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SYMPOSIUM

Future Tail Tales: A Forward-Looking, Integrative Perspective on Tail Research

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Synopsis **Synopsis** Tails are a defining characteristic of chordates and show enormous diversity in function and shape. Although chordate tails share a common evolutionary and genetic-developmental origin, tails are extremely versatile in morphology and function. For example, tails can be short or long, thin or thick, and feathered or spiked, and they can be used for propulsion, communication, or balancing, and they mediate in predator–prey outcomes. Depending on the species of animal the tail is attached to, it can have extraordinarily multi-functional purposes. Despite its morphological diversity and broad functional roles, tails have not received similar scientific attention as, for example, the paired appendages such as legs or fins. This forward-looking review article is a first step toward interdisciplinary scientific synthesis in tail research. We discuss the importance of tail research in relation to five topics: (1) evolution and development, (2) regeneration, (3) functional morphology, (4) sensorimotor control, and (5) computational and physical models. Within each of these areas, we highlight areas of research and combinations of long-standing and new experimental approaches to move the field of tail research forward. To best advance a holistic understanding of tail evolution and function, it is imperative to embrace an interdisciplinary approach, re-integrating traditionally siloed fields around discussions on tail-related research.

Introduction

Although the post-anal tail is considered a defining chordate characteristic, tails are also present in taxa outside of this phylum. Tails have extraordinarily diverse functions, including, but not limited to use as a fifth limb, as a visual signal for warning and courtship, and as an essential physiological and morphological driver for functions related to propulsion, stability and maneuverability, prehension, energy storage, and thermoregulation (Wake and Dresner 1967; Aleksiuk 1970; Lindsey 1978; Fish 1979, 1982; Hickman 1979; Tucker 1992; Thomas 1997; Patel et

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al. 2016). In other words, the tail plays multiple roles critical to many animals' survival. Such multifunctionality of the tail has captured the imagination of engineers and roboticists, leading to remarkable advances in the development of versatile bio-inspired robotic systems (Kopman et al. 2015; Patel and Boje 2015; Saab et al. 2018; Zhu et al. 2019; Fish 2020).

Despite its apparent importance, tails are vastly understudied. For example, we still have little understanding for why tails are conserved, reduced, or lost in certain lineages; or why analogous structures exist among invertebrates. Likewise, developmental pathways and regenerative mechanisms of tails are only recently gaining greater attention. Within biomechanics research, the tail is often ignored, with a greater focus toward paired appendage function. Yet, tails precede the evolution of paired appendages by ~200 million years (Donoghue and Keating 2014). As such, increasing our understanding of tail function, development, and evolution may provide valuable insight into the physiological costs and benefits of also using paired appendages, as well as how the holistic coordination of multiple appendage types—a concept common to fish swimming research but not elsewhere—enables smooth motion. Research on tails continues in a broad range of fields, from Evolutionary Developmental Biology (EvoDevo) to behavior to robotics, but these fields remain largely isolated from one another; yet there is immense conceptual overlap among these fields that have transformative potential if collaboration was more common. It is therefore imperative that we re-integrate these fields to fully capture the complexity and diversity of tails from an interdisciplinary viewpoint.

With this forward-looking perspective paper, we aim to cross boundaries between research fields, summarize what is known, and highlight exciting future tail research directions with the hope of inspiring greater interdisciplinary discourse. Here we outline five key areas to deepen and broaden our knowledge on the breath of tail and tail-related topics. We discuss the current state of the field including knowledge gaps, potential areas for future studies, and interdisciplinary research approaches in (1) evolution and development, (2) regeneration, (3) functional morphology, (4) sensorimotor control, and (5) computational and physical models.

Evolution and development

Although the notochord is a homologous structure across chordates and an integral part of post-anal tails, questions remain about the homology of skeletal tail structures. A clear definition of what comprises the tail is surprisingly elusive. If we define the tail as the "post-anal extension of the body axis," that creates a predicament since that definition in fishes would include parts of the dorsal fin and the anal and caudal fin as part of the tail. Developmental processes may provide some clarity, as there is evidence pointing toward unique genetic modules that individually control the development of these unpaired fins (Letelier et al. 2018). Thus, we should not lump all fins together as part of the tail. Sallan (2016) proposes that the fish caudal region is actually a combination of two components: (1) the caudal fin and (2) the "tail," defined as the post-vertebral notochord extension. This theory further postulates that differential outgrowth of these two structures generated the variation in the caudal region across fishes, including tetrapods (Sallan 2016). Moving forward, a careful examination of the gene regulatory networks (GRNs) controlling the development of these individual components of the post-anal caudal region will thus be necessary to evaluate homologies among chordate and vertebrate tails.

Compared with caudal structures, paired appendages that led to the origin of tetrapods have received a lot more attention in EvoDevo research. When anatomy alone was not enough to determine homology between the structure of the paired pectoral and pelvic fins in fishes and tetrapod fore and hindlimbs, development of molecular techniques allowed deep genomic homologies to be drawn between paired fins and limbs (Shubin et al. 1997; Mercader 2007; Yano and Tamura 2013; Gehrke and Shubin 2016). Similar use of genetic techniques could provide missing links in determining homologies among chordate tail structures. Analyzing developmental GRNs in the evolutionarily old caudal region may also shed light on the evolutionary origin of the younger paired appendages that first emerged in an ancestor of jawed vertebrates, potentially by co-opting genetic programs from other body appendages such as tails.

There are three key GRN components known to be involved in tail development across chordates: *Homeobox* (*Hox*) and *T-box* transcription factor genes, as well as Hedgehog signaling genes. However, large gaps still exist in our understanding of tail-specific regulatory landscapes. Here, we highlight what is already known about expression and control of these genes in relation to tail Evo-Devo and point out what is yet to be understood.

Hox genes in most vertebrates are organized into four duplicated (paralogous) clusters (*Hox A*, *B*, *C*, and *D*). Together, these pattern the antero-posterior body plan and the proximo-distal axis of paired appendages in the developing embryo (reviewed in, e.g., Burke et al. 1995; Duboule 1998; Holland 2013). Gene order along the chromosome reflects expression order along the body axis; the first *Hox* genes are expressed in the anterior of the embryo, and the last *Hox* genes are expressed in the most posterior regions of the embryo as well as the most distal ends of the fin/limb bud. In paired fins/limbs, only *Hox A* and *Hox D* cluster genes are expressed in limbs in vertebrates (Freitas et al. 2012; Tulenko et al. 2016; Longellato et al. 2018; Desanlis et al. 2020). We still lack an understanding of how the posterior *Hox* genes are expressed and regulated during caudal development across vertebrates. It has become clear that posterior genes of paralogy groups *Hox 9–13* are expressed in post-anal tails of all chordates as well as in hemichordates (Fodor et al. 2021). Most of our current knowledge comes from mouse models, which suggest a major role for posterior *Hox B* and *Hox C* cluster genes in tail development (Economides et al. 2003; Aires et al. 2019).

The key notochord gene *brachyury* (*bra*), generally known as *Tbxt*, is essential for chordate tail development. This is referred to by many names: *bra* in tunicates, *T* in mouse, *Xbra* in frog, and *no tail* (*ntl*) in fishes. This gene was present as one copy in early chordates. Two paralogous copies (*Tbxta*, *Tbxtb*) appeared during the early two rounds of vertebrate genome duplication, before one of these two paralogs (*Tbxta*) was secondarily lost again in the tetrapod common ancestor (Amemiya et al. 2013). The expression pattern of *Tbxt* genes in the notochord and the tail bud is conserved across chordates (Hermann 1995; Corbo et al. 1997; Thisse 2001). Loss of function of *Tbxt* genes leads to complete loss of tail in zebrafish and incomplete tail development in mice (Wilson et al. 1993; Schulte-Merker 1995). In zebrafish tail development, *tbxta* and *tbxtb* are required for expression of Wnt signaling genes during posterior mesoderm formation (Martin and Kimelman 2008). A recent study shows that although *bra* has been considered a master regulator of notochord development, *bra* alone is not sufficient to regulate notochord development in *Ciona*, highlighting the importance of further research into understanding the chordate tail GRN (Reeves et al. 2021).

In the Hedgehog signaling pathway, the vertebrate ligand gene *sonic hedgehog* (*shh*) plays many roles during development, one of which is establishing the Zone of Polarizing Activity (ZPA) that patterns fin and limb development (Gehrke and Shubin 2016). Its expression in the paired fin/limb is regulated by the ZPA regulatory sequence enhancer and in fish, a similar enhancer has been found to specify *shh* expression during the development of the unpaired dorsal fin (Letelier et al. 2018). The vital role of *shh* in paired and unpaired appendage development in fishes suggests that it could also play an important, yet elusive, role in fish tail development (Hadzhiev et al. 2007). Hedgehog signaling has been implicated in tail development in zebrafish (Hadzhiev et al. 2007), and loss of *shh* signaling in mouse models leads to abnormal tails (El Shahawy et al. 2019), but the specific involvement of this pathway in vertebrate caudal development has yet to be determined. Hedgehog signaling does not seem to be involved in tail development in ascidians, but does play a role in amphioxus. More work is thus necessary to understand the evolution of Hedgehog signaling in chordate caudal development (Di Gregorio 2020).

There is considerable overlap in gene expression in the tail and the paired appendages. However, this overlap is not necessarily an indication of a co-option, perhaps it is an indication of common processes (e.g., the similarity between posterior and distal axis extension). Despite the obvious similarities in gene expression, such as posterior Hox gene expression, few studies have focused on the possible caudal origin hypothesis: that the paired appendages are a co-option of GRNs specifying the posterior body axis (Shubin et al. 1997). There are several other competing hypotheses that the paired appendages and their GRNs originated from (1) the gills, (2) a hypothetical lateral fin fold, or (3) the median unpaired fins (dorsal and anal fin). No single hypothesis stands out because there are data supporting all of them (Abe and Ota 2017; Letelier et al. 2018) and some have hypothesized a combination of these origins (Diogo 2020; Sleight and Gillis 2020). Understanding the genes that pattern the non-vertebrate chordate tail compared with those that pattern the vertebrate tail as well as the vertebrate fin/limb will elucidate whether the tail really is the “first fin” and help answer a longstanding question that has interested scientists for over a century.

Although the post-anal tail is a key characteristic of chordates, the tail has also been reduced or secondarily lost in many lineages, as exemplified in birds and in the absence of a great ape tail. It is possible that a thorough investigation of instances of tail loss across chordate evolution would help us understand human tail loss, as well as other cases of tail reduction or loss among vertebrates (e.g., in frogs and birds). Different from ancestral, multi-segmented vertebrate tails, birds have fused caudal vertebrae that form pygostyles, which support tail feathers important for maneuvering during flight. Development of these pygostyles only happens after hatching (Rashid et al. 2018), indicating that birds retain the ancestral tail morphology in-ovo. In all cases of vertebrate tail loss, the tail is present throughout embryonic/larval development, but then is lost during development into the adult form—as can be seen among frogs and humans. Extending to non-vertebrate chordates, tunicates generally follow this pattern as well: the embryonic tail is lost upon reaching adulthood. However, there are some ascidian tunicates that have also lost the embryonic tail. Understanding the evolutionary and developmental processes that have led to instances of tail loss or tail vertebrae fusion across chordates could lead to a comprehensive study that encompasses the comparison of tail loss across many examples in chordate evolution.

Regeneration

Among some vertebrates, the tail demonstrates an unusual capacity for wound repair and regeneration (Bellairs and Bryant 1985; Higham et al. 2013; Jacyniak et al. 2017; Gordeev et al. 2020; Verissimo et al. 2020; Xu et al. 2020). Instead of scarring, these species are able to spontaneously regrow a replacement. Regeneration begins as an aggregation of proliferating cells called a blastema. Blastema cells eventually give rise to most new tail tissues. Although blastema-mediated regeneration is also associated with paired appendage regrowth among some anamniotes, the tail is the only appendage capable of regenerating in amniotes. Further, unlike the limbs, the tail (in various species of plethodontid salamanders and lepidosaurs) can be self-amputated or autotomized—an anti-predation mechanism that permits the controlled release of a portion of the tail. Once released, the detached tail will thrash, thereby providing a distraction as the prey escapes. It is worth noting, however, that while tail autotomy is often paired with tail regeneration, the two mechanisms are independent of one-another. More specifically, while some species capable of tail autotomy are incapable of tail regeneration (e.g., some snakes and amphisbaenians), other species that do not autotomize are capable of tail regeneration (e.g., teleost fish, non-plethodontid– and some plethodontid-salamanders, tadpoles, and crocodylians).

While tail regeneration recreates the overall shape and function of the original appendage, the fidelity of the replacement often varies. Whereas zebrafish and salamanders effectively replicate the pattern and structure of the amputated tail, reptiles do not. For example, leopard geckos primarily regenerate autotomized tails through cartilage and fat deposits, retaining a key function for fat storage, and are morphologically simple relative to their original counterparts (Gilbert et al. 2013). Among lizards, the loss in fidelity is most readily observed in the spinal cord (regenerated spinal cords lack gray matter), skeleton (bony vertebrae are replaced by a hollow cone of cartilage), skin (variation in the pattern of scalation), and a simplified musculoskeletal arrangement. The regenerated tails of *Sphenodon* and crocodylians are even less exact replacements, composed largely of a cartilaginous cone surrounded by connective tissue with limited skeletal muscle.

The amount of physiological energy and resources that are diverted into regenerating a lost tail is often indicative of their importance. Organisms that rely on tails for functional roles such as locomotion, anti-predation, and fat storage are predicted to suffer reduced fitness following autotomy (Barr et al. 2019; Triay-Portella et al. 2019). As such, energy that is allotted to maintaining regular body functioning may be funneled into caudal tissue regeneration, sometimes through multiple tail regeneration events in a lifetime (each loss occurs progressively closer to the tail base), or even "re-regeneration" of the exact same tail region (Barr et al. 2019). Energy allocation strategies between tail regeneration and reproduction vary among species and even between sex within a species (Dial and Fitzpatrick 1981; Salvador et al. 1995; Fox et al. 1998; Yurewicz and Wilbur 2004; Triay-Portella et al. 2019). Alternatively, birds use tail feather autotomy and regeneration as anti-predator strategy, which is found to be physiologically inexpensive and does not affect flight performance (Møller et al. 2006; Johansson and Hedenstrom 2009). These suggest an evolutionary cost–benefit approach to the facilitation of tail regeneration, and a hierarchy of energy allocation according to different pressures, potentially explaining why some species may not be capable of tail regeneration, or "choose" to suppress this capability entirely, in favor of other biological investments. However, this hypothesis remains to be tested.

Our understanding of the genetic and molecular mechanisms of tail regeneration is still limited and deeper analysis among different organisms is required to fully understand tail regeneration over various taxa (vertebrates, chordates, planarians, etc.). So far, studies examining regeneration in planarians, lizards, and tadpoles show very different pathways to regeneration: increased expression of genes that control cell proliferation, critical roles for transforming growth factor β signaling pathways, upregulation of *Wnt* signals, and less expression of inflammatory-immune genes (Ho and Whitman 2008; Almuedo-Castillo et al. 2012; Hutchins et al. 2014; Vitulo et al. 2016; Xu et al. 2020). A substantial amount of work has been done with plethodontid salamanders to understand the factors that influence tail autotomy and regeneration (Marvin 2010; Marvin and Lewis 2013). These findings lead to a need of further investigation of similarity in these pathways and genes in organisms capable of successful regeneration across the phylogenetic tree. Technology in genomics and molecular science can be useful tools to compare and contrast the mechanisms and gene expressions leading to observed variations in tail regeneration efficiency. For example, it allows for comparison of the restorative regeneration of planarians, that rebuild their complete lost anatomy, with modified anatomy in regenerated lizard tails (Elliot and Alvarado 2012). Moreover, in order to further investigate the depth of such questions there must be a greater effort to genome sequence species aside from currently used models such as *Anolis carolinensis* (has a complete and annotated genome sequence) and *Eublepharis macularius* (Alföldi et al. 2011; Xiong et al. 2016). Thus far, it is unknown how new structures can proliferate, differentiate, and organize while surrounded by adult cells. Comparative studies among species with high and low regenerative fidelity could elucidate why some adult animals can regenerate entire structures and why some lose this capacity.

Tail regeneration is hypothesized to have broad consequences for ecology and behavior; however, direct experimental evidence for these consequences is limited. Much of what we know is based on locomotor performance of salamanders and a small number of lizard species, namely leopard geckos and green anoles (e.g., Higham et al. 2013; Hsieh 2016). The results of these studies provide little consensus. Salamanders, for example, regenerate tails with fidelity; can regain full swimming capacities with only 50% regeneration; and regeneration speed is dependent on temperature, body size, and amount of tail length lost (Marvin 2010, 2011, 2013; Marvin and Lewis 2013; Joven et al. 2019). In contrast, most lizards lose locomotor capacity following autotomy, and it is slowly regained during regeneration. This directly impacts predator avoidance and mate selection during and even after regeneration (Gillis et al. 2009; Higham et al. 2013; Jagnandan et al. 2014; Hsieh 2016; Jagnandan and Higham 2017). Equivocal evidence from tadpoles, however, indicates that tail damage and regeneration may or may not have functional consequences on adult body size and adult locomotor performance (Ding et al. 2014; Koch and Wilcoxen 2019; Zamora-Camacho et al. 2019), emphasizing the need for comparative approaches to understanding the interplay between tail regeneration and ecology.

To rectify the gap in current knowledge, tail-regenerating species across a phylogenetic tree should be included in a cross-disciplinary analysis. For example, arboreal lizards that use tails to help climb and balance and lizards that use tails to enhance sprint speed or communicate would be better models to measure how regenerated structures support movement. Given the variation in the capacity to (1) autotomize using fracture planes, (2) the fidelity of regenerated structures, and (3) the secondarily simplified regenerated tails of lizards, we suggest leveraging the diversity of lizard habitat niches to measure the value of tails (Pianka 1973; Skeels et al. 2020). If a comparative and ecological approach is taken to sample the diversity of tail regeneration capacity in vertebrates, then the evolutionary pressures of maintaining or evolving the ability to regenerate a lost appendage could be better known.

Functional morphology

The tail provides a variety of functions that attest to its evolutionary and ecological importance. As noted earlier in this review, while some organisms—including humans—have reduced or lost the tail, a large percentage of vertebrates have maintained, elongated, elaborated, or repurposed this caudal extremity. In early vertebrates that descended from their chordate ancestors, the tail initially functioned as a device for swimming and stabilizing the body from both internal and external perturbations (Webb 2002). Embellishment of the tail with a broad caudal fin enhanced the propulsive effect by its interaction with the fluid environment (Flammang 2014). The hydrodynamics of the undulatory tail motions with a substantial caudal fin resulted in greater accelerations, swimming velocities, and efficiency due to action on an increased mass of fluid, facilitating momentum transfer from the axial musculature and vertebral column to the tail, to the water (Drucker and Jensen 1996; Müller et al. 2001; Tytell and Lauder 2004). Additionally, some fish can move outside of the water with the help of their tail (Swanson and Gibb 2004; Hsieh 2010; Gibb et al. 2013; Ashley-Ross et al. 2014), whereas certain salamanders can perform tail-assisted jumps (Hessell and Nishikawa 2017; Brown and Deban 2020).

The importance of a tail and its terminal fin for high performance swimming is a quintessential example of morphological and physiological modifications by evolution to a common successful form (Hildebrand 1995; Liem et al. 2001; Kardong 2019). The examples of the shark, ichthyosaur, and dolphin illustrate the effectiveness of this adaptation via convergent evolution. These disparate organisms exhibit similarities in shape and mechanics of the tail, despite their phylogenetic separation. This textbook example demonstrates how similar functional requirements of the tail are met by different clades that have evolved as identical solutions to analogous environmental challenges. For example, tail morphology is associated with environmental pressures selecting on the need to operate in the open ocean for fast, efficient propulsion. Convergence in morphology is then also exploited for similar trophic opportunities by highly derived aquatic predators.

As vertebrates moved out the water and conquered the terrestrial environment with limbed locomotion, the tail evolved new functions rather than simply being dragged on the ground (McInroe et al. 2016). Fast running animals use the tail as an aerodynamic inertial appendage to rapidly maneuver when changing direction (Wilson et al. 2013; Patel and Braae 2014). Saltatorial animals and bipedal runners employ the tail as a counterbalance (Alexander and Vernon 1975; Gillis et al. 2013; O’Connor et al. 2014). Even slow-moving tetrapods make use of the tail as an effective passive defensive strategy by sacrificing the extremity to allow the body an opportunity for escape (Vitt et al. 1977; Humphreys and Ruxton 2019). Rapid whip-like motions of the tail can provide a weapon for hunting and defense, which can be further enhanced by the incorporation of a massive tail club as displayed by the extinct *Ankylosaurus* (Arbour 2009; Oliver et al. 2013). A highly mobile tail affords the ability for prehension. The seahorse (*Hippocampus*) can wrap the tail around stationary objects for anchorage (Hale 1996; Neutens et al. 2014). In addition, a prehensile tail facilitates climbing in a variety of tetrapods except for birds (Hickman 1979; Lemelin 1995; Luger et al. 2020). However, the reduced fused pygostyle of birds supports the tail feathers that are necessary to foster stability in flight and swimming (Gatesy and Dial 1996; Felice and O’Connor 2014). Finally, the tail with its high surface-to-volume ratio can act as a thermal window in liberating excess heat, particularly from mammals (Fish 1979; Hickman 1979).

Two extant tetrapod vertebrate lineages that evolved flight, birds and bats, further modified tails for aerodynamic and other functions. Reduced fused pygostyle of birds supports the tail feathers while allowing unrivaled levels of modification of the full tail shape and position (Gatesy and Dial 1996) allowing it to variably act as an added wing, rudder, stabilizer, and drag reducer (e.g., Maybury et al. 2001; Maybury and Rayner 2001; Sachs 2007; Usherwood et al. 2020). Bat tails, made of a membrane stretched between hind limbs and including the caudal vertebrae, also provide a flight control surface (Gardiner et al. 2011). In both cases, the added lift and reduced drag provided by the tails decrease energetic costs relative to wing-only flight. Bird tails can also provide visual and even auditory signals for courtship and predator avoidance (Woodland et al. 1980; Clark et al. 2011) and can aid prey capture (e.g., Jackson and Elgar 1993). Bat tail membranes can even act as an insect net (Webster and Griffin 1962).

For so long, anatomical descriptions and proposed functions of the tail were investigated by simple dissections and morphometric measurements. There have been considerable advances in medical imaging and computational and physical modeling techniques that have opened a new window into understanding the relationship between form and function of the caudal extremity. computed tomography (CT) scans now allow a non-invasive means of examining both the external and internal composition of hard and soft anatomical features of tails (Watkins-Colwell et al. 2018; Buser et al. 2020). These scans can be used to create 3D models of skeletal anatomy which can be used in a variety of ways. Finite element analysis can then take these 3D models and apply loads to different bones and joints to investigate strain propagation and range of motion (Hsieh et al. 2005). 3D geometric morphometrics and other statistical techniques can tell us how morphology changes within a group or over evolutionary time (Buser et al. 2018). The powerful technique of X-ray of moving morphology can be directed toward analysis of the complex arrangement of the multiple joints and their movements by the tail (Brainerd et al. 2010). Investigations of structural mechanics (i.e., stress and strain) of real specimens can assess tail strength, flexibility, and range of motion and provide the data to examine tail autotomy and regeneration (Hsieh et al. 2005; Peixoto et al. 2019). Models generated from CT scans can be 3D printed and tested on universal testing machines to investigate how shape restricts movement (Connors et al. 2019). The importance of the tail as a thermal window can be investigated with thermographic cameras (McCafferty 2007).

With incorporation of new technologies and a perspective that views tails as an important feature in mechanics and physiology of organisms, there are opportunities to address long-standing questions and develop new possibilities for research. Tails function as a transmission directing the forces generated from muscles to the eventual exchange of momentum from swimming animals to the fluid environment. How this is accomplished has not been fully understood. Likewise, the role of the tail in stability and maneuverability is incomplete and needs to be appropriately modeled. Evolutionarily, what anatomical and morphological adaptations lead to the diversity of tail functions? Can we use the wide range of morphological data from CT scans along with kinematic data and computational modeling to create a system that "predicts" function in extant and extinct animals? Such questions can direct research projects along several avenues that demonstrate how the tail is an integral component of animals and essential in their biology.

Sensorimotor control

The wide variety of behaviors for which animals use their tails, as highlighted in the sections above, require them to extract sensory information from the surrounding environment, filter and sort through that information to determine the environmental relevance, and adapt its movements to reach a predetermined course. During locomotion, the behavior is quite complex because all of these steps have to be achieved while the animal is moving, thus the animal is constantly adjusting its motor output to changing visual, olfactory, auditory, and mechanosensory feedback (***Fig. 1***; Goulding 2009; Huston and Jayaraman 2011; Wyart and Knafo 2015; Koch et al. 2018).

The sensorimotor system lies in the ability to transform multiple sensory modalities into a locomotor movement (Schouenborg and Weng 1994; Levinsson et al. 1999; Nishikawa et al. 2007; Schouenborg 2008; Goulding 2009). Multisensory processing is essential to adapting to noisy sensory environments, enhances the robustness of the animal's motor output, and increases efficiency of sensorimotor tasks (Wyart and Knafo 2015). Studying multisensory integration with respect to the animal's tail can provide insight in how animals use this appendage to navigate and overcome obstacles in the real world. An example of multisensory processing through sensorimotor integration, with an essential role of the tail, is the startle escape response seen in fish, which is an integral behavior needed for the fish's survival (Hale et al. 2002). The precise timing and movements of a fish's body and tail into a c-shape, coupled with a tail flick, to generate a fast escape response after detection of a predator is driven directly by the sensorimotor system (Hale et al. 2002; Tytell and Lauder 2002; Faber et al. 2006; McHenry et al. 2009). This behavioral response consists of coordination of neural activity, rhythmic pattern generating networks, contraction of muscles, movement of the fish, and feedback networks to modulate the speed and direction of the movement. Yet, the contribution of the multisensory information and the neural circuits that regulate the behavioral output is still not completely understood (Hale et al. 2002; Nishikawa et al. 2007; Schuster 2012).

Although tail related motor tasks are key components of locomotion in many animals (e.g., Lauder 2000; Higham and Russell 2010; Freymiller et al. 2019), developing practical experimental models that require one to reproduce behaviorally relevant multisensory environments with consistent motor outputs is strenuous (Goulding 2009; Wyart and Knafo 2015). On the one hand, some of the reasons behind the lack of tail sensorimotor control studies are that tail morphology and tail-related behavioral repertoires exhibit variable and complex patterns of motor activity, which make practical considerations of tail-related experimental designs quite difficult to develop. On the other hand, the neural circuits that drive these tail movements have been less tractable due to the complexity of those circuits with highly variable patterns of activity and unreliable experimental tools to identify them. In addition, analyzing complex datasets with many levels of kinematic parameters per animal, including interactions between animals, raises an important technical challenge (Wyart and Knafo 2015; Mathis et al. 2018). One solution proposed in the field of neuromechanics is to use computational and physical models, such as bioinspired robotics (e.g., Jusufi et al. 2010; Libby et al. 2012; Patel et al. 2016; Zhu et al. 2019; Lin et al. 2021), to help predict some of the behavioral computations without observing the variability of non-linear motor outputs from the animal's tail. However, sensory integration and the neural circuits that underlie the movements of the tail are an essential component of sensorimotor studies, which cannot fully be explained by simplified computational and physical models.

Reflex-based tail movements are well suited for experimental analysis and can provide insights into how a moderately complex sensorimotor system can generate tail-based locomotion. At this scale, sensorimotor integration at the "high-level" cortical areas, normally associated with many complex networks of neuronal projections and interactions in the central nervous system, can be simplified to "low-level"

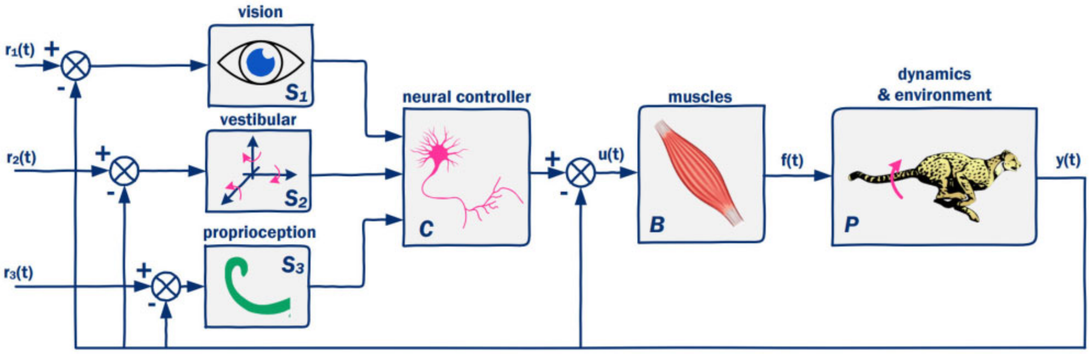

Fig. 1. Neuromechanics of tail responses in animal locomotion. Diagram encompassing underlying neuromechanical control. The tail behavior of a model animal (e.g., cheetah) expressed through a feedback control theoretic framework. The cheetah body interacts with the environment (P) for locomotion. Three outer control loops are proposed, the first is the visual processing of the cheetah chasing the prey (S1), the second is the vestibular processing of the cheetah trying to maintain its balance (S2) and the third is proprioceptive processing of the cheetah tail (S3) using muscle spindles. These parallel sensor mappings are processed by a neural controller (C) which then activates the tail musculature (B) to produce forces on the cheetah body. These muscles are also activated by high frequency mechanical feedback when interacting with the environment.

regions such as the spinal cord. Sherrington's pioneering studies have provided insights into the nature of such neural pathways, with illumination of the reflex arc and the control of reciprocal motor actions through inhibitory neural networks in vertebrates (Sherrington 1908; Brown and Sherrington 1912; Sherrington 1913). In addition to early studies from Eccles, Lundburg, Brown, and Jankowska (Brown and Sherrington 1912; Brown 1914; Lundberg 1979; Jankowska 2001), there has been increasing evidence to suggest that sensorimotor integration also occurs at the spinal cord (Grillner et al. 1991; Schouenborg et al. 1995; Mentel et al. 2006; Schouenborg 2008; Nakanishi and Whelan 2012; Hilde et al. 2016; Uemura et al. 2020; Picton et al. 2021), a region that has been originally hypothesized to contain intrinsic networks of neurons that generate rhythmic locomotor-like patterns of activity known as the central pattern generator (CPG) (Brown and Sherrington 1912; Brown 1914; Lundberg 1979; Jankowska 2001). Sensory inputs can modulate and shape the outputs of the CPG. However, whether the CPG is involved in driving tail movements needs further exploration. Studying sensorimotor control of tails, even at this reasonably low level, still requires one to select a behaviorally relevant multisensory environment that is tail-driven and can be reproducible consistently.

In practice, an important goal of neurobiologists is to understand how the nervous system is organized and functions to generate the locomotor movement (Hale et al. 2002; Nishikawa et al. 2007; Goulding 2009). Therefore, we propose some key questions to understanding the sensorimotor control of tails: (1) How do neural circuits that contain millions of neurons integrate multisensory information and flexibly contribute to specific motor patterns involved in tail-driven locomotion? (2) How are these ensembles of neurons organized and coordinated to interact with rhythm and pattern generating circuits to produce the overall motor output or behavior? (3) What is the neural computation of the circuit underlying tail-driven movements and how are these movements encoded? (4) What is the behavioral computation that includes both the active and passive mechanical properties of the movement? And (5) are these sensorimotor systems evolutionarily tuned to the locomotor mechanics and are they conserved across taxa?

Sensorimotor integration is highly dynamic where the animal is constantly responding to changes in the environment and updating its sensory inputs according to its behavioral output: for example, as a kangaroo rat detects a snake strike, vestibular and visual stimuli are constantly changing in the middle of an escape jump (Freymiller et al. 2019). Ideally, one would be able to capture every level of behavior with real-time monitoring of the sensorimotor integration as it occurs in the circuits, but practical considerations of such an experiment often make it challenging and difficult. In classical experimental settings, to probe these neuronal networks responsible for generating some of the behavioral output, the animal must often be restrained, paralyzed, or reduced to a "fictive" experimental preparation, often without sensory inputs (e.g., semi-intact, decerebrated, deafferented, and ablation), to allow recordings of active neurons—a combination of electrophysiology, pharmacological manipulation, and anatomical identification is often required

(Nishikawa et al. 2007; Goulding 2009; Wyart and Knafo 2015; Koch et al. 2018). Even in reduced animal preparations, these experimental designs are limited by difficulties in manipulating the neurons directly in the circuits, overcoming the large locomotor-driven activity of the CPG, and producing reproducible behaviors consistently. In recent years, the convergence of developmental genetics and physiological and behavioral systems approaches has expanded the possibilities of directly mapping behavioral sensorimotor computations onto specific neural circuits, targeting circuits of interests genetically, and monitoring the activity *in vivo* as the sensorimotor integration occurs (Goulding 2009; Wyart and Knafo 2015; Dobrott et al. 2019). As we move forward in the field, sophisticated genetic manipulations in powerful model systems such as mice and zebrafish have allowed for more precise characterization of the neural populations and its function in behavior. Tail sensorimotor control can essentially be dissected and pieced together using modern tools such as ontogenetics, chemogenetics, optogenetics, multi-array electrophysiology, and automated behavioral tracking systems that utilize deep learning artificial neural networks (Levine et al. 2014; Mathis et al. 2018; Dobrott et al. 2019; Lotfollahi et al. 2020).

Computational and physical models

In contrast to querying what animals are doing to implement use of the tail in a complex system, an alternative approach applies computational and physical modeling approaches. The advantage of these methods is that they permit simplification of the remainder of the system to a degree unachievable in biological systems, to identify governing principles driving tail function. In other words, they promote a template-based approach that permits progressive increases in complexity of the examined system toward the biological anchor (Full and Koditschek 1999). When combined with experimental robotics, this can provide a powerful framework for achieving valuable biological insight and facilitating discovery of novel physics principles (Flammang and Porter 2011; Aguilar et al. 2016) and a better understanding of sensorimotor control of tail movements (Fig. 1).

A classic example of a templates-anchor approach is that of the locomotor spring-mass model used for running gaits. The spring-mass model holds no clear representation to the multi-segmented, multi-material, highly complicated organism; but by virtue of its simplification to a mere mass mounted on a spring, it is capable of capturing a surprising sophistication of dynamic behaviors inherent to legged locomotor systems (e.g., Blickhan 1989; McMahon and Cheng 1990; Schmitt and Holmes 2000; Geyer et al. 2002). By gradually adding layers of complexity to this template, it then became possible to identify the roles of other subtleties critical to legged locomotion, that otherwise would have been impossible to isolate, such as leg retraction kinematics, hip torque, and stiffness modulation (e.g., Seyfarth et al. 2003; Daley and Biewener 2006; Spence et al. 2010; Shen and Seipel 2012). Like the spring-mass model, a tail template model of comparable simplicity could provide insight into basic physical principles guiding its function. For example, whereas a simple mass on a stiff or spring-tether may be sufficient to capture its dynamics for basic inertial function, imbuing greater sophistication via a distributed mass-spring model can reveal how subtle changes in position or curvature impact function. These, and increasingly more complex tail models, could then advance our understanding of tail mechanics and functional evolution.

Somewhat more sophisticated template-based models can be tested using physical models. For example, these physical models can be obtained using a combination of micro-CT scans and 3D printing, to derive shapes of varying levels of sophistication and with different stiffness and elasticity (Esposito et al. 2012; Porter et al. 2015; Flammang et al. 2017; Behm et al. 2018). In doing so, it becomes possible to isolate aspects of a tail's complex morphology and material properties and examine how each component contributes to the overall function of the entire structure. Likewise, it allows testing of biologically "impossible" shapes, to query why they might not exist. Porter et al. (2015) relied on this approach to discover why seahorse tails are square, and also why most other vertebrates have tails with a round cross-sectional geometry. Another important application of physical models is that they can be used to "revive" extinct species (e.g., McInroe et al. 2016; Johnson and Carter 2019; Ibrahim et al. 2020). Using extant species as a guide, it becomes possible to reconstruct aspects of an extinct animal's ecology and evolutionary history with a greater degree of specificity than previously possible.

Implementation of these models digitally in a computationally simulated environment provides additional insight on appendage–environmental interactions. Although this approach is already commonly used to quantify tail function during flight and swimming (Borazjani and Sotiropoulos 2008, 2009) using computational fluid dynamics models, it is much less frequently applied during explorations of terrestrial tail use. Implementation of finite element methods embedded within a discrete element model would permit simultaneous quantification of appendage force production and environment response—a topic that has been gaining increasing attention only during the last decade or so. Additionally, the digital realm provides an opportunity for rapid computational evolution of appendage morphology (Moore et al. 2013), and thus an ability to test a diverse range of shapes subjected to different kinematics and/or environmental parameters that would otherwise be extremely time-consuming if working exclusively with physical models. Ever-increasing computational power and availability of open-source modeling software (e.g., Large-scale Atomic/Molecular Massively Parallel Simulator [LAMMPS] and LAMMPS Improved for General Granular and Granular Heat Transfer Simulations [LIGGGHTS]; Plimpton 1995; Kloss et al. 2012) is making this approach ever more tractable.

The field of bioinspired and biomimetic robotics was born from the recognition of the incredible versatility, stability, and grace with which animals move through the world, and the subsequent desire to emulate their form and function in a wide variety of models and robots. Because of the broad range of tasks for which animals use their tails, researchers have focused on this appendage on several robotic platforms (e.g., Chang-Sui et al. 2011; Lauder et al. 2011; Zhang et al. 2016; Rosic et al. 2017; Saab et al. 2018; Liu and Ben-Tzvi 2021). Terrestrial bipedal and quadrupedal robots and vehicles have been equipped with tails for manipulation, climbing, maneuvering, and balance (Spenko et al. 2008; Chang-Sui et al. 2011; Rone and Ben-Tzvi 2015; Zhang et al. 2016; Flammang et al. 2017; Saab et al. 2018). And there has been increasing interest in design and development of aquatic robotics and vehicles that use fishlike, tail-propelled swimming (e.g., Triantafyllou and Triantafyllou 1995; Long et al. 2006; Lauder et al. 2011; Kopman et al. 2015; Rosic et al. 2017; Lin et al. 2021), motivated by a need for robots that are capable of prolonged, efficient swimming, and/or making difficult and smooth maneuvers. As a whole, experimental robotics is largely driven by task-based goals: using the addition of a physical tail to add greater functionality for manipulation or balance, or to allow the robot to make swifter turns or maneuver mid-air (Chang-Sui et al. 2011; Briggs et al. 2012; Libby et al. 2012; Rone and Ben-Tzvi 2014). The next-generation tail models should include more than rigid body dynamics alone, and instead integrate multi-joint flexibility and stiffness properties that afford animal tails their adaptability and 3D dexterity. An area of priority is the development of actuators that more closely model muscle mechanics. These actuators could then be tested in future tail models, reducing weight and increasing smoothness of motion. With these considerations in mind, the implementation of tail models using soft robotics could be another productive direction to pursue. Soft actuators allow for shape changes and bending actuation with potentially infinite degrees of freedom, thus facilitating modeling of prehensile tails, while soft sensors enable sensory feedback to provide insight on the neuromechanics of locomotion, such as the closed loop control of body caudal fin swimming of soft robotic fish (Lin et al. 2021), in addition to permitting measurement of curvature in conditions where videography is not feasible (e.g., nocturnal and low visibility medium).

In conjunction with bioinspired robotics is an emerging field of robophysics (Aguilar et al. 2016). A robophysical approach is highly complementary to experimental robotics, but instead of being driven by optimization of task-driven goals, it seeks to use instances of success and failure to reveal underlying principles of the interaction. A broad exploration of parameter space also permits the discovery of new locomotor strategies as well as novel physics principles that might otherwise be impossible to deduce when working with the full complexity of a system (e.g., Li et al. 2009; Marvi et al. 2014; Aguilar et al. 2016). Where robophysics is most powerful when dissecting contributions from multiple, complex sources is of interest. This includes understanding the role of the tail relative to the applied dynamics of other appendages on the body, or even adding in considerations of the complex, natural environment in which the animal is performing a behavior of interest, which may shift unexpectedly as the animal moves (e.g., Schwaner et al. 2021, this issue; Shield et al. 2021, this issue).

Conclusion

Tails are a common characteristic in animals but the diversity in development and repertoire of functional behaviors varies greatly across and within taxa. Depending on the species, the tail can have a singular or multi-functional purpose. In addition, tails exhibit a wide range of dexterity and morphological characteristics. The development, evolution, shape, and function of an appendage that seems otherwise relatively simple, such as a tail, has led researchers, scientists, and engineers to a proliferation of bio-inspired designs of dynamic robotic devices that use tails for an even wider range of tasks. Yet, there are many questions to be answered to understand the evolution, development, sensorimotor capabilities, morphology, ecology, and functions of tails across the phylogenetic tree and applications in bioinspired designs.

Expanding our knowledge of tails has important implications and has the potential to answer many long-standing questions. For example, understanding the morphology and genetic foundation of post-anal appendages can elucidate the evolutionary origin(s) and functions of tails, and opens opportunities to begin to grasp concepts like secondary loss, as seen in humans. In addition, understanding the relationship between the form and function of the tail, we can make informed predictions of tail function based on their appearance, with implications for studies of both extant and extinct species. Kinematics, sensorimotor, and morphological tail characteristics can also be used to further develop computational models and bioinspired robotics. Lastly, comparison of next generation tail models with vertebral column models may have important medical implications for treatments for human vertebral dysfunction (e.g., Ishihara 1996; Handa et al. 1997; Iatridis et al. 1999; Demers et al. 2004; Han et al. 2008).

Tail research crosses many disciplines, and here we presented just a focused review of some of them. We discussed the current state and future directions for tail-related research in five key topic areas. Although they were presented as distinct categories, these topics are inherently interrelated. For example, the post-anal tail is a phylum-defining component of the chordate bauplan, and similar genetic pathways are found to be important for both tail development and regeneration (Martin and Kimelman 2008; Vitulo et al. 2016). Tail regeneration—or lack thereof—has important consequences for sensorimotor control strategies and functional morphology, which in turn inform experimental robotics and robophysics inquiry. Examining tail function using a combination of these approaches, as well as computational and physical modeling, will provide deep insight into the evolutionary pathways and functional importance of tails to the locomotor system and beyond. As a result, a re-integration of biological disciplines is critical to the progress of multiple fields. This can be facilitated by future symposia, workshops, and seminars, focused on advancements of tail and tail-related research. Such interactions among tail researchers can serve as a foundation for cross-disciplinary research collaborations to shed light on the form, function, EvoDevo, and technical applications of animal tails.

Authors' contribution

S.T.H., C.P.M., and M.J.S.: initial manuscript ideas. S.T.H., C.P.M., M.J.S., S.B., C.B.C., C.E.C., C.M.D., F.E.F., O.E.F., B.E.F., B.E.J., A.J., P.J.M., A.P., B.J.S., and M.V.: conceptualizing ideas. S.T.H., C.P.M., M.J.S., I.B., S.B., C.B.C., C.E.C., C.M.D., F.E.F., O.E.F., B.E.F., B.E.J., A.J., P.J.M., A.P., B.J.S., and M.V.: first manuscript draft (I.B., O.E.F., and B.J.S.: evolution and development. S.B., C.B.C., C.E.C., and M.V.: regeneration. C.M.D., F.E.F., and B.E.J.: functional morphology. B.E.F., A.J., P.J.M., and A.P.: sensorimotor control. S.T.H., C.P.M., and M.J.S.: computational and physical modeling). S.T.H., C.P.M., M.J.S., I.B., S.B., C.B.C., C.E.C., C.M.D., F.E.F., O.E.F., B.E.F., B.E.J., A.J., P.J.M., A.P., B.J.S., and M.V.: editing manuscript. S.T.H., C.P.M., and M.J.S.: final edits.

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Conflict of interest

Authors declare no conflict of interest.

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