Sensory Ecology and Neuroethology of the Lateral Line

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1 Introduction

The lateral line is found in all fish groups, and aquatic amphibians. Like hearing, it is a hair-cell based mechanoreceptor system. But in contrast to hearing, it is a distributed sensory system, with clusters of hair cells grouped into neuromasts dispersed over the head and trunk of the animal. The distributed nature of the lateral line sensors (see Webb, Chapter 2) provides some similarities with touch, and indeed the early description of the lateral line system as providing "touch at a distance" is still remarkably apt (Dijkgraaf, 1934). It is the dense, viscous nature of water interacting with the cupulae of the neuromasts that allows animals with lateral lines to 'feel' their immediate surroundings and to sense water movements

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relative to the body surface such as water currents or the water disturbances caused by other animals.

Like all major sensory systems, the lateral line makes an important contribution to the sensory capabilities of fish and aquatic amphibians and contributes to a wide range of core behaviors including: feeding, avoidance of predators, and communication. In these behaviors, the lateral line is detecting the hydrodynamic fields produced by other animals. Fluid dynamics determines that these source/receiver interactions are relatively short-range in comparison with hearing. Correspondingly, the lateral line provides a short range contribution to multimodal input for basic sensory abilities – namely, the ability to detect, localize, and at least in some respects, identify biological sources of interest. The close-range operation of the lateral line also means that in some instances the behavioral reactions and neural pathways need to be fast and somewhat stereotyped to be effective.

In addition to sensing biotic sources of interest, the lateral line also plays an important role in detecting abiotic or stationary features of the local environment. In blind Mexican cavefish (*Astyanax fasciatus*) though probably in other fish species as well, the fluid flows and pressure changes generated by the animal's own swimming movements get altered by surrounding stationary objects. This provides a stimulus to the lateral line that enables a fish to actively image its environment in a way that is somewhat analogous to active electroreception or echolocation. Large scale, ambient water flows created by wind and gravity are also of obvious importance to aquatic animals and the lateral line allows fish to sense, and orient, to flows, and then in turn, to use this information in combination with other senses to mediate a range of behaviors. Recent work on lateral line has moved into the complex domain of flow fluctuations generated by obstacles in the flow, the swimming activity of other animals including prey and schoolmates, and flows generated by the animal's own swimming.

This chapter will focus on the role of the lateral line in natural fish behavior, in effect, the sensory ecology of the lateral line. The approach is more conceptual than comprehensive, choosing representative behaviors and especially those that lend themselves to a neuroethological analysis. Understanding sensory and brain function in the context of natural behavior is the foundation for neuroethology. It provides a clear focus for the determination of the relevant parameters of the physical stimulus, the physical and physiological mediation of stimulus encoding, and a targeted approach as to how the central nervous system processes and transforms sensory inputs to behavioral action. A comprehensive neuroethological understanding of lateral-line behavior is still some way off, but the approach provides an organizing scaffold from which to work. Elements of this neuroethological framework are also covered in greater depth in other chapters, including those on the morphology and evolution of the lateral line (Webb, Chapter 2), and on information processing by the peripheral (Chagnaud & Coombs, Chapter 6) and central nervous system (Bleckmann & Mogdans, Chapter 8).

2 Surface Feeding (Source localization in 2D)

The water surface provides a nice example of source localization simplified to the case of two dimensions. The air-water interface provides an important food source for a number of fish and amphibian species. Particularly in forested areas, sunlight is captured by the forest canopy which limits the productivity of freshwater systems. In these, and similar, circumstances, insects falling onto the water surface, and struggling in the surface tension layer, provide an important food source (Lang, 1980). During the day, many visual-feeding fish utilize this resource but in addition, there are also some fish like the striped panchax (*Aplocheilus lineatus*) (Fig. 1) that use their lateral line to detect and locate prey on the water surface. Surface feeding fish (Schwartz, 1971), but also the African clawed frog (*Xenopus laevis*) (Görner, 1973), hunt predominantly at night, and can locate surface prey in complete darkness.

Typical wind generated surface waves contain only frequency components below 10 Hz. In contrast an insect struggling at the water surface creates concentric surface waves that have frequencies up to about 100 Hz (Lang, 1980; Bleckmann, 1994; and Fig. 2). Insect generated surface waves propagate out from the source in a series of concentric rings. At the source sizes and target distances relevant to the detection of small prey, the surface waves have a mix of capillary and gravity properties and propagate with well-defined characteristics (Bleckmann & Schwartz, 1982; Bleckmann, 1993). In addition to the concentric nature of the waves, higher frequency wave components travel faster than lower frequency components. Furthermore, higher frequency wave components are attenuated more strongly than lower frequency components during stimulus propagation (Bleckmann et al., 1989). Thus the water surface behaves like a low-pass filter. The depth impact of surface waves is very small. At a depth of one wavelength (e.g. 23.6 mm at 10 Hz and 2.9 mm at 140 Hz) the vertical movement of water particles is less than 1/500 of that observed at the water surface. Therefore whilst foraging in the dark, fish specialized in surface feeding sit with the dorsal surface of their head in the surface film (Fig. 1a). The behaviorally-measured threshold curve to single frequency wave stimuli shows that the surface feeding striped panchax is highly sensitive in the frequency range < 10 up to about 100 Hz (Fig. 3). Even if only a short lasting wave stimulus is presented, i.e. under open loop conditions, surface feeding fish accurately orient towards the source and then move towards it and stop with an accuracy of about 10%. These behavioral responses indicate that information on source direction and distance is encoded by the lateral line.

In the striped panchax the lateral line system across the top of its head consists of a steoeotyped array of 18 neuromasts situated in open grooves (half-formed canals) (Fig. 1b), the borders of which have been described as fleshy ridges (Schwarz et al., 2011). Each neuromast has a unique receptive field (Bleckmann et al., 1989), in part defined by the inherent directional sensitivity of the neuromast, which corresponds to the long axis of the open grooves in which it sits. The inherent directional sensitivity of the neuromast results from the directional properties of its hair cells

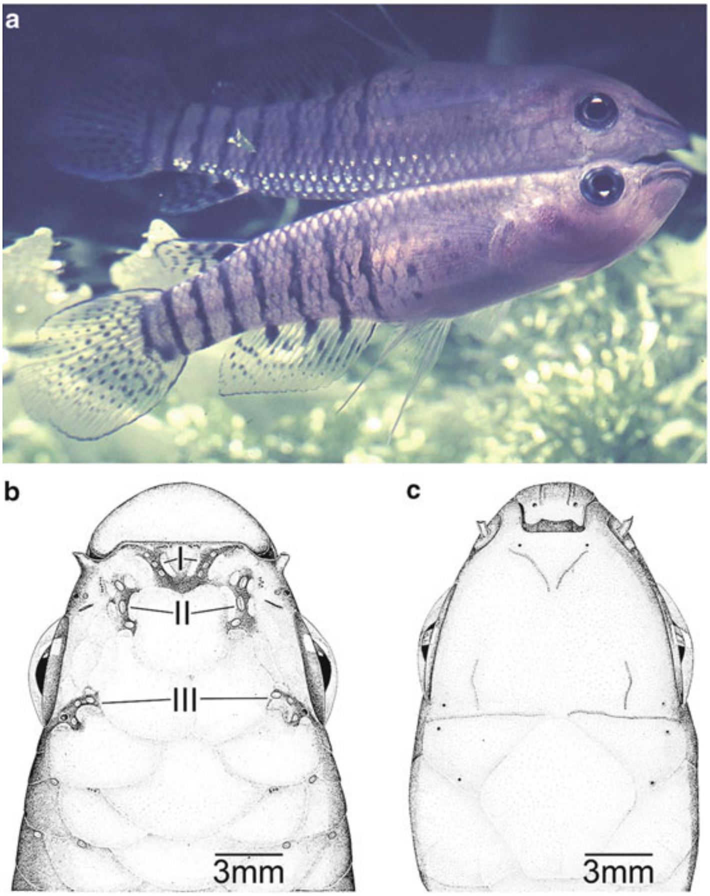

Fig. 1 (**a**-**c**). (**a**) The surface feeding striped panchax *Aplocheilus lineatus*. At night surface feeding fish hunt immediately below the water surface, maximizing their sensitivity to capillary surface waves. B. Dorsal view of the heads of the striped panchax (**b**) and the African butterfly fish *Pantodon bucholzi* (**c**) In striped panchax large dorsal head neuromasts are arranged in three groups (labeled I, II and III from rostral to caudal), each of which consists of three single organs all of which are bordered by fleshy ridges. In the African butterfly fish 6 rows of up to 70 very small (about 50 x 30 μm) superficial neuromasts are seen. The cephalic lateral line of the African butterfly fish in addition has 8 large banana shaped canal neuromasts (each of which has up to 3000 hair cells) situated below membranous coverings of widened head lateral line canals (Bleckmann et al., 1989). The drawings of both fish species were kindly provided by G. Tittel

and the fact that each hair cell responds maximally to displacement of the neuromast cupula in a single direction, producing a cosine response characteristic with respect to directional stimulation (Flock, 1965; Bleckmann et al., 1989; Chagnaud & Coombs, Chapter 7). As in other fish, there are two populations of hair cells within each neuromast, each aligned on the same axis, but with opposite polarities and directional sensitivities. The open canal grooves described above

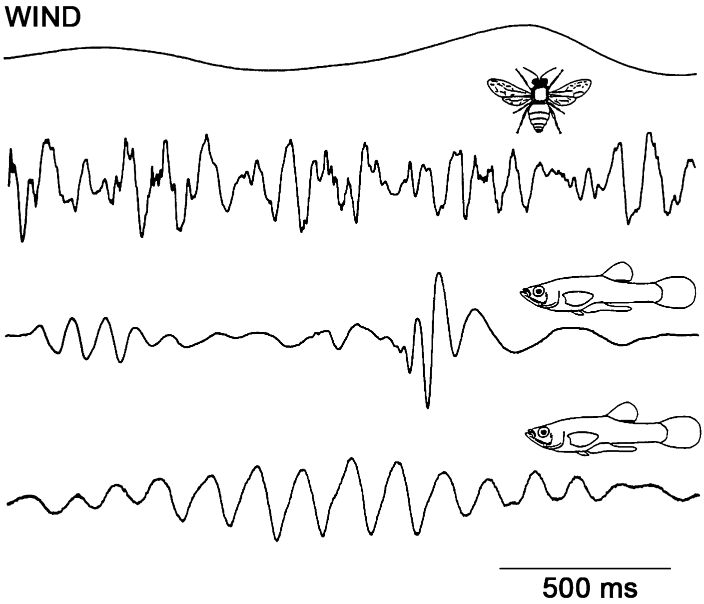

Fig. 2 Examples of water surface waves (displacement). From top to bottom: caused by wind, a struggling fly *Calliphora vicina*, and a guppy *Poecilia reticulate*. The guppy was contacting the water surface for breathing (top) and taking dry food from the water surface (bottom). Amplitudes are not to scale

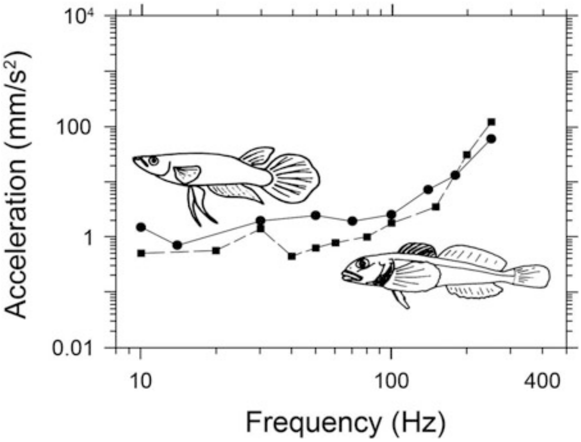

Fig. 3 Behavioral acceleration thresholds of the surface feeding striped panchaz (top curve) and the bottom dwelling mottled sculpin. Redrawn from Bleckmann (1980) and Coombs and Janssen (1990)

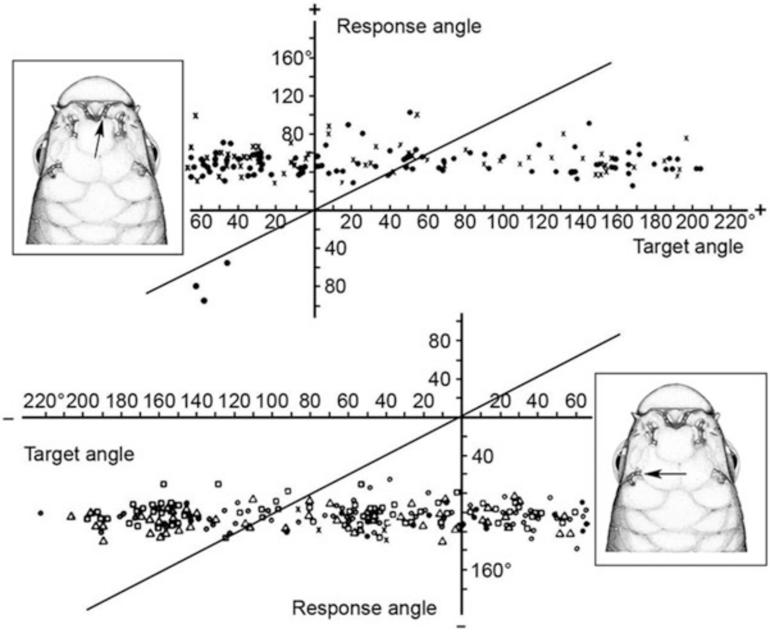

Fig. 4 Relationship between target- and response angle for striped panchax *Aplocheilus lineatus* with only one out of the 18 neuromasts located on the dorsal side of the head was left intact (arrows). Different symbols belong to different test series with the same animal (redrawn from Müller and Schwartz, 1982)

may alter the direction of water in the groove and over the neuromast relative to that outside of the groove. In short, the population of cephalic neuromasts provides intensity and spectral information that depends on target location, and hence can be decoded by the CNS to produce the orientation behavior. As the propagation speed of water surface waves is low (in the relevant frequency range of 10 to 100 Hz between 23 and 36 cm s^{-1}), the neuromasts most likely also provide temporal information that could contribute to directional orientation. Details of the CNS processing of the information from the spatial array of neuromasts, or how target direction is represented, are unknown. However, when all neuromasts except one are removed from the cephalic lateral line, striped panchax always turn in a particular direction regardless of target position (Fig. 4). Furthermore, the response angle correlates with the location of the neuromast: anterior neuromasts drive responses through small angles whereas posterior neuromasts elicit responses through large angles. This position code is consistent with direction estimation based on the relative timing of activity between neuromasts.

Having turned towards the stimulus, surface feeding fish glide towards the location of the target and stop. This provides direct behavioral evidence that target distance is also estimated. Stopping close to the prey facilitates a final orientation and strike particularly if the prey is still moving. The question then becomes: how does the lateral line encode target distance? An elegant series of behavioral experiments using the prey-orienting behaviors of the striped panchax (Bleckmann & Schwartz, 1982) and the African butterfly fish (*Pantodon buchholzi*) (Hoin-Radkovski et al., 1984) shows that this ability taps into the way in which the shape, and frequency composition, of the passing waveform varies with target distance. Because higher frequency wave components travel at higher velocities and attenuate more strongly during propagation, prey waves have more high-frequency components close to the source, and the wave packet is relatively compressed. At longer distances from the source, the wave packet has fewer high-frequency components and is extended in time. The use of these complex patterns of the wave packet to estimate target distance is shown by producing a 'phantom' stimulus: synthetic patterns from a close target that mimic the wave patterns of a more distance source. Under these conditions, the fish acts as predicted by the use of wave pattern for distance estimation. It overshoots the closer source and approaches the 'phantom' target.

These experiments are a nice reminder of the hierarchy of evidence that relates to animal orientation and behavior. Firstly, characterization of the physical stimulus is important to be able to propose a specific orientation mechanism. Secondly, neurophysiology is then necessary to demonstrate that the sensory system in question responds to and encodes the requisite features of the stimulus. Finally, only behavioral experiments can provide evidence that the animal not only can, but indeed does, utilize the proposed orientation mechanism. The direct behavioral evidence becomes even stronger when the physical stimulus can be manipulated in such a way as to generate a 'phantom' stimulus to which the animal responds in the way predicted.

That surface feeding fish use not only the spectral cues in the complex wave pattern, but also other wave features for distance estimation is indicated by the following experiments. If single frequency wave stimuli are presented, distance determination still occurs, but is less effective. The fish now tend to underestimate the distance if it exceeds 6 to 8 cm. In general, the relative localization error at a given source distance increases with frequency and at a given frequency, increases with source distance. This indicates that the fish compute the curvature of the wave front and that spectral cues are also used for distance determination. In other words, if no other cues are available, a high-frequency wave train is interpreted to have travelled a shorter distance than a low frequency one (Bleckmann, 1988; Bleckmann et al., 1989). Thus surface feeding fish utilize redundant cues for wave source localization. That the curvature of a concentric wave stimulus is one of the cues used for distance estimation is supported by CNS recordings from midbrain cells in the African clawed toad which show curvature-dependent spike rates (Claas et al., 1989; Behrend et al., 2008).

3 Detecting Prey in Midwater

Below the surface, the physics of water disturbances produced by potential prey are quite different from surface waves (Kalmijn, 1988). In addition, the problem becomes one of locating, or tracking, a target in 3D space. The type of water disturbances and the effective lateral line stimulus depend on how the disturbances are created. The flows generated by the beating limbs of a small crustacean differ from the ventilation or filter feeding currents of a larger crab or bivalve, which differ again from the stimulus generated by a small but fast moving animal, or the complex flows generated by larger swimming or breathing fish (e.g. Bleckmann et al., 1991; Hanke et al., 2012). There have been extensive behavioral studies of lateral line mediated prey detection across a wide range of species. The physics of the flows mediating these predator prey interactions are complex and differ on a case-by-case basis. The general description is that local or near-field flows around a vibrating object will provide the stimulus to the lateral line. The simplest of these types of flows will be produced by a pulsating sphere (monopole) or by a constant volume sphere vibrating backwards and forwards (dipole). The latter of these two is a better representation for some common types of lateral line stimuli and hence has become one of the standard stimulus generators for lateral line studies. Some species of fish, most studied being the mottled sculpin (*Cottus bairdi*) show an unconditioned approach and strike at a small vibrating sphere (Hoekstra & Janssen, 1985). This behavior supports the use of the dipole stimulus as a reasonable proxy for the more complex fields of the small epibenthic prey on which these species feed.

The dipole field for a given sphere size, vibration frequency and amplitude is well defined and the oscillating flow can be specified for each point in space around the dipole (Kalmijn, 1988). Midwater and bottom dwelling fish like mottled sculpin are very sensitive to dipole stimuli, their behavioral threshold curve is similar to the threshold curve of a surface feeding fish (Fig. 3). One can, in principle, model the pattern of activation over the entire lateral line system as a function of dipole location, given some simplifying assumptions and knowledge about the number, sensitivity, orientation and spatial distribution of superficial and canal neuromasts. In practice, however, this is very difficult to do, and moreover, the precise location and number of neuromasts that mediate any given behavioral response is unknown, meaning that the underlying pattern of stimulation that evokes a behavioral response is difficult to determine.

A few examples of particular predator–prey interactions can serve to illustrate the complexity and diversity of the requirements for the detection and 3D localization of stationary targets, and the tracking and interception for a moving target. One of the best models for lateral line based detection and localization of stationary prey has been the mottled sculpin (e.g. Coombs et al., 2001). As noted above, this fish shows an initial, unconditioned orienting response, followed by a step-by-step approach and final strike at a small vibrating sphere that effectively mimics their natural prey (e.g. *Daphnia*; small water fleas that effectively hover in the water

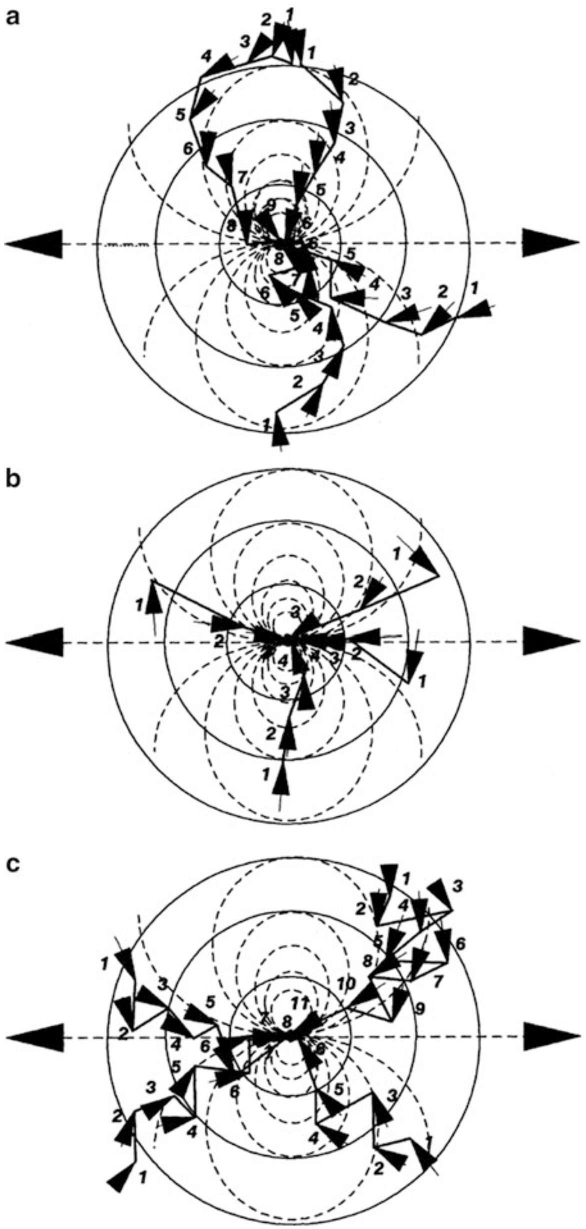

Fig. 5 (**a**-**c**) Examples of typical, unconditioned step-by-step approach patterns to an 'artificial' prey (a 50 Hz vibrating sphere). (**a**) smoothly arching approaches in which the fish keeps its head to one side of the source. (**b**) direct path in which the source is kept mainly in front of the fish's head. (**c**) zigzag approaches in which the fish alternates between being to the left and right of the source. Dashed lines indicate flow lines about the sphere (center of graph), whereas thin-lined circles represent fixed radial distances of 3, 6, and 9 cm from sphere center (from Coombs and Conley, 1997)

column). Prey localization, approach and strike are suited to a small, low-intensity target that is effectively stationary. Blind mottled sculpin approach the target in a series of movements (Fig. 5), and once the target is within a given range of the mouth, the strike is made. The interpretation of this step-like approach is that target direction and distance is estimated during the stationary phase of each step, after which the sculpin then moves closer to the prey and stops to re-estimate target position. It is likely that the water flows generated by the mottled sculpin's own movements swamp the lateral line signal from the prey. This effect is well illustrated in the chronic recording from implanted electrodes in the anterior lateral line nerve of freely swimming oyster toadfish, *Opsanus tau* (Palmer et al., 2005). Afferent fibers experienced a dramatic increase in firing during predatory strikes caused by the movement of the animal itself as part of the strike. This issue of small signals and potentially large self-generated 'noise' is central to understanding the effective use of the lateral line system and will be considered in Section 6. It is also worth noting that the movement towards the prey must be programmed in a way that minimizes physical displacement of the prey away from the predator.

Information contained in the spatial excitation pattern along the arrayed sensors of the lateral line system of mottled sculpin, as well as other sub-surface feeding fish and amphibians, is thought to play a fundamental role in guiding prey-orienting behaviors. However, the way in which prey location is encoded by the excitation pattern of the peripheral lateral line and used by the central nervous system is still largely unknown. Coombs & Patton (2009) tested the hypothesis that mottled sculpin use excitation peaks (local 'hot spots') to determine the somatotopic location of an artificial prey (vibrating sphere/dipole source) along the body surface. Dipole orientation (axis of sphere vibration relative to the long axis of the fish) was manipulated to produce excitatory peaks in different body locations without changing the actual sphere location. The results show that orienting accuracy is largely independent of source orientation, but not source distance and that turning directions are not guided by local hot spots in the somatotopic activation pattern of the lateral line.

From a wide range of evidence in fish and other vertebrates (summarized in Coombs & Patton, 2009) it is likely that the optic tectum contains a map of the turning magnitudes and directions needed to orient to a lateral line stimulus source. As Coombs and Patton (2009) pointed out, however, it is also clear that this map cannot be a simple topographic map of the body surface because stimulus sources at the same somatotopic location, but at different distances away from the body, lie at different visual angles, and thus require different orienting movements. The fish must therefore combine somatotopic information about both source distance and source location to determine the direction of the source with respect to the head and eyes. To produce the map, information about these two stimulus parameters must be computationally transformed from a somatotopic to an egocentric coordinate system that is in register with other sensory direction maps in the midbrain.

Computed space maps have been found in the auditory system of barn owl (*Tyto alba*) (Knudsen 1987), but also in the lateral line system of the African clawed toad (Claas et al., 1989) and the axolotl (*Ambystoma mexicanum*) (Bartels et al., 1990). Since source localization by the lateral line relies on spatial (somatotopic) activation patterns rather than bilateral cues (Conley & Coombs, 1998), the computations will necessarily be different and will likely need to take source orientation into account as well. Theoretically, fish could use an array of neural filters tuned to

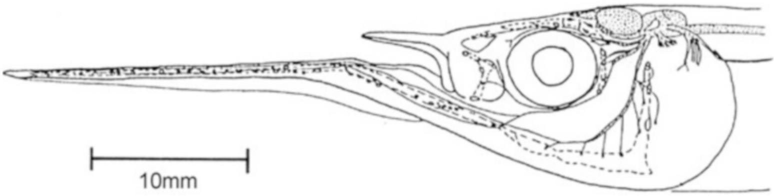

Fig. 6 The nocturnal planktivorous half beak *Hyporamphus ihi* showing the extended mandibular lateral line canal along the bill. These fish feed at night on fast moving mobile plankton using their lateral line. Laboratory feeding studies show that prey moving along the lateral line array in either direction are intercepted whereas prey moving across the array are missed (from Montgomery and Saunders, 1985)

particular combinations of source orientation, distance, and somatotopic location. Such a filter array could classify entire lateral line pressure gradient or velocity patterns rather than relying on a few key features, thereby increasing robustness against noise.

The description above applies to orientation towards and capture of a relatively small, low-intensity target that is effectively stationary within the receptive field of the lateral line array. Like the mottled sculpin, the half-beak (*Hyporamphus ihi*) is a planktivore. However, their prey are fast moving mobile plankton (Montgomery & Saunders, 1985; Saunders & Montgomery, 1985), and successful prey capture depends on the movement of the prey tracking along the sensory array of the lateral line (Montgomery, 1989). These fish have a distinctive lengthy lower jaw that gives them their common name of half-beaks (Fig. 6). The beak and extended mandibular lateral line canal provide an extended lateral line sensory array that allows for non-visual tracking and interception of small, but relatively fast moving, prey.

As shown above, the lateral line provides for target localization and tracking to enable successful prey capture, but successful predation also requires effective prey search. Under normal conditions in the wild, lateral line feeders, like visual predators, must sit and wait for prey to come to them, or actively search the environment for suitable prey. Sit-and-wait predation based on lateral line alone has been shown in the stargazer (*Leptoscopus macropygus)* (Montgomery & Coombs, 1998). Active search behavior has been well documented for visual feeders, but only recently explored from the standpoint of lateral-line mediated predation. The observation is that nocturnal predators like the dwarf scorpion fish (*Scorpaena papillosa*) (Fig. 7) adopt a saltatory search pattern consisting of alternating periods of time when the fish is stationary, and when it moves forward by a set distance. The stationary phase is the search period during which a prey may be detected inducing an orientation and attack. Prey capture occurs throughout the search space (Fig. 7). The dwarf scorpion fish feeds only on benthic prey (Montgomery & Hamilton, 1997) so like the surface feeding fish, the search space is essentially 2D. After a relatively set time with no detection, the fish moves forward to the edge of the previous search space, and pauses to 'listen' for

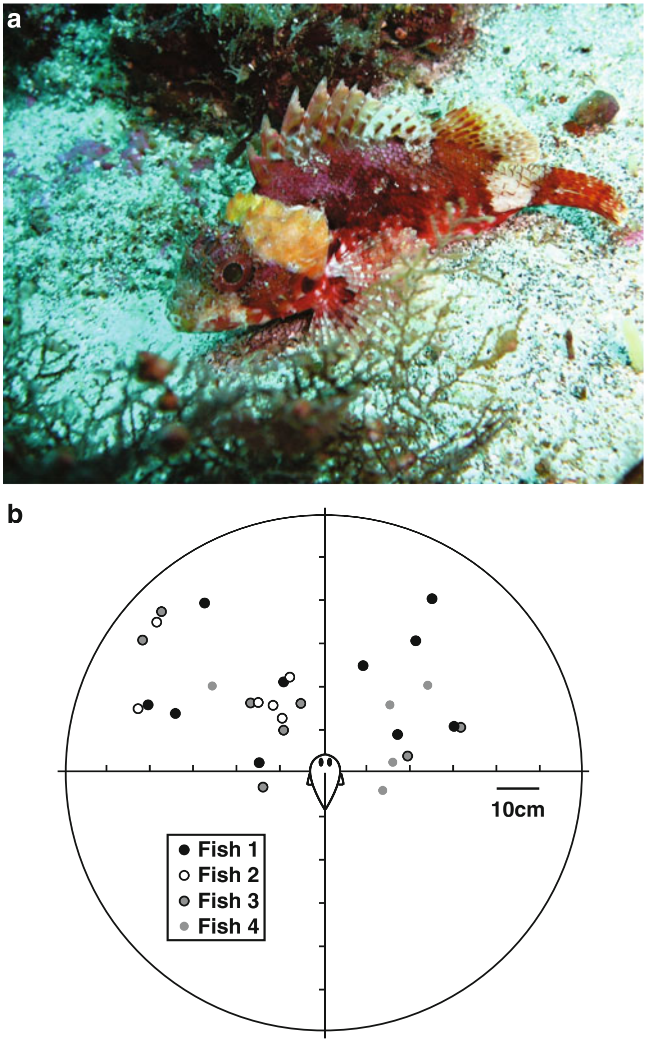

Fig. 7 A The dwarf scorpionfish *Scorpaena papillosa* detects the hydrodynamic signals produced by prey with the mechanosensory lateral line. This species hunts with a pause and move/search, or saltatory, pattern. The pause phase of the search cycle is used to detect prey and pauses often end early in order to initiate an approach at prey which are detected throughout the search space. B Polar plot showing the positions of prey relative to the fish at the time of prey detection. Note that most prey is found within a semicircular space. Data from different individual fish is represented by a different color circles (From Bassett et al. 2007)

prey in the new search space (Bassett et al., 2007). The spatial distribution of attacks relative to the fish's position defines the search space, and the time spent stationary, and the distance and direction of movement between the search phases, all contribute to the search efficiency.

Swimming fish leave a hydrodynamic trail consisting of vortices that provide information about the swimming direction and swimming velocity. In still water, the hydrodynamic trail of goldfish (*Carassius auratus*) could be visualized for up to 5 minutes (Hanke & Bleckmann, 2000). Hydrodynamic trails may provide hydrodynamic signatures associated with the swimming styles of different fish species (Hanke & Bleckmann, 2004). Behavioral evidence for hydrodynamic wake tracking of piscivorous fish has been provided by Pohlmann et al., (2001, 2004). Although the use of olfactory information could not be completely ruled out in these studies (Montgomery et al., 2002), they did show that predatory fish can intercept and follow the trail produced by prey fish using predominantly their lateral line system.

In many circumstances, the lateral line will also work alongside other senses in prey search. A number of studies explored these issues of multimodal sensory interactions, including: (1) the use of lateral line in chemosensory search (Baker et al., 2002; Carton & Montgomery, 2003; Jayne et al., 2007; and Section 9); (2) the use of lateral line in electrosensory search (von der Emde & Bleckmann, 1998); (3) the switch from visual search at a distance to lateral-line guided strike up close (New et al., 2001); (4) the comparison of information-processing demands for prey capture in lateral line and electrosensory systems (Coombs et al., 2002), and (5) the functional relationship between hearing and the lateral line in prey detection and localization (Braun et al., 2002; Braun & Coombs, 2010; Braun & Sand, Chapter 10). The relative role of the lateral line and other senses also changes with light conditions. As light levels decrease, the mechanosensory lateral line will increase in importance. The relative role of lateral line and other senses in predation also changes during development. Vision typically dominates, but in some species and some stages of development, the lateral line plays a more dominant role (Liao & Chang, 2003).

4 Predator avoidance

Predator/prey interactions are two-sided; as discussed above, predators can detect and attack prey based on lateral line information, but prey can also detect the approach or strike of a predator using the lateral line. It is particularly in this case that the speed of the strike and close range of operation of the lateral line dictates that the behavioral pathways and reactions for lateral line mediated predator avoidance must be fast to be effective. In this regard is has been known for a long time that the lateral line provides direct input onto the two Mauthner cells (e.g. Korn & Faber, 1975). The Mauthner cells are critical, decision-making neurons in the recticulospinal network of the hindbrain (Korn & Faber, 2005). They mediate an escape response (C start) that has a minimum latency of only 6.4 ms in goldfish (Eaton & Hackett, 1984). Recent research on the role of the lateral line in predator avoidance and escape response initiation has concentrated on developing a model system with zebrafish (*Danio rerio*) larvae showing that the

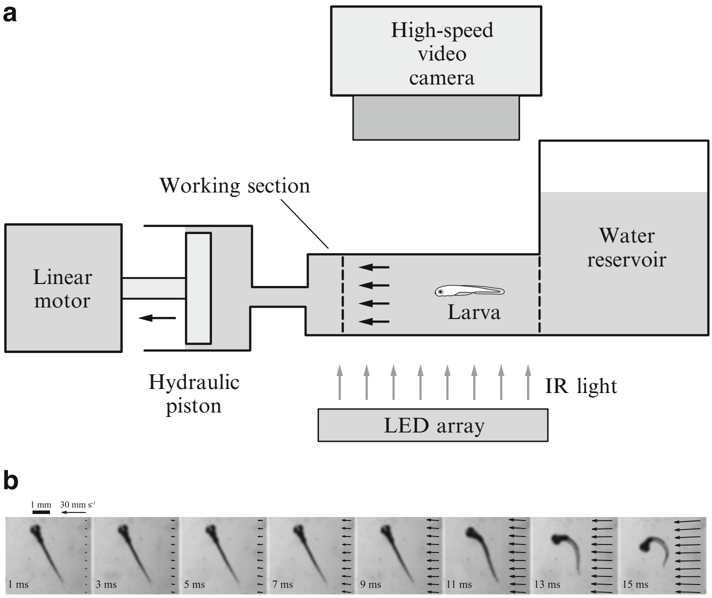

Fig. 8 Water flow stimulates an escape response in zebrafish *Danio rerio* larvae. (**a**) The impulse chamber used to generate flow includes a computer-controlled linear motor that actuates a hydraulic piston. The motion of the hydraulic piston (black arrow) creates flow through the working section. A high-speed video camera (250 frames sK1) recorded the responses of larvae that were backlit with an array of infrared LEDs in a darkened room. (**b**) Video stills of a representative fast start response for a single larva (5.90 dpf) from a dorsal view with velocity vectors from the representative flow stimulus ((i) 1 ms, (ii) 3 ms, (iii) 5 ms, (iv) 7 ms, (v) 9 ms, (vi) 11 ms, (vii) 13 ms and (viii) 15 ms) (From McHenry et al. 2009)

lateral line system plays a substantive role in predator evasion at this vulnerable stage of growth in this species (McHenry et al., 2009; Fig. 8). This research has also explored the effects of swimming and aspects of development on the lateral line stimulus. Swimming larvae are only half as likely as motionless larvae to respond to the flows produced by a suction predator (Feitl et al., 2010), and the reduction in fish density that follows the inflation of the swim bladder during development dramatically reduces the stimulus to the lateral line during a simulated strike (Stewart & McHenry, 2010).

The reduction in the effective stimulus to the lateral line after swim bladder inflation suggests a developmental change in the relative role of lateral line inputs to the Mauthner-mediated escape response. Indeed, lateral line inputs to the Mauthner cells are insufficient by themselves for initiating escape responses in adult fish and are thought to play more of a modulatory role (Casagrand et al., 1999). In contrast, either auditory or visual inputs alone are sufficient for this purpose (Eaton et al., 1977), but auditory inputs are particularly important in otophysan fishes, such as the goldfish and zebrafish (Canfield & Eaton, 1990; Casagrand et al, 1999). In these species, audition involves the swim bladder, which functions as a sound pressure transducer and amplifier. Whereas visual or pressure-driven auditory inputs dominate the initiation of the escape response, lateral line inputs guide the direction of the response once it has begun so that fish don't collide with nearby obstacles (Mirjany et al., 2011).

5 Intraspecific communication – spawning, parenting, aggression and schooling

As a close range sensory system, the lateral line is an obvious candidate for close range communication. With external fertilization being the norm across fishes, spawning synchronization is an important element of fish behavior and communication. In addition to spawning synchronization, mating communication may also play a role in mate selection. Although a lateral line component to mating communication has only been studied in a few species such as salmon (*Oncorhynchus nerka*) (Satou et al., 1994) and cave-dwelling Atlantic mollies (*Poecilia mexicana*) (Plath et al., 2004) the likelihood exists that this is not uncommon in fishes. The evidence from the two studies cited above shows that the lateral line is involved in both spawning synchrony and mate selection.

Male Siamese fighting fish (*Betta splendens*) constantly guard their juveniles. If threatened the male adopts an oblique position below the water surface and starts to produce surface waves with the pectoral fins. Even without vision the juveniles approach the male. On reaching it they are sucked up and transported back by the male to the air bubble nest (Kaus & Schwartz, 1986).

Fire-bellied toads (*Bombina sp.*) produce large surface waves by strokes of the hind legs during mating behavior and these waves are used as signals that define the territory of the respective male (Walkowiak & Münz, 1985). In addition, some fishes produce hydrodynamic stimuli during aggressive interactions (e.g. Lamprecht, 1973). For instance, in the golden dwarf cichlid (*Nannacara anomala*) one animal, the actor, pushes water with its tailfin in the direction of the other fish (Enquist et al., 1990). The two animals often change role (from beater to recipient and vice versa) and usually orient laterally to each other. They thus ensure that the hydrodynamic stimulus can be perceived by the recipient fish. Although direct evidence is missing, the lateral line is most likely involved in this behavior.

Schooling behavior is another candidate for close range communication. Tight schooling coordination in response to predator threat is very demanding in terms of the high temporal and spatial resolution characteristics required for sensory coordination of the school (Ritz et al., 2011). Observations and studies of complex schooling behavior (Pitcher & Parrish, 1993) tend to evoke descriptions of the school as a 'super organism'. Discrete 'behaviors' of the school are observable such as 'splits, vacuoles and flash expansion'. The sensory basis of these school behaviors is hard to study, but is almost certainly due to the sensory detection of an attack by the fish on the 'front line' via the visual looming stimulus of the predator, and/or the associated pressure pulse of a lunging strike. The behavior of the school will result from the way in which this information propagates into the school, both directly in response to the predator, and indirectly, in response to the propagated startle responses of the 'front line' fish. Thus, communication between neighbors is likely central to the schooling response when under attack, but it is also a key to understanding schooling behavior as a general evolutionary strategy for optimizing the transmission of threat information.

In this context, there is good experimental evidence and theoretical reasoning to support the interactive involvement of both vision and lateral line (Partridge & Pitcher 1980; Faucher et al., 2010) in the maintenance of school structure. Nearest-neighbor distance appears to be maintained by opposing forces of attraction (via visual feedback) and repulsion (via lateral line feedback). Whereas an individual's relative position and orientation with respect to neighboring fish appears to be maintained by vision, the relative velocity and direction of travel seems to be regulated by the lateral line (Partridge & Pitcher, 1980). Essentially, the lateral line enables individuals to maintain close associations with each other without colliding. The lateral line may also interact with hearing in schooling behavior, especially in clupeids (e.g. sprat, herring, shad), arguably 'champions' among schooling species. These fish have air filled cavities in their head that are mechanically linked to both the inner ear and a portion of the head lateral line system (Denton & Blaxter, 1976). Rapid schooling maneuvers of clupeids produce pressure pulses (Gray & Denton, 1991), which, like those produced by rapidly approaching predators, can be detected by the air bubble/inner ear/lateral-line system. In fact, this represents one of the rare cases in which the lateral line system responds to pressure, rather than to pressure-gradients or flow, although the precise nature of auditory/lateral line interactions in schooling behavior is still poorly understood.

Schooling behavior may also provide hydrodynamic benefits to fish, depending on an individual's position within the school relative to the hydrodynamic structures (trailing wakes of shed vortices) produced by other nearby fish, particularly those in front (Breder, 1965). Liao (2007; Fig. 9) provides an excellent review, as well as the theoretical rationale for a hydrodynamic basis to school structure. The prediction is that a fish located behind and in between two members of the school can take advantage of the average reduced flow velocity associated with the thrust wakes of those ahead. In effect, fish in schools can benefit from flow refuging (exploiting regions of reduced flow or reduced pressure) and vortex capture (harnessing the energy of environmental vortices). Direct experimental determination of vortex capture, associated energetic benefits and its sensory basis have not been done for schooling fish. However, as covered in Section 9, individual fish swimming in a flume use lateral line information to position themselves in an energetically favorable position behind a cylinder (Sutterlin & Waddy, 1975; Montgomery et al., 2003), and to entrain to shed vortices from a bluff, or non-streamlined, object in the flow (Liao et al., 2003a,b; Przybilla et al., 2010; Bleckmann et al., 2012).

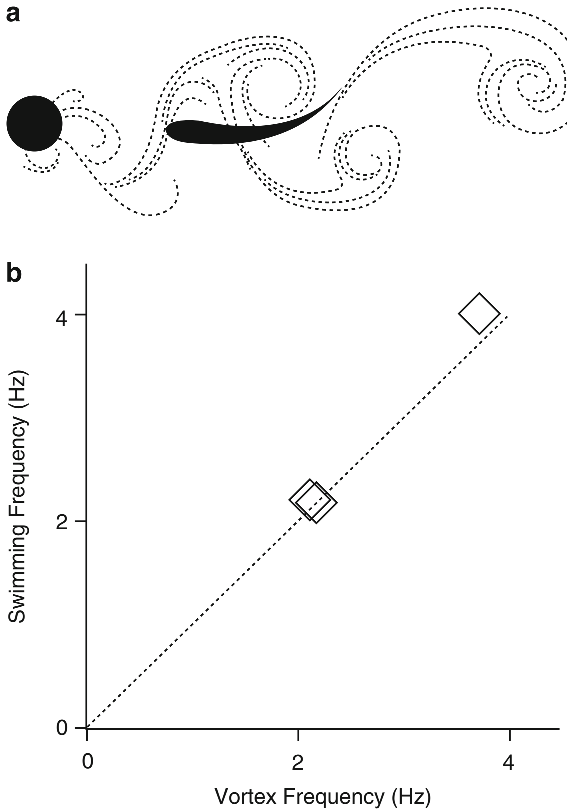

Fig. 9 (**a**) Schematic illustrating the hydrodynamic benefit gained by a fish swimming behind a bluff body, such as a cylinder, in the flow. Fish can exploit the energy of discrete vortices as well as the average reduced velocity in the Kármán street. In a two-dimensional fish school side-by-side thrust wakes generated by two individuals create an analogous Kármán street. (**b**) The graph of swimming frequency vs shed vortex frequency shows a strong match for 3 different combinations of cylinder size and flow velocity. This indicates that the fish are not just 'drafting' in the wake behind the cylinder, but tuning their swimming frequency to match that of the shed vortices. Dotted line is the line of equality. (Redrawn from Liao 2007)

6 Signals and Noise

Aquatic environments are often contaminated with hydrodynamic noise (broadband velocity and pressure fluctuations caused by unsteady flow or turbulences). Therefore the real challenge for the lateral line is not simply a sufficient sensitivity to detect water motions, but rather the ability to detect a signal in the presence of noise. Therefore, separating signals from noise is essential in understanding the sensory ecology and neuroethology of the lateral line. In this regard, the submodalities of the fish lateral line (superficial neuromasts on the skin surface and canal neuromasts located in subdermal canals) (Webb, Chapter 2) are relevant.

The simple description is that with respect to water displacement, superficial neuromasts are low-pass filters encoding low-frequency water motions of up to about 80 Hz. In comparison, canal neuromasts do not respond to DC flow, but are sensitive to higher oscillating flows up to approximately 250 Hz.

The essential idea is that superficial neuromast respond to unidirectional or low frequency AC flow (Coombs & Montgomery, 1994; Voigt et al., 2000), whereas canal neuromasts are less influenced by low frequency large scale flows (noise) such as those in a creek or river, or movements of the animal itself. The division of labor between superficial and canal neuromasts is well illustrated by the effects of background flow on the responses of these two submodalities to a small vibrating source (Engelmann et al., 2000). At zero back-ground flow (in still water), all afferent fibers phase-lock to a vibrating sphere stimulus; however, with increasing background flow rates the responses of one class of afferents is progressively masked whereas another class continues to encode the higher frequency source. It is likely that superficial neuromast input can be equated with the class of afferents masked by the flow "noise" and canal neuromasts as the unaffected class. This functional distinction between superficial and canal neuromasts is further reinforced by the behavioral findings that flowing water decreases hydrodynamic signal detection in a fish with an epidermal (superficial) lateral-line system (Bassett et al., 2006) to a greater extent than it does in a fish with a more typical lateral-line canal system (Kanter & Coombs, 2003). That superficial neuromasts are nevertheless important in a fluvial environment is supported by the behavioral findings that superficial neuromasts mediate rheotaxis (orientation to water flow; Montgomery et al. 1997), whereas canal neuromasts mediate prey detection (or orientation to a small vibrating source) (Coombs et al., 2001; Kanter & Coombs, 2003). For further details on the biomechanical and functional dichotomy between these two lateral line submodalities see McHenry and van Netten (Chapter 4) and Chagnaud and Coombs (Chapter 6).

7 Self-generated Flows as Noise

Even in still water, fish and aquatic amphibians may move around and thus generate hydrodynamic noise. Self-generated noise can be recognized as an issue for many sensory systems, but given the sensitivity of lateral line receptors and the observation that most fish are seldom motionless, self-generated noise may be a particular problem for the lateral line. The scale of the problem is under-recognized because almost all physiological studies have been made on immobilized animals. However, lateral line afferent activity has been recorded in freely swimming fish (Palmer et al., 2005), swimming tethered lampreys (*Petromyzon marinus*) (Ayali et al., 2009), and in restrained breathing fish (Montgomery et al., 1996). In all cases the movements generated by swimming and breathing produce strong modulation of the lateral line afferents. In the particular case of the breathing fish, self-stimulation of lateral line receptors occurs close to the head and respiratory flows.

One advantage self-generated noise has over other noise sources is that, at least to a certain degree, it is under the control of the animal. So the simplest strategy for noise reduction is to cease movement. As covered earlier in this chapter (section 3), complete motionlessness is a behavioral strategy adopted by sit-and-wait predators like the stargazer (Montgomery & Coombs, 1998). Cessation of gill movements during prey location by the oyster toadfish (Tricas and Highstein, 1991), and "the pause and then move search strategy" of dwarf scorpionfish (Bassett et al., 2007) are but two examples of how motionlessness can be controlled to suit the needs of the predator.

Another relatively simple approach to self-generated noise is to down regulate lateral line sensitivity during active movement (Russell & Roberts, 1972). This approach is appropriate to rapid movements where lateral line sensitivity can be reduced by activation of the efferent system (see Chagnaud & Coombs, Chapter 6 for further details on this system). However, efferent down-regulation of sensitivity need not be all-or-nothing or always in response to self-motion. Chronic nerve recording in active oyster toadfish showed incomplete inhibition during locomotion and selective action of the efferent system on one class of lateral line afferents in response to visual presentation of natural prey (Tricas & Highstein, 1991).

As a final noise-reduction strategy, the brain can use *a priori* knowledge to actively cancel afferent inputs that are linked to the animals own movements. Undulatory movements will provide a regular and predictable pattern of afferent input. Because the movements are generated by the animal itself, it has, in effect, an *a priori* knowledge of movement and the potential to predict and cancel the associated afferent inputs. Studies on both lateral line and electrosense, but particularly electrosense, show that the hindbrain processing centers for both of these senses form an adaptive filter that learns to cancel predictable input (Bodznick et al., 1999; Montgomery & Bodznick, 1999). The basis of this ability is the cerebellar-like structure of these hindbrain centers (see also Wulliman & Grothe, Chapter 7). The *crista cerebellaris*, that overlies these structures, has a molecular layer composed of parallel fibers that carry information about ongoing movements. This information comes as efference copy from motor centers, proprioceptive information about movement, and from a number of other sources. In effect, the molecular layer contains a rich matrix of information about movement. The principal cell type of the lateral line hindbrain center is the crest cell. Crest cells have dorsal spiny molecular layer dendrites that receive parallel fiber information, but also direct lateral-line afferent input on their ventral dendrites. A rather simple synaptic plasticity learning rule allows the input from the parallel fibers to generate a "negative image" of the re-afferent noise arriving at the ventral dendrites. In this way, the re-afferent noise is cancelled, yet the crest cells remain sensitive to external biologically important signals (Montgomery & Bodznick, 1994). Ventilation is one example of a movement that produces unwanted sensory re-afference. Recordings from lateral-line afferents, particularly in the area of the gills, show strong ventilation mediated responses. By comparison, the crest cells show greatly reduced responses to ventilation movement (Montgomery et al., 1996).

8 Self-generated Flows as Signal – Hydrodynamic Imaging and Control of Swimming

In low and zero light environments, the lateral line provides an alternative to vision. In addition to encoding abiotic flows and water movements produced by other animals, the lateral line senses self-generated flow to mediate collision avoidance and object detection. The flow field around a gliding fish is distorted by nearby objects, and these distortions can be sensed by the lateral line. This active use of self-generated flows has been termed “hydrodynamic imaging.” The blind Mexican cavefish uses active flow sensing for a variety of spatial tasks, including obstacle avoidance (Teyke, 1985; Windsor et al., 2008), discrimination of spatial features that differ in their orientation (Campenhausen et al., 1981) or spacing (Hassan, 1986), and exploration of novel environments (Burt de Perera, 2004; Burt de Perera & Braithwaite, 2005; Braithwaite & Burt De Perera, 2006).

For a gliding fish, the information available for hydrodynamic imaging depends on the properties of its flow field and how this flow field is altered by the presence of objects. Particle image velocimetry has been used to measure the flow fields around gliding blind cave fish as they moved through open water and when heading towards a wall (Windsor et al., 2010a). These measurements, combined with computational fluid dynamics models, were used to estimate the stimulus to the lateral line. Results show that there is a high-pressure region around the nose of the fish, low-pressure regions corresponding to accelerated flow around the widest part of the body and a thick laminar boundary layer down the body. When approaching a wall head-on, the changes in the stimulus to the lateral line were confined to approximately the first 20% of the body. When swimming parallel to the wall, characteristic changes in the form of the flow field occur when the fish are within approximately 0.2 body lengths of the wall. The stimulus to the lateral line is estimated to be sufficient for fish to detect walls when they are 0.1 body lengths away (the mean distance at which they normally swim from a wall), but insufficient for the fish to detect a wall when 0.25 body lengths away. These fluid dynamics analyses of the nature of the flow fields surrounding the fish (Windsor et al., 2010b) reinforce the view from simpler potential flow models (Hassan 1992a, b) that hydrodynamic imaging can only be used by fish to detect surfaces and objects at short range.

Self-generated flows may also play a useful role in providing sensory feedback for swimming control. This suggestion has been made for many years, but experimental evidence in support of an active contribution of lateral line to swimming efficiency has been scarce. Two roles for lateral line feedback have been proposed. Lighthill (1993) suggested that the lateral line sensors in the subcerebral canal system of the herring provide an appropriate feedback signal into a possible system for controlling yaw by oscillatory neck deflections so as to minimize the effective pressure difference and any associated cross flow effects across the head of the fish. It was proposed that swimming clupeid fishes may use this as an ’active’ mechanism for reduction of hydrodynamic resistance.

This theory was supported by an analysis of the mechanics of the subcerebral perilymph canal, which crosses the head between the lateral lines of clupeid fishes (Denton and Gray, 1993), and an analysis of the head turning movements in herring and other fishes (Rowe et al., 1993). However, direct evidence for a role of lateral line feedback in this behavior was not provided. In the golden shiner *Notemigonus crysoleucas* drag reduction was not adversely influenced by disabling the lateral line system (McHenry et al., 2010).

The second suggested role for lateral line feedback in the efficient control of swimming came from the measurements of the boundary layer in swimming fish (Anderson et al. 2001; see also McHenry & Liao, Chapter 3). This study observed inflected boundary layers that appeared to be stabilized during the later phases of the undulatory cycle, and suggested that these boundary layer profiles may provide evidence of a contribution of hydrodynamic sensing to the optimization of swimming performance. Again, this suggestion remains to be directly tested, however, Yanase et al. (2012) have recently found that unilateral disruption of the superficial neuromasts impairs hydrodynamic performance and increases the metabolic cost of swimming in the yellowtail kingfish (*Seriola lalandi*).

9 Orientation to Flows

In the aquatic environment of fish, orientation to flow (rheotaxis), finding refuge from flows, and reducing the costs of locomotion in turbulent flows are all important behaviors. It would seem obvious that flow sensing should play a useful role in all these behaviors. However, even the simplest of these, orientation to uniform flows, is not without complexity. To know that it is transported by the current, a fish needs an external reference frame. For many fish, this reference frame is the substrate and surrounding environment as sensed by the visual system. For example, station holding for a fish in midwater in a uniform current is largely mediated by optomotor responses to stabilize the image of the surroundings on the retina and to minimize ‘optic flow’. Although a fish being swept downstream results in an optic flow stimulus to the visual system, little if any hydrodynamic flow stimulus to the lateral line is generated in this circumstance. For this reason, the long-held view was that the lateral line played little or no role in rheotaxis (e.g. Dijkgraaf, 1963). However, for fish sitting on the substrate in slow flows that are insufficient for displacing it downstream, the lateral line can sense the flow relative to the body surface, thus enabling the fish to orient into the flow (Montgomery et al., 1997; Montgomery et al., 2000; Fig. 10). In these circumstances, the threshold for positive rheotaxis (orientation into the flow) is markedly lower for a fish with the lateral line, and in particular, if the superficial neuromasts of the lateral line are intact.

This form of rheotaxis, using intermittent physical contact as the external reference frame, is also used by the Mexican blind cavefish. In this species, again, a low rheotactic threshold depends on an intact superficial neuromast system

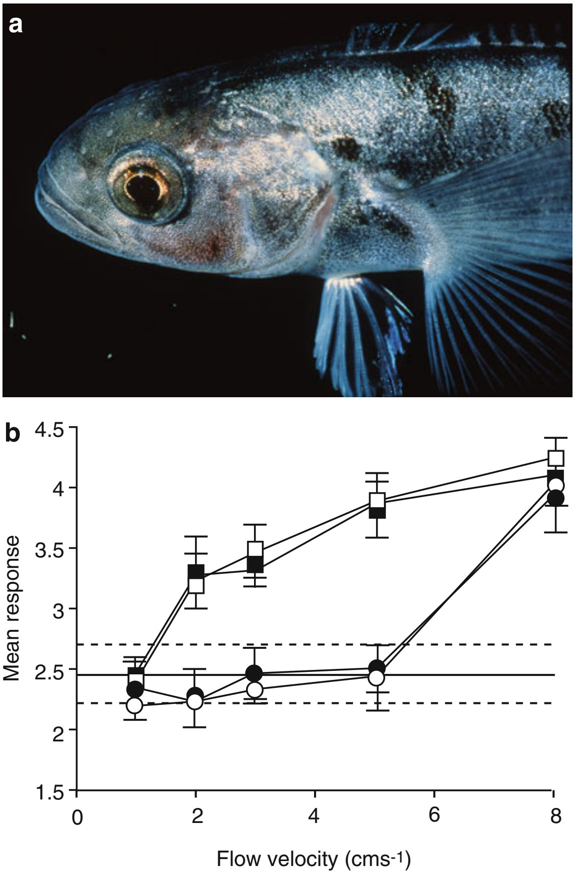

Fig. 10 Rheotactic responses of the antarctic fish *Pagothenia borchgrevinki*. Rheotactic responses; horizontal solid and broken lines indicate mean + 95% confidence intervals of the orientation response in the absence of current; filled squares, normal fish; open squares, gentamicin-treated fish; filled circles, streptomycin-treated fish; open circles, after physical ablation of the superficial neuromasts. Mean response, number of fish facing upstream

(Baker and Montgomery, 1999; Montgomery et al., 2001). Also of interest is that the normal threshold for rheotaxis is certainly not equal to the lowest current these fish can detect. The unconditioned rheotactic response to uniform flows was exhibited with a threshold of less than 3 cm s^{-1}. The effect of pairing an odor stimulant with water current dropped the rheotactic threshold to less than 0.4 cm s^{-1}. Olfactory released rheotaxis is likely to play an important part in tracking odor sources underwater and has been reported in a number of fish species (Baker et al., 2002; Carton and Montgomery, 2003; Jayne et al., 2007).

Understanding the contribution of the lateral line to rheotaxis has a number of potential practical applications ranging across a wide spectrum, from fish conservation to hair cell drug and toxicity testing (Coffin et al., Chapter 11). With respect to fish conservation, many, if not most of our inland waterways have been modified by dams or canals which impede or facilitate, the movement of fishes through these systems. Fish passage at these structures clearly has many implications for conservation, ranging from disruption of fish movement and migration during important life-history phases, to unwanted spread of introduced and invasive species. Understanding the role of flow detection in shaping the behavior of fish around these structures provides an important contribution to the 'tool box' for effective design and management of modified waterways (Hasler et al., 2009). At the other end of the spectrum, in the zebrafish model unconditioned rheotaxis and superficial placement of hair cells in the lateral line system provide some interesting possibilities for hair cell toxicity and protection screening (Coffin et al., 2010; Coffin et al., Chapter 11).

Orientation to uniform flows may have its complexities, but clearly flow refuging and swimming in turbulent flows requires an altogether higher level of sophistication in flow sensing and control proficiency. Flow sensing has been shown to be involved in station holding behind an object in a flow (Sutterlin & Waddy, 1975; Montgomery et al., 2003), but perhaps more interesting is the way in fish can use their lateral line to track hydrodynamic trails left by prey (Pohlmann et al., 2004), and to surf vortex streets (Liao et al., 2003a, b; Liao, 2007). Liao (2003) showed that trout *Oncorhynchus mykiss* alter their body kinematics to synchronize with the shed vortices generated by a stationary object in the flow. These shed vortices are known as a Kármán street, and the tuning of the body movements to these vortices has been termed a Kármán gait. Subsequent work showed that using this gait, fish can capture the energy of environmental vortices and hence consume less oxygen in turbulent flows than would otherwise be expected (Taguchi & Liao, 2011).

10 Summary

The lateral line of fishes and amphibians has some unique characteristics and makes a few 'signature' contributions that will apply to a wide variety of behaviors and species. For example, the lateral-line mediated ability of fish to react rapidly to nearby obstacles or neighboring fish is important to the navigational and spatial orientation abilities of blind cavefish, to the abilities of fish to school and avoid predators with highly synchronized maneuvers, and the ability of solitary fish to escape predators in cluttered environments. Because the distance range of the lateral line in most cases is relatively short and avoidance reactions must be quick, it is reasonable to hypothesize that the Mauthner cells and/or other fast-response reticulospinal systems are involved in many, if not all of these fundamental abilities. The importance of the Mauthner cells to the lateral line system is underscored by the fact that afferent connections between the lateral line periphery and the Mauthner cells are some of the earliest to develop in larval zebrafish (Pujol-Marti et al., 2011). These afferent neurons are also some of the largest, meaning that the propagation of information to the brain will be very rapid.

Although it is well known that the lateral line system is involved in many behaviors, the exact role this sensory system plays in the various behaviors is often not well understood. There are several reasons for this. First, to design the relevant behavioral experiments we need to know the temporal and spatial characteristics of the biologically meaningful stimuli for each species we are investigating. Unfortunately this knowledge is hard to get since it requires three-dimensional particle image velocimetry and/or other sophisticated measuring techniques. Second, sensory systems are to a degree matched filters designed to separate signals from noise. Therefore we also need to know the hydrodynamic noise to which the lateral line system of the species we are investigating is exposed to in its natural environment. Hydrodynamic measurements in the field are even more challenging than those in the lab. Third, the behavior of most fish and amphibian relies on multimodal (chemosensory, visual, somatosensory, acoustic, vestibular) input, thus blocking the lateral line often results in subtle modifications of the behavior under study. For instance, fish exposed to a stationary cylinder still Kármán gait, entrain, or swim in the bow wake when their lateral line is blocked (see above). However, if the vortex shedding cylinder is moved perpendicular to the bulk flow direction in the horizontal plane with a velocity of only 1 cm s^{-1}, they fail to perform the task in darkness (Bleckmann et al., 2012). Another example is surface-feeding fish and aquatic amphibians. If parts of their lateral line are blocked, they still orient to a surface wave source, but with a prolonged latency and, depending on the number of neuromasts ablated, with a reduced precision (Bleckmann et al., 1989; Görner & Mohr, 1989).

This chapter has summarized knowledge of the capabilities of the lateral line and its contribution to behavior, neuroethology, and sensory ecology. In particular, studies have been reviewed that provide examples of the role of the lateral line in prey detection, predator avoidance, communication, and orientation, and studies that illustrate the issues of signals and noise in this sensory system. Although much has been learned about the neuroethology of the lateral line in terms of its general function across fish and amphibians, there is still much to do in terms of studying the details of form and function of lateral lines across development, and across the huge diversity of species found in these groups. The understanding of such adaptations is especially intriguing in view of the peripheral diversity of the lateral line. For instance, more needs to be known about the hydrodynamic environment and the lateral line mediated behavior of fishes that have only superficial neuromasts, are dominated by canals with many pores, have canals without pores, or have multiple trunk and/or highly branched canals. Some of this diversity will be of adaptive significance and provide insight into the details of form and function in the lateral line. However, some of the diversity will also be related to retention of key functional attributes, such as filtering properties, in the face of structural changes driven by other evolutionary/developmental considerations (Montgomery et al., 1994; Montgomery and Clements, 2000). In addition, the observed variation in lateral line structure on the head of surface feeding fish remind us that different types of lateral lines may also serve identical behavioral functions (e.g. Bleckmann et al., 1989).

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