Response properties of scorpion pectinal nerves to chemical and mechanical stimulation.

D.D. Gaffin & E.A. Camp. University of Oklahoma, Norman, Oklahoma, U.S.A

1 Background.

Since at least the last century, the function of the comb-like pecten organs of scorpions has remained enigmatic. Recently, however, through a combination of behavioral (Gaffin & Brownell 1992; Krapf 1986), morphological (Ivanov & Balashov 1979; Ivanov 1981; Foelix & Muller-Vorholt 1983), and physiological (Gaffin & Brownell 1997a,b) approaches, it has become clear that the primary function of these organs is chemosensation and that they are important during mating activities of these animals.

The pectines are paired, ventral appendages that hang from the 2nd mesosomal body segment of scorpions (Fig $1A_1$). Pectines are composed of a flexible spine from which extend a series of moveable teeth (Fig $1A_2$). Behaviorally, the pectines are dragged, or swept intermittently, along the ground as the animal walks. The distal, ground-directed surfaces of the teeth contain dense fields of minute, peg-shaped sensilla (Fig $1A_3$) that are similar in structure to taste sensilla of other arthropods (Slifer 1970). Each peg possesses a slit-shaped terminal pore to allow entry of chemostimulants (Fig. 1B). Inside the double-walled shaft of each peg terminate dendrites of 10-15 chemosensory neurons. At least one additional neuron, a mechanoreceptor, terminates at the peg base.

Figure 1

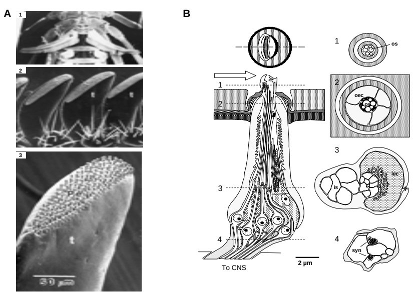

Figure 1 Gross structure of scorpion pectines and fine morphology of peg sensilla. **A1** Ventral view of *Paruroctonus mesaensis* male showing the pectines (p) with sensilla-bearing teeth (t). **A2** SEM of three pectinal teeth. Note the overlap of teeth in the horizontal axis; only peg sensilla (Pe) and tactile hairs (h) contact substrate when the pectines are swept forward during locomotion. **A3** SEM of distal face of tooth showing dense arrays of peg-shaped sensilla (Pe). **B** Diagram of a longitudinal section through peg sensillum showing arrangement of dendrites, cell bodies, inner and outer enveloping cells and structural elements. Cross-sections taken from levels 1-4 show: (1) double-walled shaft containing several dendritic outer segments (os) inside receptor lymph; (2) cuticular base of sensilla with extensions of outer enveloping cells (oec)and dendritic outer segments; (3) arrangement of dendritic inner segments (is) relative to microvillar projections of inner enveloping cell (iec); (4) axo-axonic synaptic profiles (syn) just below sensory cell body layer. (after Ivanov & Balashov 1979, Foelix & Müller-Vorholt 1983, Foelix 1985 and Brownell 1989)

A peculiar feature of scorpion peg sensilla is the presence of synaptic interactions between sensory neurons. The presence of synaptic densities between sensillar afferents was first mentioned by Foelix and Muller-Vorholt (1983) while describing the fine morphology and innervation of peg sensilla (Fig. 1B). The physiological manifestation of these synapses is seen when correlating the activity of one spiking unit with another in a peg recording (Gaffin & Brownell 1997a). The synaptic plexus is dense and wide-ranging, and is located proximal to the cell body region, about 50 microns below the surface of the tooth. Functionally, these synaptic interactions appear to shape the pattern of neural response prior to its relay to the central nervous system (Gaffin & Brownell 1997a,b).

The utility of having a complex circuit of interactions at the level of the chemosensory organ is unknown. We speculate that such an organization might be related to the use of the pectines as transducers of relatively non-volatile, ground-associated chemostimulants (Gaffin & Brownell 1992). We are interested in understanding what information value the animal gains from such a synaptic plexus and how these synaptic interactions function as the animal decodes its environment. Therefore, we are attempting to implant electrodes adjacent to the pectinal nerves of animals, loosely tether them to a recording apparatus, and record neural impulses as the animal naturally explores its home environment and is confronted with various stimuli. Below we highlight the preliminary steps in this project.

2 Electrode insertion site for pectinal nerve recording.

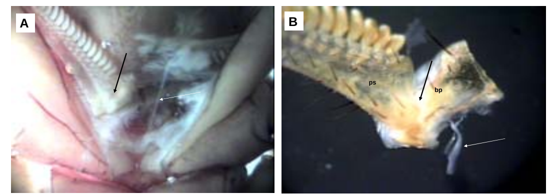

Figure 2 A Ventral view of *Vaejovis sp.* in which the right pectinal nerve has been isolated (white arrow). Black arrow points to electrode insertion point on the intact left pecten. **B** Isolated left pecten showing a piece of pectinal nerve (white arrow) and electrode insertion point (black arrow) in flexible cuticle between pectinal spine (ps) and basal piece (bp).

3 Sample extracellular recordings from pectinal nerve.

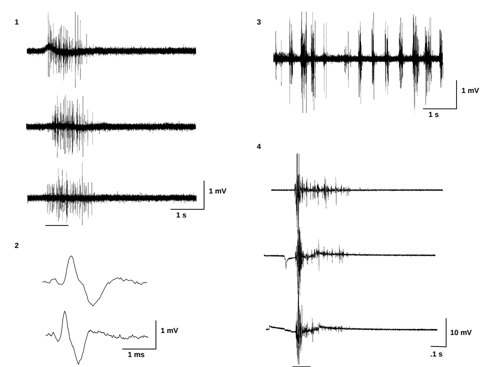

Figure 3 Sample extracellular recordings from right pectinal nerve of restrained *Hadrurus arizonensis*. **1** Three replicates of acetic acid response. In each record, a small piece of paper towel, soaked in acetic acid, was brought within 1cm of the pectinal teeth and quickly withdrawn; bar at bottom of traces indicates approximate duration of stimulus. **2** Expanded waveforms of two putative sensory spikes from traces in B1. **3** Mechanosensory response to multiple, brief contacts of peg fields with dry paper towel. **4** Response to brief breaths across pecten; bar at bottom indicates approximate duration of air puffs.

4 Proposed setup for simultaneous monitoring of pectinal nerve activity and animal movement.

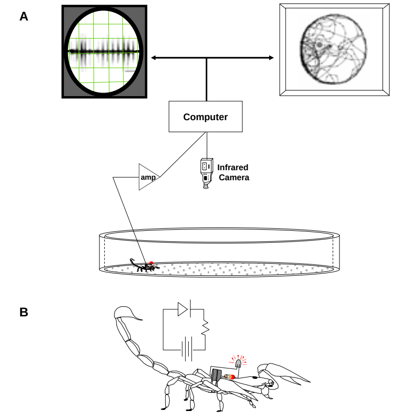

Figure 4 A *Hadrurus arizonensis* fitted with infrared diode is monitored by an infrared-sensitive video camera while an implanted electrode detects pectinal nerve activity. Computer is programmed to automatically track scorpion location within the arena (1 m diam). **B** Closeup of infrared diode and hearing-aid battery pack mounted on scorpion. Total weight of "backpack" is 0.6 g; useful life of battery is about 24 hr.

5 Conclusions

- Small filter paper strips, soaked with pure chemicals, elicited electrical responses in the pectinal nerve when brought near the peg fields.
- Nerve recordings contained cell firings that were similar in both waveform and duration to neural responses recorded from individual peg sensilla.
- Responses were obtained to dry filter paper controls only when physical contact was made between the paper and the peg fields. Such responses were highly phasic and similar in duration to mechanosensory responses of individual peg sensilla.
- Eventually we are interested in making *in vivo* electrophysiological recordings from the pectinal nerves of freely navigating scorpions to determine the neural signature of sensory afferents as the animal sweeps its pectines over natural chemostimulants. Ultimately we want to understand the role of peripheral synapses in the detection and processing of ground-based chemical information.

Literature Cited

Brownell PH (1989) Neuronal organization and function of the pectinal sensory system in scorpions. Neurosci Abst 15:1289
Foelix RF (1985) Sensory nerves and peripheral synapses. In: Barth FG (ed) Neurobiology of arachnids. Springer-Verlag, Berlin, pp 189-200
Foelix RF, Müller-Vorholt G (1983) The fine structure of scorpion sensory organs. II. Pecten sensilla. Bull Brit Arachnol Soc 6:68-74
Gaffin DD, Brownell PH (1992) Evidence of chemical signaling in the sand scorpion, *Paruroctonus mesaensis* (Scorpionida:Vaejovidae). Ethology 91:59-69
Gaffin DD, Brownell PH (1997a) Electrophysiological evidence of synaptic interactions in single peg sensilla of scorpion pectines. J Comp Physiol A (in press)
Gaffin DD, Brownell PH (1997b) Response properties of chemosensory peg sensilla on the pectines of scorpions. J Comp Physiol A (in press)
Ivanov VP (1981) The sense organs of the scorpions (Scorpiones). Proc Zool Inst Leningr 106:4-33
Ivanov VP, Balashov YS (1979) The structural and functional organization of the pectine in a scorpion, *Buthus eupews*, studied by electron microscopy. In: Balashov YS (ed) The Fauna and Ecology of Arachnida. Trudy Zool Inst Leningr 85:73-87
Krapf D (1986) Contact chemoreception of prey in hunting scorpions (Arachnida:Scorpiones). Zool Anz 217:119-129
Slifer EH (1970) The structure of arthropod chemoreceptors. Ann Rev Entomol 15:121-142

Supported by a grant from the Whitehall Foundation.