PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

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Phil. Trans. R. Soc. Lond. B 2000 **355**, 1325-1327
doi: 10.1098/rstb.2000.0693

THE ROYAL SOCIETY

doi 10.1098/rstb.2000.0693

Sensory processing of water currents by fishes

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Water currents are extremely important in the aquatic environment and play a very significant role in the lives of fishes. Sensory processing of water currents involves a number of sensory modalities including the inner ear, vision, tactile sense and the mechanosensory lateral line. The inner ear will detect whole-body accelerations generated by changes in flow, or by turbulence, whereas visual and tactile inputs will signal translational movement with respect to an external visual or tactile reference frame. The superficial neuromasts of the mechanosensory lateral line detect flow over the surface of the body and have the appropriate anatomical distribution and physiological properties to signal the strength and the direction of flow and, hence, contribute to the detection of regional differences in flow over different parts of the body.

Keywords: water currents; sensory processing; superficial neuromasts; inner ear; vision; tactile sense

1. INTRODUCTION

Water currents in the aquatic environment provide a structuring influence arguably of comparable importance to gravity and light. Large-scale currents structure the temperature and productivity of the oceans and transport animals over great distances. Mesoscale currents and gyres likewise influence physical parameters, areas of local productivity and faunal distributions. Tidal currents and turbulence too are of great importance, generating, amongst other things, the patchiness seen in the distribution of planktonic organisms (Abraham 1998). On the shore, wave-generated currents dictate the faunal composition, and in rivers and streams, flow regimes again dominate many aspects of the biology. Given their undeniable importance, it is not surprising to find that aquatic organisms are well equipped anatomically, physiologically and behaviourally to detect, respond to and take advantage of water currents.

2. IMPORTANCE OF WATER CURRENTS

Recent studies continue to document the importance of water currents in many aspects of the lives of fishes. For example, in diadromous fishes, flow direction and rate provide essential cues during migrations. The early stages of upstream migration of sockeye salmon and glass eels are synchronized with the appropriate tidal cycle (Levy & Cadenhead 1995), while movements of migrating silver eels in the lower reaches of rivers and estuaries appear to be synchronized with ebbing tides (Parker & McCleave 1997). Furthermore, many stream-dwelling fishes select microhabitats based on species-specific preferences for one or more hydrodynamic parameters. These preferences can result in spatial variations of species abundance that can be attributed to variations in water depth and velocity (Jowett & Richardson 1995; Harding *et al.* 1998). Drifting food items are most easily intercepted by a fish orientated towards the prevailing flow. Therefore, food availability and energetic cost of searching are also dependent on flow conditions (Montgomery *et al.* 1995). Accordingly, many species use current–velocity shelters, created by substrate heterogeneity. Fishes hold low-velocity positions that are adjacent to high-velocity flows and that provide an abundance of invertebrate drift (Fausch 1993). This reduces the energetic cost of holding station without affecting the frequency of foraging attempts, thereby increasing the net energy gain (McLaughlin & Noakes 1998). Determination of flow direction may also be an important component of olfactory-search strategies. In sharks, food odour induces an olfactory-released rheotaxis. On detecting the odour the shark swims up-current towards the general area of the stimulus source (Hodgson & Mathewson 1978). Although the sensory mechanisms mediating many of these behaviours are still unknown, these examples serve to illustrate the importance of water currents to fishes.

3. THE ROLE OF SUPERFICIAL NEUROMASTS

Without an external reference frame, a fish embedded within a large-scale current and moving at a constant velocity has no basis on which to determine its movement with the current. Accelerations, due to unsteady flows or turbulence, could be detected by the otolith organs of the inner ear. However, rheotaxis, or orientation to water currents, has traditionally been thought to be mediated by sensory information signalling movement relative to some external reference. For a fish in midwater but close to landmarks, the most potent source of this information is vision, and classical experiments have demonstrated an optokinetic reflex that provides for station holding in a

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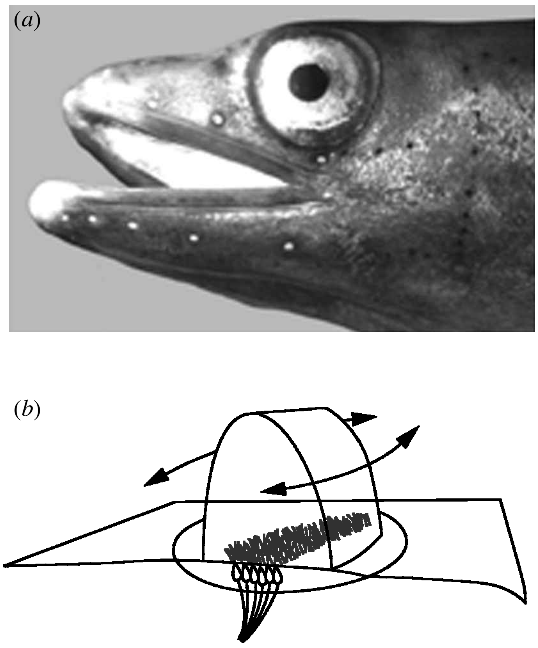

Figure 1. (*a*) Superficial neuromasts of the eel (*Anguilla dieffenbachii*) are located as an array of receptors on the surface of the head. The rows of pigmented dots below and behind the eye are superficial neuromasts. The white openings of the lateral line canals are visible above and below the mouth. (*b*) Each superficial neuromast consists of a patch of hair cells with an overlying cupula. Water flow past the cupula generates a frictional drag that displaces the cupula and the cilia of the hair cells.

stream alongside visual landmarks. For benthic fishes, additional information is available from contact slippage with the substrate, induced by passive movement in the current. In addition to visual and tactile information, a recent study shows that superficial neuromasts of the mechanosensory lateral line make a significant contribution to rheotaxis (Montgomery *et al.* 1997).

Superficial neuromasts consist of patches of hair cells on the body surface where the cilia of the hair cells are embedded in a gelatinous cupula (figure 1). The hair cells are displacement sensitive and the cupula is friction coupled to the surrounding water, hence cupula displacement is a function of the velocity of water flow over the body, and superficial neuromasts can act as flow-velocity detectors. The presence of flow detectors on the surface of the body allows benthic fishes to detect stream flow at velocities that are insufficient to displace them across the substrate. Ablation of the superficial neuromasts leads to a substantial increase in the threshold flow for rheotactic behaviour (Montgomery *et al.* 1997).

Hair-cell-based systems can be extremely sensitive, and the above experiments also demonstrate that fishes can detect flows at levels well below those that induce an upstream-orientation behaviour. For example, blind cave-fishes (*Astyanax fasciatus*) show a rheotactic threshold at flow velocities of 2–3 $\mathrm{cm\,s^{-1}}$, but a diffuse olfactory stimulus added to the water drops the threshold to $< 0.4\ \mathrm{cm\,s^{-1}}$ (Montgomery *et al.* 1997). This demonstration also alerts us to the fact that although the principal sensory input that mediates station holding in pelagic fishes may be visual, the mechanosensory lateral line will also be providing information on flow velocity and other flow characteristics.

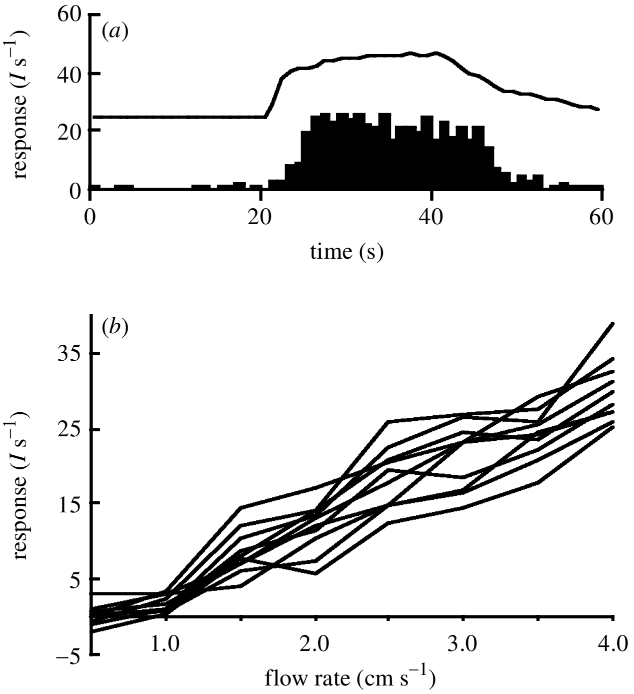

Figure 2. (*a*) Peristimulus histogram of spike activity in a single anterior lateral line afferent fibre. The upper trace is the output of the flow meter rising from the background flow of 0.5 $\mathrm{cm\,s^{-1}}$ to 4 $\mathrm{cm\,s^{-1}}$. (*b*) The stimulus response functions of the ten most sensitive fibres.

What are the response properties of superficial neuromasts to flow? This question has been answered in the New Zealand long-fin eel, *Anguilla dieffenbachii*. Animals were anaesthetized and decerebrated before the posterior dorsal cranium was removed to expose the anterior lateral line nerve adjacent to the edge of the brain (these procedures are approved by the University of Auckland Animal Ethical Committee). Eels were then placed in a computer-controlled flume with the dorsal surface of the head exposed allowing micro-electrode penetration of the nerve to record the activity of single lateral line afferent fibres. The results of this study show that many lateral line afferent fibres show a tonic non-adapting response to step increases in flow rate (figure 2). The ten most sensitive fibres had threshold responses of around 0.5–1.0 $\mathrm{cm\,s^{-1}}$ and the mean slope of the stimulus response profiles of these same fibres was around 8.7 ± 0.27 $(\mathrm{spikes\,s^{-1}})/(\mathrm{cm\,s^{-1}})$. No evidence of response saturation was observed over the applied stimulus range of 0.5–4 $\mathrm{cm\,s^{-1}}$.

These response properties of lateral line receptors provide an adequate basis for the observed contribution of the lateral line to rheotactic behaviour. The required sensitivity to generate behavioural responses to flows of $< 0.4\ \mathrm{cm\,s^{-1}}$ is already present in the responses of single afferent fibres. In many sensory systems the behavioural sensitivities greatly exceed those found in electrophysiological thresholds, so it might be expected that flows of much less than 0.4 $\mathrm{cm\,s^{-1}}$ can be detected by fishes.

Lateral line receptors (presumed to be superficial neuromasts) show a linear response up to the maximum flows that could be generated in the test flume. However, at higher flows, these responses would be expected to saturate. Superficial neuromasts have an axis of maximum sensitivity that is aligned with the directional sensitivity of the hair-cell populations in the sensory epithelium. As the angle of the stimulus shifts from aligned with that axis to orthogonal to it, the response of the neuromast drops off, approximately following a cosine function. Having a preferred axis of sensitivity, or directional tuning, may extend the dynamic range of the flow-detection system and should also form the basis of determining water-flow direction.

4. DETERMINATION OF REGIONAL VARIATIONS

Superficial neuromasts provide an array of sensors over the surface of the body. How these inputs are handled centrally is as yet unknown. However, as suggested above, integration of inputs from several, or many, neuromasts may improve the sensitivity of the system and integration of inputs from neuromasts of different orientations would be required to decode flow direction. Once current direction and strength are known at different positions on the body, it then becomes possible to determine regional variations in flow across different parts of the body. In this way information from superficial neuromasts may be important in detecting flow gradients or areas of current shear. Regional differences in flow should also stimulate canal neuromasts, since by Bernoulli's principle differences in flow across adjacent canal pores should produce flow within the canal. So it is certainly possible that both canal and superficial neuromasts may make a contribution to the detection of flow gradients or areas of current shear.

5. CONCLUSION

The sensory processing of water currents by fishes is a multimodal sensory task. Inner ear, vision, tactile sense and mechanosensory systems all make significant contributions. In addition to this, information on water currents is linked to other sensory inputs to provide the basis of more complex behaviours such as selective tidal-stream transport, feeding on stream drift, olfactory-released rheotaxis and olfactory search. In these ways sensory processing of water currents contributes to many multimodal sensory behaviours and makes an important contribution to the general sensory processing of the aquatic environment.

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