Processing of Gustatory Information by Spiking Local Interneurons in the Locust

PHILIP L. NEWLAND
Division of Cell Sciences, School of Biological Sciences, University of Southampton, Southampton SO16 7PX, United Kingdom

Newland, Philip L. Processing of gustatory information by spiking local interneurons in the locust. J. Neurophysiol. 82: 3149–3159, 1999. Despite the importance of gustation, little is known of the central pathways responsible for the processing and coding of different chemical stimuli. Here I have analyzed the responses of a population of spiking local interneurons, with somata at the ventral midline of the metathoracic ganglion, during stimulation of chemo- and mechanoreceptors on the legs of locusts. Volatile acidic stimuli were used to selectively activate the chemosensory neurons. Different members of the population of local interneurons received depolarizing or hyperpolarizing inputs during chemosensory stimulation. Many of the same interneurons that received chemosensory input also received mechanosensory inputs from tactile hairs on the leg, but others received exclusively mechanosensory inputs. Chemosensory inputs occurred with a short and constant latency, typical of monosynaptic connections. The chemosensory receptive fields of the spiking local interneurons mapped the surface of a hind leg so that spatial information relating to the location of a taste receptor was preserved. The amplitude of potentials in interneurons during chemosensory stimulation varied in a graded manner along the long axis of the leg, thus creating gradients in the chemosensory receptive fields of interneurons. Some interneurons were depolarized to a greater extent by chemical stimuli applied to basiconic sensilla on distal parts of the leg, whereas others were depolarized more by chemical stimulation of more proximal sensilla.

INTRODUCTION

Sensory information from taste receptors is vitally important for all animals and is essential if an animal is to make appropriate selections of food. In insects, contact chemoreception plays a major role in a number of behaviors, including avoidance of noxious chemicals (White and Chapman 1990), the selection of egg-laying sites (Ma and Schoonhoven 1973; Stüdler et al. 1995), and the detection and selection of food (Dethier 1976). The gustatory receptors involved in these responses are called basiconic sensilla and are found on the mouthparts, where they have been extensively studied, on the body, wings, and legs (Blaaney 1974; Chapman 1982; Kendall 1970; Thomas 1966).

On the locust leg each basiconic sensillum is thought to contain a single mechanosensory neuron and at least four chemosensory neurons (White and Chapman 1990). We now know that the mechanosensory afferents from basiconic sensilla converge onto the same spiking local interneurons that process signals from tactile hairs (Burrows and Newland 1994), and together they form an elaborate tactile detector system covering the surface of the legs (Newland and Burrows 1994). Although much is known of how the sensory neurons within each receptor respond to chemical stimuli (Blaney 1974; White and Chapman 1990) and touch (Newland 1991; Newland and Burrows 1994), we know little of where and how the chemosensory signals are subsequently processed and integrated in local circuits in the CNS.

Only one study has described interneurons involved in processing gustatory signals (Mitchell and Itagaki 1992), but that did not analyze the physiological properties of particular populations of interneurons in any detail, nor was there any attempt made to understand the role of those interneurons in any taste related behavior. Part of the problem in analyzing the networks of central neurons involved in taste processing lies in the difficulties inherent in working with taste receptors in insects. Because each taste receptor is innervated by a mechanosensory neuron, conventional methods of stimulation using drops of chemical stimuli activate that mechanosensory neuron in addition to the chemosensory neurons. Recently, however, I showed that gustatory receptors on the hind leg of the desert locust respond to acidic odors, and that such stimulation leads to a characteristic avoidance reflex of the leg (Newland 1998). The great benefit of this method of stimulation for analyzing central pathways involved in aversive taste processing is that it is free of the very rapid sensory adaptation associated with chemical stimuli placed directly over the sensillum tip, and more importantly, specific to the chemosensory neurons themselves. This means that there is no simultaneous stimulation of the mechanosensory sensory neuron within the receptor, and that any evoked responses are a consequence of purely chemical cues. The avoidance reflex evoked by acid-odor stimulation is somewhat different to that evoked by tactile stimulation (Pflüger 1980), but the movements and activation of the underlying motor neurons imply that they share common neuronal elements and pathways. This then points to important contributions from the different types of local interneuron that are part of the local circuits that control leg movements in the processing of chemosensory signals. Spiking local interneurons are involved in the initial processing of sensory signals in those local circuits (see review by Burrows 1992). One group of these interneurons has its somata on the ventral midline of the thoracic ganglia and is known to play a key role in the motor pattern formation (Siegl and Burrows 1986). This ventral midline population of interneurons uses the transmitter \(\gamma\)-aminobutyric acid (Watson and Burrows 1987), and hence has inhibitory outputs (Burrows and Siegl 1982). It is possi-
able that the inhibitory influences found in the responses of some of the tibial and tarsal motor neurons during odor stimulation of the taste receptors (Newland 1998) may directly reflect the action of some of these spiking local interneurons.

Given this possibility, the aim of this study was therefore to analyze the responses of this population of spiking local interneurons in the locust during chemosensory and mechanosensory stimulation, to start to describe the pathways involved in the processing of gustatory signals.

METHODS

Experiments were performed on adult male and female desert locusts, Schistocerca gregaria (Forskål), taken from our crowded laboratory colony at Southampton University. Each locust was restrained ventral side uppermost in modelling clay with its left hind leg fixed so that the anterior surface was accessible. All other legs were firmly fixed at the femur, but with the tibiae and tarsi free to move.

The meso- and metathoracic ganglia were exposed by removing a small window of cuticle from the ventral thorax and then supported firmly on a wax-coated silver platform. The abdominal connectives were cut posterior to the metathoracic ganglion, and the connectives between the meso- and metathoracic ganglia crushed. To aid electrode penetration, the sheath of the metathoracic ganglion was treated with protease (Sigma type XIV) for 45–60 s before recording. The thorax was continuously superfused with locust saline at 22–25°C throughout an experiment.

Intracellular recordings were made from the somata of spiking local interneurons of a ventral midline group (Burrows and Siegler 1984; Siegler and Burrows 1984) using glass microelectrodes filled with 2 M potassium acetate and with DC resistances of 50–80 MΩ. Intereurons of this population were identified by their responses to stimulation of tactile hairs on the leg that define their receptive fields (Burrows 1985; Burrows and Siegler 1984; Siegler and Burrows 1983). Intracellular recordings were made using an Axoclamp 2A amplifier (Axon Instruments).

The activity of chemosensory neurons was recorded in one of two ways depending on whether odor or aqueous solutions of chemicals were used as the method of stimulation. For odor stimulation, a glass microelectrode filled with standard locust saline was driven through the soft cuticle at the base of a receptor close to the somata of its sensory neurons. Signals were fed to a standard high-impedance DC amplifier and then AC coupled. This method of odor stimulation has already been shown to be specific to chemosensory neurons; it does not cause injury damage to sensory afferents and does not activate the mechanosensory afferents (Newland 1998). For chemical stimulation with aqueous solutions, the tip-recording technique was used (Hodgson et al. 1955) in which a blunt recording microelectrode containing 50 mM sodium chloride was placed directly over the tip of a receptor. Movements of the electrode deflected the sensillum and elicited spikes in the mechanosensory afferent that were clearly distinguishable from spikes in chemosensory afferents (Newland and Burrows 1994). The same electrode was therefore used to simultaneously evoke and record the spikes of both the mecano- and chemosensory afferents. Tactile hairs (trichoid sensilla) were first cut to approximately half their lengths and stimulated and recorded using the same tip-recording technique.

For odor delivery, controlled pulses of compressed air were delivered through a World Precision Instruments Picopump and passed through a small bottle containing filter paper soaked in glacial acetic acid (Newland 1998). The output from this bottle was then connected to a metal pipette (2.0 mm OD) and odors of acetic acid delivered in an airstream at a rate of 1.75 cm·s⁻¹. The odor delivery pipette was positioned 2–3 mm from the receptor being analyzed. All recordings from the sensory neurons and interneurons were stored on a Biologic DAT recorder for subsequent analysis and display on either a digital oscilloscope (Tektronix), or on a computer following digitization using a Cambridge Electronics Design interface (CED1401) and Spike 2 software. The results are based on recordings from 65 interneurons in 41 locusts. Data were collected only for interneurons in which the resting potential remained constant throughout the entire experiment. Moreover, any interneuron that showed adaptation to a stimulus presented to a specific location on the leg at the start and at the end of an experiment was excluded from this analysis.

RESULTS

Spiking local interneurons respond to chemosensory stimulation

Many spiking local interneurons of the ventral midline population (Burrows and Siegler 1984; Siegler and Burrows 1983) that responded to mechanosensory stimulation also responded to gustatory stimuli. For example, the interneuron shown in Fig. 1A had a tactile receptive field restricted to the tibia and tarsus of the hind leg. Thus mechanical stimulation of tactile hairs and basiconic sensilla on the tibia and tarsus, but not on the femur, evoked depolarizations and spikes in the interneuron (Fig. 1A). Stimulation with an odor of acetic acid (Newland 1998) evoked a long-lasting depolarization and spikes in the same interneuron (Fig. 1B) when directed toward basiconic sensilla on the ventral tarsus, but had little effect when directed toward the femur. Moreover, drops of water or 250 mM sodium chloride applied to groups of basiconic sensilla on the tibia also evoked depolarizations and spikes in the same interneuron (Fig. 1C). Although these drops may also have activated the mechanosensory afferents of both tactile hairs and basiconic sensilla, interneurons responded differently (i.e., with different durations) to different chemical solutions, with 250 mM NaCl evoking a response with twice the duration of that evoked by water. These differing responses of the spiking local interneurons to NaCl and water were consistent from animal to animal (n = 19 interneurons). Stimulation using an acid odor, however, avoided the problem of simultaneously activating mechanosensory and chemosensory neurons and was therefore used as the preferred method for analyzing the physiological properties of the spiking local interneurons. Not all members of this midline population of local interneuron received inputs during chemosensory stimulation (Fig. 2), but all that did also received olfactory inputs from mechanosensory neurons innervating both tactile hairs and basiconic sensilla.

Chemosensory stimulation of basiconic sensilla on the locust leg with a number of volatiles showed that the spiking local interneurons only responded to odors of acids (Fig. 3), such as formic and acetic acid (in a similar manner to the responses of leg motor neurons to odorants (Newland 1998)), and not to any other volatile, including amyl acetate, xylene, and clove oil, which are known to have powerful olfactory effects (Laurent and Naraghi 1994; Slifer 1954, 1956). This contrasts with the responses of interneurons that receive olfactory inputs from receptors on the antennae of insects (Laurent and Davidowitz 1994; Laurent et al. 1996).

Mechano- and chemosensory signals converge on spiking local interneurons

With the use of the “tip recording” technique, it is possible to simultaneously record and stimulate mechanosensory neu-
rons of the basiconic sensilla. Small movements of the recording electrode caused deflections of the sensilla, and each deflection evoked a spike in a mechanosensory neuron that was followed by a depolarizing potential in an interneuron (Fig. 4A). Superimposing sweeps of the oscilloscope triggered from the mechanosensory afferent spike showed that these potentials occurred with a constant latency (Fig. 4B), typical of known monosynaptic mechanosensory inputs from basiconic sensilla onto these interneurons (Burrows 1992; Newland and Burrows 1994). A recording from a neighboring tactile hair (trichoid sensillum) showed that mechanosensory input from this class of receptor converged onto the same interneurons as those receiving mechanosensory input from basiconic sensilla. Superimposed sweeps of the oscilloscope triggered from the afferent spike of the tactile hair show excitatory postsynaptic potentials in the interneuron that again followed with a short and constant latency (Fig. 4C). An odor of acetic acid directed to a similar location on the leg also evoked a depolarization and spikes in the interneuron (Fig. 4D), revealing a convergence of mechanosensory and chemosensory signals onto members of the same population of interneurons.

The connections made by mechanosensory neurons of tactile hairs and basiconic sensilla with these interneurons are mediated through monosynaptic pathways (Burrows and Newland 1994). The connections made by the chemosensory neurons with the same interneurons were more difficult to analyze because signal averaging failed to reveal chemosensory afferent spikes in nerve 5, which could be used to analyze synaptic latency. In addition, although chemosensory spikes could be readily elicited in an individual receptor by application of different chemicals in the recording electrode, these spikes adapted so rapidly that signal averaging failed to reveal a potential in an interneuron. To analyze the patterns of connectivity of the chemosensory neurons, it was therefore necessary to stimulate the basiconic and trichoid sensilla electrically and analyze the evoked potentials in an interneuron (n = 7). Superimposed sweeps of the oscilloscope triggered from the stimulus pulse showed that the potentials evoked by stimulation of a trichoid sensillum with a stimulus intensity just above threshold (Fig. 5A, —) and another suprathreshold (· · ·) were of a similar amplitude. Similar results were obtained for two other neighboring tactile hairs on the dorsal distal femur (numbered 2 and 3). The amplitude of the potential evoked by electrical stimulation of a basiconic sensillum, however, depended on the amplitude of electrical stimulation. At threshold, the depolarizing potential in an interneuron was of a relatively small unitary type, with an amplitude and delay characteristic of input from the mechanosensory neurons of the basiconic...
sensilla. Suprathreshold electrical stimulation recruited a later delayed component that summed with the initial depolarization (Fig. 5B), that is assumed to be from one or more chemosensory neurons from the same sensillum. Neighboring basiconic sensilla on the distal dorsal femur again also produced similar responses in the interneuron, and similar results were obtained with stimulus durations of 0.5, 1.0, and 2.0 ms. Of the interneurons tested, the example in Fig. 5B showed the clearest

**FIG. 2.** Responses of spiking local interneurons to mechano- and chemosensory stimulation. Not all interneurons that received mechano-sensory input also received chemosensory input. **A:** stimulation of tactile hairs and basiconic sensilla on the femur and tibia of the hind leg (arrows) evoked depolarizations and spikes in an interneuron. **B:** stimulation with an odor of acetic acid directed to the dorsal tibia failed to evoke a response.

**FIG. 3.** Odor-evoked responses of interneurons are specific to acidic vapors. All interneurons that received chemosensory inputs responded to odors of acids. Acetic and formic acids evoked a depolarization and spikes in an interneuron (*top 2 traces*). Odors of other volatiles such as amyl acetate, clove oil, and xylene failed to evoke a response in any of the interneurons encountered (*n = 65*).
increase in amplitude during stimulation of a basiconic sensillum. More commonly, the increased amplitude of stimulation of a basiconic sensillum led to a 10–20% increase in the amplitude of the potential in an interneuron, which often gave rise to spikes. It is unlikely that current spread to neighboring basiconic sensilla is causing the delayed component because similar electrical stimulation to the tactile hairs results in a single amplitude of evoked potential even though the tactile hairs have a similar spatial distribution on the leg.

Receptive field properties of local interneurons

Spiking local interneurons were not always depolarized by odor stimulation. Instead the polarity of input during chemosensory stimulation always matched that during mechanosensory stimulation of basiconic and trichoid sensilla. Thus interneurons that were inhibited during mechanosensory stimulation were also inhibited by chemosensory stimulation with acetic acid (Fig. 6, A and B). Other interneurons were depolarized when sensilla on the leg were displaced and also when an odor of acetic acid was directed toward basiconic sensilla (Fig. 6, C and D). Interneurons that were inhibited were encountered less often than those that were depolarized and represented only 6 of the total of 65 interneurons that were encountered in this study.

Each interneuron was excited or inhibited by stimulation of particular arrays of basiconic sensilla and tactile hairs on the leg, so that its receptive field could be described according to the distribution of those receptors on different parts of the leg. The mechanosensory receptive fields of spiking local interneurons have been described in detail for tactile hairs alone (Burrows 1992) and for tactile hairs and the mechanosensory afferents of basiconic sensilla (Burrows and Newland 1994). I analyzed in detail the receptive fields of 39 interneurons, and these could be divided into 16 types. The receptive fields were plotted by mechanically stimulating arrays of receptors with a fine brush and also by directing acidic odors to those same arrays of receptors. Given the problems associated with assessing the contributions of individual chemosensory receptors to the receptive fields of interneurons (rapid adaptation, small amplitude of extracellular spikes, and lack of signal averaging), stimulation with an odor of acetic acid was used to analyze the extent of the chemosensory receptive fields over the three distal segments (femur, tibia, and tarsus) of the hind leg. The interneuron shown in Fig. 7A was depolarized and produced spikes when tactile hairs and basiconic sensilla on the dorsal tarsus were deflected using a fine paintbrush. No mechanoreceptors on other surfaces or other leg segments provided an input to this interneuron, and therefore its mechanosensory receptive field was restricted to the dorsal surface of the tarsus. An odor of acetic acid directed toward various sites on the leg showed that the chemosensory receptive field overlapped, or matched, its mechanosensory field. Thus an odor directed toward the dorsal distal femur evoked no responses in the interneuron.

FIG. 4. Convergence of mechano- and chemosensory inputs from basiconic sensilla and tactile hairs on the legs onto the same spiking local interneurons. A: deflection of the shaft of a basiconic sensillum evoked spikes in its mechanosensory neuron, and those, in turn, evoked depolarizing potentials in an interneuron. B: the potentials in the interneuron occurred with a short and constant latency as shown by superimposed sweeps triggered from the afferent spikes. C: superimposed sweeps of a neighboring tactile hair, trichoid sensillum, triggered from its afferent spikes showed that it also evoked short and constant latency excitatory potentials in the same interneuron. D: an odor of acetic acid directed to a similar location on the leg also evoked a depolarization and spikes in the interneuron.
some interneurons received both excitatory and inhibitory inputs, but they did not contribute equally to the mechanosensory receptive fields. Thus for example, an interneuron that was excited by mechanosensory stimuli to receptors on the dorsal tibia and tarsus was inhibited by mechanosensory stimulation of the ventral tarsus. Chemosensory stimulation resulted in an inhibition of the same interneuron, but the excitatory inputs were absent.

**Interneurons express gradients of excitability in response to chemosensory stimulation**

A key feature of the mechanosensory receptive fields of spiking local interneurons is their gradients of excitability from receptors on different locations on the leg (Burrows 1992; Burrows and Newland 1994). This means that for particular interneurons receptors on one part of the leg have a greater effect on the interneuron than receptors on another area of the leg. Similar gradients in chemosensory receptive fields were also commonly found in this study. For example, the interneuron shown in Fig. 9 had a chemosensory receptive field covering most of the hind leg; however, odor pulses of acetic acid directed to the distal region of the femur had a far greater excitatory effect on the interneuron than similar odor pulses directed toward surrounding areas. The latency to the onset of the depolarization was similar for all areas of the leg that evoked a response in the interneuron, suggesting that this gradient in response amplitude was not the result of spread of the odor from areas that had no effect to areas that did.

**DISCUSSION**

In this study I have demonstrated that a population of identified spiking local interneurons processes chemosensory signals from basiconic sensilla on the leg of the desert locust. All of the interneurons of the ventral midline population that received chemosensory input from the basiconic sensilla during aversive odor stimulation also received convergent exteroceptive input from mechanosensory neurons of both tactile hairs and basiconic sensilla. Other members of the midline group, however, did not receive chemosensory inputs, although it is possible that these particular interneurons could receive input during stimulation with other chemicals. The input from the mechanosensory afferents of basiconic sensilla was mediated through monosynaptic connections (see also Burrows and Newland 1994), but it is not yet firmly established whether the inputs from the chemosensory neurons were made through mono- or polysynaptic pathways. The results obtained indicating a recruitment of synaptic inputs with short and constant latency in response to an increased amplitude of electrical stimulation were indicative of a monosynaptic input from at least one chemosensory neuron. In addition, we already know that, although chemosensitive afferents are thought to project to a slightly more dorsal area of the ganglion than exteroceptive afferents (Burrows and Newland 1994), there is considerable overlap of the branches of spiking local interneurons with afferents of both modalities (Burrows and Newland 1993). Further tests of connectivity have not been possible because electrical stimulation, which necessarily activates the mech-
FIG. 6. Input properties of spiking local interneurons. The polarity of the response of an interneuron was always the same in response to mechano- and chemosensory stimulation. A: touching tactile hairs on the leg inhibited an interneuron, as did chemosensory stimulation with an acetic acid odor (B). Note the interneuron was depolarized by 1–1.5 nA to evoke a constant barrage of spikes. C: a different interneuron received excitatory inputs in the form of depolarizations and spikes in response to tactile hair deflection (C) and also when an odor of acetic acid was directed toward basiconic sensilla in a similar location on the leg (D).

FIG. 7. Mechano- and chemosensory receptive fields overlap. Receptive fields on the leg that provide inputs to the spiking local interneurons were similar in location for both mechano- and chemosensory inputs. A: an interneuron with a mechansensory receptive field restricted to the dorsal tarsus received chemosensory inputs only from the tarsus (B) and not from any other parts of the leg. C: a different interneuron with a mechansensory receptive field restricted to the femur received chemosensory inputs only from the femur (D) and not the tarsus.
FIG. 8. Receptive fields of 16 types of spiking local interneuron from the ventral midline population. To the left of each pair of block diagrams is the chemosensory field and to the right is the mechanosensory field. Diagrams show the receptive fields of interneurons on a hind leg as if it were opened with a ventral midline incision and laid flat (as shown in inset). Excitatory regions of a receptive field are shown cross-hatched, and inhibitory regions are stippled. Numbers (n) of interneurons of each type are given. For interneurons marked with an asterisk, the precise dorsal/ventral boundary of the receptive field of the tarsus during stimulation with an acetic acid odor was unclear. a, anterior; p, posterior; d, dorsal; v, ventral.
anosensory neuron innervating the same receptor, is the only reliable method of stimulating the basiconic sensilla. Direct contact with aqueous solutions of chemicals results in a sensory response that adapts rapidly (Newland 1998) precluding this method during tests of synaptic connectivity (Burrows and Newland 1994). The consistency and constant latency of the responses in the spiking local interneurons provide compelling evidence that the connections are monosynaptic.

Organization of receptive fields of interneurons

Spiking local interneurons of the midline group, including those analyzed in this study, are known to play a major role in forming the pattern of movements of the hind leg (Burrows 1985). Through their characteristic receptive fields these interneurons provide a map of the mechanoreceptors on the surface of the hind leg (Burrows 1992; Burrows and Newland 1994) in which spatial information is preserved (Burrows and Siegler 1985). Information about the spatial location of a stimulus on a leg is essential for the production of appropriate local reflex movements of that leg that move it away from the source of stimulation. The precise movement depends on the location of the stimulus on the leg so that the movements are different when ventral receptors are stimulated compared with when dorsal receptors are stimulated (Pflüger 1980).

The chemosensory receptive fields of these same interneurons are also very specific so that spatial information relating to the location of the chemoreceptors is again preserved across the population. Chemosensory stimulation, however, appears to evoke only a single reflex pattern of movements of the leg (Newland 1998), and the need for information about stimulus location appears unclear. Stimulation of chemoreceptors on different surfaces or segments of the leg results simply in a change in amplitude of responses of the leg motor neurons (Newland 1998) and not a reversal in the sign of input that occurs in tactile reflexes (Siegler and Burrows 1986). Although it remains unclear why it is necessary to preserve the spatial information related to the location of the chemoreceptors, it is more than likely that the input the local interneurons receive from the chemoreceptors will modify their contribution to reflex effects in local circuits and controlling leg movements (Burrows 1996).

Role of local interneurons in processing taste signals

Because the spiking local interneurons described here play a major role in shaping movements of the legs, this implies that chemosensory inputs will also contribute greatly to their output effects on nonspiking local interneurons (Burrows 1987) and motor neurons (Burrows and Siegler 1982). The only other study to examine the central processing of taste inputs also describes local interneurons receiving chemosensory inputs. In the blowfly, Mitchel and Itagaki (1992) showed that many of the interneurons responding to taste stimuli applied to the labelum were spiking local interneurons with extensive branching patterns in the suboesophageal ganglion. The detailed analyses of interneurons in the local circuits of locusts (see Burrows 1996) have implicated spiking local interneurons in the initial processing of sensory signals from many types of receptor on the leg, and of different sensory modalities. For example, in addition to processing exteroceptive signals from tactile hairs on the legs (Burrows 1992; Siegler and Burrows 1983) spiking local interneurons also process inputs from the mechanosensory afferents of basiconic sensilla and from cam-

![FIG. 9. Interneurons express gradients of excitability in response to chemosensory stimulation. For any given interneuron, the amplitude of the response to acetic acid odor stimulation depended on the site of stimulation within the receptive field. For this interneuron a stimulus directed to the distal dorsal femur evoked the greatest response, with weaker responses to stimuli directed toward the tibia, and no apparent input from the tarsus and unguis.](http://jn.physiology.org/doi/10.220.33.6/fig9)
paniform sensilla that monitor cuticular stress (Siegler and Burrows 1983). They may also receive convergent proprioceptive input from receptors in a leg (Burrows 1988). Because these interneurons are responsible for the integration of so many sensory inputs, it is perhaps not surprising that the same interneurons are also involved in processing chemosensory signals from taste receptors on the leg, especially because the stimulation of the gustatory receptors evokes an avoidance reflex (Newland 1998) similar in form to that evoked by tactile hairs on the leg (Pflüger 1980).

**Functional role of basiconic sensilla on the leg of the locust**

It is intriguing as to why the surface of the body and limbs of insects are covered with taste receptors (Stocker 1994). The role of some of these receptors has been demonstrated in some species. For example, the work of Dethier (1976) and Getting (1971) showed that stimulation of tarsal chemoreceptors on the forelegs of flies elicits an extension of the proboscis. If the proboscis makes contact with the same stimulant, then feeding is likely to occur. Those on the palps of *Manduca sexta* are thought to be involved in food rejection (Glenedenning et al. 1998), whereas those on the antennae of cockroaches are involved in food selection and conspecific recognition (Hansen-Delkeskamp 1972). This, however, is only a small subset of taste receptors on the body, and the role played by the majority has yet to be described.

The receptive field properties of the spiking local interneurons and their role in local circuits controlling leg movements provide some clues to the role of the basiconic sensilla on the legs. I have shown that the areas on the leg providing inputs to an interneuron, its receptive field, were overlapping for both mechanos- and chemosensory inputs. Basiconic sensilla within the receptive fields of an interneuron did not appear to contribute equally to its receptive field; one area evoked a greater response, whereas surrounding areas have a lesser effect. This pattern of input had been analyzed in detail by Burrows (1992) and Burrows and Newland (1994) for the mechanosensory afferents innervating the tactile hairs and basiconic sensilla, respectively, and points to a general organization feature of these interneurons and their presynaptic neurons. The convergent input from both neurons of mechanosensory and chemosensory modalities indicates a summation of inputs. The implication is that the responses to mechanosensory signals will be enhanced by the appropriate chemical stimulation of the same receptors, in addition to the tactile hairs. This is only one possible role of the basiconic sensilla, and it is likely that information about different chemicals is also transmitted to other centers. Furthermore, it is also possible that different chemicals activate spiking local interneurons in other populations and that processing of different tastes could occur at separate sites. The role of local spiking interneurons is likely to be one that would enhance an avoidance movement of the leg (Newland 1998; Pflüger 1980; Siegler and Burrows 1986) and could possibly play a role in food rejection.

Although the coding of different odors has been analyzed in detail and is now known to involve oscillatory coding and temporal shifts in the oscillations and neurons involved in a network (Laurent and Davidowitz 1994), nothing is yet known about the coding of different chemicals in the local circuits, and it remains the next step in this analysis. Initial experiments suggest that the interneurons described here respond differently to different chemicals. Now I have identified a class of interneuron that is known to receive chemosensory input; the task now is to analyze how these interneurons encode different tastes and how that information is integrated in the networks that control movements of the locust leg, and how that information may be used by an animal in the selection or rejection of food.

I am grateful to Drs. Hitoshi Aonuma, Stephen Rogers, Hans Schuppe, and David Shepherd for valuable comments on earlier drafts of this manuscript. This work was supported by an Advanced Fellowship from the Biotechnology and Biological Sciences Research Council (U.K.) and a research grant from the Royal Society (U.K.).

Address for reprint requests: P. L. Newland, School of Biological Sciences, University of Southampton, Biomedical Sciences Building, Bassett Crescent East, Southampton SO16 7PX, United Kingdom.

Received 21 June 1999; accepted in final form 13 August 1999.

**REFERENCES**


