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Electrophysiological evidence of synaptic interactions within chemosensory sensilla of scorpion pectines

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Abstract The pectines of scorpions are ventral bilateral appendages supporting 10^4–10^5 chemosensory sensilla called pegs. Each peg contains 10–18 sensory neurons, some of which show ultrastructural evidence of axo-axonic synapses with other sensory neurons in the same sensillum. In extracellular recordings from single-peg sensilla, individual sensory units can be distinguished by impulse waveform and firing frequency. Cross-correlation analysis of impulse activity showed that at least two of these units, types 'A1' and 'A2', are inhibited during the 100-ms period immediately following activity of a third unit, type 'B'. This interaction between sensory units in a single sensillum also occurs in surgically isolated pectines, indicating that it does not involve efferent feedback from the central nervous system. Other sensillar neurons appear to have excitatory interactions. Thus, in scorpion pectine, chemosensory information undergoes some form of processing within individual sensilla prior to its relay to the CNS, making this an unusually accessible preparation for study of first-order chemosensory processing events.

Key words Scorpion · Electrophysiology · Chemosensory · Synapse · Sensilla

Introduction

The first synaptic interaction between neurons in the chemosensory pathways of mandibulate arthropods (e.g., insects, crustaceans) nearly always occurs within the central nervous system. In the antennae of insects, for example, the axons of primary chemosensory neurons pass from setaform hairs on the antenna through the antennal nerve to the olfactory lobe where they first converge on dendrites of second-order neurons in a glomerular neuropil (Bullock and Horridge 1965; Ernst and Boeckh 1983; Kaissling 1987; Homberg et al. 1989; Kanzaki et al. 1989). This arrangement makes physiological studies of chemosensory processing tedious and may largely explain why so little is known about it compared to other sensory modalities (e.g., vision, audition). Chelicerate arthropods appear to use a different organizational plan that may facilitate physiological studies. Ultrastructure of several chemosensory structures in xiphosurans (Griffin and Fahrenbach 1977; Hayes and Barber 1982) and arachnids (Foelix 1985) show that primary neurons innervating chemotactic sensilla have elaborate synaptic structures along the spike-initiating regions of their axons. The accessibility of these peripheral structures to high-resolution electrophysiological measurements could provide insights into initial stages of chemosensory integrative processes. To date there have been no successful attempts to develop experimental models for such studies.

The pectinal appendages of scorpions are likely to be one of the most suitable arachnid preparations for physiological investigation. These are the most elaborate chemosensory organs found in chelicerate arthropods and possibly within the phylum. In some species the pectines support as many as 10^5 chemosensory sensilla, called pegs because of their truncated setal form. In nearly all respects the pegs have microanatomy and cellular organization typical of contact chemoreceptors in other arthropods (Carthy 1966, 1968; Ivanov and Balashov 1979; Foelix and Müller-Vorholt 1983). The pegs of all examined species contain 10–18 sensory neurons whose cell bodies and axonal origins form a laminar plate 50–100 μm beneath the two-dimensional field of receptors on each pectine tooth (Foelix and

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Müller-Vorholt 1983). It is in this lamina, close to the point where electrophysiological records are conveniently taken (Gaffin and Brownell 1997), that the axons of chemosensory neurons make synaptic contacts (Foelix 1985).

In previous behavior studies we presented evidence that the pectines are intimately involved in several important orientation behaviors, most notably mate recognition and possibly localization of water (Gaffin and Brownell 1992; Gaffin et al. 1992). Similar functions are attributed to antennae of mandibulate arthropods. While the pectinal organs have the capacity to discriminate various volatilized odorants (Gaffin and Brownell 1997), their behavior in freely active animals suggests a primary role in contact chemoreception of the substrate (e.g., scorpions touch the pectines to the substrate frequently as they walk). From a practical standpoint we found that extracellular recordings made from the pectines at the base of the peg sensilla gave stable records of impulse activity for individual neurons, most of which could be identified by their characteristic spike amplitude and waveform (Gaffin and Brownell 1997). These properties enable long-term recordings from the small population of neurons innervating each peg sensillum, at least some of which show morphological evidence of synaptic interaction (Foelix 1985). Since the neurons themselves are small and relatively inaccessible to intracellular recording, we used cross-correlation analysis of their extracellular spike activities to search for synapse-like interactions between them.

Materials and methods

Adult sand scorpions, *Paruroctonus mesaensis* (Vaejovidae) captured in the Mojave Desert in Southern California were the primary subjects of these investigations. Cursory observations (not presented here) of scorpions from two other families (*Hadrurus arizonensis*, Family Iuridae, and *Parabuthus* sp., Family Buthidae) confirmed the generality of our results. Animal maintenance, electrophysiological techniques, and procedures for olfactory stimulation are described in Gaffin and Brownell (1997).

Cross-correlation analysis

Synaptic interaction between neurons can be detected indirectly as a temporal correlation between one cell's activity and another. In this study, interactions between sensory neurons in peg sensilla were detected by cross-correlating activities of identifiable units using an automated spike-sorting and analysis program. Extracellular recordings were digitized and individual units within these multiunit records were discriminated above an adjustable threshold voltage and stored in digitized form on disk along with a time marker encoding their time of occurrence. Spikes from different cells were segregated by waveform and grouped into discrete classes for redisplay as individual records of activity.

The activities of any one unit processed in this manner can be correlated in time with the activity of other units, thus revealing possible interactions between them. Spikes occurring within discrete intervals (''bins'') of time before and after the occurrence of a reference spike are counted and displayed in histogram form (see bottom of flow chart in Fig. 1A). Several hypothetical examples showing excitatory, inhibitory, and no interaction are presented in Fig. 1B. Auto-correlations (activity plots of a cell referenced against itself) are useful for verifying that spikes assigned to a particular spike class originate from a single source. In Fig. 1B the upper auto-correlation profile shows the characteristic pattern expected of spikes produced by only one cell. The action potential refractory period of the cell leaves periods of inactivity before and after the referenced spike. Auto-correlations of classes containing more than one cell would appear as shown in the second profile. The top three histograms in Fig. 1B are cross-correlation profiles for spikes from two different classes. The histograms show the patterns expected for inhibitory, excitatory, and no interaction. For expanded discussion of correlation analysis see Eggermont (1990).

Results

Spontaneous activity of peg sensillar neurons

Extracellular recordings of spontaneous electrical activity from peg sensilla of *P. mesaensis* typically displayed low-frequency (approx. 0.5–2 Hz) impulse activity originating from fewer than one-third of the neurons known to innervate each peg. Moreover, these multiunit traces generally contained only two classes of spikes: a larger amplitude type 'A' unit and smaller amplitude 'B' unit; other distinguishable units (types 'C', 'Z', and 'Y') were present at much lower frequency (Gaffin and Brownell 1997). Each of these units had constant waveform and amplitude even at high rates of discharge. The constancy of their spike signatures made it possible to identify the neurons with confidence and to quantify their activities relative to each other in recordings lasting several hours. Figure 2 is a segment of one such record of spontaneous activity. While the activity of the larger (type 'A') neuron was relatively constant, the occurrence of type 'B' spikes nearly always suppressed the activity of A for several tens of milliseconds. To quantify this apparent inhibitory action of 'B' units on 'A' units we used cross-correlation analysis.

Interactions between sensory neurons

Cross-correlation analysis was used to display the relationships between one cell's spontaneous activity and that of others in the same sensillum, especially during the time that synaptic effects between the cells were expected to occur (within approximately 100 ms before and after impulse). In the experiment shown in Fig. 3, 54 10-s long samples were taken at regular intervals from a 20-min record of spontaneous activity; these were found to contain three discrete classes of spikes – 'A1', 'A2', and 'B' – identifiable by their distinctive waveforms. Each panel of Fig. 3 is a histogram displaying the activity of one unit against a reference unit of different (cross-correlation) or similar (auto-correlation) classification. From the two upper panels it is evident that the activity of 'A1' and 'A2' units were stable prior to the occurrence of spikes in type 'B' units, but suppressed in the period immediately following. In contrast, the ac-

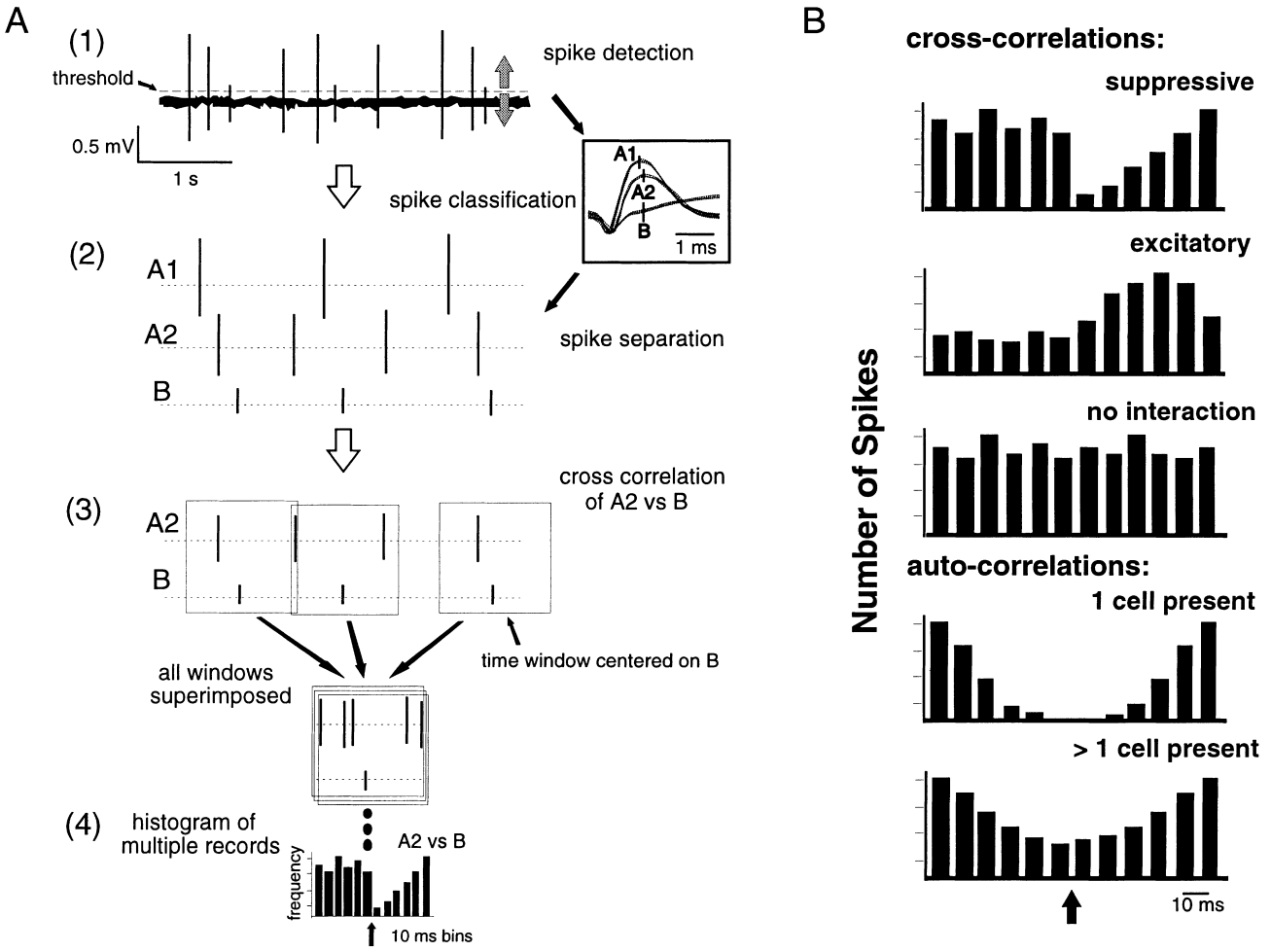

Fig. 1A, B Spike identification, classification and correlation analysis from extracellular electrophysiological records. **A** Schematic summary of spike sorting and analysis algorithm. (*1*) Spikes were detected by adjustable threshold discrimination and the digitized waveform of each was captured and stored on disk with its time of occurrence (± ms). Captured spikes were redisplayed at high sweep speed for automated (waveform template matching algorithm) or interactive manual sorting into discrete classes. (*2*) Each identifiable spike type ('A1', 'A2', 'B' in this example) was then displayed on an expanded time scale as separately reconstructed traces to visualize their activities relative to others in the original recording. (*3*) Cross-correlation analysis of one unit's activity relative to the occurrence of another revealed interactions between them as momentary changes in frequency of firing. (Note: In this example, unit 'B' spikes are centered along the time axis and another spike, 'A2', is displayed in proper temporal relation to it. (*4*) By summing several of these windows, the frequency of one unit's activity (e.g., 'A2') relative to the referent spike (e.g., 'B') can be displayed in histogram form. **B** Types of histograms expected from cross-correlating the activities of units with inhibitory, excitatory or no interaction. Auto-correlation analysis (correlating spikes of one's class with others in the same class) determines whether the spikes originate from one or more units

tivities of spike types 'A1' and 'A2' appeared unaltered when referenced against each other (third panel of Fig. 3), indicating that these neurons do not influence each other's spontaneous firing. Auto-correlation analysis of each of the three spike types showed a symmetrical absence of spike activity before and after the reference spike, confirming that each signal originated from a single, independent source.

Analysis of the spiking patterns in chemically-stimulated sensilla showed patterns of unit interactions similar to those observed in the unstimulated (spontaneously active) sensillum. In Fig. 4, stimulation of a sensillum with pure hexane excited both 'A' and 'B' type units. Auto-correlation of class 'B' units (Fig. 4C, third profile) gave the characteristic absence of activity around the centered spike, confirming that only one spiking unit contributed to this class. Referencing 'A' type spikes against themselves (Fig. 4C, second profile) did not produce the same inactivity near the reference spike, an

Fig. 2 Spontaneous electrical activity recorded from a peg sensillum of *P. mesaensis*. At least two classes of spikes of distinct amplitude were spontaneously active at about 1 Hz in this preparation. Activity of larger amplitude spikes (type 'A' units) appears to be suppressed immediately after spike discharge from smaller amplitude type 'B' units (*)

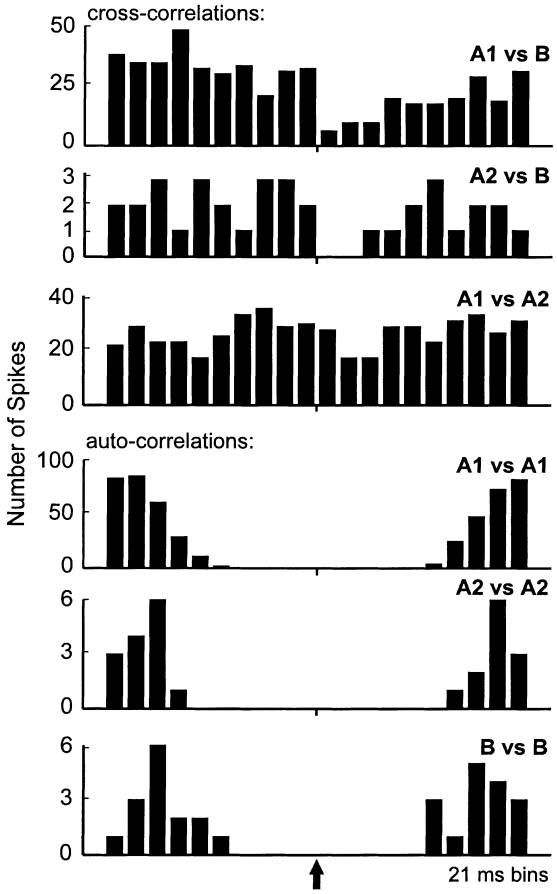

Fig. 3 Interactions between spontaneously active units in a peg sensillum. Sensory units of classes 'A1', 'A2' and 'B' were distinguished by waveform in 54 10-s samples taken over a 20-min period of spontaneous activity. Histogram profiles of all possible auto- and cross-correlations of these three spike classes are shown. For example, the *upper panel* labeled "A1 vs. B" displays unit 'A1' activity relative to firing of reference unit 'B' (*centered in the profile at arrow*). Cross-correlation of 'B' unit activity with either 'A1' or 'A2' unit activities clearly shows a suppression of spike types 'A1' and 'A2' within 100 ms following activity of type 'B' units. Spike types 'A1' and 'A2' show little to no effect on each other (*third panel*). Auto-correlations (*bottom panels*) verify that each identifiable spike probably originates from only one neuron

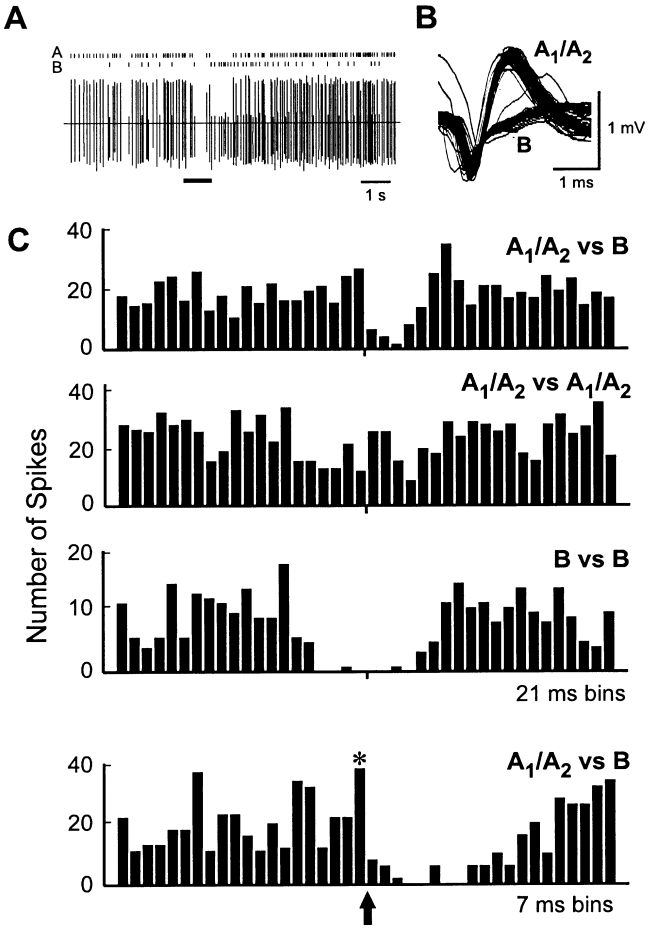

Fig. 4A, B Interactions between sensory units responding to chemical stimulation. **A** Stimulation of the peg sensillum by hexane elicited activity from at least two identifiable spike classes, 'A' and 'B', present in the peg as revealed by time-expanded display of spike waveforms **(B). C** Auto-correlation analysis of spike class 'A' ('A' vs 'A' histogram) reveals that these spikes probably originate from at least two neurons. Auto-correlation of spike class 'B' ('B' vs 'B' histogram) indicated one cell of origin for these units. During olfactory stimulation with hexane, type 'A' spike activity declines immediately after the firing of type 'B' units ('A' vs 'B' histograms). The bottom profile shows an expansion of 'A' vs 'B' (7-ms bins) to show the time-course of recovery from inhibition of unit 'A' activity. An increase in activity of 'A' prior (*) to spiking of 'B' may indicate facilitative action of unit 'A' on unit 'B'

indication that two or more neurons were generating these signals. Cross-correlation analysis between classes 'A' and 'B' showed that type 'B' units inhibited type 'A' units. On an expanded time scale (Fig. 4C, bottom profile) the suppression of 'A' begins within the first 7 ms of the 'B' unit spike and continues for at least 80 ms thereafter. A period of mild post-inhibitory rebound occurs about 140–160 ms after firing of 'B' (Fig. 4C, top profile). There is also the possibility of a facilitative effect of 'A' unit activity on the probability of firing of spike type 'B' as indicated by the increase in activity of 'A' in the 7-ms bin immediately prior to firing of 'B' (*, bottom profile in Fig. 4C).

Given the long duration of this influence, it is possible that the inhibitory action of 'B' type units on 'A' type units was mediated through feedback inhibitory pathways from the central nervous system. To investigate this possibility, we recorded from an intact pectine (body attached) then severed the pectine while continuing to observe activity in the same sensillum. Three spike types, 'A1', 'A2', and 'B', were easily resolvable in the intact animal. After 1 h of baseline recording, the pectine was severed at its point of attachment to the body. The activities of 'A1', 'A2' and 'B' units recovered to their original activity (unablated condition) within a few seconds, following hyperexcitation (approx. 20 s) caused by severance of the pectine nerves. The same 'A1', 'A2', and 'B' spike types were present throughout the recording from the severed pectine, and this activity persisted approx. 5 h. Sixty 10-s samples representing

30 min of spiking activity in the severed preparation were categorized into the three discrete spike types and examined for interactions by correlation analysis. Figure 5 shows the histogram profiles generated by this analysis, with spiking activity before and after referent spikes grouped into bins of 21 ms. As in previous examples, spike type 'B' appeared to inhibit the activity of spike types 'A1' and 'A2' while 'A1' and 'A2' showed no apparent influence on each other. Auto-correlations indicated that each spike class consisted of a single spiking unit with irregular interspike intervals lasting 100 ms or longer. Average firing frequency for 'A1' varied from 1 to 5 impulses per second, or about five times greater than the frequency of 'A2' and 30 times that of type 'B'. Spike type 'B' units typically discharged in bursts of impulses as indicated by the frequent occurrence of spikes in bins adjacent to the center of the auto-correlation profile.

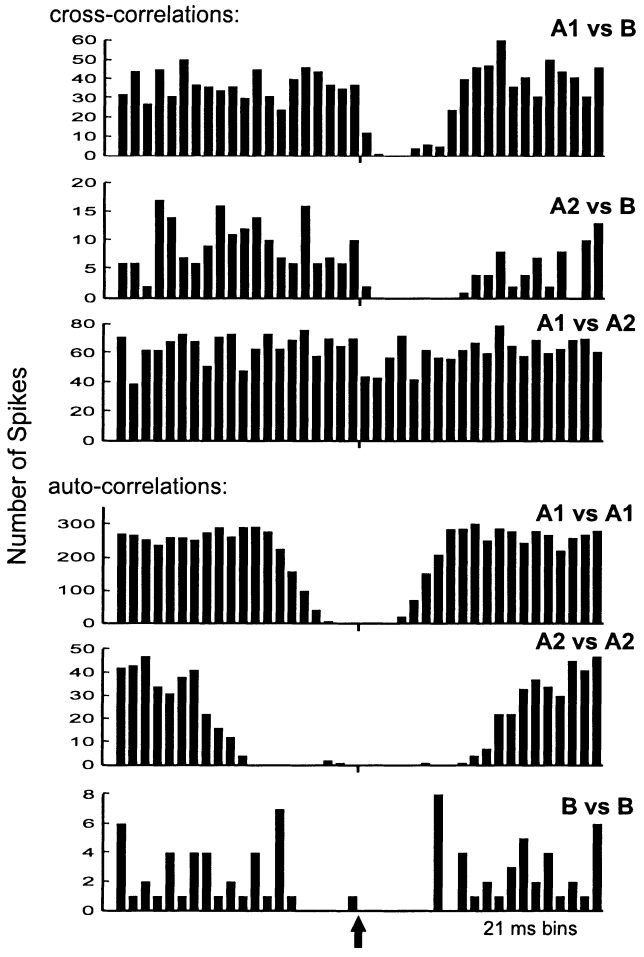

Fig. 5 Interactions between spiking units in isolated pectine. Spike classes 'A1', 'A2' and 'B' were identified in 60 10-s samples from 30 min of continuous recording from one peg sensillum after severance of the pectinal nerve. Histograms display correlation analysis of these three spike types, as described in Fig. 3. Activity of spike type 'B' was correlated with suppressed activity of 'A1' and 'A2' units. The auto-correlation histograms verify that each spike type originates from one cell

Cross-correlation analysis of spikes occurring infrequently in our recordings suggest that other neurons within the sensillum may interact. In one recording (Fig. 6A), units with very distinctive waveforms (types 'Y' and 'Z'; Gaffin and Brownell 1997) discharged together during a period of tonic 'A' unit activity, permitting analysis of the interactions between these three neurons. Cross-correlation analysis (Fig. 6B) indicates that 'Z' unit activity was inhibited by 'A' spikes with a time-course similar to the inhibitory interaction of type 'B' and type 'A' cells. In contrast, cross-correlation of types 'Y' and 'A' in this record suggest that 'Y' units are more likely to fire immediately before firing of type 'A' spikes, suggesting 'Y' units have an excitatory or facilitative influence on the firing of 'A' units. There is also an indication that 'Y' spikes are, in turn, inhibited by the activity of 'A' as judged by the reduction in 'Y' activity immediately following firing of 'A'. Cross-correlation of 'Y' with 'Z' unit activity also indicates an excitatory interaction ('Z' excites 'Y'), but more delayed than the 'Y'/'A' interaction. Auto-correlations of 'A' spike ac-

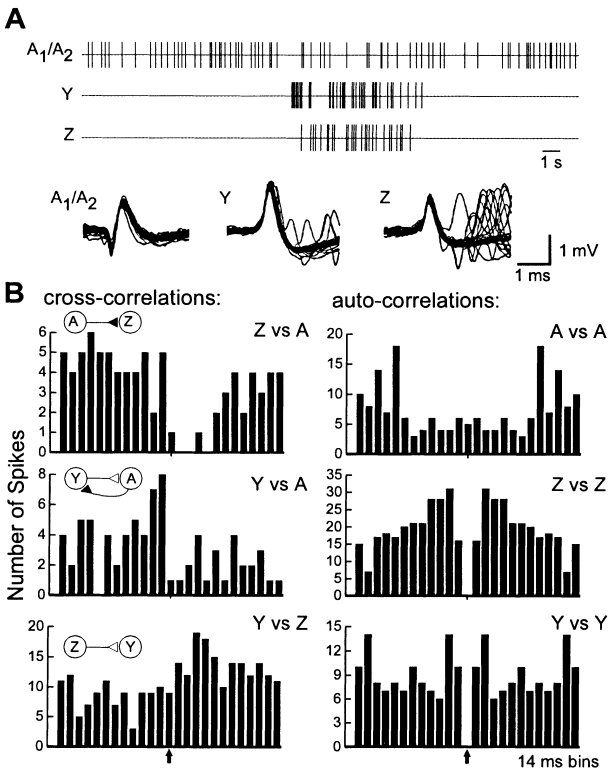

Fig. 6A, B Correlation analysis of spike bursts from type 'Y' and 'Z' units. **A** *Top*: sample of segregated recording shows a 7-s burst of spikes from type 'Y' and 'Z' units amid tonically active spikes of type 'A' ('*A1*/*A2*'). *Bottom traces* show superimposed waveforms of each spike type. **B** Histogram profiles generated by cross- and auto-correlations of spikes within the burst record in **A** above. The simplest interpretations of interaction indicated by these cross-correlation histograms is represented diagrammatically in the insets (*open triangles* = excitatory interactions, *closed triangles* = inhibitory interactions). Auto-correlations show type 'A' spikes probably originate from more than one neuron, while 'Y' and 'Z' spikes originate from single cells

tivity indicated that at least two units contribute to this class, while 'Y' and 'Z' originated from a single source.

Discussion

The impulse activities of several sensory neurons within single peg sensilla of *P. mesaensis* are not independent: for spontaneously active units, or cells activated by olfactory stimuli, there is a clear effect of some identifiable neurons on the activity of others originating from the same sensillum. These interactions are both excitatory and inhibitory, and they typically last several tens of milliseconds. In all respects they appear to be mediated by a synaptic process. Since they are independent of the pectine's neuronal connection to the central nervous system, we hypothesize that these synapses occur within the peg sensillum or very near the site of impulse initiation for its first-order chemosensory neurons.

A summary of the sensory cell interactions we observed by cross-correlation analysis is represented diagrammatically as a synaptic circuit in Fig. 8. Synaptic connectivity within each peg sensillum is likely to be extensive since most of the identifiable units we analyzed showed some evidence of interaction. Morphological studies suggest this network may be a plexus, not unlike the plexus observed in arthropod compound eyes (Bullock and Horridge 1965; Gur et al. 1972). Each peg sensillum is innervated by 10–18 sensory cells (Ivanov and Balashov 1979; Brownell 1989) each with their cell bodies in a common layer 50–100 μm beneath the two-dimensional array of peg sensilla. Morphologically, multiple configurations of synaptic contact exist between axons of these cells (Foelix and Müller-Vorholt 1983), the most common being dyadic (one presynaptic fiber contacting two postsynaptic fibers). Serial connections (postsynaptic element presynaptic to a third fiber) are also observed, as are reciprocal synapses. Each of these synaptic morphologies has an analog in the physiological interactions observed in this study. The dyad synapse may be reflected in the suppression of 'A1' and 'A2' units by 'B' units (Figs. 3–5). Serial synaptic processing may underlie the interactions between 'A', 'Y', and 'Z' units (Fig. 6), where 'A' units inhibited 'Z' units which, in turn, excited 'Y' units. Finally, a possible reciprocal interaction between 'Y' and 'A' units is shown in Fig. 6, where 'Y' units appear to simultaneously excite, and be inhibited by, 'A' units.

Interactions between primary sensory neurons may have functional significance for processing of chemosensory information. In a preceding study (Gaffin and Brownell 1997) we found that a small population of spontaneously active neurons in each sensillum (three to five units) gave distinguishable responses to a wide variety of chemostimulants. An example of this is shown in Fig. 7A of this paper, where the 6-carbon alcohol (hexanol) and 6-carbon aldehyde (hexanal) evoked strikingly different activity in two neurons: type 'B' units that were excited by both stimuli and type 'A' units that were excited by the alcohol and inhibited by the aldehyde. Given that 'B' unit activity inhibits activity of 'A' units, it is likely that at least some part of the aldehyde-induced inhibition of 'A' could be accounted for by hexanal's excitation of 'B'. Figure 7B shows a simple synaptic circuit that would produce these results. Such local circuitry could reshape the response of chemosensory neurons near the point of signal transduction,

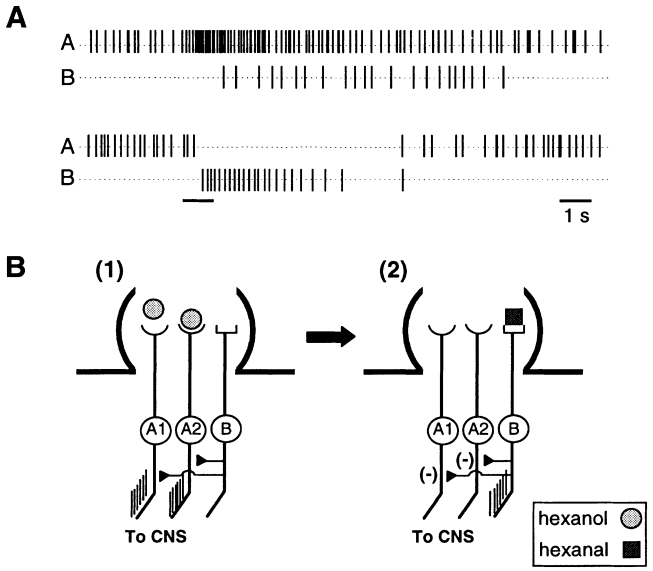

Fig. 7A, B Differential chemosensitivity of interactive units within a peg sensillum. **A** Type 'A' and 'B' units are displayed as segregated spike recordings during stimulation by hexanol and hexanal. Stronger stimulation of type 'B' units by the aldehyde may account for the inhibitory response of type 'A' units to hexanal. *Solid bar* indicates period of stimulus application. **B** Possible sensillar circuitry mediating interactions shown in A and in Figs. 3–5

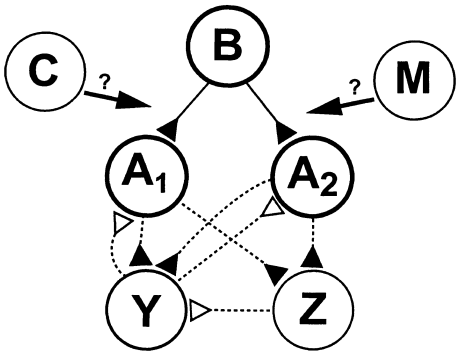

Fig. 8 Proposed circuitry for synaptic interactions within single peg sensilla. Excitatory (*open triangles*) and inhibitory (*closed triangles*) synapses modify the activity of several identifiable neurons ('*A1*', '*A2*', '*B*', '*Y*', '*Z*') within the peg sensillum. Additional chemosensory neurons ('*C*') and mechanosensory neurons ('*M*') may also influence sensory output from the peg. The inhibitory interactions involving 'A1', 'A2' and 'B' cells (*solid lines*) were observed in all recordings; interactions involving 'A1', 'A2', 'Y', and 'Z' cells (*dotted lines*) are based on a single observation (see Fig. 6)

thereby encoding subtle differences in stimulus quality before its relay to the CNS.

Synaptic connections have been recognized morphologically in the peripheral nervous systems of xiphosuran chelicerates (Griffin and Fahrenbach 1977) and in several terrestrial arachnids (Foelix 1975) and insects (Moulins and Noirot 1972; Steinbrecht 1989). In addition, physiological evidence of synaptic coupling exists for a few insect chemosensory (Getz and Akers 1994; White et al. 1990) and thermo/hygro (Gödde and Haug 1990) sensilla. Physiological investigations of these potential channels for interaction have been difficult because of the intractability of electrophysiological recordings capable of resolving the activity of single units within a multiunit record. In this regard, the peg sensilla preparation described here offers an important avenue for future descriptive and comparative studies. Most importantly, the peg sensilla appear to contain one of the most extensive and effective networks of intrasensillar neuronal interactions of any arthropod. As such it should be a useful system for study of the initial events of chemosensory processing.

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