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Fins as Mechanosensors for Movement and Touch-Related Behaviors

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Synopsis Mechanosensation is a universal feature of animals that is essential for behavior, allowing detection of animals' own body movement and position as well as physical characteristics of the environment. The extraordinary morphological and behavioral diversity that exists across fish species provide rich opportunities for comparative mechanosensory studies in fins. The fins of fishes have been found to function as proprioceptors, by providing feedback on fin ray position and movement, and as tactile sensors, by encoding pressures applied to the fin surface. Across fish species, and among fins, the afferent response is remarkably consistent, suggesting that the ability of fin rays and membrane to sense deformation is a fundamental feature of fish fins. While fin mechanosensation has been known in select, often highly specialized, species for decades, only in the last decade have we explored mechanosensation in typical propulsive fins and considered its role in behavior, particularly locomotion. In this paper, we synthesize the current understanding of the anatomy and physiology of fin mechanosensation, looking toward key directions for research. We argue that a mechanosensory perspective informs studies of fin-based propulsion and other fin-driven behaviors and should be considered in the interpretation of fin morphology and behavior. In addition, we compare the mechanosensory system innervating the fins of fishes to the systems innervating the limbs of mammals and wings of insects in order to identify shared mechanosensory strategies and how different organisms have evolved to meet similar functional challenges. Finally, we discuss how understanding the biological organization and function of fin sensors can inform the design of control systems for engineered fins and fin-driven robotics.

Introduction

Mechanosensation is fundamental to behavior, allowing sensation of one's own body movements and orientation as well as physical features of the environment. The appendages of many animals have evolved both as mechanosensory devices for touch and as adroit movement systems that require proprioceptive feedback for fine motor modulation. In a locomotor context, animals rely on mechanosensory feedback to modulate movement, allowing performance of complex behaviors even in unstable and cluttered environments. Mechanosensation is also intrinsic to many non-locomotor behaviors including prey detection and various forms of social signaling. Human tasks as simple as buttoning a shirt, discerning a texture, or using your finger to scratch your nose rely on mechanosensory feedback.

The appendages of animals, from insect wings to vertebrate limbs, integrate their sensation and movement to generate a range of behaviors, which is particularly relevant in locomotion. Proprioception, the ability of an animal to sense their own movement and position of body elements in space, and the impact of its loss, has been extensively studied in the limbs of humans (e.g., Rothwell et al. 1982; Sanes et al. 1985; Ghez et al. 1990; Sainburg et al. 1993), cats (e.g., Miller et al. 1975; Goldberger 1988; Abelew et al. 2000), and insects (e.g., Pearson and Wolf 1987; Dickerson et al. 2014; Eberle et al. 2015; Tuthill and Wilson 2016; Yarger and Fox 2016; Pratt et al. 2017). Mechanosensors innervate muscles, joints, connective, and epithelial tissues to encode the position, movement, and force of processes ranging from respiration (Ballintijn and Bamford 1975) to the movement of an entire limb (reviewed by Prochazka 2011). Proprioception is critical to motor performance across a wide range of animals, allowing animals to complete complex and precise movements with high accuracy and adaptability (e.g., Grillner and Zangger 1984; Sanes et al. 1985; Nathan et al. 1986; Giuliani and Smith 1987; Sainburg et al. 1993).

Animals also gather mechanosensory information via touch. Tactile sensation provides feedback on the geometry (i.e., shape, size, and orientation) and surface features (i.e., roughness and texture) of contacted objects. Touch can provide important sensory input during avoidance behaviors (Kaplan and Horvitz 1993), for object manipulation (Westling and Johansson 1987; Jenmalm et al. 2003), and in social interactions including mating, grooming, and child rearing (Liu and Sternberg 1995; Bshary and Würth 2001; Dunbar 2010; Feldman et al. 2010). Touch sensation has been extensively studied in the nematode *Caenorhabditis elegans* (e.g., Chalfie and Sulston 1981; Way and Chalfie 1989) and the primate hand (reviewed by Vallbo and Johansson 1984; Johnson 2001) where diverse populations of touch sensitive neurons and/or specialized receptors detect a wide range of tactile stimuli, including motion along the skin, vibration, pressure, and texture.

Fish fins provide a particularly useful system for studying the impact of both proprioception and touch in different behavioral contexts because of their extraordinary morphological and behavioral diversity across species. We focus on the pectoral fins, homologs to the tetrapod forelimb, which have been the most studied fins to date. Here, we review the anatomy and physiology of sensors innervating the fins of fishes, paying particular attention to the role of these sensors in proprioception and touch. With this paper we aim to synthesize our current understanding of the anatomy and physiology of fin mechanosensation in fishes and integrate information on mechanosensation with that of other taxa to highlight gaps in our understanding and important opportunities for future work. Finally, we end by discussing how the study of fish fin mechanosensation can inform sensory instrumentation of underwater vehicles and other devices as well as how robots can be used to systematically test biological hypotheses.

The anatomy of fin mechanosensation

The paired and median fins of fishes are invested with arrays of sensory nerve fibers, a number physiologically demonstrated to be mechanosensitive. Both the musculoskeletal base of the fins and the fin rays and membranes themselves have mechanosensory mechanisms. Pectoral fins of many species including sea robins (Morrill 1895; Bardach and Case 1965; Ono 1979; Finger 1982, 2000), bluegill sunfish, *Lepomis macrochirus* (Williams et al. 2013; Williams and Hale 2015), multiple species of wrasses (Aiello et al. 2017), catfish, *Pimelodus pictus* (Hardy et al. 2016), zebrafish, *Danio rerio* (Thorsen and Hale 2007), and dogfish shark, *Squalus acanthias* (Lowenstein 1956) are known to be mechanosensitive. The modified pelvic fin rays of squirrel hakes (*Urophycis chuss*) are highly innervated, showing responses to both chemical and mechanical stimuli (Bardach and Case 1965). Mechanosensitive receptors are also located at the base of the pelvic fins of stingrays (Fessard and Sand 1937). Dorsal fin innervation has been described in the rockling fish, *Gaidropsarus mediterraneus* (Kotrschal et al. 1984) although its physiological properties have not been reported. Innervation has also been observed in dorsal midline fins of other fishes. The adipose fin of the bronze catfish, *Corydoras aeneus* (Fig. 1A; Aiello et al. 2016) and the brown trout, *Salmo trutta* (Buckland-Nicks et al. 2012; Buckland-Nicks 2016), are highly innervated by sensory nerves (Fig. 1B, C). These fibers have been shown to be mechanosensitive in *C. aeneus* (Aiello et al. 2016). Surprisingly, the caudal fin has received little attention though it is known to be innervated (Thomas et al. 2012). While no examples of anal fin innervation exist in the literature, we have observed through immunohistochemistry the presence of nerve-like fibers and endings in a number of additional species. We suggest that innervation by the sensory system is a general feature of all fish fins. The role of fins as sensors must now be considered in studies of their morphology, behavior, and evolution. However, the organization and role of fin innervation has yet to be studied in a vast array of fin types, particularly among the median fins. Dorsal and anal fins, for example, have very diverse morphologies including ribbon fins that are used for fine control over position and movement (Curet et al. 2011; Ruiz-Torres et al. 2013; Neveln et al. 2014) and might be

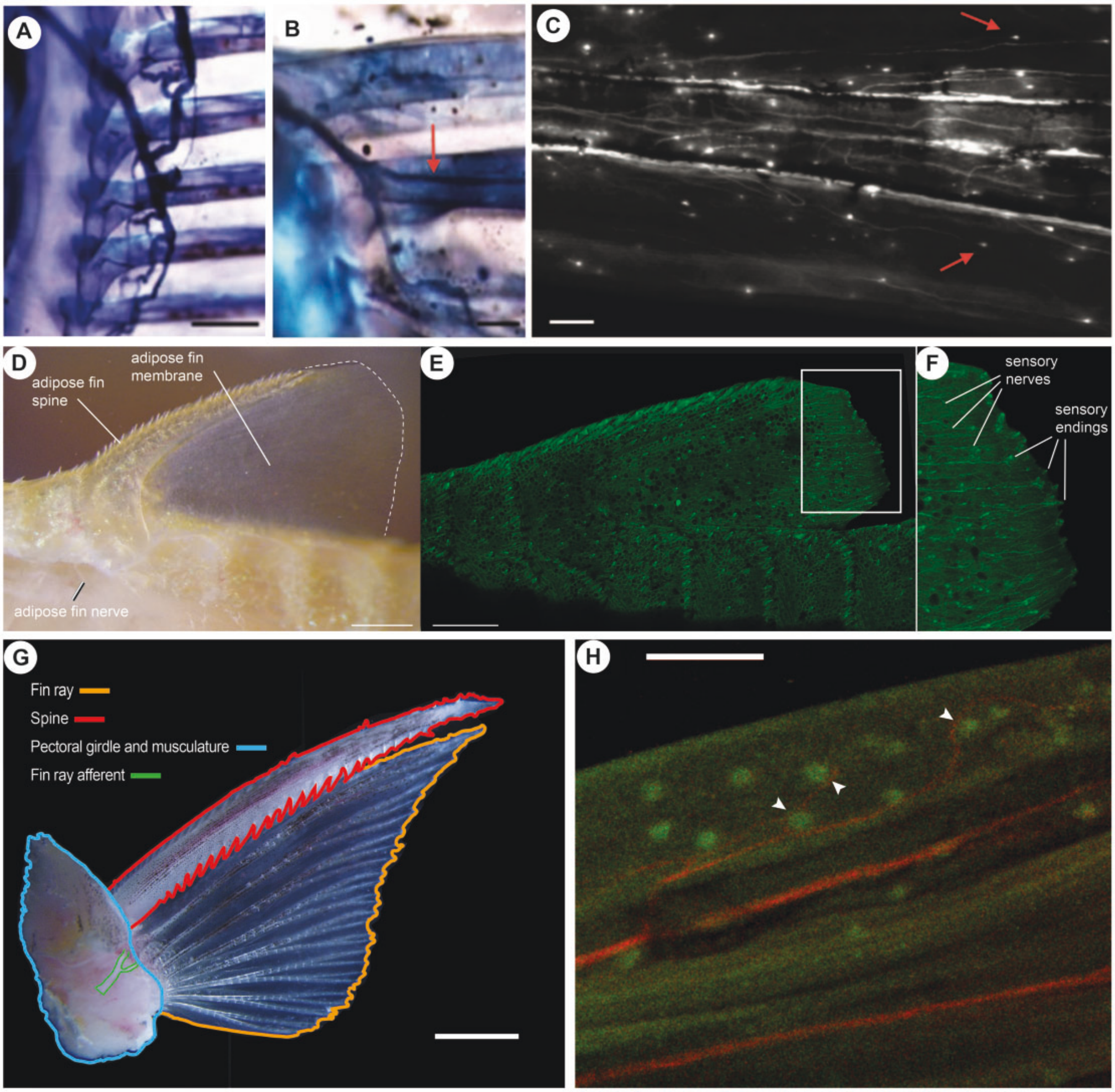

Fig. 1 Anatomy and innervation of pectoral and median fins. (**A**, **B**) The pectoral fin nerves of the bluegill sunfish (*Lepomis macrochirus*) stained with Sudan black are shown entering the proximal base of the fin ray and extend distally through its core. Panel A: scale bar: 1 mm. Panel B: scale bar: 0.4 mm. (**C**) Nerves stained with anti-acetylated tubulin are shown traveling distally throughout the length of the fin ray and follow fin ray branching patterns. The fin edges of the bony fin ray can be visualized in this image. Examples of sensory endings are highlighted by red arrows. Scale bar: 100 μm. (**D**) The adipose fin of Cory catfish (*Corydoras aeneus*) includes an anterior spine and a membrane. A nerve innervating the membrane can be seen entering the spine. Scale bar: 1.0 mm. (**E**) Sensory fibers stained with anti-acetylated tubulin are oriented approximately parallel to the actintorichia in the adipose fin and enter the fin anteriorly, behind the adipose fin spine. Scale bar: 0.5 mm. (**F**) A magnification of the trailing edge of the adipose fin membrane showing sensory nerves and endings. (**G**) Pictus catfish (*Pimelodus pictus*) pectoral fin and girdle (right fin; dorsal view) with elements outlined for clarity. Scale bar: 4 mm. (**H**) Immunostained pectoral fin ray showing nerves (red) and associated putative mechanoreceptors. Structures (green) present along the nerves stain with an antibody to cytokeratin 20, a Merkel cell marker. These putative mechanoreceptor cells are present throughout the fin and in places (denoted by white arrows) that are closely associated with nerve endings. Scale bar: 200 mm. Panels A–C adapted from Williams et al. (2013); panels D–F adapted from Aiello et al. (2016); and panels G and H adapted from Hardy et al. (2016).

expected to need feedback modulation. Caudal fins vary greatly in their shape, stiffness, function during swimming, and coordination with axial bending, and might also be expected to rely on mechanosensory feedback to modulate movement. Much of our understanding of fin innervation comes from studies of the pectoral fin and we focus on pectoral fin mechanosensation below; however, we see enormous opportunity and need to understand mechanosensation in other fins, especially in the context of median fin-based locomotor behaviors.

Sensory innervation of the distal fin

In adult bluegill sunfish (*L. macrochirus*), a nerve comprised of many fibers enters the core of each ray through its proximal base and extends nearly the full length of the fin ray (Fig. 1), following fin ray branching patterns (Williams et al. 2013). Individual fibers exit the ray to innervate the peripheral membrane (Williams et al. 2013). The nerve fibers running along the length of the fin rays have been found to terminate as either free nerve endings or expanded nerve endings (Fig. 1D, E; Williams et al., 2013; Hardy et al., 2016). For some fibers, the associated sensory cells are labeled with an antibody to cytokeratin 20 (Hardy et al., 2016), a histologic marker of Merkel cells (Moll et al. 1995). Merkel cells are one of the four main types of mechanoreceptors in the glabrous skin of mammals and have been found in the skin of all vertebrate classes except chondrichthyans (e.g., Whitear 1989; Andres and v Düring 1990). Merkel cells will be discussed further with touch mechanosensation below. The physiological significance of different receptor endings is currently unknown in bluegills and other species; however, through spike sorting approaches to analyzing multiunit physiology, at least some have been shown to have the capacity for proprioception and touch sensation. Future experiments combining cell labeling techniques and intracellular physiological recordings will be necessary to match the activity patterns of a given cell to its morphology.

Sensory innervation of the musculoskeletal system of fins

Little is known about mechanosensors that innervate the musculature or other aspects of the fin system proximal to the fin rays. In mammals and other tetrapods, muscle spindles are a critical component of mechanosensory feedback (Akay et al. 2014). In mammals, muscle spindles, which consist of a capsular enlargement surrounding intrafusal muscle fibers innervated by sensory nerves, are contained within skeletal muscle (reviewed by Prochazka 2011). Mammalian spindle afferents respond to muscle movement, encoding muscle length changes as well as the velocity and acceleration of muscle length changes (reviewed by Prochazka 2011). Muscle spindles have not been found in muscles of fish fins. Other than a study on jaw muscle (Maeda et al. 1983) that has not been replicated, spindles have not been identified in the muscles of fishes despite investigation (e.g., Barker 1974; Baum 1900).

Evidence for other types (non-muscle spindles) of mechanosensors innervating fin musculature is scarce, but their histology has been described in several chondrichthyan species (Poloumordwinoff 1898; Fessard and Sand 1937). The Poloumordwinoff endings are described as thin nerves situated between the fibers of muscles that actuate paired fins in skates (Poloumordwinoff 1898; Bone and Chubb 1975). The Poloumordwinoff endings respond to muscle stretch (Fessard and Sand 1937), and have been suggested to serve a similar function to muscle spindles (Bone and Chubb 1975). The variation of fin innervation across fishes raises intriguing questions regarding the evolutionary history of these sensory systems. How have the physiological properties of the proximal sensory endings associated with the fins of teleosts and chondrichthyans evolved in the lobe-finned fishes? When and why do muscle spindles evolve? How is muscle spindle function different than the sensory endings found proximally in the fin systems of teleosts and chondrichthyans? Future exploration of fin structure, function, and mechanosensation focused on living members of groups that have early roots in the vertebrate tree of life might be particularly revealing in regard to key transitions in the neuromechanics of limbs.

Mechanosensors are also associated with the connective tissues of limbs. In tetrapods, Golgi tendon organs innervate tendons to encode the mechanical load imposed on the tendon, and joint receptors innervate joint capsules to provide feedback on the relative position of the limb (reviewed by Prochazka 2011). In fishes, in addition to the innervation of the proximal musculature associated with fins, the tendons and joint capsules of fins are also innervated. In teleost fishes, free nerve endings with and without "vicrose" (expanded or swollen) endings have also been found to innervate the joint capsule in the modified pectoral fin rays of the sea robin, *Aspitrigla cuculus*, (Bone 1964; Ono 1979). In chondrichthyans, sensory endings are located at the base of the pectoral (Wunderer 1907; Bone 1964) and pelvic fins (Fessard and Sand 1937). Outside of teleosts and chondrichthyans, free nerve endings have also been observed in the perichondrium associated with the joints of the pectoral and pelvic fins of the African lungfish, *P. annectens* (Barker 1974). Free nerve endings are also described innervating the tendon of the dorsal fin muscle in a seahorse, *Hippocampus* sp., (Pansini 1888) and the tendons attached to the caudal fin in the tench, *Tinca tinca*, and the goldfish, *Carassius vulgaris* (Ciaccio 1890). Thus, it is apparent that (at least putative) mechanosensory cells innervate all of the same tissues associated with the appendages of fishes that are also innervated in the appendages and other tissues of tetrapods. The similarities between the mechanosensory systems of tetrapods and fishes reveal a common set of tissues associated with mechanosensory feedback across vertebrates. Therefore, it is reasonable to suggest that despite interspecific differences in environment and means of locomotion, mechanosensory innervation of the muscles, tendons, and joints of an appendage as well as information on the deformation of that appendage represents a common strategy in the placement of mechanosensors to encode a fundamental set of variables necessary for the successful use of an appendage.

The proprioceptive capability of flexible fin rays

Although proprioceptive mechanisms of the musculoskeletal system of fins are not yet understood, the rays and membranes of fins are also proprioceptive, responding to fin bending and position. The first mentions of fin ray mechanosensation were in studies focused on the chemosensory capability of the modified pelvic fin rays of the squirrel hake, *U. chuss* (Bardach and Case 1965) and the modified pectoral fin rays of the searobin, *Prionotus carolinus* (Silver and Finger 1984). Since then, the physiology of fin ray mechanosensation has been quantified in the pectoral fin rays of the bluegill sunfish, *L. macrochirus* (Williams et al. 2013), a catfish, *P. pictus* (Hardy et al. 2016), and several species of wrasses (Aiello et al. 2017). Further, the passive adipose fin of a catfish, *C. aeneus*, was also found to be proprioceptive (Aiello et al. 2016). Across species and among fins, the afferent response to fin bending is very consistent, suggesting that the ability of the fin rays and fin membrane to sense deformation is a generalizable and fundamental feature of fish fins.

The position and movement of the pectoral fin rays of fishes appear to be sensed through rapidly adapting (RA) and slowly adapting (SA) afferents and their associated sensory endings or sensory cells within the fin. Rapidly adapting (RA) fibers respond in a burst-like manner only at the onset and offset of a stimulus as the fin is in motion (Fig. 2A, B, G; Williams et al., 2013; Hardy et al., 2016; Aiello et al., 2017). At higher bend amplitudes, SA fibers continue to respond to a stimulus over its hold period, while the rays or membrane of the fin are held in a bent position (Fig. 2A, B, G; Williams et al., 2013; Hardy et al., 2016; Aiello et al., 2017). Additionally, afferent response increases as the amplitude of fin ray bending increases (Fig. 2C; Williams et al., 2013; Hardy et al., 2016; Aiello et al., 2017). Both the duration and number of spikes of the initial bursts associated with fin ray movement increase with increasing bending amplitude, as does the firing rate of SA fibers that continue to fire as the fin is held in a bent position, allowing the system to also encode the magnitude of the stimulus or fin deformation. The functional differences between SA and RA afferents allow the mechanosensory system to provide information about both the static and dynamic qualities of a stimulus, or the position and movement of the fin, which could be relevant for many of the different behaviors that might incorporate sensory feedback from fins.

Other general features of fin mechanosensation are the ability of afferents to encode the velocity of fin bending as well as respond to cyclic stimuli of biologically relevant frequencies. The activity of fin ray afferents can encode the velocity of fin ray bending (Williams et al. 2013) by increasing spike rate as the velocity of fin ray deformation increases (Fig. 2D, E). Williams et al. (2013) also found that, in the bluegill sunfish, pectoral fin ray afferent activity undergoes a cyclic response to sinusoidal stimuli within the frequency range of fin beat frequencies (1–2 Hz) at typical swimming speeds (Fig. 2F), suggesting that the mechanosensory system innervating fins is capable of providing stroke-by-stroke feedback. Much of our understanding of fin mechanosensation comes from quantifying the response of fin ray afferents to step-and-hold, ramp-and-hold, and simple sinusoidal stimuli, which allow us to characterize the general linear response properties of the afferents innervating fins. As mentioned previously, future work will need to incorporate the labeling of individual cells in order to relate the type and position of the sensory ending to the response of the afferent as well as the use of band-limited white noise stimuli to characterize the specific features of a stimulus that are encoded by fin afferents and any potential nonlinearities in the afferent system. In addition, the use of *in vivo*, behaving preparations will ultimately allow for the exploration of mechanosensation in more natural fin movements.

Across species and among fins, the response to fin ray and membrane deformation is remarkably consistent. The consistency across species and among fins in the afferent response to mechanical stimuli suggests that the ability to encode the position, movement, and rate of movement of fins is a fundamental and feature of the actinopterygian mechanosensory system. Even a fin with no associated

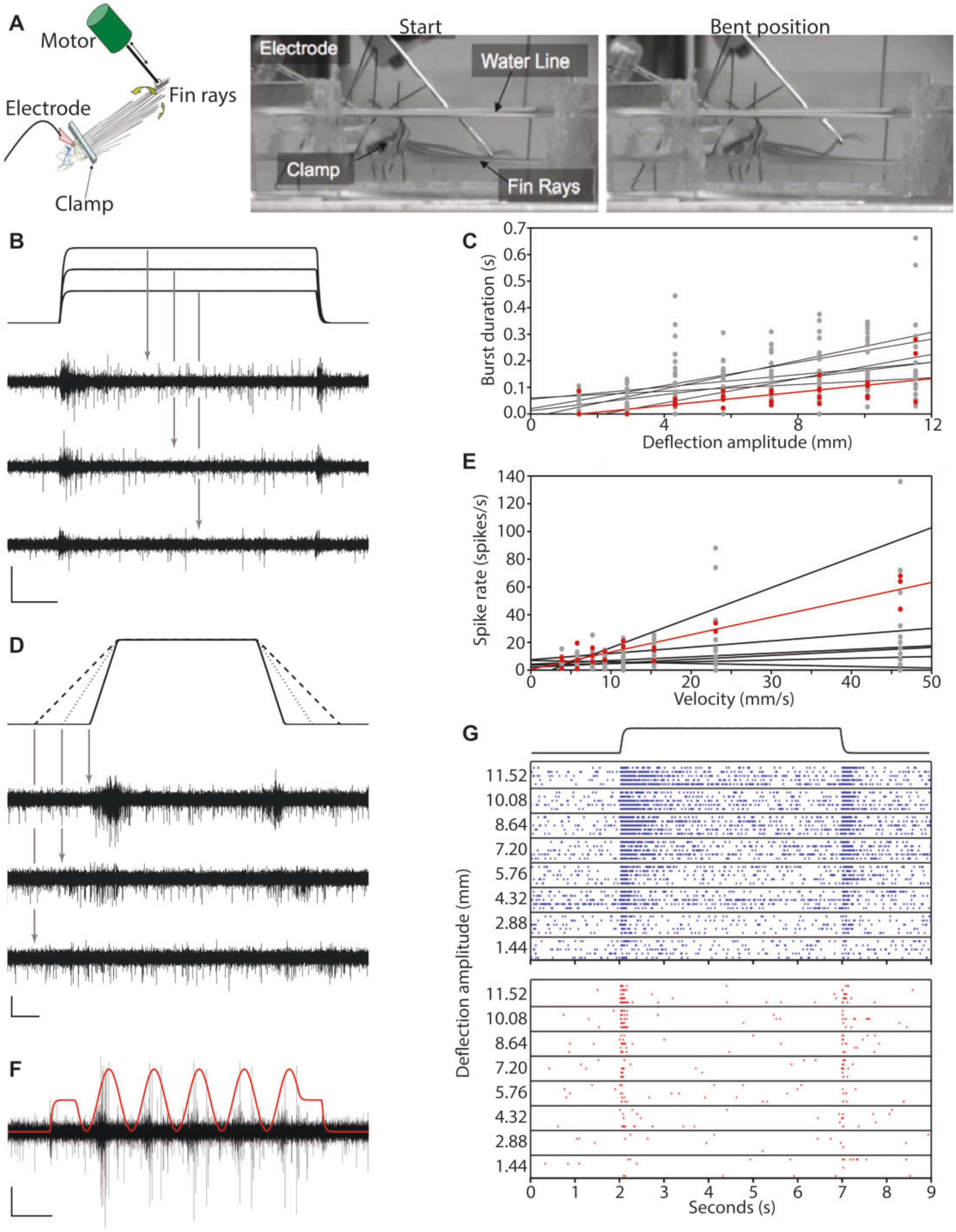

Fig. 2 The response of pectoral fin ray afferents to bending stimuli in bluegill sunfish (*L. macrochirus*). (**A**) The electrophysiology preparation used to record afferent responses to fin ray bending. The electrode highlighted in red is connected to the fin ray nerves proximal to entering individual fin rays. A motor is connected to a single fin ray (isolated from adjacent rays) to provide a mechanical stimulus. (**B**) Extracellular physiological responses to step-and-holding bending stimuli of three bend amplitudes (top): 5.76, 8.64, and 11.52 mm. Scale bar, $x=1$ s, $y=0.04$ mV. A burst of activity from RA afferents occurs at the onset and offset of the stimulus as the fin ray is in motion, and a sustained response is observed in the 5.76 mm bend when the fin ray is held in a bent position. (**C**) The activity

musculoskeletal system, the adipose fin of *C. anneus*, responds to bending and has the capability to encode these same variables (Aiello et al. 2016). While the ancestral adipose fin was likely passive and lacked an associated musculoskeletal system, the adipose fin of at least one species of catfish, *Horabagrus brachysoma*, has evolved a musculoskeletal system capable of actively controlling the position of the fin (Stewart and Hale 2012). Similarly, the active control of fins is also thought to be secondarily derived (Coates 1994). Therefore, as proprioceptive feedback is necessary for the precise control of actively generated movement (reviewed by Prochazka 2011), evidence of proprioception in a passive fin suggests that the evolution of proprioceptive feedback might have evolved prior to the evolution of active limb control.

The proprioceptive system innervating the pectoral fin is tuned with differences in fin mechanics and motion among species. In the wrasses (Labridae), a behaviorally and morphologically diverse family of fishes, propulsion is primarily driven by the pectoral fins across a wide range of speeds (Wainwright et al. 2002; Walker and Westneat 2002b; Thorsen and Westneat 2005). Labrids employ pectoral fin-based propulsion ranging from rowing to flapping, where rowing species use relatively flexible, broad fins to perform drag-based propulsion whereas flapping species use stiff wing-like fins to perform lift-based propulsion (Walker and Westneat 1997, 2000, 2002a, 2002b; Westneat et al. 2004; Westneat et al. 2017). These interspecific differences in limb mechanics contribute to differences in the magnitude of fin ray bending that routinely occurs during swimming in these fishes. A comparison across species revealed that mechanosensory sensitivity is greater (requiring a lower minimum fin bending amplitude to elicit a response) in stiff-finned flappers than in flexible-finned rowers (Aiello et al. 2017), suggesting that the components of the neuromechanical system can be tuned to interspecific differences in limb biomechanics. This work found that fin diversification was highly dynamic across the evolutionary history of the labrid fishes, and that the evolution of locomotor mechanisms includes the evolutionary tuning of mechanosensation to concurrent changes in propulsor biomechanics. Because mechanosensory feedback is common among animals (Kung 2005) and neuromechanical tuning is an evolutionary principle likely to impact many functional capabilities, rich opportunities for future comparative work on mechanosensation exist using diverse groups such as fishes and insects.

Insights on fin proprioception through a comparison between the wings of insects and fins of fishes

The proprioceptive system of the pectoral fins of fishes might be considered to be most similar to that of insect wings. Insect wings are another example of a flexible membranous appendage that rhythmically oscillates during locomotion and maneuvering. Similar to the pectoral fins of fishes, the wings of insects are also actuated through proximally located muscles (Snodgrass 1935), and the wing blade is covered in sensors, campaniform sensilla (e.g., Fudalewicz-Niemczyk and Rosciszewska 1972; Albert et al. 1976; Palka et al. 1979; Kutsch et al. 1980; Cole and Palka 1982; Gnatzy et al. 1987). Rapidly and slowly adapting mechanosensors innervating the wings of insects spike with low temporal variation in response to wing deformation (Dickinson 1990a, 1990b, 1992; Dickerson et al. 2014; Pratt et al. 2017) and are capable of phasically responding to stimuli of the same frequency of typical wing beats during flight (Dickinson 1990a, 1990b). Therefore, reciprocal insight into these two highly diverse systems might help further elucidate evolutionary principles of mechanosensation and its role in the generation of limb movements.

At high fin beat frequencies, the sensors innervating the fins of fishes might serve as event detectors. While the sensors innervating the pectoral fins of bluegill sunfish respond throughout the period of a single cycle of a 1 and 2 Hz sinusoidal stimulus (Williams et al., 2013), many pectoral fin swimmers beat their fins at frequencies between 3 and 6 Hz as adults (Walker and Westneat 2002b), and average 20 Hz for juveniles of some species (Hale et al. 2006). It is not known how the mechanosensory

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of the initial burst as well as that over the hold period both increase with increasing fin ray bending magnitude. (**D**) Nerve activity also reflects the speed of fin ray deflection. (**E**) In response to ramp-and-hold stimuli, increasing the ramp velocity to a set amplitude in the hold period results in increased pectoral fin ray nerve activity. Responses to 3.84, 5.76, and 11.52 mm s^{-1} ramps are shown. Scale bar, x=1 s, y=0.03 mV. (**F**) Pectoral fin ray afferents respond cyclically to oscillations of frequencies typical of those used during swimming in this species. This panel shows pectoral fin ray nerve activity in response to a 1 Hz sinusoidal stimulus. (**G**) Multiunit activity recording during experiments was spike sorted into individual units. This panel shows a spike-sorted raster of afferent activity for a SA (blue, top) and a RA (red, bottom) unit in response to a step-and-hold stimulus. Scale bar, x=1 s, y=0.03 mV. Adapted from Williams et al. (2013).

system will encode fin deformation at frequencies greater than 1–2 Hz. In the blowfly, *Calliphora vomitoria*, which employs wing beat frequencies of ~150 Hz, both SA and RA sensors fire only once per wing beat with high temporal precision (Dickinson 1990b), serving as an event detector for the strain of a specific location on the wing surface at a certain instance of the wing beat cycle. Because different sensors will spike at different portions of the wing beat cycle, the cumulative response from sensors across the wing, and their relative spike time throughout the cycle, can be used to detect deformation across the wing over the course of a wing stroke. In fishes, we expect that at higher fin beat frequencies, spike number, and thus sensory information content from the fin, will decrease, and might ultimately serve a similar role for event detection as in blowflies, that could be integrated over the surface of the fin to encode its deformation over the course of a fin beat cycle.

Despite similar physiological properties of the afferents innervating the fins of fishes and wings of insects, the density and distribution of sensors encoding features of propulsor movement are fundamentally different. Relevant to both flying insects and swimming fishes, the three-dimensional deformation of a flexible propulsor will impact its fluid-dynamic capabilities (Daniel and Combes 2002; Young et al. 2009). Therefore, it is not surprising that both insects and fishes have evolved sensors to encode this feature of propulsor movement. However, it is clear that fishes and insects must deal with different constraints in the distribution of sensors across the propulsors. In fishes, a bundle of afferents runs within the core of each fin ray (Fig. 1), but afferents can exit the lateral aspect of a given ray through the gap between the opposing hemitrichia, allowing sensors to innervate a large area of the fin. In contrast, in insect wings, campaniform sensilla are restricted to the veins of the wing (Fig. 3), which act as conduits for afferents, among other things, to travel proximally toward the body (Pringle 1957; Cole and Palka 1982; Gnatzy et al. 1987; Wootton 1992). The sensors innervating insect wings are also typically grouped at the base (Fig. 3; Pringle 1957; Cole and Palka 1982; Gnatzy et al. 1987; Wootton 1992; Dickerson et al. 2014; Pratt et al. 2017), but can be more distributed across the distal aspect of the wing. Further, in insects the number of sensors innervating a given wing ranges in the order of hundreds (Pringle 1957; Cole and Palka 1982; Gnatzy et al. 1987; Wootton 1992; Dickerson et al. 2014; Pratt et al. 2017), while the fins of fishes appear to have many more sensors. Despite these differences in sensor arrangements, distribution, and density, it is clear that the physiology of sensors innervating both the fins of fishes and the wings of insects, and likely the details of propulsor deformation encoded, is similar.

The differences in sensor arrangement and distribution raise questions about the role of individual sensors in both systems and why there are vast differences in the total number of sensors innervating each propulsor. Why does the sensory system innervating the fins of fishes utilize so many sensors to encode its deformation when the system innervating the wings of insects can accomplish a similar (if not, the same) feat utilizing nearly an order of magnitude fewer sensors? One functional difference between insect wings and fish fins is that the entire wing structure of insects is actuated as a whole, while fishes have control over the movement (Standen and Lauder 2005), curvature (Alben et al. 2007), and stiffness (Alben et al. 2007) of individual fin rays. Therefore, the independent and fine control of individual fin rays might complicate sensory processing and require feedback from individual rays, while an insect wing, because it is actuated as a whole, can sufficiently encode details of its movement and deformation through patches of sensors placed in positions ideal for sensing the relevant aspects of its movement and deformation. Further comparisons, once more details on the anatomy and physiology of the mechanosensory system innervating both insect wings and fish fins are revealed, will be helpful in determining the consequence of varying the number, position, and arrangement of sensors across a propulsor.

Touch sensation in fish fins

Fishes often make contact with the bottom substrate, plants, or other animals using their body and fins. The tactile sensitivity of fins has been shown through electrophysiological studies. The finger-like pectoral fin ray of sea robins (*Prionotus* sp.) as well as the filamentous pelvic rays of the squirrel hake (*U. chuss*), both used as mobile appendages to explore the substrate, respond to deformation, and light surface brushing (Bardach and Case 1965; Silver and Finger 1984). By systematically presenting tactile stimuli to fins, recent work by Hardy et al. (2016) showed for the first time that membranous pectoral fins, in addition to the free fin rays discussed above, also function as effective tactile sensors even in the absence of observable fin ray movement. Such mechanosensory feedback can have important implications in modulating locomotor, orientation,

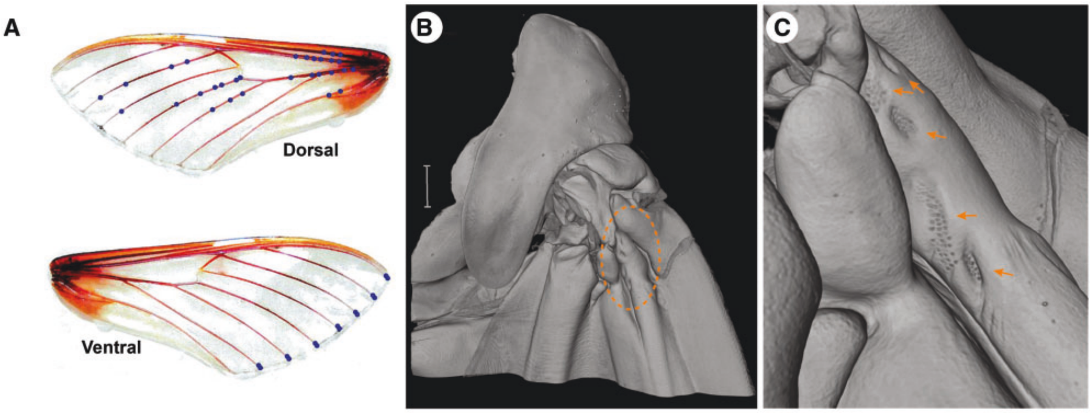

Fig. 3 Forewing campaniform sensilla of *Manduca sexta*. (**A**) Individual or patches of campaniform sensilla (represented by dots), a mechanoreceptor found in the exoskeleton of invertebrates, are found distributed across the dorsal and ventral surface of the forewing of *M. sexta*. A sensilla rich section of the forewing is highlighted by a dashed circle in (**B**) and under increased magnification, five campaniform sensilla patches are highlighted by the arrows. Scale bar=1 mm. (**C**) Panel A adapted from Dickerson et al. (2014). Panels B and C adapted from Pratt et al. (2017).

stabilization, and burial behaviors particularly in complex structural or social environments. For example, Flammang and Lauder (2013) showed that bluegill sunfish (*L. macrochirus*) tap obstacles using their pectoral fins proposed to aid in the navigation of complex environments and that the frequency of fin contact increased with the loss of visual and lateral line input. Thus, touch possibly combining with proprioception, provides feedback to aid in navigation.

As useful comparisons to touch in fins, we look to research on organisms ranging from the nematode *C. elegans* to mammals, where the morphology and physiology underlying touch sensation are well known. In *C. elegans*, distinct sets of mechanoreceptive neurons are selective for particular mechanical stimuli such as gentle or harsh touch (Li et al. 2011). In contrast, mechanoreceptive afferents in mammalian skin often terminate in sensory endings or sensory cells that respond to particular aspects of skin deformation. Together, responses from multiple afferent types contribute to the perception of shape, texture, motion, and vibration (reviewed by Saal and Bensmaia 2014). In response to contact, afferent populations can encode the modality, location, intensity, and timing of a stimulus. Previous psychophysical and neurophysiological work in primates has differentiated afferent types according to their functional response properties and morphology (reviewed by Johansson and Vallbo 1983; Johnson 2001). These afferents' ability to encode both the static and dynamic aspects of a stimulus is due in part to the differential adaption rates to sustained indentation. Mechanoreceptors also vary in the size and spatial architecture of their receptive field, or area of stimulation that leads to a neuronal response. Slowly adapting type 1 (SA1) afferents that end in Merkel cells exhibit small receptive fields (3–5 mm) with sharp borders that facilitate their ability to resolve spatial detail (Johansson 1978; Phillips and Johnson 1981; Vega-Bermudez and Johnson 1999). The distribution and density of mechanoreceptors varies across the skin but are often concentrated in regions of great functional significance for tactile sensitivity such as the finger pads of primates (Johansson and Vallbo 1979), the nose of moles (Sawyer and Catania 2016), or the bill tip of birds (e.g., Gottschaldt and Lausmann 1974; Gentle and Breward 1986).

Similar to the sense of touch observed in other systems, the fin ray mechanosensory system can encode features of both the static and dynamic aspects of tactile stimuli. Hardy et al. (2016) investigated the physiological capacities for touch in pectoral fins of the pictus catfish (*P. pictus*), a bottom dwelling species native to low-visibility riverine environments. Through sets of step-and-hold and ramp-and-hold stimuli it was revealed that afferent activity can encode the intensity, speed, and duration of contact (Fig. 4). Similar to the mammalian somatosensory system, SA fibers continued to fire throughout periods of sustained contact thus providing feedback on the duration and intensity of tactile events. This feature of fin mechanosensation may facilitate a diversity of benthic fishes such as the hawkfishes (family Cirrhitidae), gobies (family Gobiidae), and other ambush predators, known to rest on their pectoral fins for extended periods, to maintain fin position and contact with the substrate while waiting for prey. Fin ray afferents also respond to brushing the skin

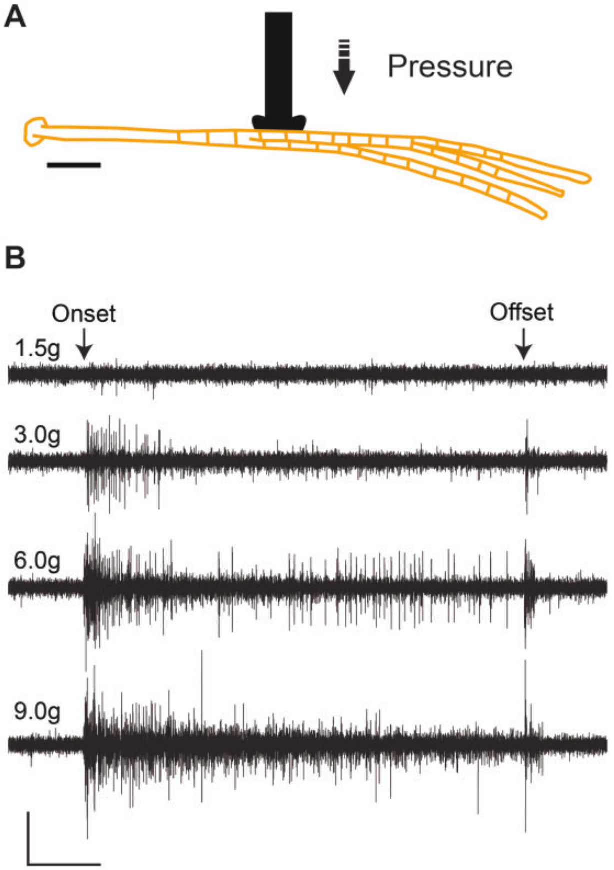

Fig. 4 The response of fin ray afferents to tactile stimuli in pictus catfish (*P. pictus*). (**A**) Tactile stimulation was generated via a probe connected to a linear actuator. Fin rays were exposed to pressure perpendicular to their dorsal surfaces via the flat head of a pin (1.4 mm diameter). Scale bar: 1 mm. (**B**) Physiological response to pressure exerted perpendicular to the dorsal surface of a pectoral fin ray. Responses to 1.5, 3.0, 6.0, and 9.0 g step indentations are shown. Nerve activity reflects the force of indentation. The duration of the burst of activity associated with the initial contact increased with increasing force. Scale bar: $x=1$ s, $y=0.02$ mV. Adapted from of Hardy et al. (2016).

along the proximodistal axis of the fin (Hardy et al. 2016). As touch often involves motion between the skin and the surface of an object, the speed and direction of motion may enhance a fish's awareness of its physical surroundings and its interactions with it. Together, the available morphological, behavioral, and electrophysiological data suggest that fins have the capacity to act as sophisticated systems for touch and share features commonly observed in mammals such as afferents with differential adaptation rates.

Insights from the mechanosensory system of other animals have led to many additional questions about touch sensation in fins. As mentioned previously, cutaneous mechanoreceptors are often localized to functionally important regions of the body where high sensory ending density facilitates greater sensitivity and an increased spatial resolution of tactile stimuli. It is unclear whether mechanoreceptors in fins are similarly localized to particular regions of the fin such as the distal tips of fin rays where touch events may more readily occur. Likewise, are the receptive fields of fin ray mechanoreceptors small enough (on the order of a few millimeters) to discriminate spatial stimuli like the SA1 afferents of primates? Feedback on the surface features of contacted objects may be beneficial for fishes. Sensory input regarding the shape, texture, and/or roughness of contacted surfaces could inform habitat selection as well as behaviors such as navigation, station holding, and burying. For example, the size and texture of sediment (i.e., mud, sand, pebbles) influences the distribution of many benthic species as these factors help to determine prey type availability and these fishes' ability to bury themselves (Gibson and Robb 1992; Moles and Norcross 1995). Texture perception among animals is best studied in the primate finger pad system where coarse textural features (on the order of millimeters) are most faithfully encoded in the spatial pattern of activation across SA1 afferents. Fine textures (on the order of micrometers), however, are encoded by texture-specific vibrations that produce characteristic temporal patterns of spikes in RA and Pacinian (PC) afferents (Weber et al. 2013). It is unclear whether fins exhibit similar capabilities and if so whether fish and tetrapods use conserved encoding mechanisms. The role of fins in determining relevant features of the contacted surfaces such as texture remains an exciting question for future study.

Fishes that live in benthic or structurally complex environments provide rich opportunities to investigate touch sensation. Maintaining a close physical connection to the substrate, fishes in these habitats often exhibit morphological adaptations to their fins that presumably facilitate substrate-based behaviors. For example, blennies (family Blenniidae) and sculpins (family Cottidae) exhibit a highly differentiated pectoral fin where the ventralmost fin rays function as hooks to cling to the substrate and resist water movement (Brandstätter et al. 1990; Taft et al. 2008; Kane and Higham 2012; Taft and Taft 2012). Hawkfishes (family Cirrhitidae) also exhibit adaptations as the five to seven ventralmost pectoral fin rays are often elongated and thickened relative to the rest of the fin to provide body support while at rest on the substrate (Randall 1963). It is clear that fish have adapted to a benthic existence yet little is known about the specifics of the physical interactions between fins and the external environment. For example, how much of a fin's surface area makes contact with the substrate and for what duration does contact occur during typical behaviors? Knowing this type of information across fishes of varying ecology and pectoral fin shape will inform how fins or even particular fin rays interact with the environment and may be adapted for substrate contact and touch sensation.

Form and function comparisons between fins and limbs may shed light on the evolution of appendage-based touch sensation given their shared developmental and evolutionary histories. While vertebrates exhibit both SA and RA receptor types, variation in receptor structure and function exists among vertebrate classes (i.e., fish, reptiles, birds, mammals) (reviewed by Iggo and Andres 1982; Andres and v Düring 1990). Free nerve endings and putative Merkel cells have been found in membranous pectoral fins (Williams et al. 2013; Hardy et al. 2016), but it is unclear whether other types of touch receptors are present and whether putative Merkel cells in fins respond to stimulation consistent with other taxa. Merkel cells have been found innervating the body trunk, barbels, and oral cavity in at least 12 species of fish (Whitear 1989), but information on their presence in fins is lacking. A more targeted account of fin sensory structures is therefore needed to inform the evolutionary histories of cutaneous mechanoreceptors across vertebrate appendages and the functional demands they meet.

Although information on touch in fins is scarce, there is a wealth of information on the mechanosensation in fishes from studies of the lateral line. The lateral line comprises mechanoreceptors called neuromasts arranged along the head and body that allows the detection of movement, vibration, and pressure gradients in the surrounding water (Dijkgraaf 1963). Often referred to as "touch at a distance," sensation by the lateral line provides organisms with a spatial awareness of their surroundings critical to a number of behaviors including predator avoidance (McHenry et al. 2009), schooling (Partridge and Pitcher 1980), and orientation (Montgomery et al. 1997). Functioning at different distances relative to the body, lateral line, and fin membrane mechanosensation could be thought of as complementary systems that provide information on a wide range of parameters that describe their physical surroundings. Both systems rely on multiple types or varieties of sensors that are tuned to encode spatial and temporal aspects of behaviorally relevant stimuli. Furthermore, as information from the periphery (i.e., skin) in both systems must be integrated at central processing centers, understanding how the lateral line simultaneously integrates feedback from neuromasts distributed across the body and head may provide clues as to how fish process fin ray feedback.

The application of fin mechanosensation to underwater robotic devices

The incorporation of mechanosensory feedback in bioinspired robots still remains a significant engineering challenge. Many of the sensorimotor problems experienced by robots have already been solved through natural selection in biological systems and there is growing use of biologically inspired sensory systems in robots to acquire information from the external environment and use it to adjust the output of the robot. A holistic understanding of mechanosensory feedback and its impact on the effective generation of behavior and acquisition of information in animals can demonstrate principles of sensory feedback applicable to novel engineered devices.

The fins of underwater robots are capable of complex motions that mimic the kinematics of biological fins, and research on the integration of sensory feedback in these systems is now underway. The kinematics and three-dimensional deformation (Daniel and Combes 2002; Young et al. 2009) as well as the stiffness (Tangorra et al. 2010) of a propulsor will strongly influence its propulsive capabilities. Bioinspired fin-based robotic systems have made great strides matching these characteristics of biological fins (Flammang et al. 2017; Westneat et al. 2017). As the movement and deformation of robotic fins becomes more complex and fins that can dynamically change stiffness become the norm (Tangorra et al. 2010; Kahn et al. 2015), so too will the integrated sensory system need to become more complex. Pressure (Kahn et al. 2012) and strain (Kahn et al. 2015) sensors have both been distributed across a robotic fin, and feedback from strain sensors can reasonably predict the propulsive forces associated with certain low frequency fin movements (Kahn et al. 2015). Here, we synthesize biological principles of mechanosensation to focus on two topics that are likely of interest to engineers: tuning the sensory system to match appendage mechanics and incorporating touch sensation into robotic fins. Further, the study and use of robotics can be used a platform or mechanism to test biological hypotheses relating to the fish fin mechanosensory system.

While performance tradeoffs, which are often correlated with morphological variation, exist in biological systems, it would be possible for engineers to integrate different fin-based sensorimotor strategies into a single robotic fin model. In a morphologically and behaviorally diverse group of coral reef fishes, the family Labridae, fishes employ pectoral fin-based propulsion ranging from rowing to flapping, where rowing species capable of high degrees of maneuverability use relatively flexible broad fins to perform drag-based propulsion and flapping species capable of highly efficient cruising and high speeds use stiff wing-like fins to perform lift-based propulsion (Aiello et al. 2017, 2018a, 2018b). The employment of adaptive propulsors with sensory feedback would be useful in a robot that will need to engage in both highly efficient long-distance cruising as well as slower tasks that require high degrees of maneuverability. Modulating the stiffness of a propulsor will change the magnitude of bending that occurs in response to the application of force. Just as with biological mechanosensors, engineered sensors have limited operating ranges and their output can saturate with the application of a high intensity stimulus. Sensors with wide receptive ranges could be used in adaptive systems in order to encode the stimulus throughout the entire range of the stiffness spectrum; however, this will likely limit the intensity resolution of the sensor (the ability to discern between different intensities of the same stimulus). In closed loop systems, inaccurate sensory information and sensor error, which could be caused by low intensity resolution, can have devastating effects in the production of the desired output signal (Kuo 2002).

Data from comparative studies are critical to the development of engineered solutions because comparative studies provide insights into the diverse ways different species have solved the same problem. Aiello et al. (2017) found that the stimulus range of a sensor changes with the stiffness of the fin it innervates, so that sensors innervating stiff fins are more sensitive (a lower stimulus threshold is needed for activation) than those innervating more flexible fins. The difference in sensor threshold allows the sensory systems innervating both stiff and flexible fins to maintain the same intensity resolution across fins of different stiffness regimes. Therefore, it appears that the ability to accurately discern the intensity or magnitude of a stimulus is an important feature of mechanosensory systems. The development of robots employing fins capable of adapting their stiffness should thus benefit from sensors and control algorithms designed to maintain intensity resolution over a wide range of intensities of a given stimulus.

The use of sensory feedback from robotic fins has been limited to the prediction of propulsive forces during swimming, yet the incorporation of tactile sensation can be important in other contexts. Biological fins are a particularly useful system to study for applications involving underwater touch as they are capable of deforming to the contours of contacted surfaces yet rigid enough to support the body at rest on the bottom and/or to generate propulsive forces necessary for movement. These qualities are advantageous in the applied realm where bioinspired fin-based systems could be used to sense and navigate situations involving complex environmental features, structures, turbid and other low visibility environments, or physical interactions with other objects. Robotic fins have typically been designed for use in open water, but applications certainly exist for substrate dependent systems where tactile feedback from the bottom could enhance obstacle avoidance or positional stability in wave swept environments. In order to facilitate the incorporation of touch into robotic fins it will be critical to gather detailed knowledge of the extent to which biological fins touch and conform to contacted surfaces. The physical dynamics of fin-based touch will serve to inform optimal sensor placement as well as the necessary flexibility of these robotic systems to extract sufficient feedback on contacted surfaces during a variety of movements and behaviors.

Robots can be used to test biological hypotheses on the relationships between sensor density, placement, and physiology (form and function) as well as answer questions on the degree of sensor redundancy. In comparison to biologically inspired robotic fin systems, biological fins are covered by more than an order of magnitude more sensors. In contrast, Kahn et al. (2015) employed eight pressure and six strain sensors across a robotic fin, which resulted in a reasonable prediction of the propulsive forces generated during fin movement. The disparity in sensor number raises questions on whether there is a given density and arrangement of sensors needed to accurately encode a given stimulus, and whether biological systems are outfitted with sensors transmitting redundant information. As researchers continue to study interspecific differences in the count and spatial distribution of mechanoreceptors in biological fins, only the use of a robotic fin can allow researchers to strategically manipulate sensor density and the specific location/placement of a given sensor across the surface of a fin. These manipulation experiments can then be combined with sparse sensor theory to determine the specific features of a stimulus encoded by a given sensor (Brunton et al. 2016) and information theory can be used to determine the information encoded by a given sensor as well as the degree of redundancy in the information encoded among sensors (Timme et al. 2014). While engineers often look to biology for inspiration when designing robots, it is clear that the use of robots and computational methods is similarly useful for answering difficult biological questions.

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