Mechanosensation is evolutionarily tuned to locomotor mechanics

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The biomechanics of animal limbs has evolved to meet the functional demands for movement associated with different behaviors and environments. Effective movement relies not only on limb mechanics but also on appropriate mechanosensory feedback. By comparing sensory ability and mechanics within a phylogenetic framework, we show that peripheral mechanosensation has evolved with limb biomechanics, evolutionarily tuning the neuromechanical system to its functional demands. We examined sensory physiology and mechanics of the pectoral fins, forelimb homologs, in the fish family Labridae. Labrid fishes exhibit extraordinary morphological and behavioral diversity and use pectoral fin-based propulsion with fins ranging in shape from high aspect ratio (AR) wing-like fins to low AR paddle-like fins. Phylogenetic character analysis demonstrates that high AR fins evolved independently multiple times in this group. Four pairs of species were examined; each included a plesiomorphic low AR and a high AR species. Within each species pair, the high AR species demonstrated significantly stiffer fin rays in comparison with the low AR species. Afferent sensory nerve activity was recorded during fin ray bending. In all cases, afferents of stiffer fins were more sensitive at lower displacement amplitudes, demonstrating mechanosensory tuning to fin mechanics and a consistent pattern of correlated evolution. We suggest that these data provide a clear example of parallel evolution in a complex neuromechanical system, with a strong link between multiple phenotypic characters: pectoral fin shape, swimming behavior, fin ray stiffness, and mechanosensory sensitivity.

neuromechanics | mechanosensation | evolution | locomotion | Labridae

The appendages of animals, from insect wings to tetrapod limbs, have evolved and diversified with the functional demands associated with a species' behaviors and the environments in which it lives (1–4). Whereas the evolution of appendage structure and movement has been identified as critical, both to key evolutionary innovations and to more subtle taxonomic specialization (1–3, 5, 6), it is clear that mechanosensation, which includes the ability to sense the relative movement and position of one's own body elements, is also critical for effective appendage function and control. For example, people who have lost mechanosensation of their limbs must attend visually to their affected limbs to know where they are in space and to modulate motor output effectively (7, 8). Experimental sensory denervation of limbs (9–12) and other appendages (13–15) in a range of other species has also been shown to result in significant disruption of normal movement. The recent discovery of mechanosensation in the pectoral fins of fishes (15–17) provides an opportunity to explore evolutionary patterns of mechanosensation relative to interspecific variation in limb locomotor biomechanics.

Sensory capabilities evolve with behavior to reflect the diverse sensory needs across species (18–20). The absolute range of perceptible sensory cues varies among species for a given sensory modality, as seen in the diversity of auditory frequency ranges represented among insects (18, 21) and rodents (22–24), and the olfactory detection thresholds among primates (25, 26). In addition, activity in particular regions of a sensory range may be enhanced to reflect biologically relevant inputs. For example, the olfactory system has been highly specialized through evolution to the relevant olfactory cues (27–29). Appendage mechanosensation is different from these sensory modalities in that the appendages of animals are integrated sensorimotor structures that perform dual roles, acting as both sensory and motor structures during a given behavior (16, 30). Interspecific variation in appendage mechanics will influence the magnitude of bending and shape change incurred from the application of forces during locomotion (31, 32), which will consequently change the range of mechanosensory stimuli relevant to each species. The diversity of pectoral fin shape and behavior among fishes provides a unique opportunity to test whether the mechanosensory system undergoes correlated changes in relation to the mechanical properties of locomotor appendages, which would suggest that limb mechanics and the limb's associated mechanosensory system are major axes of structural and functional variation in neuromechanical systems.

In this study, we investigated the correlated evolution of mechanosensation and limb mechanics in fish pectoral fins, the homologs of tetrapod forelimbs. Pectoral fin nerves have recently been shown to provide feedback on fin ray bending amplitude and rate as well as on fin ray position (15, 16). Here we examined proprioception in the fish family Labridae (wrasses), a group that demonstrates considerable morphological, biomechanical, and movement diversity (33). Aspect ratio (AR) is a measure of the fin's span squared relative to its surface area, with higher AR indicating relatively longer and narrower, more wing-like fins, and low AR indicating a broader more paddle-like fin shape. Labrids use pectoral fin-based swimming behaviors along a continuum that

Significance

This paper provides an analysis of the correlated evolution of limb biomechanics and mechanosensation. We found that in multiple independent evolutions of stiff fins there was concurrent evolution of increased mechanosensory afferent sensitivity to low amplitude bends, compared with the nerve responses of more flexible fins. These results indicate that sensory systems are tuned to fin mechanical properties, revealing that limb mechanics and the limb's associated mechanosensory system are a new and important axis of structural and functional variation in locomotor systems. Further, we find high levels of parallelism between swimming behavior, fin shape, mechanics, and mechanosensation across a rich phylogeny of fishes, suggesting that neuromechanical tuning may be a general feature of evolution in neuromechanical systems.

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Data deposition: The sequences reported in this paper have been deposited in the GenBank database (accession nos. provided in Dataset S1). Aspect ratio sources and data, mechanical property data, electrophysiology data and phylogenetic tree files have been deposited in the Dryad Digital Repository (http://dx.doi.org/10.5061/dryad.0463n).

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ranges from drag-based rowing with broad, low AR fins for high maneuverability, to lift-based flapping driven by high AR, wing-like fins that maximize thrust and mechanical efficiency (33–37). The central aim of this study is to test the hypothesis that the mechanosensory response to fin ray bending undergoes evolutionary tuning with fin mechanical properties across a diversity of fin shapes and behaviors. First, we hypothesized that high AR pectoral fins have increased overall flexural stiffness due to their propensity to bend less during locomotion in comparison with more flexible low AR fins (Fig. S1). Second, we hypothesized that in comparison with more flexible fins, the reduced bending magnitude that occurs in stiff fins has driven their associated sensory system to evolve increased sensitivity to lower amplitude bending.

We sought to explore broad evolutionary patterns of fin design and function. To test our hypotheses in a phylogenetic framework, we performed a phylogenetic analysis of pectoral fin aspect ratio using a new phylogeny of 340 species of Labridae (Fig. 1 and Fig. S2). Based on this reconstruction, four species pairs were chosen, each pair from a different labrid subfamily. Within each pair, selected species used fins of divergent shapes, one with high AR fins and one with low AR fins. The four species pairs (*Gomphosus varius* and *Halichoeres bivittatus*, *Halichoeres hortulanus* and *Halichoeres melanurus*, *Scarus taeniopterus* and *Cheilinus fasciatus*, and *Clepticus parrae* and *Bodianus rufus*, high AR and low AR, respectively) were used to test patterns of correlated evolution between fin ray flexural stiffness and the mechanosensory afferent response to step-and-hold stimuli in our analysis of the evolutionary tuning of neuromechanical systems.

Results

Phylogenetics and Ancestral State Reconstruction. Our analysis of DNA sequence data for 340 species of labrid fishes yielded a well-resolved phylogeny (Fig. S1) to use in exploring phylogenetic patterns of pectoral fin shape. Character optimization and ancestral state reconstruction revealed a most likely ancestral state of low AR fins at the root node of the tree (likelihood probabilities of each fin AR: low = 0.47, intermediate = 0.29, and high = 0.24) and at least 22 independent evolutions of high aspect ratio fins associated with the flapping swimming behavior (Fig. 1, Figs. S2 and S3, and Table S1). The phylogenetic reconstruction shows a rich history of fin shape evolution, with multiple clades having evolved upward and downward on the fin aspect ratio continuum, producing complex patterns of divergence and parallelism across the tree. High AR fins (AR > 3.2) were highly significantly ($P < 0.01$) convergent across the tree. Whereas the character state at the root node is equivocal, ancestral state reconstructions show high likelihood values for character states of low, intermediate, or high AR at progressively more distal nodes. Therefore, our interpretation of multiple independent evolutions of high aspect ratio fins is not dependent on the character state at the root node. The probability of representing the low AR character state at the node of a species pair's most recent common ancestor is 0.872 for *C. parrae* and *B. rufus* (node 27), 0.756 for *G. varius* and *H. bivittatus* (node 206), and 0.750 for *H. melanurus* and *H. hortulanus* (node 296). The node (node 58) of the most recent common ancestor between *C. fasciatus* and *S. taeniopterus* has a 0.491 probability of representing the low AR fin character state. Although this node is equivocal, the parrotfish *S. taeniopterus* represents a large clade of high AR flapping species, and a particularly notable independent evolution of high aspect ratio fins from the common ancestor of the cheiline and scarine wrasses.

Fin Ray Mechanics. The morphological phenotypes of low and high AR fins (Fig. 2*A*) corresponded to a strong divergence in fin ray flexural stiffness. The average flexural stiffness, or resistance to bending, at 50% fin ray length was between 190 ± 30 and 210 ± 50 × 10^{-9} N·m^2 (average ± SD) among the high AR species and between 20 ± 10 and 40 ± 10 × 10^{-9} N·m^2 among the low AR species. These data indicate largely consistent trends in flexural stiffness among size-matched individuals in each behavioral phenotype. Within each species pair, the average flexural stiffness at 50% fin ray length of high AR fins was 5.4–11.6 times greater and significantly different from that of low AR fins (Fig. 2*B*; *t* test *P* values <0.05; Fig. S4). Across all eight species, flexural stiffness decreases exponentially along the length of the fin ray, and regressions of stiffness against fin ray position reveal significant differences in the *y* intercept between species for all four pairs and significant differences in the regression slope between species for three pairs (*G. varius* and *H. bivittatus*, *C. parrae* and *B. rufus*, and *C. fasciatus* and *S. taeniopterus*) ($P < 0.01$; Table S2). The significant differences in *y* intercept suggest that there is a strong species effect on fin ray stiffness and significant differences in the regression slope suggest that the rate fin ray stiffness changes along the length of the fin ray is different between species.

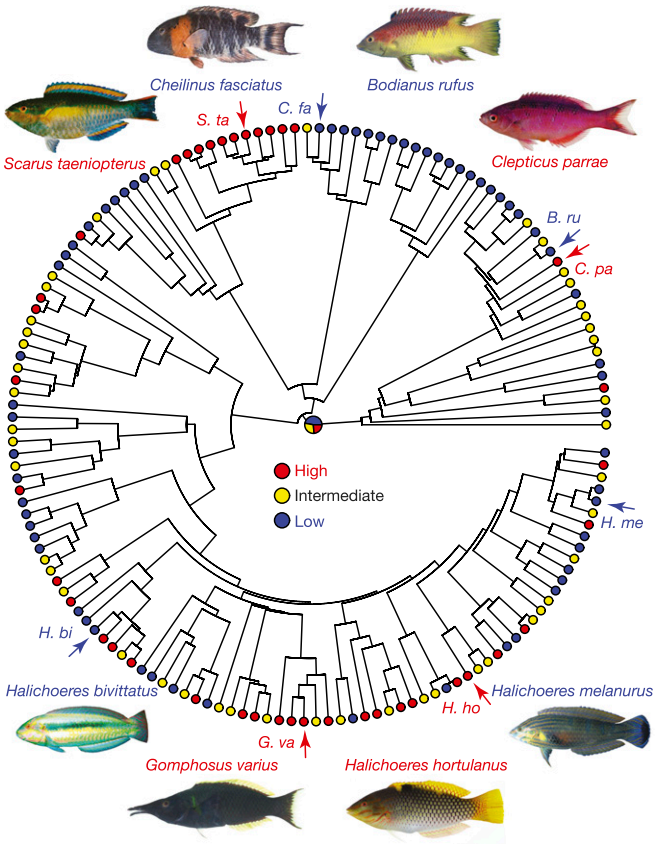


Fig. 1. The phylogenetic relationships of the Labridae and pectoral fin aspect ratio ancestral state reconstruction. The maximum likelihood reconstruction revealed a most likely ancestral state of low aspect ratio pectoral fins (low = 0.47, intermediate = 0.29, high = 0.24) and at least 22 independent evolutions of high aspect ratio fins. An arrow and the species' initials highlights the phylogenetic position of each species used in this study. The two species of each pair were always located within the same subfamily and each species pair contains an independent evolution of the high AR fin. The phylogeny presented here is pruned from 340 species to 150 species to maximize visualization. The ancestral state of the basal node is taken from the 340 species reconstruction. The full 340 species phylogeny and accompanying 340 species ancestral state reconstruction can be found in Fig. S2, and the node labels and the corresponding likelihood of the ancestral state at each node can be found in Fig. S3 and Table S1, respectively. Red, high aspect ratio; yellow, intermediate aspect ratio; and blue, low aspect ratio. Photo credits: *H. bivittatus*, Paul Humann; *H. hortulanus* and *G. varius*, Jeffrey T. Williams; and *B. rufus*, *C. parrae*, *C. fasciatus*, *H. melanurus*, and *S. taeniopterus*, John E. Randall.

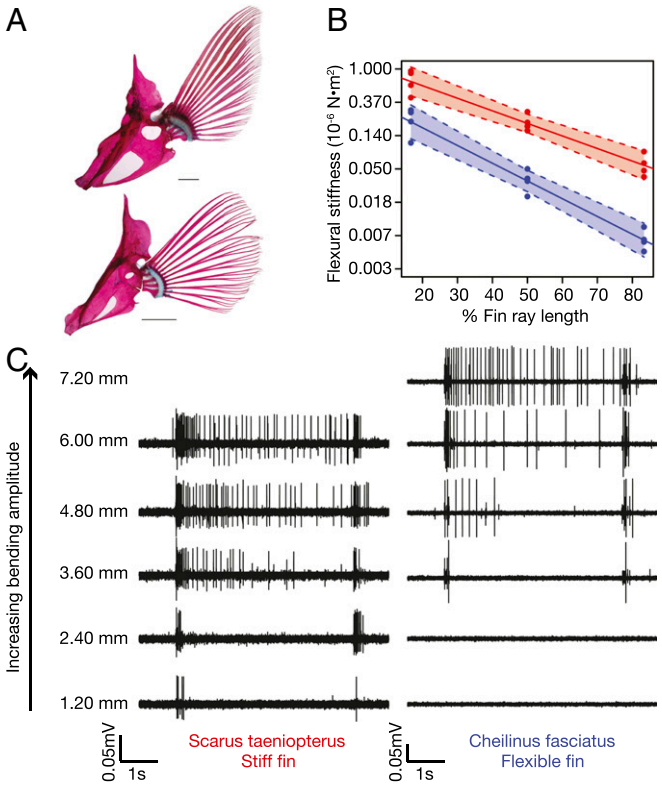
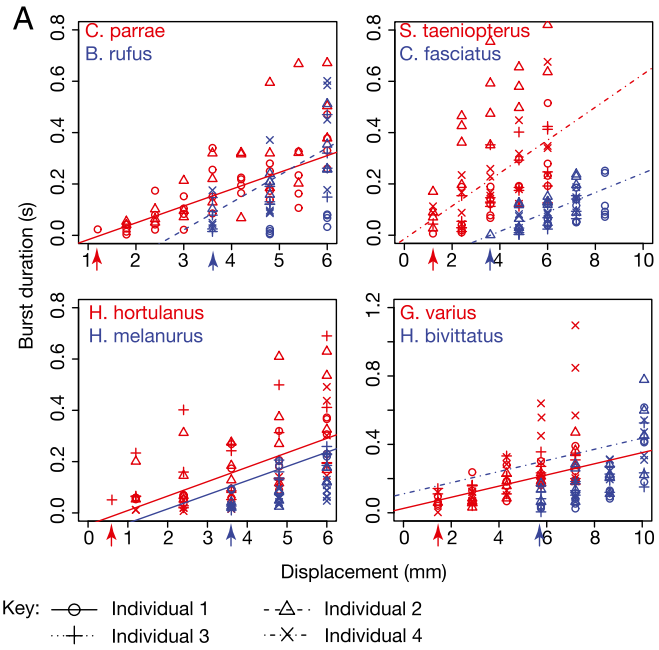


Fig. 2. Comparative pectoral fin morphology, mechanics, and proprioceptive sensitivity between closely related low AR (*C. fasciatus*) and high AR (*S. taeniopterus*) species. (*A*) Cleared and stained pectoral fins of *S. taeniopterus* (flapper; *Top*) and *C. fasciatus* (rower; *Bottom*). *S. taeniopterus* employs wing-like high-aspect ratio pectoral fins, whereas *C. fasciatus* employs broad paddle-like pectoral fins. (Scale bars, 1 cm.) (*B*) The pectoral fin rays of *S. taeniopterus* (high AR; red) are significantly stiffer than the rays of *C. fasciatus* (low AR; blue). All flexural stiffness data for each species were pooled and fit with an exponential curve (r^2 = 0.93, 0.95 for *S. taeniopterus* and *C. fasciatus*, respectively). Correspondingly, the data are presented in a semilog fashion with a logarithmically scaled *y* axis. The shaded region of each fit represents a 99% confidence interval of the linear regression. The *y* intercept and slope of the regression line was significantly different between each species ($P < 0.05$; Table S2). (*C*) Representative nerve recordings from one individual of *S. taeniopterus* (*Left*) and *C. fasciatus* (*Right*). A three times larger bending magnitude is needed to elicit a response in the size-matched pectoral fin of the flexible-finned *C. fasciatus* in comparison with the stiff-finned *S. taeniopterus*.

Mechanosensation. Afferent nerve responses to fin ray bending were recorded for all eight of the species tested and consistent trends were identified among taxa. In response to step-and-hold stimuli, where a single fin ray is bent, held in a bent position, and then returned to rest, a burst of spikes occurred both when the fin was raised from and when it was returned to its resting position. The duration of bursts (three or more spikes within 50 ms of each other) associated with stimulus onset increased significantly with increasing bending amplitude (Fig. 3*A* and Table S3). Furthermore, fibers continued to respond during the hold phase of the stimulus (Fig. 2*C*). At high bending amplitudes, the spike rate over the hold period (a 3-s portion of the trace that began 1.5 s after stimulus onset to ensure activity associated with fin movement was not included in this analysis) was significantly greater than the spike rate of a prestimulus baseline for each species used in this study (one-way ANOVAs, $P < 0.05$; Table S4). At these higher bending amplitudes, a significant and positive relationship was found between hold period spike rate and bend amplitude ($P < 0.05$) for all individuals across all species (Fig. S5 and Table S5).

Comparing across the species pairs, stiff-finned species consistently demonstrated greater sensitivity in comparison with species using more flexible fins. The average minimum bending amplitude to elicit a response (response threshold) was between 17.84 ± 0.88 and 30.67 ± 1.03% fin ray length (3.6 ± 0.0 and 6.12 ± 0.72 mm) among the low AR species and between 5.91 ± 0.58 and 8.20 ± 3.03% fin ray length (1.05 ± 0.3 and 1.5 ± 0.42 mm) among the high AR species (Table S6). Similar to fin stiffness, these data show consistent trends in response threshold among size-matched individuals in each morphological phenotype. Within each species pair, the average response threshold of the low AR species was 2.39–5.19 times greater in percent fin ray length than that of the high AR species (Fig. 3*B*). This finding corresponds to differences in average response threshold between the species of each pair ranging from approximate bending magnitudes of 11–25% fin ray length and significant differences in response thresholds between the species of each pair ($P < 0.0125$; Fig. 3*A*). Furthermore, the slope of the



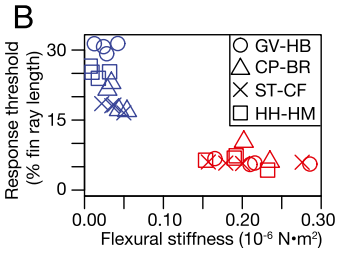


Fig. 3. Summary of afferent response to fin ray bending. (*A*) Bivariate plots of burst duration by fin ray bending magnitude per species. The duration of bursts (three or more spikes within 50 ms of each other) associated with the onset of fin ray movement is positively and significantly correlated with fin ray bending magnitude. Regression lines are presented for one representative individual of each species, and regression statistics for all individuals are detailed in Table S3. Arrows represent minimum response amplitude per species. (*B*) Response threshold (the minimum bending amplitude needed to elicit a response) is plotted against fin ray flexural stiffness for every individual of each species. In all cases, the pectoral fin rays of high AR fins are significantly stiffer than those of low AR fins, and the proprioceptive system of high AR species is significantly more sensitive than that of low AR species. Blue, flexible low AR fins; red, stiff high AR fins.

regression between the duration of the afferent's initial burst associated with fin bending and fin bending amplitude was compared between the species of each pair to determine whether the high and low AR species of each pair maintained similar stimulus intensity resolution (the ability to discern between two intensities of the same stimulus). The high and low AR species of each pair show no differences in intensity resolution (P values range from 0.186 to 0.777).

We also assessed the relationship between response threshold and fin ray flexural stiffness. A multiple regression that nests species within subfamily and includes aspect ratio as a fixed effect found no significant correlation between response threshold and fin ray flexural stiffness (P value = 0.2447; Table S7). Similarly, linear regressions conducted on these two variables for each species were never significant (P values range from 0.101 to 0.965; Table S7). An additional regression between these two variables conducted on data from a single species that covered a larger range in body size (standard length: 6.3–15.2 cm; $n = 6$) was also not significant ($P = 0.214$; Table S7).

Discussion

The key results of this study are that (*i*) a phylogenetic analysis reveals extensive parallel evolution resulting in at least 22 independent origins of high aspect ratio, wing-like appendages in the Labridae; (*ii*) the four pairs of species at low and high extremes on the AR spectrum showed significant differences in flexural stiffness; and (*iii*) we found strong evidence of neuromechanical tuning, with elevated mechanosensory sensitivity in stiffer more wing-like fins.

This study investigates the relationship between limb mechanosensation and stiffness in four pairs of closely related species that use divergent fin shapes, an independently evolved high AR species and a plesiomorphic low AR species. In each pair, the high AR species used significantly stiffer fin rays in comparison with the low AR species. Previous work has found a correlation between pectoral fin aspect ratio and swimming behavior (33). Therefore, these data suggest that differences in fin shape (aspect ratio) do not simply reflect change in movement and motor control of the fins but that the fins have evolved mechanically to function as effective propulsive structures, tuned to different performance capabilities. Importantly, the interspecific variation in fin ray stiffness observed and multiple independent evolutions of stiff fins, provided a phylogenetic framework in which to examine the correlated evolution of mechanics and mechanosensation.

In all eight species of wrasse studied here, spiking patterns of the mechanosensory afferents innervating each individual's pectoral fin rays were able to encode fin ray movement and position (Figs. 2*C* and 3*A*). These data are consistent with results from the bluegill sunfish (16). In combination with previous work in the pectoral fin (16, 17) and the adipose fin (38), a central result of this study is the mechanosensory system's ability to encode information about both the static and dynamic qualities of a stimulus (i.e., position and movement) might be a general feature of actinopterygian fins. Further, we consistently found that species using stiffer pectoral fins also exhibited greater mechanosensory sensitivity (a lower minimum bending amplitude needed to elicit a response) in comparison with species using more flexible fins. These results suggest that sensory physiology can be tuned to the fin's mechanics through adaptation of the mechanosensory system's sensitivity to fin ray bending.

Our data support the hypothesis of species-specific sensory phenotypes. We considered alternative explanations for the relationship between neural activity and mechanics. One possibility is that interspecific variation in mechanosensory sensitivity arose as a plastic response to different behavioral repertoires. However, our data do not support this alternative. If plasticity were the dominant process acting to produce the interspecific differences in response threshold, we would expect to see correlations between stiffness and sensory threshold across species and among individuals of a given species. In this situation, within a given species and across all species, response threshold would decrease as stiffness increased. Instead, the mechanosensory sensitivity data show consistent sensitivity thresholds with little intraspecific variation (P values range from 0.101 to 0.965; Table S7) for each species. To increase statistical power, a further multiple regression model that includes aspect ratio as a fixed effect to account for the two morphological groups was also conducted and no significant correlation was found between fin ray flexural stiffness and response threshold (P value = 0.2447).

Body size and ontogeny may also impact the relationship between fin stiffness and afferent nerve activity. We performed the tests in this study on size-matched individuals with little variation in fin stiffness among the individuals of each species. To determine whether species-specific nerve activity patterns resulted from the narrow size range used, additional experiments were performed on individuals of a single species (*H. bivittatus*) that covered a large range in body size (standard length: 6.3–15.2 cm; $n = 6$). We found no significant correlation between fin stiffness or body size and mechanosensory sensitivity ($P = 0.214$; Table S7), suggesting a species-specific match between stiffness and mechanosensory sensitivity across a wide range of sizes of adult wrasses.

The pectoral fin mechanosensory system is at the nexus of physics (mechanotransduction at the cellular level), biomechanics and behavior (the mechanics and motion of the fin), and neurobiology (the encoding of a signal and subsequent information processing). It is still under debate whether mechanosensory cells sense stress or strain (39, 40), and whether the same mechanism of sensation is conserved across animals (41). Our results do not suggest that species have retained a plesiomorphic response threshold where the same minimum force would elicit a response in all species. In this scenario, regardless of a species' fin stiffness, the application of the same given force would elicit a response in the pectoral fin afferents of any species. If this scenario was true, a negative correlation would exist between response threshold and fin stiffness among the individuals within a given species and within behavioral phenotypes, and fins of the same stiffness would exhibit the same response threshold. However, our data show a wide variety of response thresholds for fins of similar stiffness (Fig. 3*B*). These data provide support for the hypothesis that interspecific differences in mechanosensory sensitivity reflect species-specific phenotypes evolutionarily tuned to the different magnitude bending regimes experienced by species with fins of high or low stiffness, respectively. Further, these results suggest that the pectoral fin mechanosensory system is responding to strain rather than differences in the applied stress.

The limbs of both biological organisms and robots with integrated sensors typically rely on sensory feedback to adjust output signals (42, 43). In closed-loop control systems, the production of the desired output signal relies on extremely accurate sensory information and is sensitive to sensor error (44). Novel engineering has led to the engineering of robots that use dynamic limbs, which are capable of tuning their stiffness as they locomote to optimize limb mechanics and locomotor efficiency over variable terrain, payloads, and speeds (45–47). The application of robust sensors with wide stimulus ranges and high resolution could be implemented to meet the needs of dynamic limbs throughout the entirety of their stiffness spectrum, but this will increase bandwidth requirements and sensory processing time. Limitations in neural bandwidth and delays in sensory processing in closed-loop control systems can have devastating effects on performance and stability in robotic models (48). The results presented here are a case study for how the mechanosensory system has been finely tuned through evolution to interspecific variation in appendage mechanics and may be useful in developing new sensors or control algorithms to maximize intensity resolution while maintaining low bandwidth and processing time.

In an evolutionary context, the phylogenetic analysis of fin shape reveals strong evidence of parallel evolution across the tree topology. In this study, we focused on 4 of the 22 known independent evolutions of high AR pectoral fins (Fig. 1 and Fig. S2). In each of these 4 cases, high AR pectoral fins evolved in parallel from a similar low AR ancestor, and this same pattern is seen repeatedly across the tree topology (Fig. S1). In all 4 independently evolving species pairs, pectoral fin mechanics evolve in tandem with AR, and as fins evolve increased stiffness, the sensitivity of their mechanosensory system also increases. The close association between swimming behavior (33) and biomechanics (34–36) with pectoral fin shape in these fishes suggests that the mechanosensory system has coevolved with the anatomical and behavioral diversification of the labrid fishes. We suggest that this is a clear example of parallel evolution in a complex neuromechanical system, with a strong link between multiple phenotypic characters: pectoral fin shape, swimming behavior, fin ray stiffness, and mechanosensory sensitivity. Further exploration of mechanosensation in this system, focused on species with a diversity of fin shapes, may yield information on the function of the mechanosensory system in intermediate forms and the role that sensory neuromechanics plays in driving evolutionary trends in locomotor diversity.

Broadly across animals, a spectacular morphological and biomechanical diversity of appendages are used in a vast repertoire of behaviors. The locomotor appendages of animals, from insect wings to vertebrate limbs, perform dual roles as sensors and propulsors (16, 49, 50). We argue that the diversification of locomotor appendages involves the evolutionary tuning of mechanosensation to the concurrent evolutionary changes in the material and morphological properties of propulsors (wings, fins, and limbs). This study demonstrates that the mechanosensory system has evolved to meet the dynamic range of fin movement in multiple independently evolving pairs of closely related fishes. The broad sampling of our study demonstrates that, as the fin evolves increased stiffness, the sensory system evolves increased sensitivity. These results suggest that the correlated evolution of the mechanosensory system and appendage biomechanics is a general principle of how neuromechanical systems evolve. As mechanosensation is a universal feature of organisms (51), neuromechanical tuning may be an evolutionary principle that shapes the functional capabilities of all animals.

Materials and Methods

Species pairs were selected from the phylogenetic topology specifically to be close relatives with divergent fin shapes, representing disparate regions of the tree. Four adult *G. varius* (9.9–12.0 cm), *H. bivittatus* (8.0–10.9 cm), *H. hortulanus* (7.3–10.5 cm), *H. melanurus* (7.5–8.8 cm), *C. fasciatus* (9.5–13.2 cm), *S. taeniopterus* (9.5–11.9 cm), and *B. rufus* (7.8–10.2 cm) and two adult *C. parrae* (8.1 and 8.2 cm) were used in this study. There were no significant differences in size between the individuals of the two species in each pair ($P > 0.05$). Two additional *H. bivittatus* were used in this study to expand the range of body sizes (standard lengths: 5.3 and 16.2 cm).

A phylogenetic analysis of 340 species of labrid fishes was performed, using an aggregated dataset of 10 genes used in previous labrid phylogenetics (52, 53), new sequences generated for this study, and additional genetic data obtained from GenBank (Dataset S1). Pectoral fin aspect ratio character states for 340 species were visualized at the tips of the phylogeny and analyzed using likelihood ancestral state reconstructions using the R packages ape (54) and phytools (55). Pectoral fin aspect ratio was calculated as the square of the longest fin span (usually the leading edge), divided by fin area. Aspect ratio was binned into three discrete characters: low AR (AR: 0.73–1.5), intermediate AR (AR: 1.50–3.0), and high AR (AR: 3.0–4.6).

For each animal used, we performed mechanical testing in one pectoral fin and the physiological recording of the afferent response to fin bending in its pair. Intrinsic pectoral fin ray flexural stiffness was measured through a series of three point bending tests along the ray's span with a material testing machine (LS1, Lloyd Instruments) using a 50 N load cell. We recorded from pectoral fin nerves following published methods (16). An extracellular glass suction electrode was connected to one of the afferent nerve fibers to record multiunit physiological responses to fin ray bending. The fin rays were clamped at their proximal end and the interray membrane was cut to isolate the individual ray for bending. Randomly ordered series of step-and-hold stimuli were applied to the third fin ray of each individual. Data were analyzed in MATLAB 7.10.0 (Mathworks) using a custom routine (R. Williams IV, University of Chicago). The burst duration associated with the stimulus onset (fin movement) and the spike rate over the hold period of the stimulus were calculated. All statistical analyses were performed in RStudio 0.98.484 (RStudio, Inc.) or JMP 9.0.1 (SAS). All experimental procedures were carried out under University of Chicago Institutional Animal Care and Use Committee guidelines (protocol 71589 to M.E.H.). The unabridged materials and methods section can be found as *SI Materials and Methods*.

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