The Potential Overlapping Roles of the Ear and Lateral Line in Driving “Acoustic” Responses

Dennis M. Higgs and Craig A. Radford

Abstract Examination of fish responses to sound stimuli has a rich and varied history but it is not always clear when responses are true measures of hearing or the lateral-line. The central innervation of auditory and lateral-line sensory afferents lie in close proximity in the brainstem and both sets of receptors are, at heart, hair cell-based particle motion detectors. While it is possible to separately measure physiological activity of these two receptor subtypes, many studies of fish “hearing” use whole brain potentials or behavioural assays in complex sound fields where it is not possible to distinguish inputs. We argue here that, as often measured, what is thought of as fish “hearing” is often a multisensory response of both auditory and lateral line receptors. We also argue that in many situations where fish use sound stimuli, the behaviour is also an integrative response of both systems, due to the often close proximity of fish during sound communication. We end with a set of recommendations for better understanding the separate and combined roles of ear and lateral-line hair cells as well as an acknowledgment of the seminal and continuing contributions of Arthur N. Popper and Richard R. Fay to this field.

Keywords Fish hearing • Mechanosensory • Auditory • Lateral line • Acoustic communication • Multisensory integration

1 Introduction

As generally reported, the response of fish to a sound source is typically considered “hearing” and structural correlates to this response have focused on ears and other auditory structures, such as Weberian ossicles and laterophysic connections (e.g.

D.M. Higgs (✉)
Department of Biological Sciences, University of Windsor, Windsor, ON, Canada
e-mail: dhiggs@uwindsor.ca

C.A. Radford
Leigh Marine Laboratory, Institute of Marine Science, University of Auckland,
Auckland, New Zealand
e-mail: c.radford@auckland.ac.nz

© Springer International Publishing Switzerland 2016

J.A. Sisneros (ed.), *Fish Hearing and Bioacoustics*, Advances in Experimental Medicine and Biology 877, DOI 10.1007/978-3-319-21059-9_12

Popper and Fay 1973, 1993, 1999; Fay and Popper 2012). While this might be a reasonable approach to take for terrestrial animals, we feel it is unjustified for studying responses of fish to sound due to the complexities of sound transmission underwater (Parvulescu 1967; Akamatsu et al. 2002; Zeddies et al. 2010) as well as the short distances over which fish "acoustic" communication typically occurs (reviewed in Zelick et al. 1999; Ladich 2004). As early as 1967 Parvulescu argued that, especially in laboratory experiments, "animal behavior may be due to lateral-line response rather than to auditory system response" (Parvulescu 1967) and yet many researchers focus largely on the "auditory response" when examining responses of fish after sound presentation in tanks. By focusing on hearing as the main mechanism of sound source detection in fish, not only are we missing valuable insights into how fish respond to sound stimuli but we also may have difficulty interpreting evolutionary trends in sound detection. We argue here that detection of many sound sources, although by no means all, is best examined as a multimodal response in which fish use both the ear and lateral line, and associated structures (e.g. Weberian ossicles and laterophysic connections), to form a full picture of sound stimuli, likely incorporating all inputs into a sensory gestalt after integration by central neural structures. While we of course do not advocate going back to the views of van Bergeijk (1964) that the ear plays little role in localization or even detection, we do argue that the pendulum has swung too far toward focus on the ear as the primary detector of sound stimuli, especially in the highly artificial laboratory or nearfield environment. The ear and lateral line are complementary, but not redundant, systems and only by fully understanding their central integration will we have a true appreciation for the importance of sound to the sensory ecology of fish and how this may have evolved across the Osteichthyes particularly and across the broader grouping of animals considered "fish".

2 Basic Concepts

An underwater acoustic stimulus has two components, the nearfield and farfield, both of which provide important information to fish. The "nearfield" is dominated by hydrodynamic flow and the "farfield" is dominated by a propagating pressure wave (Fig. 1). Hydrodynamic flow is generated by the movement of water near the acoustic stimulus source, while sound pressure waves propagate from the acoustic source as a cyclic compression and rarefaction of the water (Rogers and Cox 1988; Higgs et al. 2006). The fish mechanosensory lateral line is sensitive to hydrodynamic flow within one to two body lengths from the source (nearfield), and is not generally sensitive to pressure (Montgomery et al. 1995; Sand and Bleckmann 2008). The lateral line has two types of receptors: superficial neuromasts (particle velocity sensitive), which lie on the surface of the skin; and canal neuromasts (particle acceleration sensitive), which are found in subdermal canals that open to the external environment via a series of pores. The inner ear is also sensitive to the particle movement of an acoustic field as a result of whole-body accelerations (Rogers and

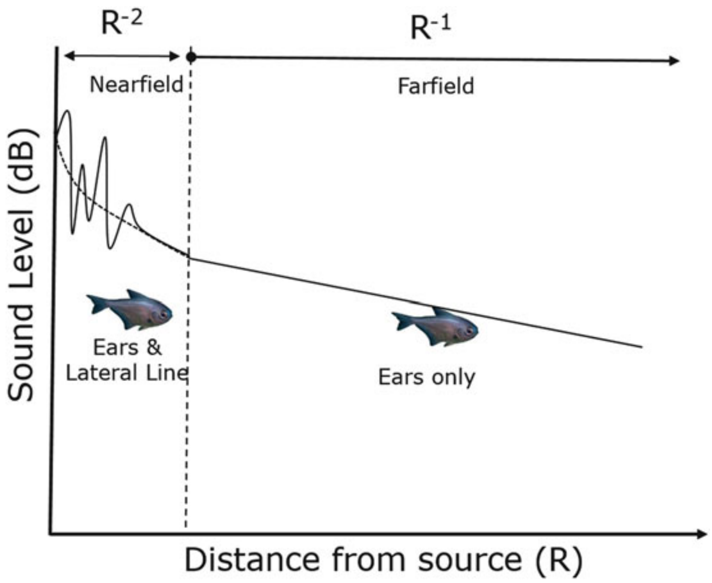

Fig. 1 Sound level as a function of distance for a representative source. Fluctuations near the source are due to source structure and would depend on direction. *Dotted line* shows sound level for an ideal point source

Cox 1988; Montgomery et al. 2006), through the differential movement of the denser otolith with the body motions of the fish. Sound pressure can be detected by fish from pressure-induced oscillations of the walls of an air pocket, such as the swim bladder, that then are transduced into mechanical stimuli appropriate to sensors (Higgs et al. 2006), such as the hair cells of the inner ear (Montgomery et al. 2006) or possibly the hair cells of the neuromasts that overlie laterophysic or otolaterophysic connections (Webb 1998; Webb and Smith 2000; Radford et al. 2013). The inner ear often lies just medial to the confluence of several cephalic lateral line canals (Fig. 2), so mechanical transduction to inner ear hair cells is also likely to be passed on to at least those neuromasts in the cephalic lateral line.

3 Underwater Sound Propagation

The behaviour of sound underwater is well characterized for ideal situations so will not be extensively reviewed here (see Rogers and Cox 1988; Montgomery et al. 2006). Sound consists of two components, particle motion and pressure, that, in theory, propagate in well-defined ways in unbounded media with the nearfield/farfield boundary dependent on wavelength. The problem with these physical descriptions of sound propagation for understanding the sensory ecology of fish is that the vast

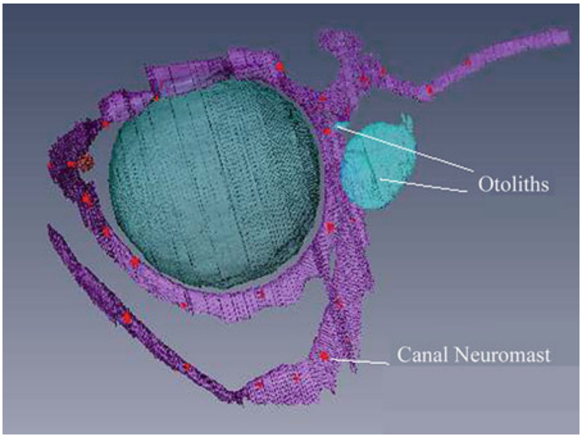

Fig. 2 MicroCT scan of a New Zealand Bigeye showing in vivo location of the otoliths and the canal neuromasts. Images were acquired on a Skyscan 1172 scanner and axial images were reconstructed as 17–35 mm slices. Anatomical structures were reconstructed from microCT slices, with Amira 5.2.1 (Visage Imaging, Inc.). Diagrams were prepared with Corel Graphics Suite X4. *Green* = eye; *blue* = otoliths; *purple* = cephalic lateral line; *red* = canal neuromasts

majority of fish species live in shallow and/or highly structured habitats (Lévêque et al. 2008) that disrupt sound propagation in highly unpredictable ways (Lugli and Fine 2007; Wilson et al. 2013). In the case of complex sound sources such as a coral reef, sound propagates much further than would be predicted from simple spreading models and it is likely that much of this propagation would be in the form of pressure waves (Fig. 3). Radford et al. (2011) described propagation of ambient reef sound from a temperate reef and observed a zone around the reef where sound loses little energy, what they termed the "reef effect" (Fig. 3c). Beyond the range of the reef effect (when the receiver is approximately 90° to the reef) sound propagation can be described by cylindrical spreading with some bottom attenuation. The reef effect essentially extends the range at which reef sound can propagate away from the reef. Even when examining the propagation of single species calls, propagation dynamics do not follow theoretical predictions (Fig. 3a, b). Courtship calls of oyster toadfish (*Opsanus tau*) propagate less than 5 m from the source (Fig. 3b), with transmission loss much higher than predicted due to interaction with the substrate on which they are calling, although low frequency pure tones can propagate further than predicted due to boundary interactions (Fine and Lehnardt 1983). Damselfish (Pomacentridae) that enter the water column to signal (Fig. 3a) likely cannot detect their own calls over approximately 10 m away due to rapid propagation loss (Mann and Lobel 1997) and freshwater goby (*Padogobius* spp.) calls attenuate up to 30 dB 30 cm from the source (Lugli and Fine 2003) due to the shallow nature of their habitat. While simple spreading models would predict greater sound propagation of many of these low frequency calls, it is clear that—in the structured world in which many vocalizing fish live—habitat structure and depth put additional constraints on the effective

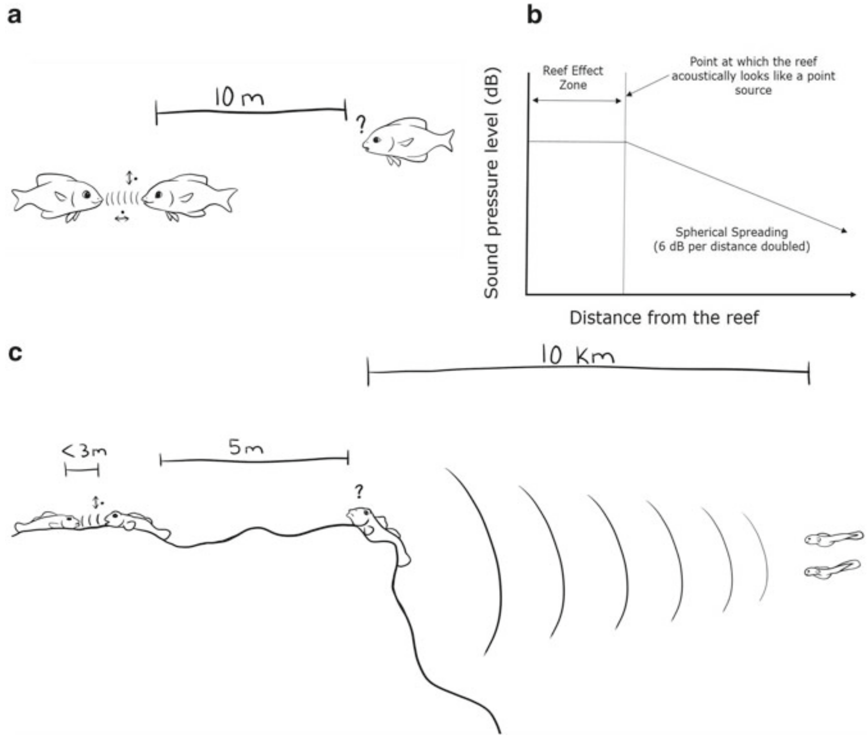

Fig. 3 Diagrammatic representation of relevant sound propagation in natural settings. (**a**) In pelagic spawning fish, communication sounds would be expected to stimulate both particle motion (*double arrows* in figure) and pressure sensors (*arcs* in figure) when fish are close together but likely are completely undetectable by either sensor at 10 m and beyond. (**b**) For benthic spawning fish, communication sounds likely are completely lost by 3 m from the source. (**c**) For reef communities there is little propagation loss even 1 km from the reef and then sound decays following idealized spherical spreading

distance of these calls and would put the effective range well within the detection range at which both ears and lateral lines would likely be stimulated (Fig. 3a, b).

4 Sound Propagation in Tanks

In experimental tanks, the propagation problem may be even harder to model due to relatively small tank sizes and variations in tank construction that have frequency-dependent disruptions to sound travel. Sounds do not travel in standard plane waves in small tanks, causing inaccurate pressure recordings (Parvulescu 1967), and significant distortions can occur due to tank resonance, water depth and the complexity of sounds presented (Akamatsu et al. 2002). If carefully measured, the direct contributions of sound pressure and particle motion can be used to the experimenters' advantage by examining behavioural responses of freely swimming fish in different components of the sound field. Using this approach Zeddies et al. (2012) were able to definitively demonstrate that plainfin midshipman (*Porichthys notatus*) can localize to tonal signals by following particle motion gradients in a tank but this approach is rare. It is much more common to only characterize the sound pressure level at a release site and assume a constant gradient from the sound source to the animal of interest. Until more careful sound characterizations are done in the model of Zeddies et al. (2012) it will be difficult, if not impossible, to ascertain exactly what component of the sound is being used to drive "acoustic" responses in the laboratory environment (Coffin et al. 2014).

5 Acoustic Ecology

Despite the supposed importance of acoustic signalling in fish, there still remain very few studies that have actually measured the propagation of fish acoustic communication in natural environments but, where these studies do exist, it appears that acoustic communication is very limited in effective range (Egner and Mann 2005; Lugli and Fine 2003; Fine and Lehnardt 1983). Many of the vocalizing species that have been studied live in association with the bottom or in shallow, structured environments and in these situations there is poor sound propagation (Forrest et al. 1993). Even damselfish (*Dascyllus albisella*) that leave the bottom during acoustic "signal jumps" have propagation of acoustic signals lasting only 11–12 m from the source (Mann and Lobel 1997). Bottom-associated species such as gobies (*Padogobius martensii*) have an even greater transmission loss, calls are likely indistinguishable from noise approximately 50–60 cm away from the source (Lugli and Fine 2003). Even fishes in the family Batrachoididae ("toadfishes" such as *O. tau* and *Halobatrachus didactylus*) that are known to have quite loud calls (Fine and Perini 1994) likely cannot detect conspecifics above background noise within 5 m of the sources (Fine and Lehnardt 1983; Amorim and Vasconcelos 2008). Thus, the vast majority of fish acoustic communication likely occurs in the nearfield, where particle motion should dominate (Rogers and Cox 1988; Au and Hastings 2008), and is likely to use lateral line receptors in conjunction with auditory receptors. Lateral line receptivity has been characterized to explain the behavioural orientations to sound stimuli for at least one fish species, the squirrelfish, (*Myripristis* spp.) and physiological responses of lateral line afferents show directional-dependent responses that are consistent with, and possibly sufficient for, orientation behaviours to these sounds (Horch and Salmon 1973), although it remains possible that auditory responses could also aid in orientation. When investigating the interplay of sound and behaviour it is also important to consider the distance (farfield or nearfield) at which the behaviour is occurring and the acoustic modality used. Here we review the role sound plays in fish communication (short range) and orientation (long range).

While fish may use sound as a long-distance attraction in some cases (see below), for conspecific communication—using Myrberg's (1981) definition of purposeful transfer of information to benefit the sender—both the signaller and the receiver are generally quite close together. In aggressive interactions involving sound cues, fish are typically within centimetres of each other (reviewed in Ladich 2004) and frequently produce high energy but low frequency (<600 Hz) sounds as aggressive displays (e.g. Tavolga 1958; Torricelli and Romani 1986; Torricelli et al. 1990; Amorim and Vasconcelos 2008; Johnston et al. 2008). In such cases, particle motion would predominate and both auditory and lateral line hair cells would likely be stimulated (Fig. 4a). For mating displays it is possible for fish to be further separated from one another, at least when calls might be used for mate attraction, and in these cases the predominant modality may change with distance from the source (Fig. 4b). In species such as midshipman (Brantley and Bass 1994), toadfish (Gray and Winn 1961), and many gobiids (Tavolga 1958; Torricelli and Romani 1986) males will vocalize without visual contact from a female. It is generally argued that directionalization is made possible by auditory processing (reviewed in Fay and Megela Simmons 1999), but lateral line inputs are known to be important in nearfield localization (Fay and Feng 1987) and have recently been hypothesized to work in conjunction with auditory processing at least for the midshipman response (Zeddies et al. 2012). For courtship sounds, the vocalization behaviour typically happens when a male and female are in close contact (Ladich 2004) and it is here that both hearing and lateral line hair cells are especially likely to be stimulated (Braun 2002; Sand and Bleckmann 2008). While it may be likely that longer-distance attractive calls are first detected and analysed by the auditory system, sounds used in final mating decisions are almost certainly analysed by both auditory and lateral-line peripheral and central mechanisms and both these systems must be considered when making functional correlates to behavioural responses.

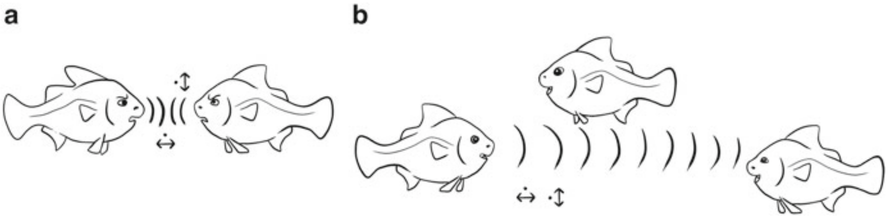

Fig. 4 In aggressive contexts (**a**), sound emission typically happens when fish are less than one body length apart and likely stimulate both particle motion (*double arrows* in figure) and pressure sensors (*arcs* in figure). Mating displays (**b**) may happen at a greater range of distances so sensory systems used will likely differ with distance, with pressure sensors needed further from the source but both ear and lateral line particle motion sensors stimulated as conspecifics come close for mating

6 Acoustic Attraction

Long range (farfield) orientation studies began in the 1960s with Nelson and Myrberg's pioneering work on sharks, investigating the frequencies which attracted distant sharks the best. Nelson and Gruber (1963) found that different species of Carcharhinidae and Sphyrnidae were mostly attracted to low frequency (20–60 Hz) pulsed sounds compared to higher frequency (400–600 Hz) pulsed sounds or low frequency continuous sounds. Myrberg et al. (1969, 1972) took this work a step further and observed that sharks showed sensitivity to low amplitude irregular pulsed sounds up to a frequency of 1000 Hz. The sharks also exhibited directional responses beyond the visual range of the camera (>25 m), which highlights that they were orienting to the sound stimulus well into what is typically thought of as the farfield (Myrberg et al. 1969). The actual nature of the attraction remains to be determined however, as sharks likely have little to no pressure sensitivity because they lack any pressure sensitive ancillary hearing structures, such as a swim bladder. Therefore, the particle motion component could be stimulating both the ear and external mechanoreceptors.

More recently, ambient underwater sound has been shown to play a major role in a key life history stage of many reef fish species—the transition from the larval pelagic stage to the benthic juvenile/adult stage (see Montgomery et al. 2001, 2006 for review). The first studies (Tolimieri et al. 2000; Simpson et al. 2004) employed the use of light traps and showed that traps with a sound source (recordings of ambient reef noise collected at night when most larvae settle) consistently caught more fish than silent traps. In free-swimming pelagic larvae followed by divers, it was also demonstrated that pre-settlement larvae will orient to a reef at night and that broadcast sounds can change their orientation behaviour, indicating that they can use sound to orient to reef habitats up to 1000 m from the reef source (Leis et al. 2002; Leis and Carson-Ewart 2003). The next step was using binary choice experiments which showed that all reef fish tested could directionally orient themselves to the sound source (Tolimieri et al. 2002, 2004; Leis and Lockett 2005). This was followed by patch reef experiments where reef fish settled onto the patch reefs associated with a sound source in greater numbers than silent patch reefs (Simpson et al. 2005). Not only do reef fish show a behavioural response towards sound, they also have the hearing capability to be able to detect these sounds (Wright et al. 2005, 2008, 2011). Combining the different hearing thresholds determined by Wright et al. (2011) with the reef sound propagation model developed by Radford et al. (2011), larval reef fish have the capability to detect a reef from between 8–15 km offshore. All these experiments highlight that sound plays a critical role as a long distance orientation and settlement cue for reef fish and at these distances it is likely that responses to sound are indeed likely dominated by true hearing responses because of the steep attenuation of particle motion sources likely to stimulate the lateral line at these distances (Figs. 1 and 3).

7 "Hearing" as a Physiological Response

While some field studies have assessed hearing in free-field situations (e.g. Chapman 1973; Chapman and Hawkins 1973; Chapman and Sand 1974), the vast majority of especially physiological work has tested "hearing" in the lab environment. Sound travel in laboratory tanks is notoriously complex (Akamatsu et al. 2002) and likely contains particle motion information well beyond what is typically thought of as the nearfield limit. A common physiological measure of fish "hearing" is the use of auditory evoked potentials (AEP, previously called auditory brainstem response or ABR). In this technique a fish is restrained under or at the surface of the water and a recording electrode implanted somewhere over the brainstem (Corwin et al. 1982; Kenyon 1996; Kenyon et al. 1998). In response to "sound" the waveform of brain activity will change in definable ways and the disappearance of this change as sound level decreases is taken to represent some sort of "auditory threshold". This technique is attractive to researchers because it is a fairly simple way to determine what sounds fish can detect and AEP can be quite useful in a comparative context to test how sound detection changes ontogenetically (e.g. Kenyon 1996; Higgs et al. 2002, 2003; Caiger et al. 2013), how experimental manipulations can affect detection (e.g. Yan et al. 2000; Radford et al. 2012, 2013; Higgs and Radford 2013), and to examine the bandwidth of detection between different species of interest (e.g. Corwin et al. 1982; Kenyon et al. 1998; Niemiller et al. 2013). While we have both used this technique extensively (e.g. Higgs et al. 2002; Radford et al. 2012, 2013; Higgs and Radford 2013) and recognize its utility in examination of sound detection, we no longer feel it can be used as an accurate test of hearing *sensu strictu*. The purpose of the present synopsis is not to review all the AEP/ABR papers that have been published, as that has been effectively done elsewhere (Ladich and Fay 2013), but rather to review the limited available evidence for the dual roles of the ear and lateral line in physiological responses to "acoustic" stimulation. The primary innervation sites for both auditory and lateral line nerves lie in close proximity in the brainstem (McCormick 1999; Higgs et al. 2006) and the same AEP recording setup that is commonly used in "hearing" studies has recently been used to measure direct lateral line stimulation (Brack and Ramcharitar 2012), therefore it seems likely that past AEP/ABR studies have been detecting responses of both systems. While there exists behavioural evidence that the lateral line can play a role in "acoustic" responses (see below), to our knowledge the only examination of the role of the lateral line in AEP responses is Higgs and Radford (2013). In that paper we showed that canal neuromasts play a role in "acoustic" thresholds previously attributed solely to the ear and that detection of sound stimuli in experimental tanks is likely an integrative response of both the ear and the lateral line, at least at low frequencies (<400 Hz). Direct recording from lateral line afferents in response to "acoustic" stimulation also shows that neuromasts can directly detect conspecific calls (Weeg and Bass 2002; Radford and Mensinger 2014) and can aid in localization of these calls in free-swimming fish (Radford and Mensinger 2014). The highlighted evidence clearly demonstrates that what was typically considered "hearing" may often be an integrative response between these two acoustic modalities. Unless the role of each system can be explicitly identified, we would recommend that future whole-brain physiological work be identified as acousticolateralis evoked potentials rather than the current ABR/AEP terminology.

8 "Hearing" as a Behavioural Response

In a more behavioural setup, there is also good evidence that lateral line afferents can also drive "hearing" responses, although the effect seems to vary with species. The Mauthner-mediated (M-cell) escape response is a reliable behavioural measure of reaction to aversive stimuli in fish that is driven by M-cell innervation of trunk musculature (Eaton et al. 1977). This M-cell escape response has been frequently used to test directional orientation to acoustic stimuli (reviewed in Eaton et al. 2001) and has been said to form a defined linkage between the ear and the trunk musculature (Moulton and Dixon 1967; Eaton and Popper 1995; Canfield and Rose 1996). While it is clear that the ear is involved in this behavioural response, the lateral line can also play an integrative role. Chemical ablation of the lateral line improves the ability of goldfish (*Carassius auratus*) to respond to sound stimuli while blocking the response of cichlids (*Astatotilapia burtoni*) (Canfield and Rose 1996) so both systems play a role in the M-cell response. The lateral line has been further implicated in both the directionality of this response and its interaction with environmental obstructions (i.e. tank walls) (Mirjany et al. 2011), showing that at least lower frequency sound stimuli are detected and processed by both auditory and lateral line systems.

9 Particle and Pressure Detection

To date there is only one published paper that has directly compared the contribution of particle motion and pressure sensitivity in fish (Radford et al. 2012). This paper compared the hearing thresholds of three species of fish (*C. auratus*, *Pempheris adspersa*, and *Forstergyian lappilum*) using a shaker table stimulus and an in-tank speaker stimulus. The results showed that all fish have the same basal hearing ability to particle motion and it is the fish's ability to detect the pressure stimulus that differentiates hearing ability between different groups, and likely drove evolutionary diversification in this modality. In a behavioural assay, female plainfin midshipman fish (*Porichthys notatus*) use particle velocity paths to directly guide their movement toward a vocalizing male with the response likely due to both hearing and lateral-line inputs (Zeddies et al. 2012). Radford and Mensinger (2014) have also shown that the toadfish (*O. tau*) can use their anterior lateral line to respond to a speaker stimulus using chronic recordings. Thus both the lateral line and inner ear may play in sound source localisation and, depending how the stimulus is presented, behavioural and physiological techniques may actually measure an integrated response from the lateral line and ears.

Fish of course can be using their auditory systems for much more than just conspecific communication and it has been cogently argued elsewhere (Popper and Fay 1993, 1997; Fay 2009) that "hearing" in fish may have evolved to function for auditory scene analysis rather than just conspecific communication. Under this model, the fish auditory system works to extract a range of relevant signals out of the background noise, forming a sensory gestalt of the entire acoustic landscape. While there is little direct evidence for this hypothesis, it does make intuitive sense and it is in analysis of the broader range of sounds that auditory and lateral line inputs may be separated. For nearfield communication sounds however, and especially for sound fields in laboratory tanks, it is likely that central processing of both auditory and lateral line inputs is combined in integration centres to form an integrative picture of sound stimuli. Until this central integration is better understood it will not be clear exactly what roles the ear and lateral line play in sound detection, although for a fish it may not matter what system predominates as long as the appropriate response is elicited.

10 Conclusions and Recommendations

Popper and Fay have had an outsized influence on the general field of vertebrate hearing through their superb compendium of Springer-Verlag volumes, their strong individual scientific work, and their training and mentoring of numerous students, postdoctoral fellows and visiting researchers and, for fish hearing in particular, in their excellent series of review papers (Popper and Fay 1973, 1993, 1999; Fay and Popper 2012) laying out the state of the field and major research questions still to be addressed. While we are far from their status as 'senior bioacousticians' (Fay and Popper 2012), we wish to end this review by emulating their model and offer three suggestions where we feel the research community could helpfully progress. As we hope we outlined above, we are not the first to suggest these research foci but by laying them out explicitly below we urge the field to consider new approaches that will better elucidate how the ear and lateral line work together to form a central image in response to sound stimuli.

1. In other vertebrates, especially mammals, the study of multisensory integration has become well established but researchers studying fish sensory function have predominantly studied sensory systems in isolation. We feel an enhanced emphasis on truly integrative physiology has the potential to advance the field in significant ways. Both single- and multi-unit recordings from integrative centres such as the torus semicircularis in response to sound stimuli as well as more natural stimuli (e.g. conspecifics or prey stimuli presented in the recording chamber, e.g. Wysocki and Ladich 2003; Maruska et al. 2007) would better inform us as to how fish encode and process sensory stimuli at the central level and turn that processing into behavioural responses. This physiological work would ideally be

coupled with anterograde and retrograde tracing to better understand how and where ear and lateral line afferents are integrated at a central level.

2. While there have been some attempts to isolate ear and lateral line inputs by selective ablation, especially of lateral line inputs (see above), more could be done in this regard. We echo Zeddies et al. (2012) suggestion that selective ablation of each input in freely behaving fish would be highly instructive in determining the role of each system. While selective ablation is not without controversy (Janssen 2000; Brown et al. 2011), if done carefully this technique can add insights into how fish perceive stimuli and how this perception drives responses.
3. While challenging, more effort must be put into physiological and behavioural responses in animals in their natural environment. At least for larger fish it is now possible to accurately track movements of free-swimming fish with either implanted passive integrated transponder (PIT) tags (e.g. www.Biomark.com) or acoustic tags (e.g. www.vemco.com) and these technologies could be effectively used to record responses of fish to a variety of sound stimuli. There has also been rapid progress in side-scan sonar applications from many companies that provide impressive details on fish movements and behaviours. Physiologically, it is now possible to record from neurons of free-swimming fish (e.g. Radford and Mensinger 2014) so more effort in this regard would be highly instructive as to how fish process sensory stimuli at both peripheral and central levels, although current technology would limit this to larger, more robust fish.

Acknowledgements Drs. Arthur Popper and Richard Fay have been the guiding influence for much of the field of fish bioacoustics throughout their careers and have advanced the field by their own primary research work as well as by the numerous commentary papers and compendia they have put together over the years. Art was a valued mentor for DH during a critical phase of his scientific career and acted as a true mentor as a scientist and as an academic. The time spent in Popper's lab continues to influence DH and contribute to his approach to science and mentoring. Dr. Fay was also an important sounding board for DH during his time as a postdoctoral fellow and, while DH never had the opportunity to work directly in Fay's lab he always appreciated the feedback and assistance when their paths crossed. While CR has not had the opportunity to work directly with either of Dr. Popper or Fay, they have really provided the foundation behind his work in understanding how larval marine fish use underwater sound as an orientation cue. In saying that, Dr. Popper has always supported CR's work through invitations and support to attend conferences.

The authors also gratefully appreciate the work of Ms. Meghan Donovan for drawing images for Figs. 3 and 4, Mr. Peter Johnston (MD) for the work on the CT-Scan images and two anonymous reviewers for many constructive comments on an earlier draft of this manuscript.

References

Akamatsu T, Okumura T, Novarini N, Yan HY (2002) Empirical refinements applicable to the recording of fish sounds in small tanks. J Acoust Soc Am 112:3073–3082

Amorim MCP, Vasconcelos RO (2008) Variability in the mating calls of the Lusitanian toadfish *Halobatrachus didactlyus*: cues for potential individual recognition. J Fish Biol 73:1267–1283

Au WWL, Hastings MC (2008) Principles of marine bioacoustics. Springer, New York

Brack CL, Ramcharitar J (2012) Assessment of lateral line function: a potential technique for studies in ototoxicity. J Clin Neurosci 19:333–335

Brantley RK, Bass AH (1994) Alternative male spawning tactics and acoustic signals in the plainfin midshipman fish *Porichthys notatus* Girard (Teleostei, Batrachoididae). Ethology 96:213–232

Braun CB (2002) What is the nature of multisensory interaction between octavolateralis subsystems. Brain Behav Evol 59:162–176

Brown AD, Mussen TD, Sisneros JA, Coffin AB (2011) Reevaluating the use of aminoglycoside antibiotics in behavioral studies of the lateral line. Hear Res 272:1–2

Caiger PE, Montgomery JC, Bruce M, Lu J, Radford CA (2013) A proposed mechanism for the observed ontogenetic improvement in the hearing ability of hapuka (Polyprion oxygeneios). J Comp Phys A 199:653–661

Canfield JG, Rose GJ (1996) Hierarchical sensory guidance of Mauthner-mediated escape responses in goldfish (*Carassius auratus*) and cichlids (*Haplochromis burtoni*). Brain Behav Evol 48:137–156

Chapman CJ (1973) Field studies of hearing in teleost fish. Helgolander wiss Meeresunters 24:371–390

Chapman CJ, Hawkins AD (1973) A field study of hearing in the cod, *Gadus morhua*. J Comp Physiol 85:147–167

Chapman CJ, Sand O (1974) Field studies of hearing in two species of flatfish *Pleuronectes platessa* (L.) and *Limnada limnada* (L.) (Family Pleuronectidae). Comp Biochem Physiol 47A:371–385

Coffin AB, Zeddies DG, Fay RR, Brown AD, Alderks PW, Bhandiwad AA, Mohr RA, Gray MD, Rogers PH, Sisneros JA (2014) Use of the swim bladder and lateral line in near-field sound source localization by fish. J Exp Biol 217:2078–2088

Corwin JT, Bullock TH, Schweitzer J (1982) The auditory brain stem response in five vertebrate classes. Electroencephalogr Clin Neurophysiol 54:629–641

Eaton RC, Popper AN (1995) The octavolateralis system and Mauthner cell: interactions and questions. Brain Behav Evol 46:124–130

Eaton RC, Bombardier RA, Meyer DL (1977) The Mauthner-initiated startle response in teleost fish. J Exp Biol 66:65–81

Eaton RC, Lee RKK, Foreman MB (2001) The Mauthner cell and other identified neurons of the brainstem escape network of fish. Prog Neurobiol 63:467–485

Egner SA, Mann DA (2005) Auditory sensitivity of sergeant major damselfish Abudefduf saxatilis from post-settlement juvenile to adult. Mar Ecol Prog Ser 285:213–222

Fay R (2009) Soundscapes and the sense of hearing of fishes. Integr Zool 4:26–32

Fay RR, Feng AS (1987) Mechanisms for directional hearing among nonmammalian vertebrates. In: Yost WA, Gourevitch G (eds) Directional hearing. Springer, New York, pp 179–211

Fay RR, Megela Simmons A (1999) The sense of hearing in fishes and amphibians. In: Fay RR, Popper AN (eds) Comparative hearing: fish and amphibians. Springer, New York, pp 269–318

Fay RR, Popper AN (2012) Fish hearing: new perspectives from two “senior” bioacousticians. Brain Behav Evol 792:215–217

Fine ML, Lehnardt ML (1983) Shallow-water propagation of the toadfish mating call. Comp Biochem Physiol 76A:225–231

Fine ML, Perini MA (1994) Sound production evoked by electrical stimulation of the forebrain in the oyster toadfish. J Comp Physiol A 174:173–185

Forrest TG, Miller GL, Zagar JR (1993) Sound propagation in shallow water: implications for acoustic communication by aquatic animals. Bioacoustics 4:259–270

Gray GA, Winn HE (1961) Reproductive ecology and sound production of the toadfish, *Opsanus tau*. Ecology 42:274–282

Higgs DM, Lui, Z, Mann DA (2006) Hearing and mechanoreception. In: Evans DH (ed) The physiology of fishes, 3rd edn. CRC Press, pp 391–429

Higgs DM, Radford CA (2013) The contribution of the lateral line to "hearing" in fish. J Exp Biol 216:1484–1490

Higgs DM, Souza MJ, Wilkins HR, Presson JC, Popper AN (2002) Age related changes in the inner ear and hearing ability of the adult zebrafish (*Danio rerio*). J Assoc Res Otolaryngol 3:174–184

Higgs DM, Rollo AK, Souza MJ, Popper AN (2003) Development of form and function in peripheral auditory structures of the zebrafish (*Danio rerio*). J Acoust Soc Am 113:1145–1154

Horch K, Salmon M (1973) Adaptations to the acoustic environment by the squirrelfishes *Myripristis violaceus* and *M. pralinius*. Mar Behav Physiol 2:121–139

Janssen J (2000) Toxicity of Co2+: implications for lateral line studies. J Comp Physiol A 186:957–960

Johnston CE, Bolling MK, Holt DE, Phillips CT (2008) Production of acoustic signals during aggression in Coosa bass, *Micropterus coosae*. Environ Biol Fish 82:17–20

Kenyon TN (1996) Ontogenetic changes in the auditory sensitivity of damselfishes (Pomacentridae). J Comp Physiol A 179:553–561

Kenyon TN, Ladich F, Yan HY (1998) A comparative study of hearing ability in fishes: the auditory brainstem response approach. J Comp Physiol A 182:307–318

Ladich F (2004) Sound production and acoustic communication. In: von der Emde G, Mogdans J, Kapoor BG (eds) The senses of fish: adaptations for the reception of natural stimuli. Narosa Publishing, New Delhi, pp 210–230

Ladich F, Fay RR (2013) Auditory evoked potential audiometry in fish. Rev Fish Biol Fish 23:317–364

Leis JM, Carson-Ewart BM (2003) Orientation of pelagic larvae of coral-reef fishes in the ocean. Mar Ecol Prog Ser 252:239–253

Leis JM, Lockett MM (2005) Localization of reef sounds by settlement stage larvae of coral-reef fishes (Pomacentridae). Bull Mar Sci 76:715–724

Leis JM, Carson-Ewart BM, Cato DH (2002) Sound detection *in situ* by the larvae of a coral-reef damselfish (Pomacentridae). Mar Ecol Prog Ser 232:259–268

Lévêque C, Oberdoff T, Paugy D, Stiassny MLJ, Tedesco PA (2008) Global diversity of fish (Pisces) in freshwater. Hydrobiologia 595:545–567

Lugli M, Fine ML (2003) Acoustic communication in two freshwater gobies: ambient noise and short-range propagation in shallow streams. J Acoust Soc Am 114:512

Lugli M, Fine ML (2007) Stream ambient noise, spectrum and propagation of sounds in the goby Padogobius martensii: sound pressure and particle velocity. J Acoust Soc Am 122:2881–2892

Mann DA, Lobel PS (1997) Propagation of damselfish (Pomacentridae) courtships sounds. J Acoust Soc Am 101:3783

Maruska KP, Boyle KS, Dewan LR, Tricas TC (2007) Sound production and spectral hearing sensitivity in the Hawaiian sergeant damselfish, *Abudefduf abdominalis*. J Exp Biol 210:3990–4004

Mccormick CA (1999) Anatomy of the central auditory pathways of fish and amphibians. In: Comparative hearing: fish and amphibians. Springer, New York, pp 155–217

Mirjany M, Preuss T, Faber DS (2011) Role of the lateral line mechanosensory system in directionality of goldfish auditory evoked escape response. J Exp Biol 214:3358–3367

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

Montgomery JC, Tolimieri N, Haine OS (2001) Active habitat selection by pre-settlement reef fishes. Fish Fish 2:261–277

Montgomery JC, Jeffs A, Simpson SD, Meekan M, Tindle C (2006) Sound as an orientation cue for the pelagic larvae of reef fishes and decapod crustaceans. Adv Mar Biol 51:143–196

Moulton JM, Dixon RH (1967) Directional hearing in fishes. Mar Bioacoust 2:187–228

Myrber AA, Spires JY (1972) Sound discrimination by the bicolor damselfish, *Eupomacentrus partitus*. J Exp Biol 57:727–735

Myrberg AA (1981) Sound communication and interception in fishes. In: Popper AN, Fay RR (eds) Hearing and sound communication in fishes. Springer, New York, pp 395–426

Myrberg AA, Banner A, Richard JD (1969) Shark attraction using a video-acoustic system. Mar Biol 2:264–276

Nelson EM, Gruber SH (1963) Sharks: attraction by low-frequency sounds. Science 142:975–977

Niemiller ML, Higgs DM, Soares D (2013) Evidence for hearing loss in amblyopsid cavefishes. Biol Lett 9. doi:10.1098/rsbl.2013.0104

Parvulescu A (1967) The acoustics of small tanks. Mar Bioacoust 2:7–13

Popper AN, Fay RR (1973) Sound production and processing by teleost fishes: a critical review. J Acoust Soc Am 53:1515–1529

Popper AN, Fay RR (1993) Sound detection and processing by fish: critical review and major research questions. Brain Behav Evol 41:14–38

Popper AN, Fay RR (1997) Evolution of the ear and hearing: issues and questions. Brain Behav Evol 50:213–221

Popper AN, Fay RR (1999) Comparative hearing: fish and amphibians. Springer, New York

Radford CA, Mensinger AF (2014) Anterior lateral line nerve encoding to tones and play-back vocalisations in free-swimming oyster toadfish, *Opsanus tau*. J Exp Biol 217:1570–1579

Radford CA, Tindle CT, Montgomery JC, Jeffs AG (2011) Modelling a reef as an extended sound source increases the predicted range at which reef noise may be heard by fish larvae. Mar Ecol Prog Ser 438:167–174

Radford CA, Montgomery JC, Caiger P, Higgs DM (2012) Pressure and particle motion detection thresholds in fish: a re-examination of salient auditory cues in teleosts. J Exp Biol 215:3429–3435

Radford CA, Montgomery JC, Caiger P, Johnston P, Lu J, Higgs DM (2013) A novel hearing specialization in the New Zealand bigeye, *Pempheris adspersa*. Biol Lett 9:21020163

Rogers PH, Cox M (1988) Underwater sound as a biological stimulus. In: Atema J, Fay RR, Popper AN, Tavolga WN (eds) Sensory biology of aquatic animals. Springer, New York, pp 131–149

Sand O, Bleckmann H (2008) Orientation to auditory and lateral line stimuli. In: Webb JF, Popper AN, Fay RR (eds) Fish bioacoustics. Springer, New York, pp 183–231

Simpson SD, Meekan MG, McCauley RD, Jeffs A (2004) Attraction of settlement-stage coral reef fishes to reef noise. Mar Ecol Prog Ser 276:263–268

Simpson SD, Meekan MG, Montgomery JC, McCauley RD, Jeffs A (2005) Homeward sound. Science 308:221

Tavolga WN (1958) Underwater sounds produced by two species of toadfish, *Opsanus tau* and *Opsanus beta*. Bull Mar Sci 8:278–284

Tolimieri N, Jeffs A, Montgomery JC (2000) Ambient sound as a cue for navigation by the pelagic larvae of reef fishes. Mar Ecol Prog Ser 207:219–224

Tolimieri N, Haine O, Montgomery JC, Jeffs A (2002) Ambient sound as a navigational cue for larval reef fish. Bioacoustics 12:214–217

Tolimieri N, Haine O, Jeffs A, McCauley R, Montgomery JC (2004) Directional orientation of pomacentrid larvae to ambient reef sound. Coral Reefs 23:184–191

Torricelli P, Romani R (1986) Sound production in the Italian freshwater goby, *Padogobius martensi*. Copeia 1986:213–216

Torricelli P, Lugli M, Pavan G (1990) Analysis of sounds produced by male *Padogobius martensi* (Pisces, Gobiidae) and factors affecting their structural properties. Bioacoustics 2:261–275

van Bergeijk WA (1964) Directional and nondirectional hearing in fish. Mar Bioacoust 1:281–299

Webb JF (1998) Laterophysic connection: a unique link between the swimbladder and the lateral line system in Chaetodon (Perciformes: Chaetodontidae). Copeia 1998:1032–1036

Webb JF, Smith WL (2000) The laterophysic connection in chaetodontid butterflyfish: morphological variation and speculations on sensory function. Philos Trans R Soc B 355:1125–1129

Weeg MS, Bass AH (2002) Frequency response properties of lateral line superficial neuromasts in a vocal fish, with evidence for acoustic sensitivity. J Neurophysiol 88:1252–1262

Wilson CJ, Wilson PS, Greene CA, Dunton KH (2013) Seagrass meadows provide an acoustic refuge for estuarine fish. Mar Ecol Prog Ser 472:117–127

Wright K, Higgs DM, Belanger AJ, Leis J (2005) Auditory and olfactory abilities of pre-settlement larvae and post-settlement juveniles of a coral reef damselfish (Pisces: Pomacentridae). Mar Biol 147:1425–1434

Wright K, Higgs DM, Leis J (2008) Auditory and olfactory abilities of larvae of the Indo-Pacific Coral Trout *Plectropomus leopardus* (Pisces: Serranidae) at settlement. J Fish Biol 72:2543–2556

Wright K, Higgs DM, Leis J (2011) Ontogenetic and interspecific variation in hearing ability in marine fish larvae. Mar Ecol Prog Ser 424:1–13

Wysocki LE, Ladich F (2003) The representation of conspecific sounds in the auditory brainstem of teleost fishes. J Exp Biol 206:2229–2240

Yan HY, Fine ML, Horn NS, Colón WE (2000) Variability in the role of the gasbladder in fish audition. J Comp Physiol 186:435–445

Zeddies DG, Fay RR, Alderks PW, Shaub KS, Sisneros JA (2010) Sound source localization by the plainfin midshipman fish, *Porichthys notatus*. J Acoust Soc Am 127:3104–3113

Zeddies DG, Fay RR, Gray MD, Alderks PW, Acob A, Sisneros JA (2012) Local acoustic particle motion guides sound-source localization behavior in the plainfin midshipman fish, *Porichthyes notatus*. J Exp Biol 215:152–160

Zelick R, Mann DA, Popper AN (1999) Acoustic communication in fishes and frogs. In: Fay RR, Popper AN (eds) Comparative hearing: fish and amphibians. Springer, New York, pp 363–411