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D. D. Gaffin · P. H. Brownell

Response properties of chemosensory peg sensilla on the pectines of scorpions

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Abstract By behavioral and anatomical criteria, the pectinal sensory appendages of scorpions appear to be chemoreceptive organs specialized for detection of substances on substrates. These comb-like, midventral appendages contain tens of thousands of minute (< 5 μm), truncated setae, called pegs, arranged in dense, two-dimensional arrays on the ventral surface. In this study we used extracellular recording techniques to examine spontaneous and stimulated activity of sensory neurons within individual pegs. Chronic recordings lasting several days showed long-term fluctuations in spontaneous activity of sensory units in single peg sensilla, with peak activity coinciding with the animal's normal period of foraging. Several units were identified by the stereotypical waveforms of action potentials they elicit. Near-range olfactory stimulation of peg sensilla by volatile alcohols, aldehydes, ketones, esters, and carboxylic acids produced dose-dependent patterns of neural response. Contact stimulation with these chemicals, or water, or mechanical deflection of the peg tip also evoked activity in identifiable units. The peg sensilla appear to be broadly sensitive to odorants and tastants, suggesting they function similarly to the antennae of mandibulate arthropods.

Key words Scorpion · Pectine · Electrophysiology · Chemosensory · Mechanosensory

D.D. Gaffin[1] (✉) · P.H. Brownell
Department of Zoology, Oregon State University, Corvallis, OR 97331-2914, USA

Present address:
[1] Department of Zoology, University of Oklahoma, Norman, OK 73019-0235, USA
Tel.: +1-405/325-2786; Fax: +1-405/325-7560;
e-mail: ddgaffin@ou.edu

Introduction

The pectines are paired, ventral appendages extending ventro-laterally from the 11th body segment (mesosomal segment 2) of all scorpions. Although the existence of these organs can be traced in the fossil record to aquatic ancestral species of the Devonian era (Kjellesvig-Waering 1986), their function remains unknown [see Cloudsley-Thompson (1955) for early references]. The pectines have a comb-like appearance with a jointed "spine" (anterior lamella) supporting a line of movable teeth ranging in number from 3 (genus *Euscorpius*) to more than 40 in some psammophilic buthids (Stahnke 1970). The ventral surface of each tooth contains a patch of peg-shaped sensilla (Schröder 1908; Carthy 1966). The number of peg sensilla increases with developmental stage, with reproductively mature males of many species having more than twice the number of pegs found in females (Swoveland 1978).

The peg sensilla of scorpions have ultrastructure similar to contact chemoreceptor sensilla of insects (Slifer 1970). The individual pegs are blunt, cylindrical structures, approximately 1–2 μm in diameter and 2–5 μm in length (depending on species); these move within a circular socket (Carthy 1966). Each peg is a double-walled shaft of cuticle, flattened near the tip, where a slit-shaped pore connects the inner sensillar chamber to the external environment (Ivanov and Balashov 1979). The dendritic outer segments of approx. 10–18 bipolar sensory neurons extend through the sensillar chamber to within a few microns of the slit opening (Brownell 1989), with an additional dendrite terminating near the base of the peg in a tubular body characteristic of arthropod mechanoreceptor cells (McIver 1975; Foelix and Müller-Vorholt 1983).

Behavioral observations of scorpions support this morphological evidence of a dual mechanosensory/chemosensory function for the pectines. The pectines seem to be important for discriminating surface texture (Abushama 1964; Carthy 1966, 1968; Boyden 1978),

particularly by males selecting a suitable site for spermatophore deposition (Alexander 1957, 1959). Krapf (1986) showed the pectines respond to natural chemostimulants in the detection of food items and the relocation of stung prey. The pectines are sexually dimorphic appendages with males of most species having notably larger organs. Tactile movements of the pectines during courtship suggest they may be important for detection of substrate-borne pheromones (Krapf 1986; Gaffin and Brownell 1992).

Nevertheless, a chemosensory function for scorpion pectines has not been demonstrated physiologically. In the only previous electrophysiological study, Hoffmann (1964) used whole nerve recordings from the base of the pectines on *Euscorpius carpathicus* and *Euscorpius italicus* (Chactidae) to show they were responsive to mechanical deflection of the peg tip; application of various chemicals failed to evoke a detectable response under these conditions. In this study we developed techniques for extracellular recording from individual peg sensilla of the desert sand scorpion *Paruroctonus mesaensis* and tested their responsiveness to a variety of chemical stimulants and mechanical displacement.

Materials and methods

Animals

Male and female *P. mesaensis* collected from sandy regions of the Mojave Desert near Indio, Calif., USA were the subjects of these experiments. Only animals judged to be sexually mature (i.e., instar stage 5 or older) were used (Stahnke 1970). Animals were kept individually in plastic containers and maintained on a diet of grasshoppers and waxworms. The results presented here and in the following paper (Gaffin and Brownell 1997) are based on more than 300 h of recording time from 54 peg sensilla on 11 adult *P. mesaensis* (eight male, three female).

Electrophysiology

Scorpions were anesthetized by cooling then immobilized ventral side up on a rigid Plexiglass stage using a mixture of carnuba and bee's waxes. The intact pectines were further secured on a metal platform ($20 \times 5 \times 0.5$ mm), using double-sided tape so the peg sensilla were maximally exposed and stable. Extracellular recordings were made using electrolytically sharpened tungsten wires (17 μm diam., tips sharpened to < 0.5 μm in 1 mol·l^{-1} $NaNO_2$) inserted through the flexible cuticle at the base of a peg (Fig. 1). A reference electrode (tungsten) was inserted into the distal end of the pectinal spine for indifferent contact with hemolymph. Impaled

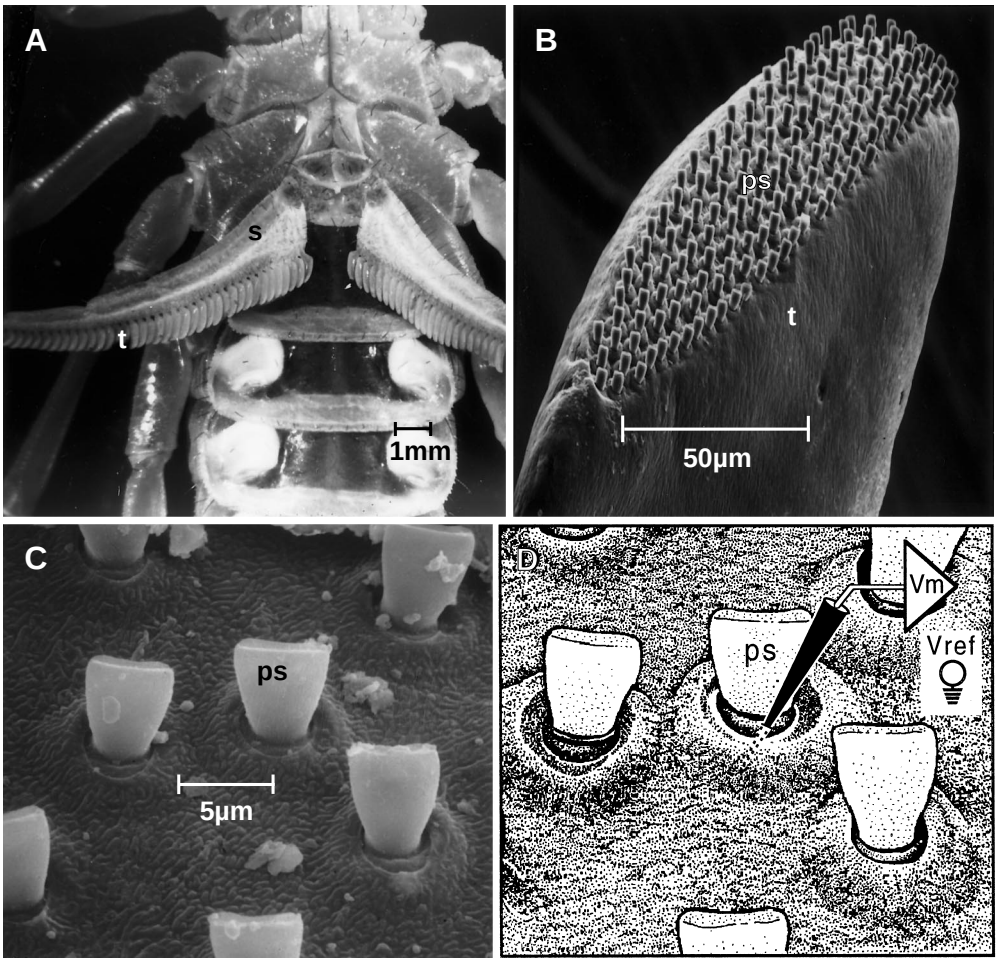


Fig. 1A–D External morphology of the pectines and extracellular recording configuration. **A** Ventral view of *P. mesaensis* showing the numerous sensilla-bearing teeth (*t*) attached to pectinal spine (*s*). **B** SEM of distal face of tooth showing dense arrays of peg-shaped sensilla (*ps*). **C** SEM of small patch of peg sensilla. **D** Diagram of extracellular electrode placement. Tungsten recording electrode inserted at the base of a peg sensillum records extracellular electrical activity (V_m) relative to a reference electrode (V_{ref})

sensilla were allowed to recover from penetration for 15 min before delivery of the first stimulus. AC-coupled, electrical signals were amplified 100-fold over a bandwidth of 1–5 kHz and displayed on an oscilloscope. Chemosensory responses were stored as 1-min records (15-s pre-stimulus baseline, 45-s post-stimulus response) on audio magnetic tape for subsequent playback, digitization and analysis.

Fluctuations in spontaneous spike activity in single peg sensilla were automatically monitored by computer for periods of several hours to several days. At 20-min intervals sample recordings (10 and 20 s duration) were taken from continuous records; spike frequencies from multiple days were averaged and plotted to obtain long-term fluctuations in spiking frequency.

Chemosensitivity of peg sensilla

To test the sensitivity of peg sensilla to odorants, volatile organic compounds known to elicit responses in insect chemoreceptors were presented in puffs of air ejected from an olfactometer (Kafka 1970). One milliliter of stimulus fluid contained within a 10-ml vial was placed inside a 20-ml syringe; 10 ml of saturated air in the syringe was ejected for each trial. Individual stimulus syringes were re-equilibrated for at least 80 s between stimulus applications. The syringe nozzle (3.0 mm diam.) was positioned about 5 mm from the tip of the impaled sensillum. The air stream (velocity approximately 3 m s^{-1}) was applied for approximately 1 s. An exhaust fan continually drew clean air over the preparation. The recording setup allowed only sensilla on medial to distal teeth of the right pectine to be analyzed. Experiments were performed at room temperature (21–28 °C).

Orientation and position of the short (< 5 μm) peg sensilla relative to the recording electrode and stimulus odor stream varied between experiments, making quantitative comparisons of response intensities unreliable. For accurate qualitative comparisons, we measured the responses of individual sensilla to an array of stimuli applied in succession over several hours. Under these conditions, stimulus presentation was constant between successive applications, allowing better temporal comparisons of unitary responses.

Olfactory sensitivity of individual peg sensilla was assessed using a variety of unbranched acylated compounds to obtain a qualitative profile of sensillar response. Stimulants included C_6–C_{10} n-alkanes, n-alcohols, n-aldehydes, n-esters, and ketones. Three additional ketones with ringed structure [(+)-fenchon, (+)-carvon, and α-ionon] were also tested. These substances were used in pure form or diluted in paraffin oil to log-molar concentrations ranging in half steps from 0.5 to −3.0. Stimuli were presented at 3-min intervals in the following order of log-molar concentrations: −1.0, −3.0, −0.5, −2.5, 0.0, −2.0, 0.5, −1.5, pure substance. Triplicate applications were given for the alcohol and aldehyde concentration series, and duplicate applications for the straight-chained ketone series. Alkanes, esters and ring-structured ketones were presented only as pure substances in saturated air and as 1 $mol \cdot l^{-1}$ concentrations (single application). An inert control (the paraffin oil diluent) was presented every fifth trial to monitor fluctuations in baseline spiking frequency.

Contact chemosensitivity and mechanical stimulation

Water was reversibly applied to the tips of individual sensilla by immersing the pectine in paraffin oil and extruding and retracting a water droplet from a glass micropipette placed near the recorded sensillum. Recordings made in this manner were stable and allowed for precise application and removal of aqueous stimuli marked by brief electrical artifacts. Non-polar chemical stimuli were dissolved in paraffin oil and applied in air to the peg tip using a glass micropipette. These applications were non-reversible and could not be used for quantitative dose-response studies. Puffs of air ejected from a Pasteur pipette mounted 1 mm from the pectine gave reliable and selective mechanosensory responses with minimal stimulus artifact. Stimulus intensity was not quantified.

Spike identification and analysis

Electrical recordings of sensillar responses were digitized through an IBM DACA analog-to-digital converter (settling time approx. 30 μs) and displayed on the computer screen. A computer algorithm was written and used to identify and sort spikes of similar waveforms from multiunit recordings. The digitized waveforms of all spike events exceeding a selectable threshold voltage were captured and stored on disk along with their time of occurrence in the electrical record. These were redisplayed at high sweep speed for automatic (waveform template matching algorithm) or interactive-manual sorting into discrete classes. The activity of each identified spike type was reconstructed in separate traces so that its activity over time relative to the stimulus could be visualized.

Results

Electrical characteristics of peg sensillar neurons

The peg sensilla of *P. mesaensis* were easily penetrated by sharpened tungsten electrodes or saline-filled glass micropipettes for extracellular recording. We chose the former for their ease of use and lack of sensillar fluid contamination by electrolyte. Although each sensillum is small (approx. 2 μm, base diam.), the soft, sleeve-like cuticle of its socket facilitated penetration. Morphologically, each peg sensillum contains about 10–18 (mean = 14) sensory neurons (Brownell 1989), but only two or three of these were spontaneously active at low frequencies (combined firing rate approx. 1–2 Hz). Extracellular action potentials were approximately 1–2 mV in amplitude with signal-to-noise ratio above 10 for the largest amplitude spikes. Recordings made through the peg base were typically stable for several hours to several days once the penetration wound sealed (usually within minutes). Tungsten electrodes sealed better than glass electrodes and some recordings lasted several days without appreciable degeneration of signal form. Most preparations were reusable for several days, thereby allowing extended experimentation on pectines from individual animals.

Identification of sensory units

In recordings of electrical activity from peg sensilla of *P. mesaensis*, three distinct types of spiking units were typically observed. These were identified broadly as class A, B, and C units. Spike class A contained two similar units, 'A1' and 'A2' (Fig. 2A,B), characterized by large-amplitude, triphasic impulses of stereotypical waveform. In baseline recordings of spontaneous activity, 'A1' units were at least twice as active as 'A2' units, thus providing a second basis for distinction. Type 'B' cells produced smaller amplitude spikes with biphasic waveforms (Fig. 2A,B) and discharged spontaneously at low frequency (typically one-tenth the frequency 'A2') in a weak bursty pattern. Peak firing frequency of 'B' spikes was less than 10 Hz even when maximally excited by chemical stimulation. Spikes of type 'C' had waveforms

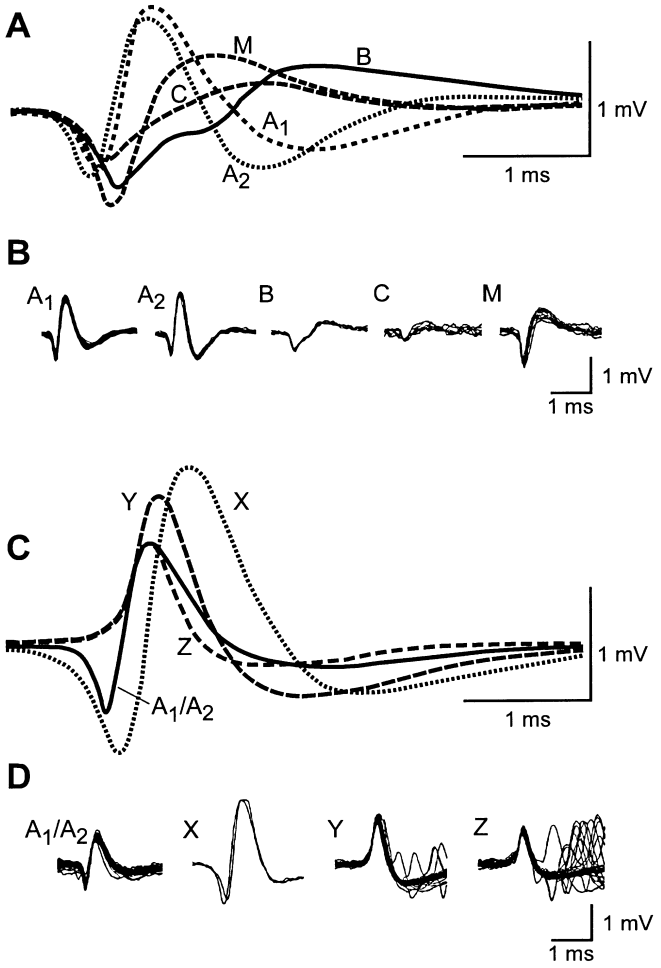


Fig. 2A–D Extracellular action potentials recorded from peg sensilla of *P. mesaensis*. **A** Five identifiable spike types are superimposed to show differences in their amplitude and waveforms. Spike types 'A1', 'A2' and 'B' are spontaneously active units most commonly observed in sensillar recordings. 'C' and 'M' spikes occur less frequently, usually in response to chemical stimuli ('C') or mechanical deflection of the peg tip ('M'). **B** Samples of > 10 superimposed spikes of each type to show consistency of their waveforms. **C** Expanded waveforms of type 'X', 'Y' and 'Z' units superimposed on 'A' unit spikes for comparison. **D** Samples of superimposed spikes of types 'A1/A2', 'X', 'Y' and 'Z' show consistency of their waveforms

of smaller and more variable amplitude (< 1 mV) and these were difficult to observe above background electrical noise in poorer recordings. 'C' spikes fired in high-frequency bursts (up to 30 Hz with hexanol stimulation) during or toward the end of the 1-s stimulus application.

Each peg contained a mechanoreceptor unit, 'M', with characteristic spike waveform. Type 'M' spikes had distinctly larger negative-phase amplitudes and longer-lasting positive-phase potentials than other spikes in the recording. Infrequently, a second unit with waveform similar to type 'M' was activated by mechanical stimulation, raising the possibility that peg sensilla contain more than one mechanoreceptor unit.

Other spike waveforms were occasionally observed in our recordings. Three of these occurred frequently enough in conjunction with A, B, and C spikes (> 10 observations within a single sensillum preparation) to be distinguished by their waveform and pattern of activity. Spike type 'X' (Fig. 2C, D) had the largest peak-to-peak amplitude (approx. 3 mV) of any spike recorded in this study. This spike occurred rarely, but always in a stereotypical form not owing to summation of smaller spikes. It was not responsive to our test stimuli. Spike types 'Y' and 'Z' (Fig. 2C, D) occurred together in one recording as a single, high-frequency burst of distinct form and sensillar origin, but the causal stimulus was unknown. The shapes of these two spike types were uniquely characterized by the initial positive phase of their waveforms, with spike type 'Y' having a larger amplitude than spike type 'Z'. Although pectines have muscle fibers that move the pectine teeth, electrical activity from muscle cells was easily distinguished by form, amplitude (> 5 mV) and duration (> 20 ms) from those of sensory origin.

Fluctuation in electrical activity

Electrical recordings from the base of individual peg sensilla are stable for several days, making it possible to monitor long-term fluctuations in spontaneous activity. Figure 3 indicates that spontaneous electrical activity of peg sensilla increased steadily during the 4-h period between 1800 and 2200 hours and decreased by a commensurate amount between 2200 and 0200 hours ($n = 4$; three male, one female). A similar fluctuation in activity with time of day was observed when sensilla were stimulated with paraffin oil controls (via olfactometer) during assays of chemosensitivity. It is noteworthy that peg sensilla of *P. mesaensis* were most active beginning a few hours after sunset until a few hours after midnight, the period when this animal normally emerges from its burrow onto the sand surface to hunt for prey

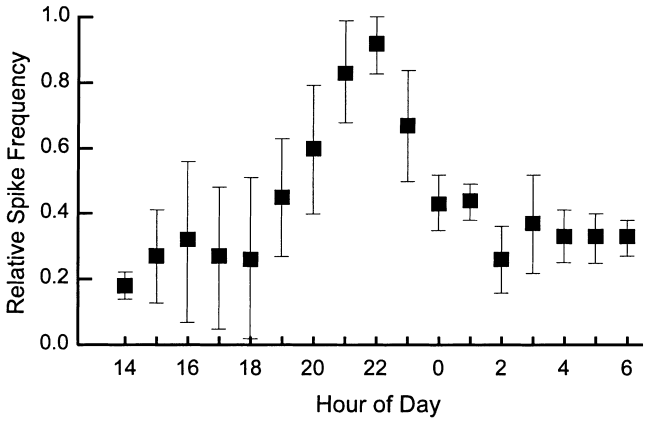


Fig. 3 Fluctuations in spontaneous impulse activity recorded from single peg sensilla in *P. mesaensis*. Mean ± SE of normalized spiking frequencies ($n = 4$). Spike frequency in each recording was normalized to the peak spiking frequency of the sampling interval. The period of greatest activity coincides with the time of day that *P. mesaensis* forages most actively for food and mates (late evening to early morning)

or search for mates (Polis 1980). The periodicity of these fluctuations is 24 h, raising the possibility that they are the expression of a circadian rhythm.

Modes of response

Mechanosensory

Mechanical deflection of peg sensilla elicited high-frequency spike discharges from a distinct class of units referred to here as 'M' (Fig. 4). Figure 4 shows a recording of 'M' unit spikes with type 'A' and 'B' units for comparison. The presence of discrete spike waveforms and absence of gradation between class 'M' cells indicates they are a unique class of neurons in the peg. The peak firing frequency of type 'M' spikes was notably higher (> 100 Hz) than that observed for type 'A' spikes, and type 'M' spikes showed fast adaptation (within 1 s to sustained deflection of the peg tip) and recovery as is typical of mechanosensitive units in other arthropod sensilla (McIver 1975). Furthermore, type 'M' units were not responsive to chemical stimulation of the peg unless such stimulation caused the peg to deflect.

Contact chemosensitivity

Sensory neurons in the peg sensilla of *P. mesaensis* responded vigorously to direct stimulation by water applied as a droplet to the sensillum tip (Fig. 5A). Peg sensilla were unresponsive to water vapor (presented as water-moistened filter paper placed within 1 mm of the sensillum) indicating a necessity for direct contact with aqueous stimuli or dissolved electrolytes.

Figure 5B shows the unprocessed, multiunit response of peg sensillar neurons to successive contacts with pure octanol. This record was sampled from a continuous recording (2 min duration) during which the stimulus was repeatedly applied for 1–2 s then withdrawn. The three traces in Fig. 5B are 20-s segments from the beginning, middle and end of this record. The initial response showed immediate phasic-tonic excitation of large-amplitude spikes ('A' type). With repeated applications, 'A' unit activity desensitized, becoming increasingly phasic (middle trace) and finally ceasing to respond (bottom trace). During this period of repetitive stimulus application the firing rate of type 'B' spikes gradually increased.

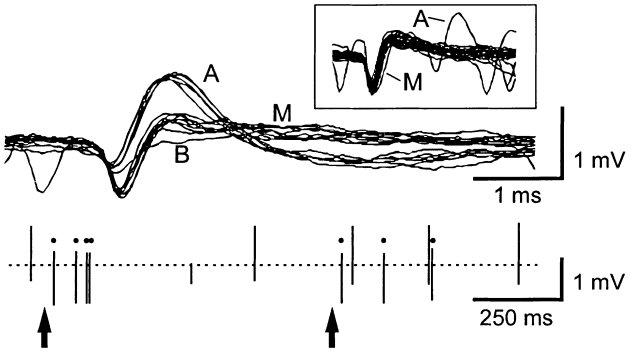


Fig. 4 Electrical response of a peg sensillum to mechanical stimulation. Deflection of peg sensilla by directed puffs of air (*at arrows*) elicited bursts of spikes (type 'M', indicated by *dots*) amidst spontaneously active 'A' and 'B' units. *Inset*: nearly coincident firing of type 'M' and 'A' spikes shows them to be independent events

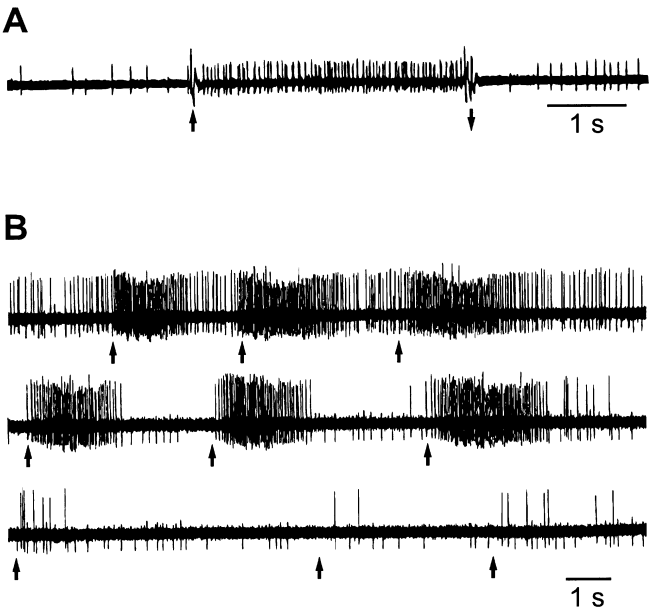
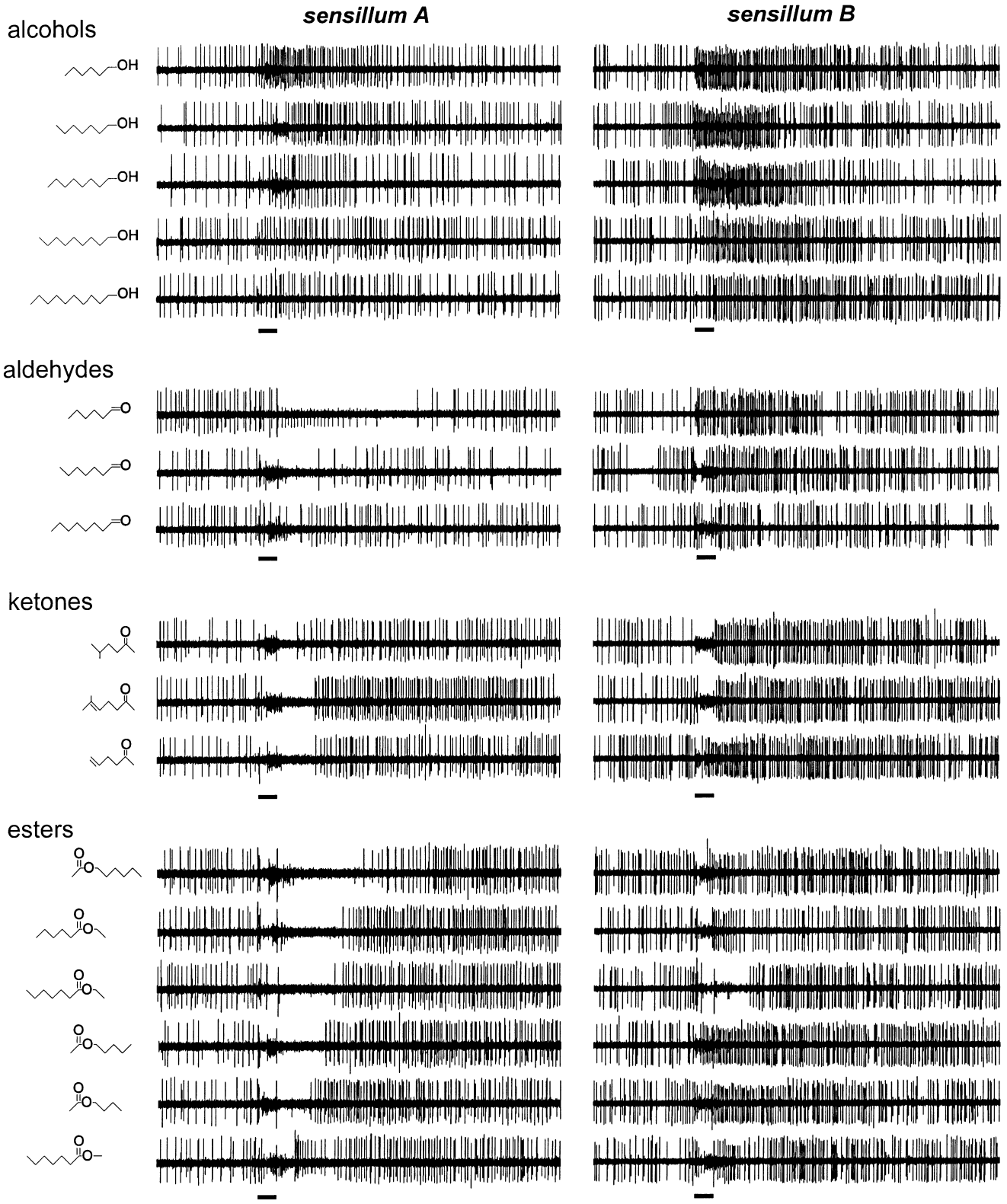


Fig. 5A, B Response of peg sensillar neurons in *P. mesaensis* to water and octanol applied directly to the peg tip. **A** With the pectine submerged in paraffin oil, peg sensilla showed a normal pattern of low frequency spike activity prior to contact with a droplet of water. When the terminal pore made contact with a droplet of water extruded from a micropipette (*up arrow*), several units discharged at high frequency until the droplet was removed (*down arrow*). **B** Desensitization of peg sensillum response to repeated contact application (approx. 1 s duration) with a droplet of octanol (samples from records of several contacts over a period of 2 min; *arrows* indicate time of contact)

Olfactory sensitivity

Individual peg sensilla produced both excitatory and inhibitory responses to volatile organic substances applied as puffs of vapor across the preparation. Several sample traces, from two sensilla, are shown in Fig. 6. In general, the threshold for response to stimulatory substances was high, on the order of 10^{-3} mol·l^{-1}. Repeatable, dose-dependent responses were obtained from a given sensillum; however, between preparations we observed significant variance in the intensity and pattern of evoked responses. This variance may reflect differences in sensillar sensitivities, but may simply be an artifact related to the means of stimulus delivery. Since we were unable to quantify the amount of stimuli accessing the terminal pore of a sensillum, statistical comparisons of intersensillar responses were impractical.



The composite sensillar responses can be described in terms of individual firing patterns of 'A', 'B' and 'C' type spikes. Some of these patterns include simple excitation or inhibition of large-amplitude 'A' type spikes. Other responses are composite patterns of two or more spike types. For example, the hexanal response of sensillum A

Fig. 6 Electrophysiological responses of two peg sensilla to volatile chemical stimuli of different classes. Olfactory stimulation of the pectines by 1-s pulses of air (*bar*) saturated with various pure substances elicited repeatable patterns of responses that were consistent for a given sensillum and stimulus presentation, but inconsistent when compared between sensilla

is composed of excitation of small-amplitude, 'B' type spikes along with suppression of 'A' type spikes. Most of the other patterns involved differential activity of 'A' and 'C' type spikes. For example, all three ketone responses for sensillum A (as well as several other responses for either sensillum) showed short, early periods of high-frequency firing of small-amplitude, 'C' type spikes along with early suppression and delayed excitation of 'A' type spikes.

The capacity of the pectines to discriminate between odorants was best assessed by observing the response of single peg sensilla to a series of olfactants delivered from a consistent stimulus syringe/sensillar pore orientation. Figure 7 shows the responses of 'A', 'B' and 'C' units to olfactory stimulation by primary alcohols varying only in carbon chain length, from C_6 to C_8. Each alcohol evoked a simple pattern of excitation characterized by dose-dependent, phasic excitation of 'A' and 'C' units. As carbon chain length of the alcohol increased, peak firing frequencies for these cells decreased and became more delayed in the post-stimulus record. The shortest alcohol (hexanol) also stimulated significant activity from type 'B' units, with peak responses occurring sooner in the record as stimulus concentration decreased.

The ability to discriminate structurally similar odorants was confirmed in similar experiments with C_6–C_8 alkyl aldehydes: hexanal, heptanal and octanal each produced readily distinguishable patterns of response (Fig. 8). Unlike the alcohol stimuli, the aldehydes produced dose-dependent suppression of type 'A' spike activity and more variable patterns of response for molecules of different size. Stimulation with hexanal gave dose-dependent excitation of type 'B' spikes and much reduced 'C' spike activity compared to heptanal and octanal stimuli. The larger aldehydes evoked moderate activity of type 'B' spikes that appeared late in the post-stimulus record.

Stimulation with 6- to 10-carbon esters also gave class-specific responses to structurally similar odorants (Fig. 9). These were characterized by early, intense firing of type 'C' units and sequential inhibition/excitation of type 'A' spikes over a period of several seconds post-stimulation. Type 'B' spikes showed delayed excitation

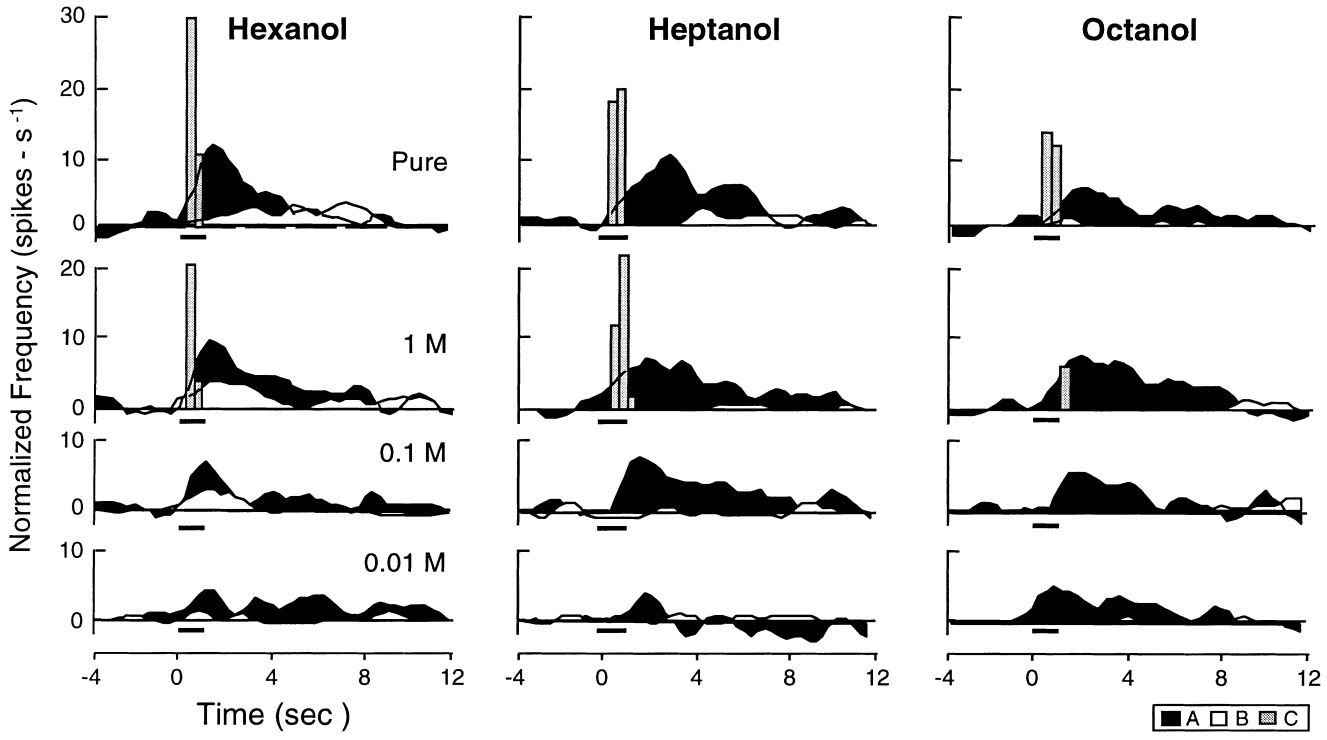


Fig. 7 Dose-dependent responses of a peg sensillum to olfactory stimulation by C_6–C_8 primary alcohols. Each graph shows 4 s of pre-stimulus baseline activity and 12 s of post-stimulus response to a 1-s pulse (indicated by *solid bars*) of stimulus blown across the preparation. Each curve was normalized by subtraction of average pre-stimulus activity. Curves for spike types 'A' (units 'A1' and 'A2' combined) and 'B' represent five-point running averages of spiking frequencies in 0.25-s bins (averaging spans 1.25 s of activity). Histogram displays of 'C' unit activity are absolute frequency of firing within 0.25-s bins. All responses were obtained between 2100 and 2300 hours

in some responses. Activity of spike type 'C' (and inhibition of spike type 'A') increased with stimulation by acetate esters as chain length of the esterified alcohol increased (butyl to pentyl to hexyl acetate). For the two heptate esters, greater activity was evoked for type 'C' units following stimulation by ethyl heptate as compared to methyl heptate. Ethyl heptate produced slightly weaker inhibition and slightly lower peak firing frequency of type 'A' spikes than ethyl hexate.

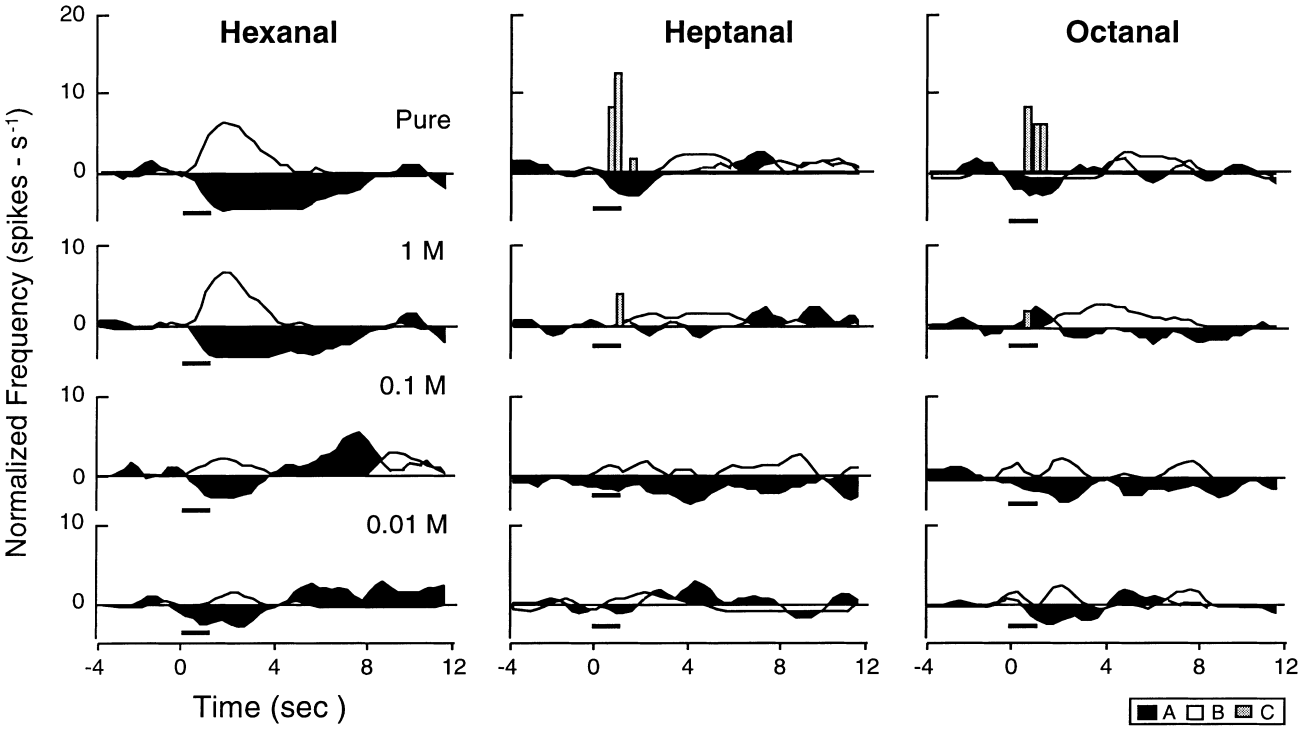


Fig. 8 Dose-dependent responses of a peg sensillum to olfactory stimulation by C_6–C_8 primary aldehydes. Same graphical display format as in Fig. 7. All responses were obtained between 2300 hours and midnight

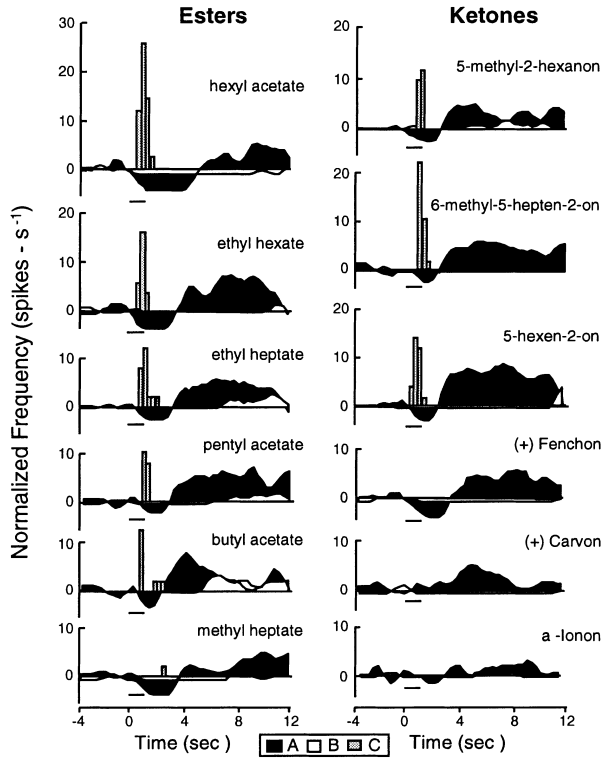


Fig. 9 Responses of a peg sensillum to olfactory stimulation by pure esters and ketones. Same graphical display format as in Fig. 7. Ketone responses were obtained between 2300 hours and midnight; ester responses were obtained between midnight and 0100 hours

Peg sensillar neurons responded differently to straight-chained and ring-structured ketones. Both classes of ketone elicited inhibitory responses from type 'A' units followed by sustained excitation; straight-chained compounds also excited bursts of type 'C' spikes. The inhibition of type 'A' spikes was considerably greater with stimulation by (+)-fenchon as compared with (+)-carvon or α-ionon stimulation.

Discussion

These results demonstrate that several of the sensory neurons innervating each peg sensillum of scorpion pectines can be identified and discriminated electrophysiologically by the impulses they generate. Most of these units are chemosensory as judged by their responses to water and simple organic compounds applied directly to the peg tip or blown across the sensillar preparation as puffs of volatilized olfactant. At least one neuron in each sensillum is a mechanoreceptor with optimal responsiveness to phasic deflection of the peg. These findings are the first physiological confirmation of chemosensory functions for the pectines and they support morphological evidence that the pegs are contact or near-field olfactory chemoreceptors with similar organization and function to those of insects and crustaceans (Ivanov and Balashov 1979; Foelix and Müller-Vorholt 1983). These similarities of structure and function suggest that the pectinal appendages of scorpions mediate behavioral functions similar to the antennal appendages of mandibulate arthropods; namely, tactile mechanoreception and detection of food (Krapf 1986) and pheromonal signals (Gaffin and Brownell 1992).

A clear distinction of the pectine organs is their specialization for sensing chemical deposits on the substrate. The high threshold for olfactory responses we observed ($> 10^{-3}$ mol·l^{-1}) and the single terminal pore found on each sensillum suggests these are organs of gustation or very close-range olfaction. During normal locomotory movements of the animal, the pectines are swept intermittently or tapped against the substrate. When males encounter substrates labeled by females or their cuticular extracts, tapping frequency increases as the pectines are swept repeatedly over the contaminated surface (Gaffin and Brownell 1992). High-speed imaging of these sweeps shows each "sniff" brings the sensilla-bearing surfaces in contact with the substrate for as little as a few tens of milliseconds (P. H. Brownell and D. D. Gaffin, unpublished observations). While this mode of sensing might suggest a form of gustation, the dryness of dune sand and, apparently, of pectine teeth make near-field olfaction seem the more likely mode.

Whatever their mode of usage, the morphology of the pectines clearly indicates they are among the most elaborate chemosensory organs reported for Arthropoda. Several species of scorpion from three families show that a typical peg sensillum is innervated by approx. 10–18 bipolar sensory neurons (Ivanov and Balashov 1979; Foelix and Müller-Vorholt 1983; Brownell 1989). Since some species may have as many as 10^5 pegs on their pectines, the afferent projection to the central nervous system could amount to more than a million chemosensory axons. Our recordings from single peg sensilla confirmed that at least seven neurons in each peg, or about half the contingent known to be there, are responsive to chemosensory stimuli. These units have sufficiently stable and distinguishable waveforms that we have identified then as units 'A1', 'A2', 'B', 'C', 'X', 'Y' and 'Z'.

Since the array of natural chemical stimuli of potential importance to scorpions is likely to be extensive and diverse, the capacity of individual neurons to discriminate odor and/or taste stimuli must be very high (Dethier 1976; Seelinger 1983; Boeckh and Ernst 1987; Kauer 1991). Indeed, we found that as few as three of these cells, the 'A', 'B' and 'C' units, produced distinguishable patterns of response to compounds of different chemistry (e.g., aldehydes, alcohols, ketones and esters), or even substances of similar chemistry but varying in size by a single acyl carbon atom. Most obvious were the differences in response to stimuli of different chemical classification. In some sensilla, for example, 'A' cells were strongly excited by C_6–C_8 alcohols and inhibited by aldehydes of the same size, and by ketones and esters; 'B' cells were immediately excited by C_6 aldehyde but showed delayed excitation to alcohols and longer chained aldehydes. By contrast, 'C' cells fired immediately in bursts of impulses for all stimuli except hexanal and ring-structured ketones. 'X', 'Y' and 'Z' were not affected by these stimuli and may require more specific signals or natural mixtures of substances to respond.

These physiological observations clearly show that at least one order of terrestrial arachnids, the scorpionids, is endowed with a major chemosensory organ, and that this structure is likely to have specialized function related to detection of substrate-borne odors or tastes. Behavioral observations (Gaffin and Brownell 1992) suggest one of these substances may be a mating pheromone, thereby promoting interest in use of the pectine preparation as a bioassay system for detecting and identifying specific pheromonal molecules. However, the most important objective of future electrophysiological studies of the pectines may be to define the information processing functions of the synaptic circuitry occurring within its individual peg sensilla (Gaffin and Brownell 1997).

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