided taxis mediated by the antennal tactile sense. A new behavioral paradigm has been developed for estimating the animal’s performance at detecting object direction, using a single antenna. The role of putative antennal proprioceptors, a hair plate (HP) at the base of scape, is investigated. The antennal HP or its homolog is considered to be the sensor for antennal position (Böh m 1911; Schneider 1964; Gewecke 1972; Masson 1972). The effects of destroying the scapal HP on the antennal thigmotaxis and the orientation towards objects are examined.

**Materials and methods**

**Animal and preparation**

Adult male cockroaches (*P. americana*) raised in a laboratory culture at 27 °C were used. Both the compound eyes and the ocelli in all the animals used throughout this study were occluded by an opaque black paint (XF-1; Tamiya, Japan) in order to exclude the effect of visual inputs.

To evaluate the contribution of the scapal hair plate (S-HP) to tactile orientation, the hairs were removed in some animals. Animals were first immobilized on ice, and as many mechanosensitive hairs as possible were shaved off with a sharp razor blade, including a thin surface layer of cuticle. Experiments on operated animals were conducted at least 2 days later, to allow recovery from the operation.

**Apparatus for behavioral experiments**

In experiments on free-walking cockroaches, each animal was released individually in an experimental arena (30 cm in diameter, with wall 12 cm high). A metal pole (1.2 cm in diameter, 4.5 cm high) was placed at the center of the arena as a stationary object.

In experiments with tethered-walking cockroaches (Fig. 1A) animals were mounted on a Styrofoam ball 10 cm in diameter, similar in basic design to the spherical treadmill introduced by Kramer (1976). A thin flexible plastic plate (0.5 cm × 3 cm) was glued to the pronotum to restrain the cockroach, it also usefully smoothed walking on the sphere, by buffering small vertical movements of the body. The animal was then attached to the adjustable probe of a clamp-stand at the other end of the tether plate. The sphere was floated on air just above a funnel fitted in a plastic tube, 7 cm in diameter. Air flow was directed into the other end of the tube from a small fan, adjusted to give friction-free movement of the sphere. A 15-cm-square metal plate with a 7-cm hole was fitted over the upper part of the sphere. This plate stabilized the rotating sphere, and also deflected the air-flow away from the protruding upper part of the sphere, where the cockroach was positioned. With the cockroach held at the top of the sphere, a moveable test object (an aluminum plate, 1 cm wide, 5 cm high) could be presented to the cockroach in one of three different horizontal positions (midline, 45° or 90° clockwise from the midline) by means of a linear drive (Fig. 1A; inset of Fig. 5). The object was presented for 15–30 s, and always on the right-hand side. Cockroaches were allowed to touch the object with the distalmost 3 mm of the antenna. At least 3 min rest was allowed between successive stimulus presentations. The direction from which the stimulus object was presented (0°, 45°, 90°) was changed randomly between trials. Static charges resulting from antennal contact with the test object were amplified, rectified, and, via a Schmidt trigger circuit, used to drive a red light-emitting diode (LED; light flash, 50 ms). This light pulse indicated antennal contact to the observer and was recorded together with the video image.

**Behavioral analysis**

Behavior was recorded by a conventional video camera set 1.2 m directly above the arena or the treadmill, using a video recorder (30...

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**Fig. 1A, B** Experimental design for tethered-walking condition. A Animals were tethered, and allowed to grasp a Styrofoam sphere floating on an air-cushion. An object (a metal plate, "stipped") was presented to allow spontaneous antennal contacts at various angles in the horizontal plane. B Method for analyses of the animal movement (top view). Displacement of a dot inscribed on the sphere (from A to B) in one time unit (0.1 s) was decomposed into two components (arc AC, described by turn angle θ) and a linear displacement parallel to the body axis (line CB). Counter-clockwise rotation of dots on the sphere was defined as a positive intention turn of the animal (note the signs of + and −).