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HINDBRAIN SIGNAL PROCESSING IN THE LATERAL LINE SYSTEM OF THE DWARF SCORPIONFISH *SCOPEANA PAPILLOSUS*

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Summary

Recordings were made from primary afferent fibres and secondary projection neurones (crest cells) in the mechanosensory lateral line system of the dwarf scorpionfish. Crest cells were identified by antidromic stimulation from the contralateral midbrain. Differences between primary afferent fibre and crest cell response characteristics are indicative of signal processing by the neuronal circuitry of the medial octavolateralis nucleus. There are a number of differences between primary afferent fibres and crest cells. Primary afferents have relatively high levels of spontaneous activity (mean close to 40 impulses s^{-1}) and many of them are strongly modulated by ventilation. By contrast, crest cells have a much lower rate of spontaneous activity that is not obviously modulated by ventilation. Primary afferents show a simple tonic response to a maintained stimulus, whereas crest cells show a variety of temporal response properties, but in general show a phasic/tonic response to the same prolonged stimulus. Afferents are most sensitive to frequencies of stimulation around 100 Hz; in contrast, crest cells show a strong suppression of activity at this frequency. Crest cells are most responsive around 50 Hz. These afferent/secondary comparisons show similarities with those reported for allied electrosensory and auditory pathways.

Key words: teleost, lateral line, hindbrain, medial octavolateralis nucleus, dwarf scorpionfish, *Scopeana papillosus*, signal processing.

Introduction

Octavolateralis systems include the electrosensory and mechanosensory lateral line systems and the sense of hearing. Many of the hindbrain nuclei servicing these senses share organisational similarities. These include the electrosensory dorsal octavolateralis nucleus (DON), the electrosensory lateral line lobe (ELL), the mechanosensory medial octavolateralis nucleus (MON) of fishes and the auditory dorsal cochlear nucleus (DCN) of mammals. From an overview of hindbrain sensory processing in these systems, it is very clear that the mechanosensory MON is the least well known (Montgomery *et al.* 1995). This overview of hindbrain processing compared the response characteristics of primary afferent fibres with those of the principal cells of the hindbrain nuclei. Principal cells are the projection neurones of these nuclei and include the ascending efferent neurones (AENs) of the DON, crest cells of the MON, pyramidal cells of the ELL and fusiform cells of the DCN. In general, principal cells differ from primary afferent fibres with respect to their spontaneous activity, gain, receptive field characteristics, temporal responses, frequency/response characteristics and dynamic signal conditioning properties (Montgomery *et al.* 1995).

Primary afferent responses have been characterised to some extent in a number of fish species: *Sarotherodon niloticus* (Münz, 1985), antarctic fishes (Montgomery and Macdonald, 1987; Montgomery *et al.* 1988, 1994; Coombs and Montgomery, 1992; Montgomery and Coombs, 1992), *Xiphister atropurpureus* (Bleckmann and Münz, 1990), trout *Oncorhynchus mykiss* (Kroese and Schellart, 1992) and mottled sculpin *Cottus bairdi* (Coombs and Janssen, 1990). Most studies have focused on frequency/response measures. These are found to be divided into two classes corresponding to the two submodalities of the peripheral lateral line system: the superficial neuromast organs and the canal neuromasts. For sinusoidal stimuli generated by a vibrating bead, a constant maximal velocity across different frequencies is obtained by halving the stimulus displacement for every doubling of frequency. Using a stimulus of this nature, the afferent fibres from superficial neuromasts have the frequency/response characteristics of a low-pass filter. Response amplitude is relatively independent of frequency at low frequencies, but declines rapidly above a certain frequency defined as the cut-off frequency. The cut-off frequency for superficial neuromasts is in the range 30–50 Hz (antarctic fishes, Coombs and Montgomery, 1994; *Sarotherodon niloticus*, Münz, 1985). The mechanical effect of enclosing the neuromast sense organ into a canal is to reduce its responsiveness to low frequencies

(Montgomery *et al.* 1994). Under these stimulus conditions, canal afferents show bandpass filter curves with the upper cut-off frequencies either equal to (antarctic fishes, Coombs and Montgomery, 1994) or higher than those of the superficial neuromasts in the same species (100–200 Hz in *Sarotherodon niloticus:* Münz, 1985).

Much less, however, is known about the second stage of sensory processing in the mechanosensory lateral line system. Some recordings have been made from mechanosensory units in the MON and surrounding hindbrain (Caird, 1978; Wubbels *et al.* 1993), but in no case have units been identified as crest cells and their response properties characterised to allow comparison with the other systems. In this study, we report on the spontaneous activity, temporal response properties and frequency/response characteristics of crest cells identified by antidromic stimulation from the midbrain. The study was conducted on the dwarf scorpionfish, a common, though inconspicuous, member of the subtidal rocky reef community in northeastern New Zealand. Since there has been no lateral line physiology reported on this species, it was necessary first to characterise the response characteristics of the primary afferent fibres as a basis from which to make the necessary comparisons.

Materials and methods

All experiments were performed on the dwarf scorpionfish *Scopeana papillosus* (Bloch and Schneider). Fish were caught in hand nets by SCUBA divers and transferred to holding tanks at the Leigh Marine Laboratory. For experimentation, individual fish were anaesthetised in 0.001 % MS222 dissolved in sea water. A hole was drilled into the upper spinal cord canal and the cord pithed with a flexible plastic rod. The drill was also used to open the dorsal cranium. The brain was then exposed and the fish decerebrated by transection of the forebrain between the diencephalon and the telencephalon. The head was firmly held in a holder which screwed into the anterior and lateral cranium, and the fish was placed in an aquarium with the water level adjusted to just below the cranial opening. The sea water in the aquarium was filtered and circulated through a cooler, which maintained the temperature at 18–19 °C. A strain gauge was attached to one of the opercular spines, using a thread and a heart clip, to generate an electrical trigger from closure of the gill operculum.

Afferent unit activity was recorded with sharp (approximately 20 MΩ) glass electrodes filled with 4 mol l^{-1} NaCl placed in the intracranial portion of the anterior lateral line nerve. Recordings from the central nervous system were made with platinum-black-tipped Woods metal electrodes (2–5 μm tips, 2–4 MΩ resistance). Crest cells were identified by antidromic spikes evoked by a stimulating electrode placed in the contralateral torus semicircularis. Stimulus electrode position was optimised by adjusting position while simultaneously recording the antidromic field potential in the MON with a blunt glass micropipette.

Adequate stimulation of the lateral line system was provided by a 4 mm radius bead attached to a minishaker driven by a power amplifier (Ling Dynamic Systems) slaved to a function generator (Trio) or the D/A output of a Labmaster interface card in a PC computer. For post-stimulus time histograms (PSTHs), the function generator provided a constant frequency stimulus for a set period of a few hundred milliseconds. For frequency/response analysis, the stimulus sequence was computer-generated to maintain a constant maximal velocity over a range of frequencies between 7.4 and 208 Hz. The computer-generated waveform took account of the dynamics of the minishaker. Correct calibration of the system was confirmed by recording the motion of the bead with an optoelectronic movement detector.

Spike activity triggered a window discriminator with spikes turned into standard 2 ms pulses to be passed to the D/A input of the computer to generate the PSTHs or responses at different frequencies. The axis of movement of the bead was parallel to the surface of the fish, and the edge of the bead was approximately 4–6 mm from the skin surface.

The responses to individual frequencies were analysed to give the probability of a spike occurring within any given 2 ms bin within one sinusoidal stimulus cycle. In effect, this is a period histogram scaled to represent the probability of a spike occurring within the 2 ms segments of the sinusoid. A perfectly phase-locked response, firing one spike per cycle, generates a probability of 1, and no response generates a probability that depends on the rate of spontaneous activity. Frequency/response curves were determined at 10–15 dB above threshold.

Results

Experiments were carried out on 10 fish and a total of 51 central units were recorded using Woods metal electrodes. Of these, 18 were positively identified as crest cells by antidromic stimulation from the midbrain. The antidromic latency was 2–2.5 ms, which corresponded well with the negative peak of the antidromic field (2.5 ms) recorded with a blunt electrode in the MON. The crest cells were recorded between 110 and 550 μm below the surface of the hindbrain. The other 33 cells recorded with the Woods metal electrodes would have included other crest cells whose identity could not be verified and other cell types in the DON. Data from these cells were not analysed in this study.

Full data sets were obtained from 12 primary afferent fibres to provide a comparison with crest cell responses. These recordings would not have included efferent fibres as these exit the brain in discrete bundles which bypass the section of the nerve from which recordings were made (Tricas and Highstein, 1991).

Spontaneous activity

The spontaneous activity of primary afferents is variable, ranging from 2.5 to 108 impulses s^{-1} in a sample of 12 afferents, with a mean of 39.5 impulses s^{-1}. A feature of primary afferents is that, in many, spontaneous activity is

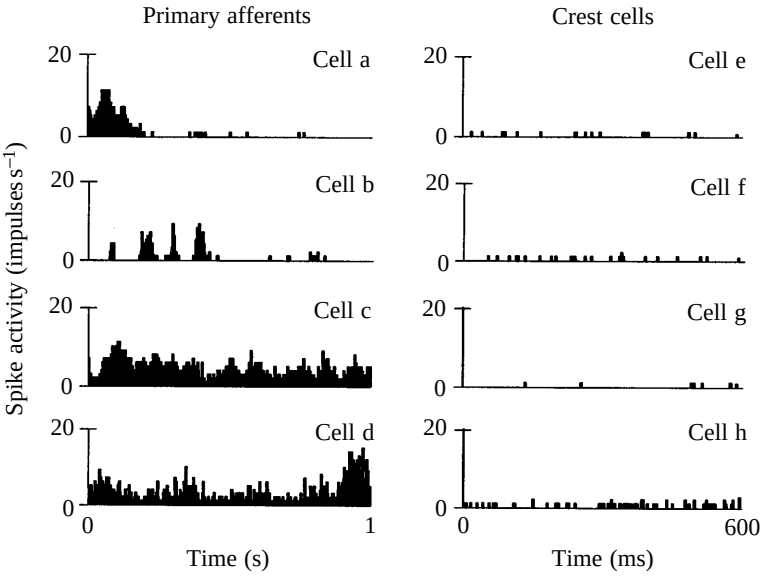

Fig. 1. Responses of primary afferents (left-hand column) and crest cells (right-hand column) to ventilation. Histograms of spontaneous spike activity for 1 s in the case of primary afferents and 600 ms in the case of crest cells extend for most, but not all, of one ventilation cycle. Collection of spike activity to produce the histograms was initiated by the trigger generated from the strain gauge attached to the operculum, so the beginning of the histogram corresponds to opercular closure. Each histogram is for a different unit, and the examples were chosen to show the range of responses observed. Note the much higher spontaneous activity of the primary afferent units and their modulation by breathing activity. The receptive fields of crest cells e and f were on the operculum, and those for cells g and h were on the lower jaw.

strongly driven by the animal's own breathing (Fig. 1). Not surprisingly, afferents whose receptive field is on the mandible or on the operculum are often those driven by breathing, and those from canal lines on the cheek or just behind the eye tend not to be. The modulation of afferent activity driven by ventilation is quite variable in different afferent fibres.

The spontaneous activity of crest cells is much lower. A sample of 17 crest cells had a range from 0.6–4.95 impulses s^{-1} with a mean of 1.69 impulses s^{-1}. The spontaneous activity of crest cells was relatively unaffected by ventilation (Fig. 1) despite the fact that many of them had receptive fields around the mouth and the gills.

Gain

Gain, or responsiveness, is difficult to measure. The intensity of the response is very sensitive to the position and orientation of the stimulus with respect to the receptor. The section of the canal containing the receptor was often located by observing the phase change that occurred as the stimulus was moved along the canal line. However, even when the receptor was so located, physical limitations in positioning the stimulus meant that the stimulus was presented only approximately parallel to the surface of the skin of the fish and could be anywhere between parallel to the canal or at right angles to it, depending on the orientation of the canal itself. Given these limitations, gain was not systematically studied, and the values given here are only indicative. They are given as the mean probability of a spike in primary afferent units and crest cells for a 50 Hz stimulus at a peak-to-peak amplitude of 240 μm. For these stimulus conditions, primary afferents showed a mean probability of spiking of 0.58 (S.D.=0.21, N=10), and crest cells a mean probability of 0.39 (S.D.=0.29, N=7, difference between the means not statistically different).

Temporal response properties

Examples of temporal response types are presented in Fig. 2. Primary afferent fibres were typically phase-locked to the stimulus with one spike per stimulus cycle and maintained a tonic response to the stimulus train (Fig. 2, column 1). The PSTHs of crest cells were more complex. One consistent finding was that the response of crest cells was suppressed at higher stimulus frequencies. The middle column of Fig. 2 shows PSTHs for one particular crest cell for a range of increasing stimulus frequencies. The clear tonic response at 60 Hz is virtually absent at 80 Hz and turns into a suppression at 100 Hz. The right-hand column shows PSTHs of three different crest cells at stimulus frequencies of 50 Hz. A range of response types is seen, from phasic through phasic/tonic to tonic.

Intensity and frequency/response characteristics

With the stimulus conditions used in this study, the responses of units had a relatively narrow dynamic range. Fig. 3A shows the intensity/response functions for two primary afferent fibres. Both had thresholds at 100 Hz of approximately −75 dB (re: 1 m s^{-1}), but had reached saturation at −55 dB. Taking account of the size of the vibrating bead and its distance from the surface of the fish, a stimulus intensity of −65 dB (re: 1 m s^{-1}) gives a calculated particle displacement at the surface of the fish of 28 nm. Fig. 3 also shows the frequency/response functions of two primary afferents each measured at three different intensities (constant velocity stimulus). The narrow dynamic range is evident in that the frequency/response curve changes from no response to fully saturated over an approximately 20 dB change in stimulus intensity. Also evident in this figure is that the 'noise floor' (i.e. response to zero stimulus amplitude) changes with spontaneous activity and is greater at low frequencies. Frequency/response curves for representative crest cells and primary afferents are shown in Fig. 4. Responses of primary afferent units were relatively homogeneous, with the response increasing over the mid-frequency range at a rate consistent with an acceleration-

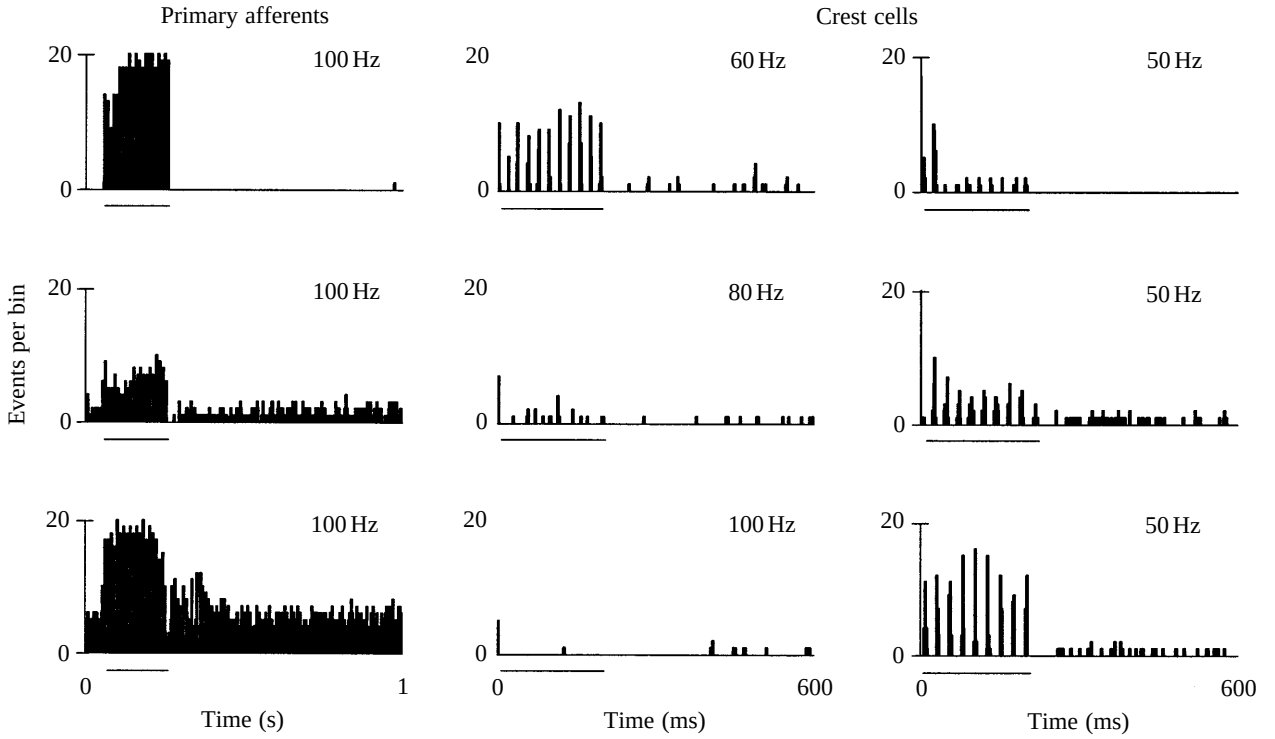

Fig. 2. Post-stimulus time histograms (PSTHs) of primary afferent and crest cell responses to maintained stimulation (stimulus length is indicated by the bar below each PSTH). Column 1: a range of primary afferent responses showing the tonic nature of their response. Column 2: responses of a particular crest cell responding well at 60 Hz, marginally at 80 Hz and suppressed by higher frequencies of stimulation. In this column, the vertical axis has been omitted to show the initial spike. Column 3 shows the range of variation in PSTHs from three different crest cells. Histograms of spike activity for 1 s in the case of primary afferents and 600 ms in the case of crest cells.

sensitive system being driven by a constant-velocity stimulus. The elevation of the response at low frequencies evident in some units was an artefact due to spontaneous activity, as shown in Fig. 3. In most units, a clear break was evident in the response at approximately 100 Hz.

The responses of crest cells were consistently different from those of primary afferents. As illustrated in the PSTHs (Fig. 2), frequencies above 50 Hz often produced a suppression in response. In some units, onset of the 'tone burst' produced a singe spike followed by suppression. These effects are clearly seen in the frequency/response curves of crest cells (Fig. 4B) which increase with frequency up to approximately 50 Hz and thereafter decline with increasing frequency.

Discussion

Crest cells in the medial octavolateralis nucleus (MON) of the mechanosensory lateral line show similar properties to

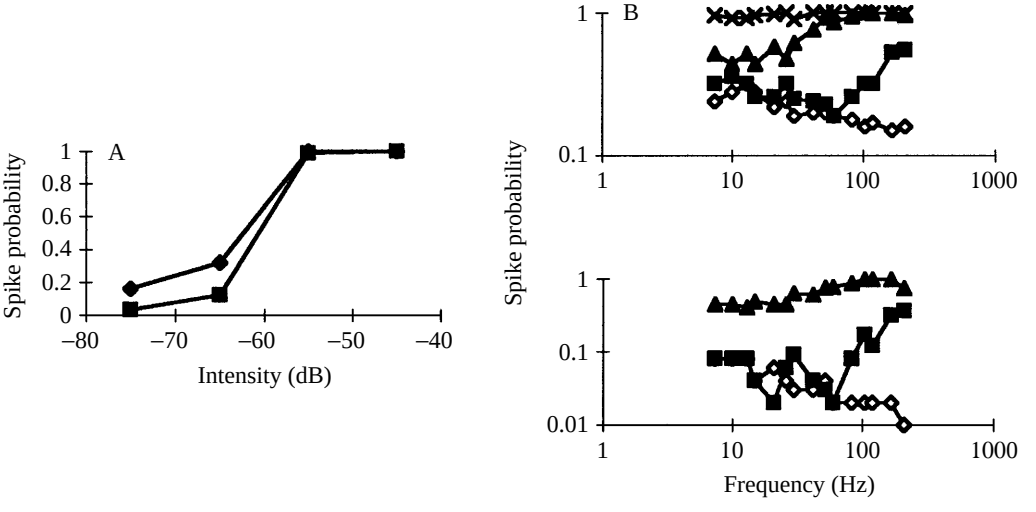

Fig. 3. (A) Intensity/response functions for two afferent fibres stimulated at 100 Hz. (B) Frequency/response functions for two different afferent fibres stimulated at a range of intensities (◇ stimulus off; ■ −65 dB; ▲ −55 dB; × −45 dB re: 1 m s^{-1}).

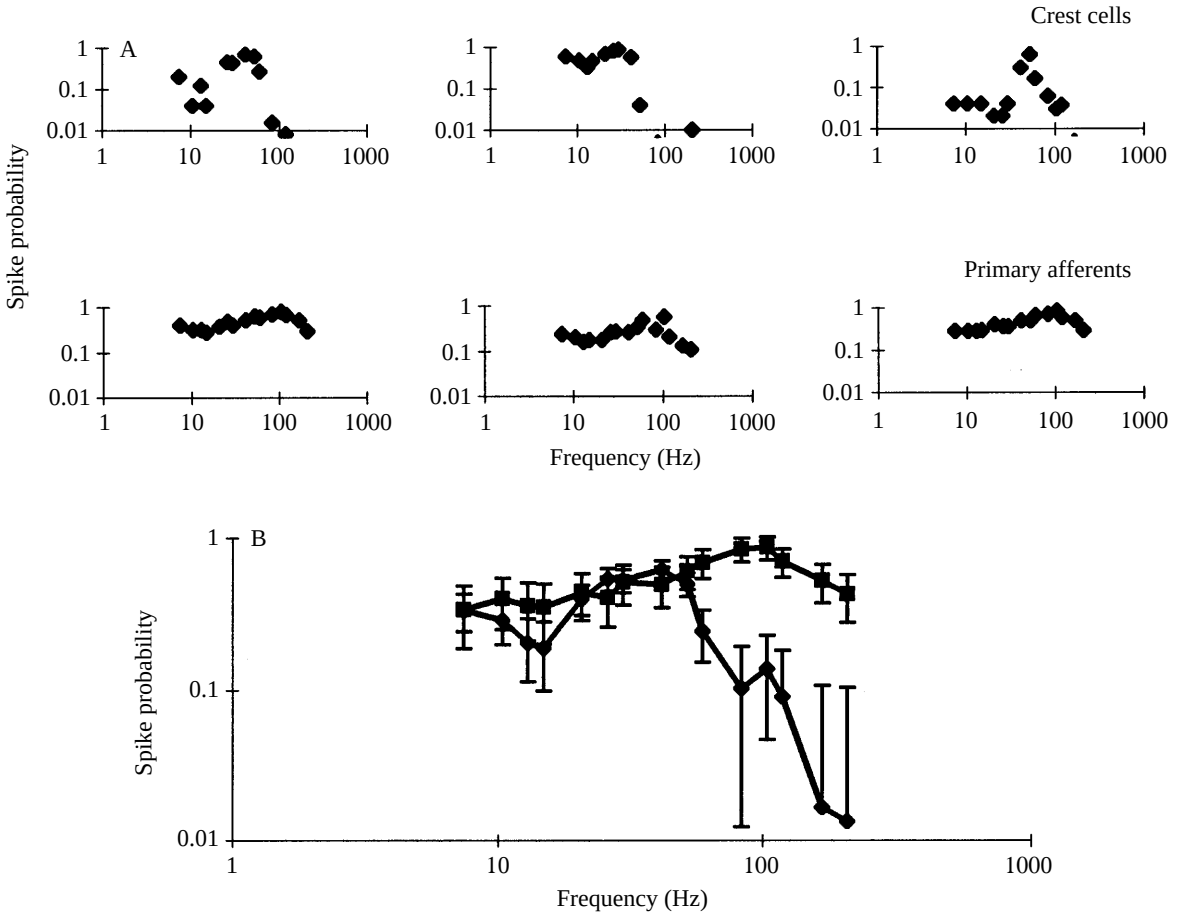

Fig. 4. (A) Frequency/response curves of representative crest cells and primary afferents; note that in every case the upper cut-off frequency of the crest cells is lower than that of the primary afferents. (B) Mean frequency/response curves for crest cells (◆) and primary afferents (■). Values are means ± S.E.M., *N*=12.

those of their electrosensory and auditory counterparts. Ascending efferent neurones (AENs) are the electrosensory equivalent of mechanosensory crest cells. One of the very distinctive differences between AENs in the elasmobranch dorsal octavolateralis nucleus and electrosensory afferents is the large difference in levels of spontaneous activity; AENs are virtually silent, whereas the electrosensory afferents have a high level of spontaneous activity (Montgomery and Bodznick, 1993; Conley, 1995). A similar difference is evident in the spontaneous activity of mechanosensory afferents and MON crest cells reported in this study. This difference appears to be a general phenomenon in these systems since the spontaneous activity of principal cells in ELL and DCN is also lower than that of afferents (Montgomery *et al.* 1995).

As in the elasmobranchs that have been studied, in the dwarf scorpionfish mechanosensory afferent activity is often strongly driven by ventilation (Montgomery, 1984). However, unlike electrosensory ventilatory activity, the modulation of mechanosensory afferents is quite variable. Both the degree and nature of the modulation depend on the location of the mechanosensory receptor. In consequence, the larger part of ventilatory modulation in the mechanosensory system cannot simply be removed by common-mode rejection, as it is in elasmobranch electroreception (Bodznick *et al.* 1992; Bodnzick and Montgomery, 1992; Montgomery and Bodznick, 1993). It appears that ventilatory modulation in the mechanosensory system is effectively removed at the first relay in the hindbrain since it fails to appear in the spontaneous activity of most crest cells (Fig. 1), including those with receptive fields in the region of the mouth or gills where afferents generally show strong ventilatory modulation.

The post-stimulus time histograms (PSTHs) of crest cells show some interesting differences from those of primary afferents. Whereas the PSTHs of afferent units are almost exclusively phase-locked tonic responses, the crest cells are phase-locked to the stimulus, but many show more phasic responses than primary afferents, particularly at high stimulus frequencies. This is similar to the finding in the DON, ELL and DCN, where principal cell responses tend to be more phasic than those of primary afferents. One distinctive property of crest cell responses is the suppression of activity by higher frequencies. Frequencies of 100 Hz, which produce maximal activity of afferents, produce a very strong suppression of activity in crest cells (Fig. 2).

The different PSTHs of different crest cells is one factor that contributes to the difficulty of comparing the sensitivity of crest cells and primary afferents using the measures available in this study. The probability statistic used for the construction of frequency/response curves, and for sensitivity comparison, is based on the response over the whole of the stimulus period, so that a cell, such as a crest cell, with a phasic response will exhibit a lower response statistic than a cell with a tonic response. The difficulty in defining an appropriate response measure coupled with the difficulty of providing a standard stimulus at the receptor preclude meaningful sensitivity comparisons between primary afferents and crest cells in this study. In general terms, however, the sensitivity of lateral line units in the scorpionfish (clear modulation at 28 nm particle displacement) is similar to other reported values. For example, Wubbels *et al.* (1993) report that high-frequency, high-sensitivity units in the MON of the trout showed a 20 % modulation of activity for a particle displacement of 16 nm.

The response criteria used in this study were based on the physiological assumption that spikes arriving within 2 ms at the postsynaptic cell (crest cell in this case) would produce excitatory postsynaptic potentials which would summate, so that phase-locking within this 2 ms window would effectively bring asynchronous activity in afferents from the same receptor converging onto the same postsynaptic cell into synchrony. This choice of response measure produces a relatively narrow dynamic range in the sensory afferents (Fig. 3), as do other response measures that have been used elsewhere (Coombs and Fay, 1993). For this reason, frequency/response curves were taken at 10–15 dB above threshold. This gave a frequency/response between no response and saturation (Fig. 3B).

It is clear from the individual curves, and from the mean responses, that the crest cells showed a significantly lower upper cut-off frequency than the primary afferents (Fig. 4). Whereas afferents showed a maximal response at approximately 100 Hz, crest cell responses peaked at around 50 Hz and dropped away precipitously at higher frequencies. One interpretation of this finding is that, in this study, the stimulus used activates not only the excitatory receptive field but also an inhibitory surround. Inhibitory postsynaptic potentials are longer-lasting (typically 20 ms or so) than excitatory postsynaptic potentials, so that strong activation of inhibitory inputs onto crest cells could reduce their responses at frequencies above 50 Hz to all but the first spike (Fig. 2). One of the main afferent/crest cell comparisons that has not been addressed in this study is that of receptive field organisation. The study of receptive field organisation is not a trivial matter in the mechanosensory lateral line. Vibrating dipoles produce a complex spatial stimulus pattern which must be taken into account in the interpretation of the receptive fields (S. Coombs and R. A. Conley, in preparation). Resolution of the above interpretation of the upper cut-off frequency of crest cells will require definition of the receptive field characteristics of crest cells, which is a matter for future study.

This study provides further confirmation that a filter operates at the level of the hindbrain to suppress movement-generated reafference in this mechanosensory system. Crest cells do not show the ventilatory modulation exhibited by afferent fibres. Montgomery and Bodznick (1994) report that some secondary cells show suppression of stimuli triggered by ventilation and, furthermore, that this suppression is achieved by the development of a cancellation signal. A possible model of how synaptic plasticity within the molecular layer of the MON could operate to produce such a cancellation signal is discussed by Montgomery and Bodznick (1994).

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