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COMMENTARY

Mechanosensory signaling as a potential mode of communication during social interactions in fishes

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ABSTRACT

Signals produced during social interactions convey crucial information about the sender's identity, quality, reproductive state and social status. Fishes can detect near-body water movements via the mechanosensory lateral line system, and this sense is used during several common fish behaviors, such as schooling, rheotaxis and predator–prey interactions. In addition, many fish behaviors, such as aggressive lateral displays and reproductive body quivers, involve fin and body motions that generate water movements that can be detected by the lateral line system of nearby fish. This mechanosensory system is well studied for its role in obstacle avoidance and detection of inadvertent hydrodynamic cues generated during schooling and predator–prey interactions; however, little research has focused on the role of mechanosensory communication during social interactions. Here, we summarize the current literature on the use of mechanosensation-mediated behaviors during agonistic and reproductive encounters, as well as during parental care. Based on these studies, we hypothesize that mechanosensory signaling is an important but often overlooked mode of communication during conspecific social interactions in many fish species, and we highlight its importance during multimodal communication. Finally, we suggest potential avenues of future research that would allow us to better understand the role of mechanosensation in fish communication.

KEY WORDS: Behavior, Communication, Lateral line, Mechanoreception, Multimodal signaling, Teleost

Introduction

Animals use multiple sensory modalities to gain information about their physical and social environment. In teleost fishes, the use of visual, chemosensory and acoustic communication is relatively well studied in different behavioral contexts such as territoriality, reproduction and parental care (Almeida et al., 2005; Amorim et al., 2003, 2004; Barata et al., 2007; Chen and Fernald, 2011; Grosenick et al., 2007; Keller-Costa et al., 2015; Korzan and Fernald, 2007; Korzan et al., 2008; Lobel, 1998; Martinovic-Weigelt et al., 2012; Maruska and Fernald, 2012; Maruska et al., 2012; Rosenthal and Ryan, 2000; Simoes et al., 2008). However, all fishes also possess another sensory system, the mechanosensory lateral line (Fig. 1), which allows them to detect water movements. Since the early descriptions of the lateral line system, researchers have proposed a potential role for mechanosensory signals during social interactions (e.g. Dykgraaf, 1933; Noble and Curtis, 1939), but direct empirical tests are few. During typical social encounters, fishes produce a variety of behaviors, many of which involve fin or body motions that generate water movements (Aronson, 1949; Barlow, 2002; Dijkgraaf, 1963; Enger et al., 1989; Fernald, 1977; Fernald and Hirata, 1977; Mackereth and Keenleyside, 1993; Munro and Pitcher, 1985; Noble and Curtis, 1939; Thresher, 1984). These water movements can then be detected by the lateral line system of nearby fish, which suggests that mechanoreception could be an important sense during many social interactions. Past research on the lateral line system has focused on its involvement in obstacle avoidance (Baker and Montgomery, 1999; Kulpa et al., 2015; Montgomery et al., 1997; Windsor, 2014) and detection of inadvertent water movements generated by other fish [e.g. during schooling (Pitcher et al., 1976) and predator–prey interactions (Coombs and Patton, 2009; Schwalbe et al., 2012, 2016)], but there are only a few studies that examine the possibility that fish purposefully generate mechanosensory signals as a form of communication (Butler and Maruska, 2015, 2016; Medina et al., 2013; Satou et al., 1991, 1994). The aim of this Commentary is to inspire future research to address the role of hydrodynamic signals as a potential form of communication during social interactions. We first provide background on the lateral line system and its distinction from the auditory system. We then discuss what is known about the role of mechanosensory signals during social interactions, and we propose that these signals may act as an important form of communication during multisensory behaviors in fishes. A brief discussion on the methodological issues surrounding lateral line ablation techniques is provided, and readers are encouraged to critically evaluate results from past studies cited throughout this Commentary. Finally, we conclude by suggesting avenues of future research that will help move this interesting field forward.

What is the lateral line system?

The lateral line is a mechanosensory system that detects water movements close to the body of the fish (Coombs, 1994; Coombs et al., 1996; Dijkgraaf, 1963; McHenry and Liao, 2014). It is composed of neuromasts – mechanoreceptive organs comprising support cells and sensory hair cells with hair bundles (made up of a single kinocillium with multiple rows of stereovilli) covered by a gelatinous cupula (Dijkgraaf, 1963). These neuromasts are located either on the skin surface of the fish (superficial neuromasts) or in bony canals embedded within the dermis (canal neuromasts; Fig. 1) (Webb, 1989). Water movements near the fish's skin surface cause the cupula to be deflected by viscous drag, opening mechanotransduction channels on the stereovilli to depolarize the sensory hair cells and generate neural action potentials (reviewed in van Netten and McHenry, 2014). The effective stimulus differs between superficial and canal neuromasts because of their morphology and location (Chagnaud and Coombs, 2014); while superficial neuromasts primarily detect velocity, fluid dynamics within the canals means that flow inside the canal is proportional to the acceleration differences between the fish and surrounding water,

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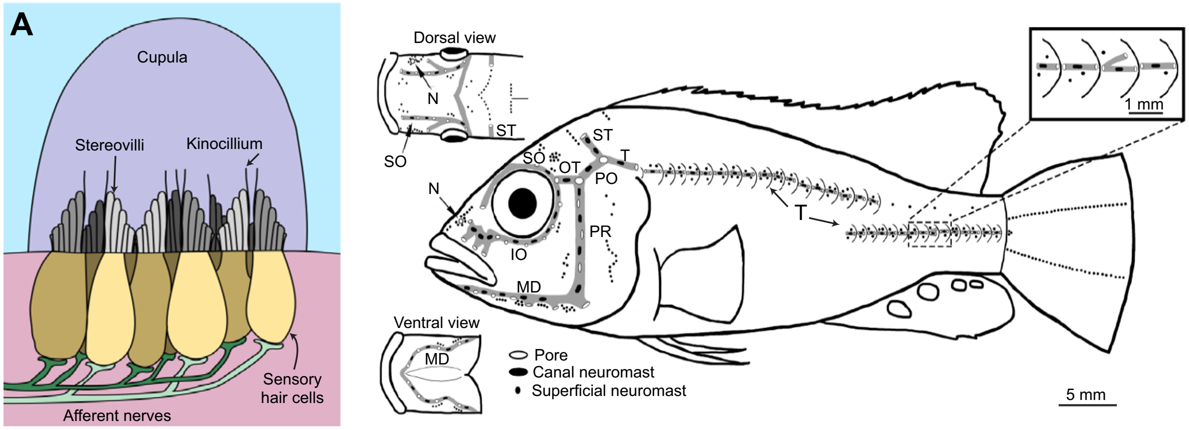


Fig. 1. Neuromast structure and distribution of the mechanosensory lateral line system in the African cichlid, *Astatotilapia burtoni*. (A) Lateral line neuromasts are composed of support cells (not shown) and sensory hair cells, each of which contains a single kinocilium and several rows of stereovilli, projecting up into a gelatinous cupula. Afferent nerves deliver mechanosensory information from water movements produced near the fish and transmit it to the brain. (B) The *A. burtoni* lateral line system consists of seven cranial canals and a disjunct trunk canal. Canal neuromasts (black ovals) lie inside bony canals (gray shading) embedded within the dermis, and each neuromast is located between adjacent canal pores (open ovals). Superficial neuromasts (small black circles) are located on the skin surface around the naris, in rows or clusters around canals and in two rows down the length of the caudal fin. IO, infraorbital canal; MD, mandibular canal; N, naris; OT, otic canal; PO, postotic canal; PR, preopercular canal; SO, supraorbital canal; ST, supratemporal canal; T, trunk canal. Modified from Butler and Maruska (2015).

which are detected by canal neuromasts. Information about the velocity and acceleration components of nearby water movements are then conducted by lateral line nerves to the brain, where they are ultimately integrated with other neural circuits to produce appropriate behavioral responses (Bleckmann and Mogdans, 2014; Butler and Maruska, 2016; Wullimann and Grothe, 2014).

Mechanosensory versus acoustic communication

In the past, the lateral line system was thought to be an accessory hearing organ (van Bergeijk, 1964). Today, electrophysiological, morphological, neuroanatomical and behavioral evidence indicates that although the mechanosensory lateral line system and auditory inner ear (composed of three otolithic endorgans – the saccule, lagena and utricle) can be stimulated by the same source, they are in fact two distinct systems (reviewed in Braun and Sand, 2014; Kalmijn, 1988, 1989). Any movement underwater will inevitably generate sound, which propagates away from the source as both a pressure wave (a scalar quantity involving compressions and rarefactions of particles) and particle motion (a vector quantity involving to-and-fro displacement of particles). Detection of sound pressure waves requires pressure-transducing morphological specializations that are found in some fish species [e.g. large swim bladder or rostral extensions of the swim bladder that increase proximity to the inner ear (Schulz-Mirbach et al., 2012); direct connections between the swim bladder and auditory otolithic endorgans, such as auditory bullae in clupeoids (Blaxter et al., 1981) and Weberian ossicles in ostariophysians (Furukawa and Ishii, 1967); and laterophysic connections between lateral line canals and the swim bladder in some butterflyfishes (Webb and Smith, 2000)]. Because the particle motion component of sound propagates further from the source underwater than it does in air, it is an important stimulus for both the mechanosensory and auditory systems of fishes. Although all fishes detect the particle motion component of sounds, the relative use of the pressure component depends on the presence or absence of the abovementioned morphological specializations. Across fishes, therefore, the perception of 'sound' can be envisioned as a continuum from species that depend on particle motion detection to those that use both pressure and particle motion, and still others that predominantly detect the pressure component (reviewed in Popper et al., 2003). Thus, acoustic stimuli can be detected by both the auditory and mechanosensory systems, depending on factors such as frequency and distance. The lateral line system detects close-range (usually within ∼1–2 body lengths), low-frequency (<∼200 Hz) stimuli; thus, perception at low frequencies and at close range can be a multimodal response (Braun and Coombs, 2000; Braun and Sand, 2014; Higgs and Radford, 2013).

The lateral line system acts independently of the auditory system in many behaviors. Similarly, the auditory system functions independently of the lateral line system, particularly further from the source. Here, we focus on the mechanosensory lateral line system, and hypothesize that it might mediate an independent form of close-range communication during social interactions, with the caveat that particle displacements from water movements produced by behaving fish can potentially stimulate both lateral line and auditory systems. Future research should attempt to distinguish the responses of these two systems to acoustic stimuli and determine the relative importance of each during social interactions.

The potential use of mechanosensory signals in the social behavior of fishes

Mechanosensory cues versus signals

The role of mechanosensory cues in mediating behaviors such as schooling, rheotaxis (orientation within a current) and predator–prey interactions is well studied (Baker and Montgomery, 1999; Coombs and Patton, 2009; Hoekstra and Janssen, 1985; Kulpa et al., 2015; Montgomery et al., 1997; Pitcher et al., 1976; Schwalbe et al., 2012), but little research has addressed the possibility that fish use water movements as a form of communication during intra-specific social interactions (Butler and Maruska, 2015). Although often used interchangeably, the terms 'cue' and 'signal' have distinct definitions in the realm of animal communication theory (Bradbury and Vehrencamp, 1998). Cues are passive and generated either inadvertently or for another purpose, whereas signals are generated by a sender with the purpose of informing the receiver. Signals are mutually beneficial to both parties and arise through evolutionary processes. For example, predators exploit mechanosensory cues in order to locate living prey (Coombs and Patton, 2009; Pohlmann et al., 2004; Schwalbe et al., 2012, 2016), but for a water movement to be considered a signal, it must also benefit the sender in some way.

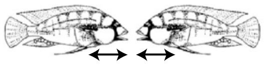
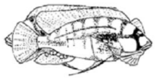
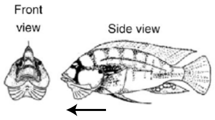
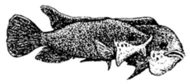
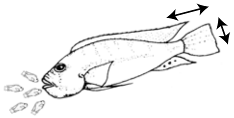
Based on a plethora of ethological studies, it is apparent that many fish social behaviors generate water movements (Aronson, 1949; Barlow, 2002; Dijkgraaf, 1963; Enger et al., 1989; Fernald, 1977; Fernald and Hirata, 1977; Mackereth and Keenleyside, 1993; Munro and Pitcher, 1985; Noble and Curtis, 1939) (Table 1), which should be detectable by the lateral line system of conspecifics. In fact, Baerends and Baerends-van Roon (1950) described a subset of cichlid fish behaviors as ‘signal movements’. Many of these behaviors are described, at least in part, as involving fin and body motions that generate water movements. Further, Bleckmann et al. (1991) found that body and tail movements produced hydrodynamic flow fields consisting of low-frequency (<10 Hz) stimuli coupled with higher-frequency acceleration components. These hydrodynamic stimuli, therefore, can be detected by both superficial and canal neuromasts, and are likely to be produced during close-range social behaviors (e.g. body quivers, lateral displays). Thus, hydrodynamic signals produced during conspecific interactions might serve as important substrates for natural and sexual selection. Below, we discuss some examples of social behaviors in which mechanosensory signals might play an important role.

Mechanosensory signals and aggressive interactions

Many species of fishes live in dominance hierarchies or territorial systems where only the most dominant, highest ranking members reproduce (Ellis, 1995; Fernald, 2009; Itzkowitz, 1974; Maruska, 2014; Wootton and Smith, 2014). For these species, aggressive encounters have extreme consequences for reproductive fitness. One commonly used agonistic ‘signal movement’ in many fishes is a lateral display, during which one fish orients parallel to another, fully erects its dorsal, anal and caudal fins, and distends its jaws to create a visual display of larger size. Several fish species accompany this visual display with potential mechanosensory signals by gently to vigorously shaking their body and beating their tails or other fins. Another common behavior performed by fish during aggressive encounters is a frontal display, in which one fish pushes water at another with flared opercula and distended jaws. Both of these behaviors involve visual signals, but they, and many other common agonistic behaviors, also create hydrodynamic stimuli.

Whether to engage in or escalate a fight is an important decision for a fish. Territorial interactions are energetically costly, increase predator exposure and often result in physical damage to both the winning and the losing fish. To make this decision, a fish needs as much information about the opponent as possible. Although the roles of visual and chemosensory signals in animal assessment are well documented (Arnott and Elwood, 2009; Bleckmann and Mogdans, 2014; Chen and Fernald, 2011; Ratterman et al., 2009), only one study has examined the role of the lateral line system in mediating mutual assessment (Butler and Maruska, 2015). In that study, we found that lateral-line-ablated male cichlids were less likely to initiate and engage in a territorial encounter compared with lateral-line-intact males (Fig. 2) (Butler and Maruska, 2015); fish lacking the ability to detect mechanosensory signals spent more time assessing their opponent prior to engaging in a fight. Visual assessment is adequate when animals are unequally size-matched (Chen and Fernald, 2011), but we propose that when fish are closely size-matched, mechanosensory signals provide relevant information for fish to decide whether to engage in a fight or retreat.

Table 1. Schematic representations of social behaviors that produce hydrodynamic stimuli in the cichlids *Astatotilapia burtoni* and *Tilapia natalensis* (=*Oreochromis mossambicus*).

Aggression	
Border fight 	Fish orient in front of each other and push foward and back to delineate the borders of their territory.
Lateral display 	Fish orient parallel to each other, erect fins, distend jaws and shake their bodies.
Frontal threat 	Fish distend jaws and flare opercula. Often accompanied by a lunge at another fish.
Mouth fight 	Fish grasp jaws and push/pull each other.
Bite/nudge 	One fish rams opponent typically on the trunk with an open mouth (bite) or closed mouth (nudge).
Reproduction	
Lead/tail waggle 	Male leads female to spawning shelter while waggling tail back and forth.
Quiver/courtship display 	Male shakes body while displaying egg spots on anal fin.
Parental care	
‘Call’ to the fry 	Parental fish abruptly raises and lowers various fins to call young back to the nest or buccal cavity.

During aggressive behaviors (border fights, lateral displays, frontal threats, mouth fights, bites and nudges), fish generate mechanosensory signals that can be detected by the lateral line system of their opponents and other nearby fish. Male *A. burtoni* (and many other fishes) court sexually receptive females by quivering their body and leading females back to the spawning territory while waggling their tails. Parental fish can ‘call’ their young back to the nest or their mouth by abruptly raising and lowering various fins. Arrows around fish indicate movement directions of body or fins. Modified from Baerends and Baerends-van Roon (1950), Butler and Maruska (2015) and Maruska and Fernald (2010).

Game theory research indicates that most aggressive interactions follow a stereotypical structure (Enquist et al., 1990; Leiser et al., 2004). For example, fights are normally instigated with a lateral display (or other non-contact behavior) and continue with the use of less-dangerous non-contact behaviors. If the fight escalates, fish then resort to more-dangerous contact behaviors, such as mouth fighting and biting. In the convict cichlid, *Archocentrus*

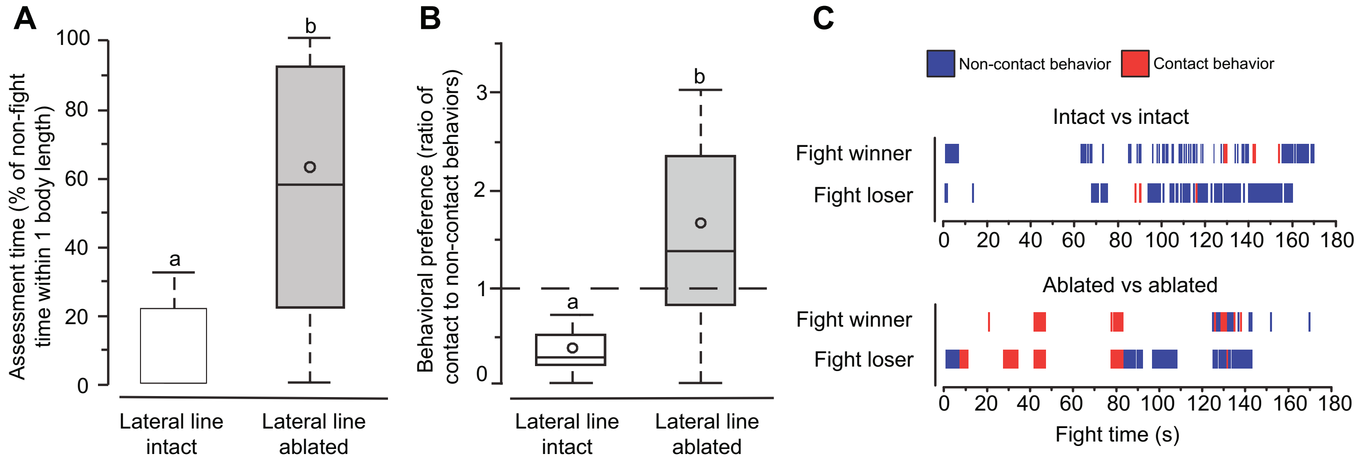


Fig. 2. *Astatotilapia burtoni* uses the mechanosensory lateral line system for assessment during aggressive interactions. (A) Lateral line-ablated *A. burtoni* males spent more time assessing their opponents (measured as the percentage of pre-fight time spent within one body length of an opponent) than lateral-line-intact males. (B) Lateral-line-intact males used predominantly non-contact aggressive behaviors while lateral-line-ablated males used contact fight behaviors. A ratio of <1 (below dashed line) signifies use of non-contact behaviors and >1 (above dashed line) signifies predominant use of contact fight behaviors. Different letters indicate statistical significance at $P<0.05$. Tukey's box plots were used to represent behavior data: the median is represented by a line and the mean by an open circle; the box extends to the furthest data points within the 25th and 75th percentiles; whiskers extend to the furthest data points not considered outliers. Absence of whiskers indicates that no data points are present outside of the 25th/75th percentile. (C) Raster plots of non-contact (blue) and contact (red) fight behaviors during territorial interactions between two size-matched males show a difference in the sequence of behavioral patterns. Fights between two lateral-line-intact fish (top) use primarily non-contact behaviors and then escalate to the use of contact fight behaviors. In contrast, lateral-line-ablated fish (bottom) used mostly contact fight behaviors from the start of the fight. Modified from Butler and Maruska (2015).

nigrofasciatus, the number of non-contact aggressive behaviors decreased as the fight progressed, while the number of mouth fights and bites (i.e. contact behaviors) stayed the same or increased (Leiser et al., 2004). In the African cichlid, *Astatotilapia burtoni*, lateral-line-ablated males performed predominantly contact behaviors and had an altered fight structure compared with males with intact lateral line systems (Fig. 2) (Butler and Maruska, 2015). Instead of beginning with non-contact behaviors, as do males with intact lateral line systems and as predicted by game theory, fish with ablated lateral line systems would use contact behaviors throughout a fight. When fish were unable to detect the hydrodynamic signals produced by their opponents, they quickly escalated the fights to involve contact behaviors such as bites, rams and mouth fights, suggesting that intact lateral line neuromasts allowed the use of mechanosensory signaling between opponents, through non-contact behaviors. Although experimental data exist for only one species, Butler and Maruska's (2015) study indicates that fish likely produce and use mechanosensory signals during agonistic interactions. This could, in part, be due to their inability to gauge the opponent's distance, resulting in more contact behaviors. With an intact lateral line system, the use of non-contact behaviors likely represents a self-preservation technique, allowing fish to be more aware of their surroundings than they would be if engaged in contact behaviors. The South American cichlid *Nannacara anomala*, for example, reacted more slowly to a predator during contact behaviors than during non-contact behaviors (Jakobsson et al., 1995). We hypothesize that mechanosensory communication is vital for territorial interactions across fishes, with impacts on dominance hierarchies and, ultimately, reproductive success – an idea that needs to be tested in future studies on diverse species.

Mechanosensation-mediated courtship and reproductive behaviors

In addition to aggressive contexts, many fishes produce water movements that could be used as mechanosensory signals during their courtship repertoire. For example, body quivers, in which males display and vibrate their bodies while in close proximity to a female, are a common courtship behavior. Furthermore, some male fish produce tail waggles to encourage a sexually receptive female to spawn. Male three-spined sticklebacks (*Gasterosteus aculeatus*) use a 'zig-zag' dance to court gravid females (Tinbergen, 1951; Tinbergen and Van Iersel, 1947), and in many species of wrasses, terminal-phase (i.e. dominant, territory-holding and reproductively competent) males combine intense body vibrations with rapid tail beats while swimming back and forth over a potential mate (Robertson and Hoffman, 1977). Despite the obvious use of hydrodynamic signal-generating behaviors, only a few studies have examined the role of mechanosensation during reproductive encounters. Because any signals produced during courtship and mating provide the receiver with crucial information on the sender's quality, motivation, readiness and social status, these mechanosignals have important implications for fitness and species persistence.

Vibrational communication involves one fish purposefully vibrating its body to send information, such as 'I'm ready to spawn' or 'stay away', to other nearby fish. This vibrational communication has been studied in only the hime (landlocked) salmon *Oncorhynchus nerka* (Satou et al., 1991, 1987, 1994) and the Amarillo fish *Girardinichthys multiradiatus* (Medina et al., 2013), and these studies suggest that the detection of hydrodynamic signals emitted from the vibrating fish elicits a behavioral response from the receiver. In the hime salmon, female body vibrations signal they are ready to spawn (Satou et al., 1991). These mechanosensory signals alone are sufficient to elicit male reproductive behaviors, as males exposed to a vibrating sphere will release sperm. However, when the males' ability to detect mechanosensory signals was disrupted, they failed to appropriately respond to the vibrating sphere (Satou et al., 1994). In the Amarillo fish, females use body vibrations to discourage male courtship (Medina et al., 2013). Females that did not emit vibrations in response to an approaching male were harassed and chased by the male. In addition, this study found that lateral-line-ablated females were less likely to respond to approaching males, suggesting that their behavioral response (i.e. vibrating) was dependent on receiving mechanosensory signals from the approaching males. Further research is needed in other fish species to better understand the role of mechanosensory communication during courtship and reproductive encounters.

In an alternative approach, Plath et al. (2004) used surface- and cave-dwelling Atlantic mollies (*Poecilia mexicana*) to compare fish size-discrimination abilities under light and dark conditions. Females from all populations could distinguish male size (measured by preference for larger males) when visual signals were present, but only females from the cave populations could distinguish male size in the absence of visual cues (Plath et al., 2004). The authors suggest that the lateral line system likely mediates the observed preference in the cave-dwelling populations (although they did not directly test this or the relative importance of chemosensory signals). Cave-dwelling mollies have widened lateral line canals that potentially compensate for their lack of vision and might have allowed for a potential sensory shift from vision to mechanoreception. Thus, mechanosensory signals may be involved in mate choice, although further research is needed.

Spawning synchronization, in which males and females release their gametes at similar times and locations, is important for externally fertilizing fish species. This ability to synchronize gamete release increases fertilization success and may also be mediated by mechanosensory signaling. For example, in many broadcast-spawning fishes (which release gametes into the water column), a single male–female pair or a larger group of males and females will swim rapidly upwards and simultaneously release eggs and sperm. As these behaviors involve rapid body movements of both sexes in close proximity (Thresher, 1984), it is likely that hydrodynamic signals play a role in synchronization, although this remains untested. In nest-building species, males and females also circle each other while releasing gametes into their nest (Aronson, 1949; Thresher, 1984), and in mouthbrooding fishes (in which the young develop inside the oral/buccal cavity), spawning partners circle each other during repeated bouts of egg release, uptake and fertilization (Salzburger et al., 2007). Marchesan et al. (2000) examined spawning behaviors in the grass goby, *Zosterisessor ophiocephalus*, and found that both sexes predominantly used behaviors involving physical contact or fin and body oscillations, concluding that mechanical stimulation via the somatosensory and mechanosensory systems is needed to synchronize spawning behaviors. They suggest that female body arching and dorsal fin oscillations signal receptivity to the male to inhibit male aggression. Unfortunately, none of these studies directly tested whether mechanosensory signals mediate spawning synchronization; however, they do suggest that mechanosensory communication may be involved in the proper timing of gamete release.

Parental care: water movement signals to ‘call’ the young

Many species of fishes offer some form of parental care to their offspring (reviewed in Wootton and Smith, 2014). Although chemosensory communication is thought to be the primary sense involved in kin recognition in fishes (salmonids: Olsén, 1992; zebrafish: Biechl et al., 2016), evidence suggests that parents also employ mechanosensory communication to signal to their offspring. In some species, parents ‘call’ to their young using abrupt raising and lowering of various fins and occasional tail-beating (Baerends and Baerends-van Roon, 1950; Fryer and Iles, 1972). These behaviors generate water movements that can potentially be detected by the lateral line systems of the offspring. In the mouthbrooding Mozambique tilapia, *Oreochromis mossambicus*, parents ‘call’ to their young, who quickly return to the calling mother’s mouth (Fryer and Iles, 1972). However, if the offspring are separated from the calling mother by a clear, solid barrier, they fail to respond to the mother’s signals. If the visual signals are paired with water disturbances in the offsprings’ tanks, the fry swim to the barrier separating them from their parent in an attempt to re-enter her buccal cavity. In *O. mossambicus*, visual cues must be paired with these mechanosensory signals to induce the fry’s behavior, indicating that hydrodynamic signaling is necessary for accurate communication between parents and offspring. However, in another cichlid, *Hemihaplochromis multicolor*, fry reportedly respond to visual cues alone, but these results have been questioned (Fryer and Iles, 1972). Although scarce, these data suggest that fishes that provide parental care may produce mechanosensory signals to communicate danger or other information to their young, which would be particularly salient under conditions of limited visibility. However, additional research is needed to fully understand the role of mechanosensory signaling between parents and offspring. Using modern techniques (i.e. lateral line ablation) in a variety of fish species with a range of parental care strategies will provide a more complete picture of the role of mechanoreception in parental care.

Investigating the neuroethology of mechanosensory signals involved in social decisions

If mechanosensory signals are important during the abovementioned social interactions (i.e. territoriality, reproduction and parental care), then where might this information be processed in the brain to mediate behavioral decisions? The conserved vertebrate social decision-making network (SDMN) is thought to evaluate the salience of social or sensory signals and integrate it with the animals’ own physiology to produce context-appropriate behaviors (O’Connell and Hofmann, 2011; O’Connell and Hofmann, 2012). Several nuclei of the SDMN receive input from mechanosensory-processing regions (Fig. 3; reviewed in Wullimann and Grothe, 2014), indicating that hydrodynamic information has the potential to affect social decisions. To date, only a single study has examined the role of mechanosensory signals in mediating activation of decision-making circuits in the brain (Butler and Maruska, 2016). Several studies have used neurophysiological and tract-tracing methods to elucidate where in the brain mechanosensory information is processed (reviewed in Bleckmann and Mogdans, 2014; Wullimann and Grothe, 2014), but these were performed on anesthetized, non-behaving animals while often using controlled artificial stimuli such as a vibrating sphere. In an alternative approach, we recently examined where in the brain socially relevant mechanosensory information is processed in awake, behaving animals, using lateral-line-intact and -ablated *A. burtoni* males (Butler and Maruska, 2016). In addition to known lateral-line-processing regions (i.e. hindbrain medial octavolateralis nucleus; midbrain torus semicircularis, ventrolateral region; central posterior thalamic nucleus), several other regions had differential activation between lateral-line-intact and -ablated males: the anterior tuberal nucleus (ATn, partial homolog of the ventromedial hypothalamus), the granular zone of the lateral part of the dorsal telencephalon (Dlg, putative homolog of hippocampus) and the supracommissural nucleus of the ventral telencephalon (Vs, homologous in part to the extended amygdala). This suggests that the activation of these behaviorally relevant regions is associated with reception of mechanosensory signals, but

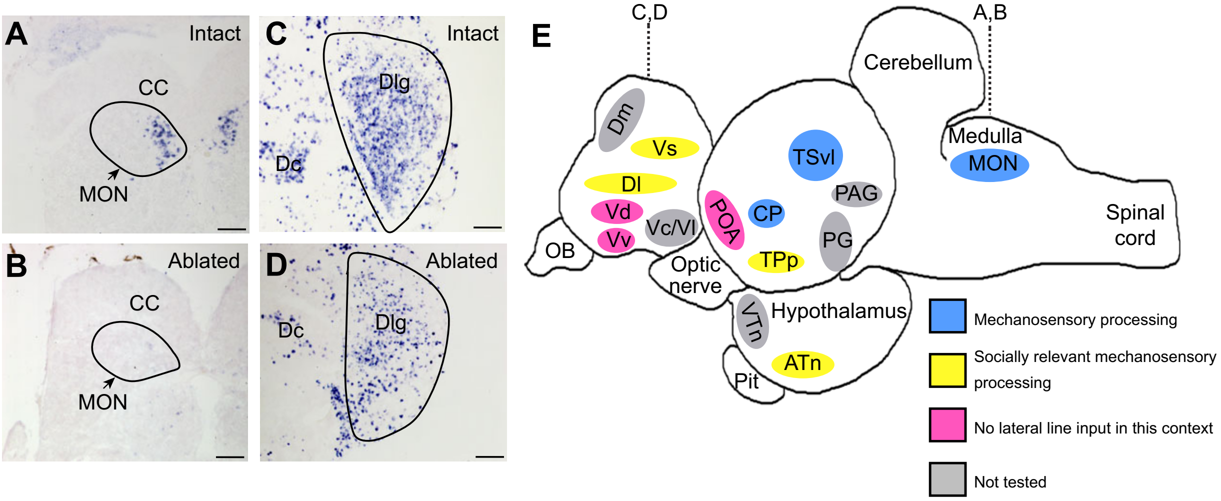


Fig. 3. Mechanosensory signals used during aggressive territorial interactions mediate activation of several socially relevant brain nuclei in male *Astatotilapia burtoni*. Photomicrographs of staining (purple label) for the immediate early gene *cfos* in cells of the medial octavolateralis nucleus (MON) and granular zone of the lateral part of the dorsal telencephalon (Dlg) of lateral-line-intact (A,C) and -ablated (B,D) animals. Lateral-line-ablated fish have fewer *cfos*-stained cells (i.e. reduced neural activation) in a lateral-line-processing (MON) and socially relevant (Dlg) brain region compared with fish with a functioning lateral line system. Solid outlines depict nuclei borders. Scale bars, 100 µm. CC, cerebellar crest; Dc, central part of the dorsal telencephalon. The approximate locations of the representative transverse sections shown in A–D are indicated on the sagittal brain in E. (E) Summary schematic of the *A. burtoni* brain to illustrate known processing regions for socially relevant mechanosensory information, based on Butler and Maruska (2016). Blue, mechanosensory-processing regions. Yellow, nuclei of the social decision-making network (SDMN) that receive lateral line input and possibly use it to modify behavioral output. Pink, SDMN nuclei without evidence for mechanosensory input in this aggressive context. Gray, SDMN and sensory-processing regions that have not been tested for a potential role in processing socially relevant mechanosensory signals. ATn, anterior tuberal nucleus; CP, central posterior thalamic nucleus; Dl, lateral part of the dorsal telencephalon; Dm, medial part of the dorsal telencephalon; OB, olfactory bulb; PAG, periaqueductal gray; PG, lateral preglomerular nucleus; Pit, pituitary; POA, preoptic area; TPp, periventricular nucleus of the posterior tuberculum; TSvl, ventrolateral portion of the torus semicircularis; Vc/Vl, central and lateral parts of the ventral telencephalon; Vd, dorsal part of the ventral telencephalon; Vs, supracommissural nucleus of the ventral telencephalon; VTn, ventral tuberal nucleus; Vv, ventral part of the ventral telencephalon. Modified from Butler and Maruska (2016).

other brain regions still need to be tested (Fig. 3). Future studies are also needed to identify brain areas involved in processing socially relevant mechanosensory information during courtship and spawning, and whether these regions differ from those involved in aggressive or other contexts.

Role of mechanosensory signals in multimodal sensory integration to mediate behaviors

Animals survey their environment and constantly receive input from multiple sensory channels during social interactions. Information gained through the senses is integrated by the brain to adjust the animal's physiological state or motivation, or to influence behavioral responses. Although the roles of visual, chemosensory and auditory signals in social behavior are well studied, recent evidence indicates that hydrodynamic stimuli also provide crucial information during social interactions (Butler and Maruska, 2015, 2016; Medina et al., 2013; Satou et al., 1994). Because of this, mechanosensory signals should not be ignored in the context of multisensory behaviors in fishes.

Sensory signaling is also dependent on the environment that the animals inhabit. Signal redundancy (i.e. when the same information is delivered via more than one sensory channel) ensures that the message is conveyed even if one sensory channel is disrupted by background noise, whereas non-redundant signals (which convey unique information via different sensory channels) allow animals to increase the information being sent (Partan and Marler, 1999). Although no studies have directly tested whether mechanosensory signals encode redundant or non-redundant information, evidence from the above studies suggests that mechanosensory cues and signals often encode non-redundant information, such that disrupting mechanoreception limits the amount of information received during multisensory interactions (Butler and Maruska, 2015; Medina et al., 2013; Satou et al., 1994). Given that many social interactions among the >30,000 species of fishes produce water movements that can be detected by the lateral line system, we suggest that future studies investigating multimodal behaviors of fish should consider mechanosensory communication and attempt to distinguish the relative importance of different sensory modalities.

Future research

Much more research is needed before we fully understand how fish use mechanosensory signaling during a variety of social interactions. Here, we propose several research questions of interest. First and foremost, additional studies are needed to test how mechanosensory signaling is used by diverse fish species during different social interactions (e.g. aggression, reproduction, parental care). One reason that previous research in this area has been limited is the difficulty in effectively ablating the lateral line system in many fishes. Throughout the past 30 years of lateral line research, a variety of ablation methods have been used [e.g. cobalt chloride ($CoCl_2$), aminoglycoside antibiotics, physical ablation]. Unfortunately, many of the studies using chemical ablation techniques failed to adequately demonstrate treatment efficacy, account for comorbid effects or test for impacts on other sensory systems, which introduces skepticism regarding their conclusions on lateral line system function. Further, at one point it was thought that aminoglycosides only disrupted canal neuromasts and left superficial neuromasts intact (Song et al., 1995). However, later research found that treatment with aminoglycosides affected both superficial and canal neuromasts, but that the effects were highly variable across species (Brown et al., 2011; Van Trump et al., 2010). Because superficial and canal neuromasts encode different stimulus properties (reviewed in Chagnaud and Coombs, 2014), and fin and body movements create hydrodynamic stimuli with both low- and high-frequency components (Bleckmann et al., 1991), the relative role of each lateral line submodality during social behaviors deserves to be further examined. In addition, several of the studies mentioned throughout this Commentary used $CoCl_2$ to chemically ablate the lateral line system (e.g. Butler and Maruska, 2015, 2016; Medina et al., 2013; Pohlmann et al., 2004). At the time of these studies, it was thought that $CoCl_2$ selectively disabled mechanosensory hair cells, but recent research indicates that $CoCl_2$ treatment can also impair olfaction (and potentially taste systems; Butler et al., 2016). When using $CoCl_2$ in behavior studies, future research should include appropriate toxicity and anosmic (olfactory-epithelium-ablated) controls, similar to those in Butler and Maruska (2015). Because of the recent knowledge surrounding lateral line ablation techniques, conclusions on lateral line system function from past studies should be interpreted with caution, keeping in mind potential toxic or unwanted effects. Future studies should also include appropriate controls to verify treatment efficacy and to ensure that different sensory modalities are isolated. In addition, the use of modern neuroscience techniques (e.g. CRISPR/Cas9, optogenetics) to examine how mechanoreception functions during social interactions promises to produce much cleaner results and will help move the field forward.

Another area of interesting future research concerns the evolution of socially relevant mechanosensory signaling. With >30,000 species of fishes, there is huge diversity in lateral line localization and morphology, which can have functional implications (Webb, 1989, 2014). Canal morphology (i.e. widened or narrow) is thought to be related to the fish's habitat. Narrow canals are ideal for highly turbulent environments, whereas widened canals have increased detection capabilities that are better suited for calmer environments (Klein and Bleckmann, 2015). In addition, widened canals are thought to enhance the ability to perform hydrodynamic-dependent behaviors (Denton and Gray, 1988; Denton and Gray, 1989; Janssen, 1997). For example, many dark-dwelling or night-foraging species have widened lateral line canals (Schwalbe et al., 2012; Schwalbe et al., 2016). Although widened canals likely evolved as a result of natural selective pressures, it is possible that fish have exploited this increased sensitivity to also expand their behavioral repertoire to include mechanosensory signaling for purposeful communication. To our knowledge, the evolution of mechanosensory signaling, or its role in sexual selection and speciation, has not yet been examined.

Finally, we suggest that future studies also take an integrative approach to investigate the neural control of mechanosensation-mediated behaviors. For example, research on mechanosensory processing in awake, behaving animals using approaches such as neural recordings with implanted electrodes in freely swimming fish (similar to Palmer et al., 2003, 2005; Radford and Mensinger, 2014) or studies using immediate early genes (or other activity markers) as a proxy for neural activation would increase our understanding of how fishes use mechanosensory signaling to mediate behavioral decisions. Further, consideration of mechanosensory signaling as part of a more complex multimodal repertoire used during social interactions is needed to better understand what type of information is conveyed in each sensory channel and the neural computations required to produce adaptive behaviors. Only after we accumulate results from carefully designed experiments in a variety of behavioral settings in multiple species will we begin to fully understand how fishes use mechanosensory signaling as a form of communication during social interactions.

Conclusions

Despite almost a century of lateral line research suggesting that mechanosensory signals act as a form of communication during social interactions, few studies have actually tested this hypothesis. Here, we have summarized what is currently known about mechanosensation-mediated behavioral interactions and propose that mechanoreception is a crucial mode of communication during a broad range of social encounters in fishes, including aggression, reproduction and parental care. We hope this Commentary will encourage more researchers to consider mechanosensory communication during multimodal social behaviors and inspire additional research on this interesting topic. With >30,000 species of fishes, most of which produce hydrodynamic signals during social encounters, a better understanding of how mechanosensory signals mediate social interactions and behavioral decisions has broad implications for the fields of sensory biology, evolution and neuroethology.

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The authors declare no competing or financial interests.

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