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RESPONSES OF ANTERIOR LATERAL LINE AFFERENT NEURONES TO WATER FLOW

RAINER VOIGT, ALEXANDER G. CARTON AND JOHN C. MONTGOMERY*

Experimental Biology Research Group, School of Biological Sciences, University of Auckland, Private Bag 92019, Auckland, New Zealand

*Author for correspondence (e-mail: j.montgomery@auckland.ac.nz)

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Summary

The mechanoreceptive lateral line system detects hydrodynamic stimuli and plays an important role in a number of types of fish behaviour, including orientation to water currents. The lateral line is composed of hair cell receptor organs called neuromasts that occur as superficial neuromasts on the surface of the skin or canal neuromasts located in subepidermal canals. Both are innervated by primary afferents of the lateral line nerves. Although there have been extensive studies of the response properties of lateral line afferents to vibrating sources, their response to water flow has not been reported. In this study, we recorded extracellularly from anterior lateral line afferents in the New Zealand long-fin eel *Anguilla dieffenbachii* while stimulating the eel with unidirectional water flows at 0.5–4 cm s^{-1}. Of the afferents, 80 % were flow-sensitive to varying degrees, the response magnitude increasing with flow rate. Flow-sensitive fibres gave non-adapting tonic responses, indicating that these fibres detect absolute flow velocity. Further studies are needed to confirm whether flow-sensitive and flow-insensitive fibres correlate with superficial and canal neuromasts, respectively.

Key words: anterior lateral line, flow-sensitive fibre, water flow, teleost, New Zealand long-fin eel, *Anguilla dieffenbachii*, neuromast.

Introduction

Fish are able to detect minute hydrodynamic stimuli *via* the mechanoreceptive lateral line system. The importance of the mechanoreceptive lateral line sense has been demonstrated in different fish behaviours such as prey detection and capture (Hoekstra and Janssen, 1985; Montgomery and Hamilton, 1997), predator avoidance (Blaxter and Fuiman, 1989), schooling (Partridge and Pitcher, 1980), obstacle avoidance (Hassan, 1989) and rheotaxis (Montgomery et al., 1997).

The lateral line system is composed of numerous receptors located either in subepidermal canals (canal neuromasts) or on the body surface (superficial neuromasts) (Bleckmann, 1993; Coombs et al., 1988; Münz, 1989). Neuromasts are composed of a population of mechanosensory hair cells whose cilia are embedded in an overlying gelatinous cupula. Hair cell potentials are modulated by cupula displacement induced by fluid motion. The directional response properties of individual hair cells are defined by the anatomical polarisation of the ciliary bundle: bending the stereocilia towards the kinocilia causes depolarisation, while bending in the opposite direction causes hyperpolarisation (Flock, 1971).

Hair cells are innervated by a sensory afferent and an efferent fibre (Roberts and Meredith, 1989). Each afferent fibre originates from a bipolar neurone whose cell body is located in the nerve adjacent to its point of entry to the hindbrain (medial octavolateralis nucleus of the medulla; Meredith et al., 1987; McCormick, 1989). Collectively, afferent fibres that innervate neuromasts on the head form the anterior lateral line nerve.

Physiological investigations of lateral line function have largely concentrated on measuring the frequency/response characteristics of both canal and superficial neuromasts (Münz, 1985; Kroese and Schellart, 1992; Coombs and Janssen, 1990; Montgomery and Coombs, 1992; Coombs and Montgomery, 1994). In these studies, response characteristics of primary afferent fibres consistently fall into two groups: those that respond to the acceleration component of water motion and those that respond to the velocity component (Denton and Gray, 1988, 1989; Kalmijn, 1989). Although the experimental limitations of such studies make it difficult to identify the type of lateral line receptor, it has been assumed on theoretical grounds that responses to water accelerations originate from fibres innervating canal neuromasts and responses to water velocity originate from fibres innervating superficial neuromasts (Kalmijn, 1989; Coombs and Janssen, 1990; Kroese and Schellart, 1992; Coombs and Montgomery 1994).

Anatomical and physiological differences between the two receptor subpopulations raise the possibility that canal and superficial neuromasts may mediate different patterns of behaviour (Münz, 1989). For example, the strike response in the mottled sculpin *Cottus bairdi* appears to be mediated by acceleration-sensitive canal neuromasts (Janssen et al., 1990), while velocity-sensitive superficial neuromasts

contribute to rheotactic behaviour (Montgomery et al., 1997). Currently, there is no description of the response characteristics of lateral line receptors to behaviourally relevant hydrodynamic stimuli generated by flow. Although vibrational stimuli generated by a dipole source may approximate hydrodynamic signals produced by invertebrate prey (Coombs and Janssen, 1990; Janssen et al., 1990), they do not represent the full range of biologically relevant stimuli present in the environment of the fish (Bleckmann et al., 1991; Montgomery and Coombs, 1998).

The New Zealand freshwater long-fin eel (*Anguilla dieffenbachii* Gray) is primarily a generalist, occupying a range of freshwater habitats with access to the sea (McDowell, 1990). It is a suitable species for this study because (i) eels are nocturnal predators, and non-visual cues are therefore likely to play important roles in a number of behaviours, (ii) orientation with respect to water currents plays a crucial role during migratory periods, a behaviour potentially mediated by the lateral line system (Montgomery et al., 1995, 1997), and (iii) the anterior lateral line system of *Anguilla* spp. is composed of both classes of lateral line receptor (Zacchei and Tavolaro, 1988).

This study is the first attempt to describe the response characteristics of anterior lateral line afferents when a fish's head is stimulated with a unidirectional water flow (streaming water), presumably the biologically relevant stimulus involved in lateral-line-mediated rheotaxis.

Materials and methods

Experiments were performed on 21 New Zealand freshwater long-fin eels, *Anguilla dieffenbachii* Gray (mass approximately 300 g, length 45–55 cm). Eels were acquired from local dealers and maintained in 150 l tanks at ambient temperature and light cycle.

Preparation

For preparation, individual eels were anaesthetised in and perfused with 500 mg l^{-1} tricaine methanesulphonate (MS-222, Sigma) dissolved in cold water and buffered to pH 6.8–7.0. A hole was drilled into the upper spinal cord, and the cord was pithed. After removal of overlying skin and muscles, the dorsal cranium was removed, the fish was decerebrated (by transection between the diencephalon and telencephalon) and the supraoccipital bone was removed to expose the root of the anterior lateral line nerve. Following surgery, the eel was immobilised with 0.5 ml of pancuronium bromide (David Bull Laboratories). A head holder was firmly screwed into the lateral cranium, and the fish was transferred to the experimental tank, where it was ventilated by a water stream supplied *via* a mouthcast. Eels were allowed to recover for at least 2 h before recording sessions began, after which the mouthcast was removed.

Experimental arrangement and stimulation

All experiments were carried out in a rectangular flow tank (100 cm×25 cm×10 cm; Fig. 1) which consisted of a water inlet section with baffles, upstream and downstream flow collimators, and the recording section holding the eel. A computer-controlled proportional valve (Bürkert, type 6223) produced a range of flow rates in the flume. The flow was produced by a pump (Dynaflo XF 171) positioned in a neighbouring room. The fish was positioned towards the flow with the water level just below the cranial opening. A strip of fabric supported its tail. This configuration allowed us to produce unidirectional water flows at different flow rates along the longitudinal body axis of the eel. Water temperature was maintained by a water cooler at 10.9±0.5 °C.

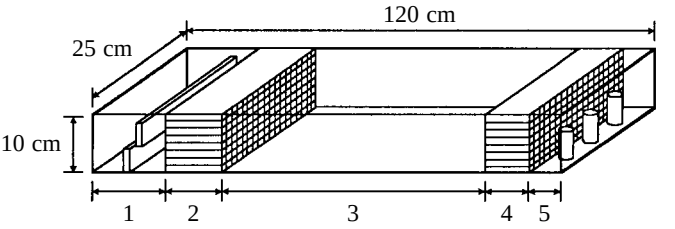

Fig. 1. Diagram of the experimental arrangement for recording from single lateral line afferent fibres in the eel. The flow tank (100 cm×25 cm×10 cm) consists of a water inlet section with a baffle (1), upstream (2) (9 cm wide) and downstream (4) flow collimators (8 cm wide; 20 mm^2 openings) and the recording section (3) holding the eel. The water level was maintained at approximately 5 cm by three standpipes in the outlet section (5).

Recording technique

Activity from single fibres of the anterior lateral line nerve was recorded extracellularly using glass microelectrodes (approximately 6–10 MΩ) filled with 4 mol l^{-1} NaCl. Standard electrophysiogical equipment (Neurolog, Digitimer Ltd) was used to amplify and filter neural activity. Responses of single fibre were identified visually from an oscilloscope trace on the basis of waveform, amplitude and interspike interval. Units were separated from background noise using a window discriminator that generated a TTL pulse for each spike above a set level. TTL pulses were digitised and stored as time of the event (1 ms resolution) on a personal computer using commercial software (Labview, National Instruments). The data were further analysed using in-house programs.

The approximate location of neuromasts on the head was determined with small jets of water delivered from a hand-held pipette. Each stimulus trial consisted of a 20 s recording of the pre-stimulus activity, 20 s of stimulus activity and 20 s of post-stimulus activity. The response magnitude was calculated as the difference in the number of spikes between the pre-stimulus and stimulus periods, and is expressed as number of spikes per second.

The stimulus/response functions of 95 single lateral line afferents were determined by increasing the flow from a low background flow rate (0.15 cm s^{-1}) to one of eight stimulus flow rates (0.5, 1, 1.5, 2, 2.5, 3, 3.5 or 4 cm s^{-1}). The response of a single fibre was measured once at each stimulus flow

rate. The presentation of different stimulus flow rates was randomised. Thirty-one of these primary afferents were further tested with the above stimulus flow rates in elevated background flows of 2 and 3 cm s^{-1}, respectively. Furthermore, 21 single afferents were repeatedly tested (10 times) with one of three stimulus flow rates (1, 2 or 3 cm s^{-1}) at a low background flow (0.15 cm s^{-1}). Stimulus delivery, i.e. valve control, stimulus measurement and spike collection, was synchronised by a computer.

Flow profiles

For stimulus quantification, the stimulus flow profile was measured with a heated-bead thermistor-based flow meter (after Vogel, 1981). The thermistor probes (sensor probe YSI 44101, compensator probe YSI 44001A) were stationed approximately 4 cm lateral of and level with the snout of the eel. The voltage output of the flow meter was digitised at 100 Hz and stored on a computer for later analysis. The voltage output of the flow meter was calibrated by video-taping and measuring the distance travelled by 100 µm neutrally buoyant plastic particles at each flow rate (Piolite, Goodyear Corp.; Breithaupt and Ayres, 1998). Flow meter output and flow rate were highly correlated (r^2=0.99). The resulting calibration curve showed the typical exponential relationship, thus making it difficult to convert voltage output into flow rate at higher flow rates. Particle visualisation of the flow profiles in the tank without the eel present indicated that flow at the position of the eel's head (during experiments) was reasonably smooth, although small-scale turbulence could be seen. The bottom boundary layer had little effect on flow rates at the level of the eel's head. In contrast, flow rates in the top boundary layer were significant lower. Therefore, we did not record from neuromasts close to the air/water interface.

Fig. 2 shows 10 superimposed flow profiles for three different flow rates (1, 2 or 4 cm s^{-1}). Increased flow reached the eel's head region within 2 s after valve opening, 90 % of maximum flow within 2 s, and maximum flow within 5 s. The maximum flow rate did not vary by more than 10 %. Flow returned to the pre-stimulus rate within 5–10 s.

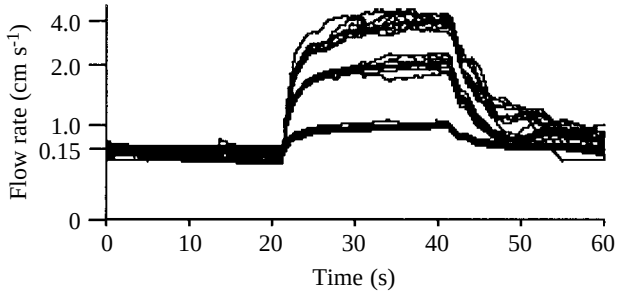

Fig. 2. Flow profiles measured in the recording section of the flow tank (see Fig. 1) by a thermistor-based flow meter (after Vogel, 1981). The flow profiles are recorded as the voltage output of the flow meter. The ordinate values indicate the approximate maximum flow rates. After 20 s, the background flow rate (0.15 cm s^{-1}) was increased to 1, 2 or 4 cm s^{-1} for 20 s; ten repetitions for each flow rate are superimposed.

Results

Full stimulus/response functions were obtained from 95 primary afferents, and in 31 of these fibres stimulus response functions were measured at three different background flow rates. In addition, we recorded in 21 afferents the responses to 10 repeated stimulations at three different flow rates. These 21 afferent fibres had peak responses that varied by less than 20 % (coefficient of variation). The experimental arrangement and on-line stimulus measurements allowed us to deliver highly reproducible flows that resulted in similar responses in a single afferent fibre (Fig. 3).

Stimulus profiles and responses in a single afferent fibre

Each plot in Fig. 4A exemplifies the measured stimulus profile (upper portion) and the corresponding peristimulus-time histogram of a single afferent fibre (lower portion) obtained at three different background flows (0.15, 2 and 3 cm s^{-1}). Typically, single afferents showed constant spiking activity during constant flow and increased or decreased spiking activity according to the change in flow rate, i.e. responses in single fibres followed the stimulus profile with no obvious adaptation (tonic responses). Each graph in Fig. 4B summarises the column above: constant pre-stimulus activity and a linear increase in response magnitude in response to increased flow rates. Similarly, increased background flows caused a downward shift in stimulus/response functions.

Population responses to the lowest background flow

Of the 95 fibres tested, 32 showed no or little pre-stimulus activity (<1 spike s^{-1}) at the lowest background flow (0.15 cm s^{-1}). Activity varied from 0 to 20 spikes s^{-1} (median

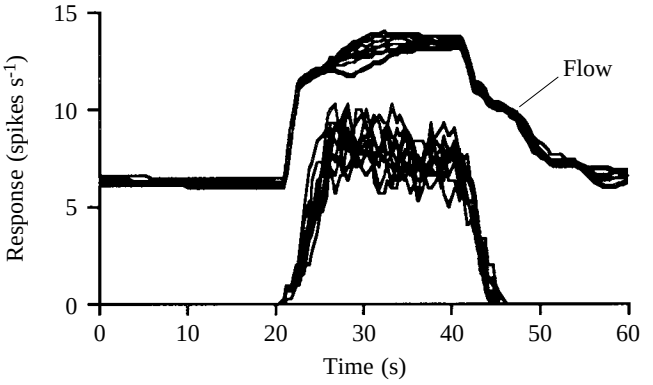

Fig. 3. Response reliability of a single anterior lateral line afferent fibre to repeated stimulation. Ten flow profiles (upper traces) are superimposed. The corresponding spike activity (lower traces) in each stimulation was binned (500 ms bins) and smoothed (three-point running average). The flow was increased (from 0.15 to 4 cm s^{-1}) between t=20 s and t=40 s.

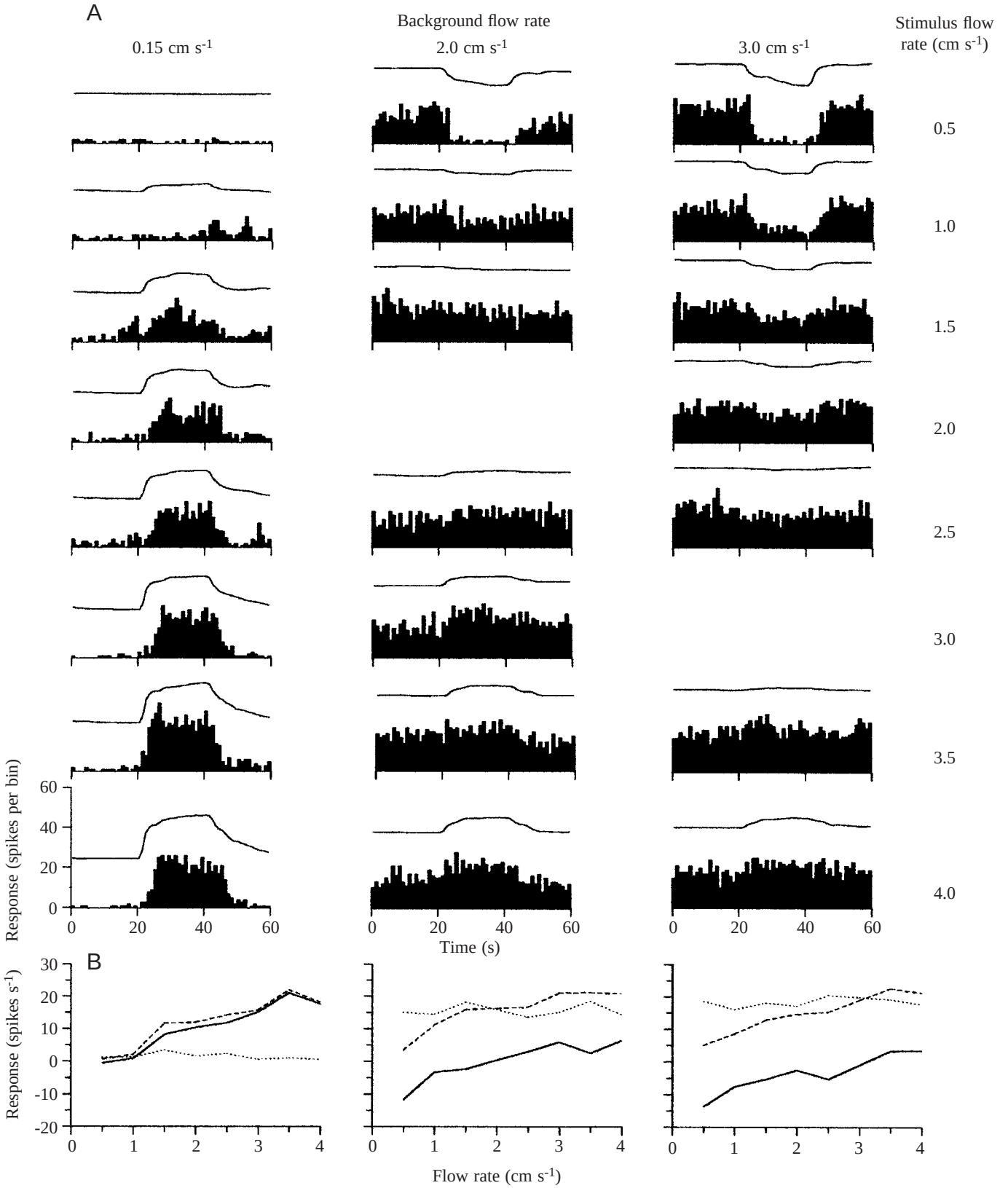

Fig. 4

2.2 spikes s^{-1}; mean 5.7 spikes s^{-1}), with no definable groups. Of these 95 fibres, 70 were found to be flow-sensitive, with the remaining fibres being flow-insensitive. Fibres were deemed to be flow-sensitive if the spike activity during the stimulus

Fig. 4. (A) Peristimulus-time histograms of a single lateral line afferent fibre stimulated at three different background flow rates (0.15, 2 or 3 cm s^{-1}). After 20 s, the background flow was changed for 20 s to one of eight stimulus flows ranging between 0.5 and 4 cm s^{-1}; in addition, 20 s of the post-stimulus period are shown. Responses are shown as the number of spikes in 1 s bins. The top line in each plot represents the flow profile measured by a thermistor-based flow meter. (B) Responses of a single lateral line afferent fibre to different stimulus flow rates at three different background flow rates. Responses (solid line) were evaluated as the difference between the number of spikes occurring during the pre-stimulus (the number of spikes in the first 20 s; dotted line) and stimulus (the number of spikes occurring between t=20 s and t=40 s; dashed line) periods. Responses are given as the number of spikes per bin (A), per second (B).

response period exceeded that during the pre-stimulus period by two standard deviations (Mogdans et al., 1997).

Responses to increased flow rates

Of 95 anterior lateral line afferents, 70 showed varying degrees of increases in response magnitude to increased flow rates, while the responses of three fibres decreased in magnitude (data not included). Twenty-five afferents did not respond to changes in flow rate (Fig. 5). In addition, we identified 15 fibres that were silent and did not respond to increases in flow (they are not included in the following analysis). Most flow-sensitive fibres showed a linear increase in response magnitude with increased flow rates, i.e. 62 afferents gave a maximum response at a flow rate of 4 cm s^{-1}, while the response of eight peaked at 3.5 cm s^{-1}. The slopes of stimulus/response functions were calculated over all stimulus flow rates and varied from 0 to 10.5 spikes s^{-1}. Again, no groups were obvious. Thresholds of single afferents varied widely (Table 1). Most flow-sensitive afferents (approximately 80 %) had thresholds below a flow rate of 3.0 cm s^{-1}.

Effects of background flow rate on population responses

The mean population responses of 31 single lateral line afferents both increased and decreased linearly according to changes in flow rates (Fig. 6). The mean slope of the stimulus/response function of the 70 flow-sensitive afferents at the lowest background flow was 4.7±0.29 spikes s^{-1} (mean ± S.E.M.). The mean slope for the 10 afferents with the steepest slopes was 8.7±0.27 spikes s^{-1}. For the 31 afferents tested at three different background flows, the mean slopes were 5.0±0.41 spikes s^{-1} at 0.15 cm s^{-1}, 4.3±0.29 spikes s^{-1} at 2.0 cm s^{-1} and 3.9±0.27 spikes s^{-1} at 3.0 cm s^{-1} (Fig. 6). The ten afferents with the steepest slopes at the lowest flow rate had mean slopes of 7.6±0.58, 5.6±0.51 and 5.1±0.3 spikes s^{-1}, respectively.

Although not all fibres were tested for their sensitivity to light, the activity of two of the 70 afferents was found to be affected when the ipsilateral eye was stimulated with a bright light. In these two fibres, bright light projected onto the ipsilateral eye caused their activity in response to background and stimulus flow rates to increase. Münz (1985) found similar responses in the cichlid *Sarotherodon niloticus* and assumed

Table 1. *Thresholds of 70 flow-sensitive primary afferent fibres*

Flow rate (cm s^{-1})	Number of afferents
0.5	1
1.0	11
1.5	27
2.0	8
2.5	16
3.0	0
3.5	7
4.0	0

Threshold was defined as the flow rate at which the response activity in each fibre exceeded the mean background activity by two standard deviations (Mogdans et al., 1997).

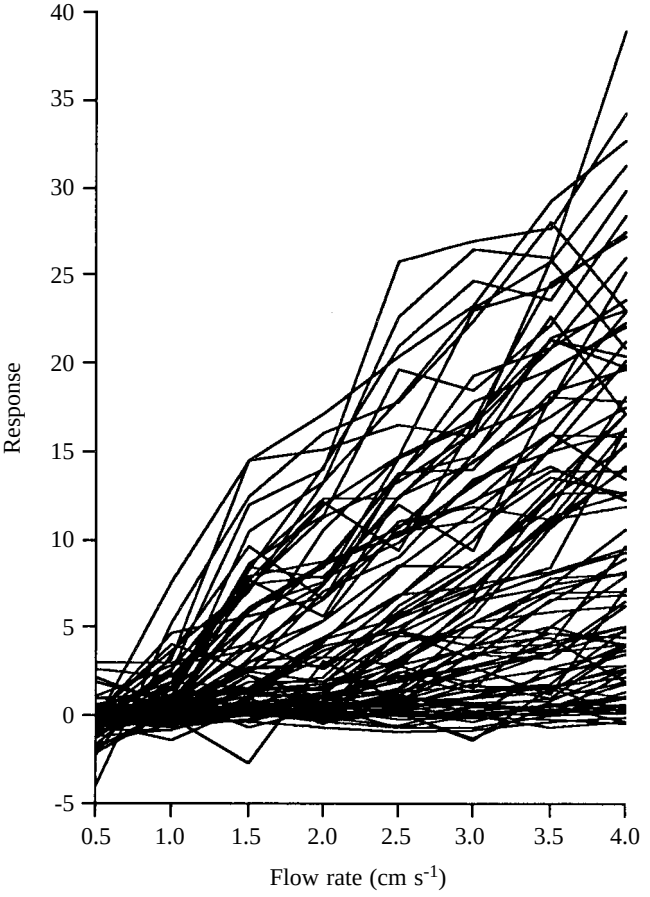

Fig. 5. Stimulus/response functions of 95 single anterior lateral line afferent fibres. Responses are shown as the difference between pre-stimulus spike activity (the number of spikes in first 20 s) at a low background flow rate (0.15 cm s^{-1}) and stimulus spike activity (the number of spikes occurring between t=20 s and t=40 s) at eight different stimulus flow rates. Response is given as the number of spikes per second.

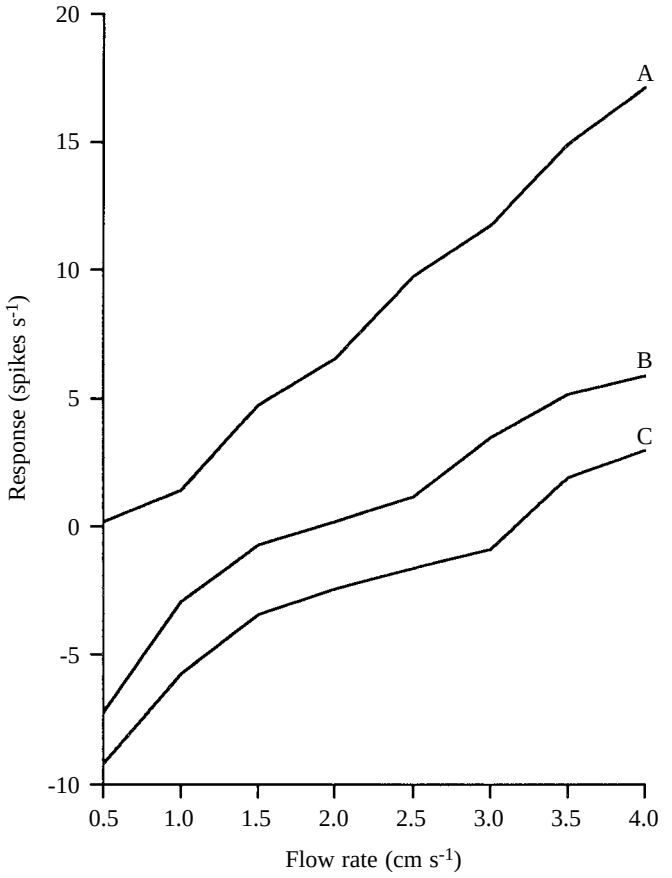

Fig. 6. Mean stimulus/response functions of 31 single lateral line afferent fibres in three different background flows: (A) 0.15 cm s^{-1}, (B) 2 cm s^{-1} and (C) 3 cm s^{-1}. For each fibre, the responses are calculated as the difference between pre-stimulus spike activity (the number of spikes in 20 s) at the background flow rate and stimulus spike activity (the number of spikes in 20 s) at different stimulus flow rates. Response is given as the number of spikes per second.

that some of these fibres belonged to the efferent system. Ronan and Bodznick (1991) reported photosensitive responses in afferents of the posterior lateral line nerve in larval sea lampreys *Petromyzon marinus*. In our study, these afferents responded to all flow rates and resembled other flow-sensitive fibres; they are unlikely, therefore, to be efferent fibres.

Discussion

Responses of lateral line afferents to flow

This study is the first attempt to quantify the responses of primary afferent fibres of the anterior lateral line system to water flow (streaming water). Using extracellular recording techniques, we measured the responses of 95 afferent fibres in the New Zealand long-fin eel *Anguilla dieffenbachii*. Seventy of these fibres responded to water flow. The sensitivity of these fibres varied widely (threshold and slope of the stimulus/response functions), ranging from low-threshold/steep-slope to high-threshold/shallow-slope responses. The remaining 25 fibres failed to show any response over the range of flow rates tested. These results suggest the existence of two distinct populations of anterior lateral line fibres, which either are flow-sensitive or flow-insensitive. Similar results have been described in frequency/response studies, in which velocity- and acceleration-sensitive fibres were identified (Münz, 1985; Kroese and Schellart, 1992; Coombs and Janssen, 1990; Montgomery and Coombs, 1992; Coombs and Montgomery, 1994). Although the recording technique used in this and previous studies does not allow identification of the receptor type, the most plausible explanation of the stimulus/response functions found in this study is that flow-sensitive fibres correlate with velocity-sensitive fibres (which presumably innervate superficial neuromasts) and flow-insensitive fibres correlate with acceleration-sensitive fibres (which presumably innervate canal neuromasts). This interpretation is consistent with theoretical (Denton and Gray, 1988, 1989; Kalmijn, 1988, 1989) and behavioural studies of lateral line function (Coombs and Janssen, 1990; Janssen et al., 1990; Montgomery et al., 1997).

Response characteristics and reliability

We repetitively stimulated 21 afferent fibres with approximately identical flows. The responses of flow-sensitive fibres were highly reproducible (Fig. 3). The response profile of a single afferent fibre resembles the measured stimulus flow profile: constant flow elicited a tonic response and caused no apparent degree of sensory adaptation, while increased flow caused an increase in response magnitude. To our knowledge, this is the first time such responses have been demonstrated in lateral line afferents. Similar responses have been demonstrated in gravity-sensitive otoconial afferents in the bullfrog *Rana catesbetana* (Baird and Lewis, 1986).

Tonic responses in flow-sensitive fibres suggest that such fibres innervate velocity-sensitive superficial neuromasts. Water motion over the cupula bends the underlying hair cells. Superficial neuromasts are friction-coupled to water motion such that displacement of the cupula is proportional to flow rate (van Netten and Kroese, 1989). In our experiments, the flow rate during the pre-stimulus and stimulus periods was constant (excluding micro-turbulence). Therefore, the mechanical force applied to the underlying hair cells was maintained, resulting in non-adapting responses. Theoretically, the filter properties of canal neuromasts would result in phasic responses, i.e. fibres should respond only to the onset and offset of the flow. In this study, phasic responses were not observed; however, some of the 25 flow-insensitive fibres may innervate canal neuromasts. Furthermore, seven fibres with high thresholds (3.5 cm s^{-1}) may also innervate canal neuromasts because the most anterior pores of the supra- and infraorbital canals face directly into the flow. Here, the filter properties of the canals may be overcome at sufficiently high flow rates, causing fluid movement inside the canals and resulting in high-threshold/shallow-slope responses.

Response characteristics of superficial neuromasts

Lateral line neuromasts are directionally sensitive. In most

teleosts, the axis of maximum sensitivity corresponds with the long axis of the sensory strip (Coombs et al., 1988, 1992; Janssen et al., 1987; Webb, 1989; Song and Northcutt, 1991; Coombs and Montgomery, 1994). Directional sensitivity has been demonstrated in surface-feeding fish (*Aplocheilus lineatus*; Bleckmann et al., 1989) and amphibians (*Xenopus laevis*; Görner and Mohr, 1989), in which the response magnitude increases as stimulus direction becomes more aligned with the axis of maximum sensitivity.

Superficial neuromasts distributed over the head in many teleosts show variable orientations (Janssen et al., 1987; Song and Northcutt, 1991; Coombs and Montgomery, 1994). Anterior superficial neuromasts in *A. dieffenbachii* also display variable orientations, especially those found on the nose and mandible (A. G. Carton, personal observation). Considering the directional sensitivity and variable orientations, the anterior superficial neuromast population seems to be well suited to respond to water flow from many different directions (Janssen et al., 1987).

Theoretically, flow direction could be determined by comparing the responses of differently orientated neuromasts within the anterior population (Janssen et al., 1987; Webb, 1989): neuromasts orientated with their axis of maximum sensitivity parallel to the flow will respond maximally, while neuromasts orientated orthogonal to the flow will respond minimally (Janssen et al., 1987; Webb, 1989). The anterior superficial neuromasts of *A. dieffenbachii* display directional tuning and may, therefore, form the basis for determining water flow direction. In this study, flow direction remained unchanged with respect to the longitudinal axis of the eel. The variable orientation of anterior superficial neuromasts, coupled with their directional sensitivity, may account for the variable stimulus/response functions. The most flow-sensitive fibres, displaying the lowest thresholds (0.5–1.0 $cm\,s^{-1}$) and steepest slopes, are most likely to be superficial neuromasts orientated parallel to the direction of the flow. Superficial neuromasts orientated orthogonal to the flow direction would presumably show minimal responses, while neuromasts orientated at 45° to the flow direction would show intermediate flow-sensitivity, displaying mid-range thresholds (1.5–2.5 $cm\,s^{-1}$) and slopes.

Responses at different background flows

Flow-sensitive fibres function as absolute rather than relative detectors of flow rate. At different background flows, the slopes of the stimulus/response functions were not altered, a consequence of the non-adapting responses to both background and stimulus flows. Similar shifts of stimulus/response functions have been described in the auditory system of the cat (Costalupes et al., 1984), suggesting that the dynamic range of flow-sensitive fibres remains unchanged in the presence of high background flows. In the most sensitive fibres, high background flows may limit the discrimination of similar stimulus flow rates as the fibre firing rate saturates at higher background flows. The responses of most flow-sensitive fibres did not saturate at the maximum flow rate, i.e. the slope of their response functions was approximately linear over the range of flows tested. This raises a question concerning the dynamic range of flow-sensitive fibres. The directional selectivity and variable orientation of anterior superficial neuromasts may also form the basis of range fractionation. In addition, the dynamic range of superficial neuromasts may be regulated by cellular properties and efferent control, resulting in different response thresholds and slopes.

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References

Baird, R. A. and Lewis, E. R. (1986). Correspondences between afferent innervation patterns and response dynamics in the bullfrog utricle and lagena. *Brain Res.* **369**, 48–64.

Blaxter, J. H. S. and Fuiman, L. A. (1989). Function of the free neuromasts of marine teleost larvae. In *The Mechanosensory Lateral Line. Neurobiology and Evolution* (ed. S. Coombs, P. Görner and H. Münz), pp. 481–499. New York: Springer-Verlag.

Bleckmann, H. (1993). Role of the lateral line in fish behavior. In *Behaviour of Teleost Fishes* (ed. T. J. Pitcher), pp. 177–202. London: Chapman & Hall.

Bleckmann, H., Breithaupt, T., Blickhan, R. and Tautz, J. (1991). The time course and frequency content of hydrodynamic events caused by moving fish, frogs and crustaceans. *J. Comp. Physiol.* A **168**, 749–757.

Bleckmann, H., Gottfried, T. and Blubaum-Gronau, E. (1989). The lateral line system of surface-feeding fish: Anatomy, physiology and behavior. In *The Mechanosensory Lateral Line. Neurobiology and Evolution* (ed. S. Coombs, P. Görner and H. Münz), pp. 501–526. New York: Springer-Verlag.

Breithaupt, T. and Ayers, J. (1998). Visualization and quantification of biological flow fields through video-based digital motion-analysis techniques. *Mar. Freshwater Behav. Physiol.* **31**, 55–61.

Coombs, S. and Janssen, J. (1990). Behavioural and neurophysiological assessment of lateral line sensitivity in the mottled sculpin, *Cottus bairdi*. *J. Comp. Physiol.* A **167**, 557–567.

Coombs, S., Janssen, J. and Montgomery, J. (1992). Functional and evolutionary implications of peripheral diversity in lateral line systems. In *The Evolutionary Biology of Hearing* (ed. D. B. Webster, R. R. Fay and A. N. Popper), pp. 267–294. New York: Springer-Verlag.

Coombs, S., Janssen, J. and Webb, J. F. (1988). Diversity of lateral line systems: Evolutionary and functional considerations. In *Sensory Biology of Aquatic Animals* (ed. J. Atema, R. R. Fay, A. N. Popper and W. N. Tavolga), pp. 553–593. New York: Springer-Verlag.

Coombs, S. and Montgomery, J. C. (1994). Function and evolution of superficial neuromasts in an Antarctic notothenioid fish. *Brain Behav. Evol.* **44**, 287–298.

Costalupes, J. A., Young, E. D. and Gibson, D. J. (1984). Effects of continuous noise backgrounds on rate response of auditory nerve fibres in cat. *J. Neurophysiol.* **51**, 1326–1344.

Denton, E. J. and Gray, J. A. B. (1988). Mechanical factors in the

excitation of the lateral lines of fishes. In *Sensory Biology of Aquatic Animals* (ed. J. Atema, R. R. Fay, A. N. Popper and W. N. Tavolga), pp. 595–617. New York: Springer-Verlag.

Denton, E. J. and Gray, J. A. B. (1989). Some observations on the forces acting on neuromasts in fish lateral line canals. In *Mechanosensory Lateral Line. Neurobiology and Evolution* (ed. S. Coombs, P. Görner and H. Münz), pp. 229–246. New York: Springer-Verlag.

Flock, A. (1971). Sensory transduction in hair cells. In *Handbook of Sensory Physiology*, vol. I, *Principles of Receptor Physiology* (ed. W. R. Loewenstein), pp. 396–441. New York: Springer-Verlag.

Görner, P. and Mohr, C. (1989). Stimulus localization in *Xenopus*: Role of directional sensitivity of lateral line stitches. In *The Mechanosensory Lateral Line. Neurobiology and Evolution* (ed. S. Coombs, P. Görner and H. Münz), pp. 543–560. New York: Springer-Verlag.

Hassan, E. S. (1989). Hydrodynamic imaging of the surroundings by the lateral line of the blind cave fish *Anoptichthys jordani*. In *The Mechanosensory Lateral Line: Neurobiology and Evolution* (ed. S. Coombs, P. Görner and H. Münz), pp. 217–228. New York: Springer-Verlag.

Hoekstra, D. and Janssen, J. (1985). Non-visual feeding behaviour of the mottled sculpin, *Cottus bairdi* in Lake Michigan. *Env. Biol. Fish.* **12**, 111–117.

Janssen, J., Coombs, S., Hoekstra, D. and Platt, C. (1987). Anatomy and differential growth of the lateral line system of the mottled sculpin, *Cottus bairdi* (Scorpaeniformes: Cottidae). *Brain Behav. Evol.* **30**, 210–229.

Janssen, J., Coombs, S. and Pride, S. (1990). Feeding and orientation of the mottled sculpin, *Cottus bairdi*, to water jets. *Env. Biol. Fish.* **29**, 43–50.

Kalmijn, A. J. (1988). Hydrodynamic and acoustic field detection. In *Sensory Biology of Aquatic Animals* (ed. J. Atema, R. R. Fay, A. N. Popper and W. N. Tavolga), pp. 83–130. New York: Springer-Verlag.

Kalmijn, A. J. (1989). Functional evolution of lateral line and inner ear sensory systems. In *Mechanosensory Lateral Line. Neurobiology and Evolution* (ed. S. Coombs, P. Görner and H. Münz), pp. 187–215. New York: Springer-Verlag.

Kroese, A. B. A. and Schellart, N. A. M. (1992). Velocity- and acceleration-sensitive units in the trunk lateral line of the trout. *J. Neurophysiol.* **68**, 2212–2221.

McCormick, C. A. (1989). Central lateral line mechanosensory pathways in bony fish. In *Mechanosensory Lateral Line. Neurobiology and Evolution* (ed. S. Coombs, P. Görner and H. Münz), pp. 341–364. New York: Springer-Verlag.

McDowell, R. M. (1990). *New Zealand Freshwater Fishes. A Natural History and Guide*. Auckland: Heinemann Reed.

Meredith, G. E., Roberts, B. L. and Suharti, M. (1987). Distribution of afferent fibres in the brainstem from end organs in the ear and lateral line in the European eel. *J. Comp. Neurol.* **265**, 507–520.

Mogdans, J., Bleckmann, H. and Menger, N. (1997). Sensitivity of central units in the goldfish, *Carassius auratus*, to transient hydrodynamic stimuli. *Brain Behav. Evol.* **50**, 261–283.

Montgomery, J. C., Baker, C. F. and Carton, A. G. (1997). The lateral line can mediate rheotaxis in fish. *Nature* **389**, 960–963.

Montgomery, J. C. and Coombs, S. (1992). Physiological characterisation of lateral line function in the Antarctic fish *Trematomus bernacchii. Brain Behav. Evol.* **40**, 209–216.

Montgomery, J. C. and Coombs, S. (1998). Peripheral encoding of moving sources by the lateral line system of a sit-and-wait predator. *J. Exp. Biol.* **201**, 91–102.

Montgomery, J., Coombs, S. and Halstead, M. (1995). Biology of the mechanosensory lateral line in fishes. *Rev. Fish Biol. Fish.* **5**, 399–416.

Montgomery, J. C. and Hamilton, A. R. (1997). Sensory contributions to nocturnal prey capture in the dwarf scorpian fish (*Scorpaena papillosus*). *Mar. Freshwater Behav. Physiol.* **30**, 209–223.

Münz, H. (1985). Single unit activity in the peripheral lateral line system of the cichlid fish *Sarotherodon niloticus* L. *J. Comp. Physiol* A **157**, 555–568.

Münz, H. (1989). Functional organisation of the lateral line periphery. In *The Mechanosensory Lateral Line. Neurobiology and Evolution* (ed. S. Coombs, P. Görner and H. Münz), pp. 17–78. New York: Springer-Verlag.

Partridge, B. L. and Pitcher, T. J. (1980). The sensory basis of fish schools; relative roles of lateral line and vision. *J. Comp. Physiol.* **135**, 315–325.

Roberts, B. L. and Meredith, G. E. (1989). The efferent system. In *The Mechanosensory Lateral Line. Neurobiology and Evolution* (ed. S. Coombs, P. Görner and H. Münz), pp. 445–460. New York: Springer-Verlag.

Ronan, M. C. and Bodznick, D. (1991). End buds: Non-ampullary electroreceptors in adult lampreys. *J. Comp. Physiol* A **158**, 9–16.

Song, J. and Northcutt, G. R. (1991). Morphology, distribution and innervation of the lateral-line receptors of the Florida gar, *Lepisosteus platyrhincus*. *Brain Behav. Evol.* **37**, 10–37.

van Netten, S. M. and Kroese, A. B. A. (1989). Dynamic behavior and micromechanical properties of the cupula. In *The Mechanosensory Lateral Line: Neurobiology and Evolution* (ed. S. Coombs, P. Görner and H. Münz), pp. 247–264. New York: Springer-Verlag.

Vogel, S. (1981). *Life in Moving Fluids. The Physical Biology of Flow*. Boston: Willard Grant Press.

Webb, J. F. (1989). Neuromast morphology and lateral line trunk canal ontogeny in two species of cichlids: An SEM study. *J. Morph.* **202**, 53–68.

Zacchei, A. M. and Tavolaro, P. (1988). Lateral line system during the life cycle of *Anguilla anguilla* L. *Boll. Zool.* **55**, 145–154.