





SYMPOSIUM

Moving in an Uncertain World: Robust and Adaptive Control of Locomotion from Organisms to Machine Intelligence

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Synopsis Whether walking, running, slithering, or flying, organisms display a remarkable ability to move through complex and uncertain environments. In particular, animals have evolved to cope with a host of uncertainties—both of internal and external origin—to maintain adequate performance in an ever-changing world. In this review, we present mathematical methods in engineering to highlight emerging principles of robust and adaptive control of organismal locomotion. Specifically, by drawing on the mathematical framework of control theory, we decompose the robust and adaptive hierarchical structure of locomotor control. We show how this decomposition along the robust–adaptive axis provides testable hypotheses to classify behavioral outcomes to perturbations. With a focus on studies in non-human animals, we contextualize recent findings along the robust–adaptive axis by emphasizing two broad classes of behaviors: (1) compensation to appendage loss and (2) image stabilization and fixation. Next, we attempt to map robust and adaptive control of locomotion across some animal groups and existing bio-inspired robots. Finally, we highlight exciting future directions and interdisciplinary collaborations that are needed to unravel principles of robust and adaptive locomotion.

Introduction

Locomotion is the crucial enabler of multiple life-history processes in many groups of animals that move across air, water, and land. Animals move to reproduce, feed, escape predation, and sustain many other processes. Without the evolution of movement and its associated control, life on Earth as we know it would look strikingly different. Yet it is humbling how poorly we understand motor control and locomotion. One might look at artificial intelligence (AI) as an analogy that has triumphed over the top human Go and chess players (Schrittwieser et al. 2020)—yet current robots cannot walk to the board or pick up a piece as dexterously as a toddler. Although it has been argued that machines are getting close to passing the Turing test, they do

so by taking advantage of our innate social ability to “infer” intelligence (Sejnowski 2023; Zador et al. 2023), and these intelligences still fail to usefully extrapolate to an uncertain future (Silva et al. 2023). So, while machine intelligence may appear to mimic many human-level aspects of cognition and reasoning, it is also intuitively obvious that, despite requiring TWh of energy (International Energy Agency) and petabytes of data (Kumar 2017), current approaches to AI reveal little if any insight into the natural intelligence that they superficially mimic and, as such, may provide little insight into movement and its control—other than its immediate use in parsing large datasets and enabling tracking of complex movement (e.g., Mathis et al. 2018). Indeed, applying bio-inspired artificial neural networks to

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Table 1 Glossary of key terms. We make a distinction for terms with different definition in engineering (e) and biology (b).

Term	Definition
adaptive (b)	A heritable trait that improves a specific function relevant for a given environment, therefore increasing the survival and reproduction of organisms of a given species.
adaptive (e)	A system, such as a control system, which can update itself “on the fly,” e.g., by changing parameters, to compensate for changes in (or <i>a priori</i> unknown) system dynamics such as changes in weight.
block diagram	Formal visualization of a dynamical system constructed by connecting subsystems (blocks) via signals (arrows).
closed-loop	Property of a system with <i>feedback</i> , often used in engineering to maintain a desired output (e.g., cruise control system).
control autonomy	Property of a hierarchical control system where lower level layers can generate outputs (e.g., behavior) without inputs from higher levels, and thus can operate autonomously or semi-autonomously (Merel et al. 2019).
delay (b)	Usually related to latency, or the transmission delay for neural spikes to travel along axons, or a synapse to transmit information to a postsynaptic cell (More and Donelan 2018).
delay (e)	Refers to a physical delay in transmission, which causes a pure phase lag.
linear time invariant (LTI)	Property of a system which obeys scaling and superposition (linearity) and for which the dynamics do not change with time (time-invariance). No such system exists, but many systems (including biological ones) can be well approximated as LTI over biologically relevant regimes.
mechanical feedback	Sensor-less feedback through environment-body interactions which can rapidly stabilize locomotion.
phase lag	Difference in phase between input and output, which can be caused by a time delay, integration, inertia, etc. Note: time delay causes phase lag, but not all phase lag is caused by delay.
robust (e)	A control system designed to maintain adequate performance despite (typically bounded) uncertainty and variation in parameters.

understand biological neural networks runs the risk of being circular. Thus, to achieve the grand challenge of passing an “embodied Turing test” (Zador et al. 2023), we should aspire toward a synthetic view of embodied intelligence (Koditschek 2021), perhaps beginning at least in part with a systematic understanding of the rules and mechanisms that underlie the physical, embodied intelligence of animals (Chiel et al. 2009; Wang et al. 2023).

Unraveling motor control remains a grand challenge in biology. As the brain functions within the body, one challenge is that the nervous system and the body

are dynamically coupled (Dickinson et al. 2000). This means that studying the nervous system or body mechanics in isolation is often not sufficient: we must be able to capture their interactions. Given that these two systems are complex on their own, studying their interactions requires theoretical frameworks that model these interactions and provide testable hypotheses. Second, movement is closed-loop (Cowan et al. 2014; Roth et al. 2014): every action generates sensory feedback that acts locally or at the level of the central nervous system. Sensory feedback is partially what makes motor control in animals robust, therefore closed-loop sensory feedback must be included in a mathematical framework of motor control (Madhav and Cowan 2020). Third, movement is flexible and adaptable. Animals can learn new movements and adapt to environmental uncertainties. Thus, the capacity for learning must be incorporated into models of motor control. Fourth, motor control is constrained by delays. Transmission speed, which is constrained by nerve conduction delays, is only one of many constraints on the total sensorimotor delay: sensory transduction, synaptic, motor nerve, neuromuscular junction, electromechanical, and force generation delays must also be considered (More and Donelan 2018). Fifth, movement is constrained by physics, meaning that it conforms to Newton’s laws (Cowan and Fortune 2007; Madhav and Cowan 2020; Tytell et al. 2011). For instance, in larger animals, inertia creates “delay-like” phase lag, owing to Newton’s laws. In contrast, smaller animals must contend with relatively high friction forces to move their appendages (Dickinson et al. 2000). Further, muscles act on joints that have hard constraints in their axes of rotation (or translation), thus limiting the range of motion. Thus, musculoskeletal constraints must be incorporated to understand how movement is generated and controlled. Lastly, motor control is organized hierarchically (Full and Koditschek 1999; Holmes et al. 2006; Merel et al. 2019). At the bottom are low-level reflexes that act rapidly and semi-autonomously. At the top are slower but more flexible task-level controllers that drive goal-directed behavior. Collectively, these six challenges make the motor control problem extremely hard to solve.

Fortunately, control theory, a branch of applied mathematics, can serve as a valuable theoretical framework to unravel these challenging problems (Madhav and Cowan 2020). It provides a mathematical “toolkit”—visualized through block diagrams—that models the complex interactions between sensing, control, actuation, delays, and feedback pathways (see Table 1 for a glossary of key terms used throughout). Further, it can make experimental predictions through mathematical manipulation of control topologies (e.g., opening or

closing sensory feedback loops by tethering an animal) (Roth et al. 2014). Of particular relevance to this review is the analogy of robust and adaptive control, two established branches of control theory (Åström and Murray 2010). A robust control system is one that can maintain performance typically in the presence of known uncertainty and variations in system parameters. Robust systems do not update in real-time (e.g., their controller gains are fixed). As such, they do not deal well with large or unexpected uncertainty. They are designed with stability and performance margins to handle expected uncertainty, e.g., inaccuracies in sensor or actuator mathematical models that are not exact representations of the real world. In contrast, an adaptive control system can maintain performance in the presence of uncertainty by tuning control parameters in real-time.

A defining feature is that an adaptive control system continuously updates controller parameters as the dynamics change (Åström and Wittenmark 2008). Through gain scheduling, an adaptive control system can compensate for changes in process dynamics by adjusting the gain of the controller (as a mathematical function or lookup table), e.g., airplanes change autopilot control parameters as mass decreases due to fuel consumption. Alternatively, model reference adaptive controllers learn from the system's behavior by reading the error between the output of the actual system and a reference model (analogous to an internal model in motor control) (Narendra and Annaswamy 2012). Of course, robustness and adaptation need not be mutually exclusive, but collectively they can serve as useful analogies to unravel principles of locomotion in animals. It can also inform the development of bio-inspired fault-tolerant strategies, integrating intelligent control and robust mechanical design.

In practice, engineering systems are often designed to be both robust and adaptive, providing flexibility while ensuring stability. As uncertainties abound in nature, locomoting organisms similarly can benefit by being both robust and adaptive to maintain adequate performance in an ever-changing world. Robustness and adaptive control arise from both physical (i.e., body design) and computational (i.e., neural network) intelligence, and can be organized hierarchically based on flexibility/complexity and response speed (Fig. 1A).

At the lowest level is sensorless mechanical feedback (Full et al. 2002; Holmes et al. 2006), which can confer stability through physical environment-body interactions [e.g., flapping counter-torque in flight (Hedrick et al. 2009), mutually opposing forces (Sefati et al. 2013; Uyanik et al. 2020), or leg impedance when running on the ground (Holmes et al. 2006)]. A defining feature is that this type of feedback is purely mechanical and therefore neurally open-loop. While such mechan-

ical feedback is a critical component of the locomotion system, it is limited in what it can achieve. For example, in the simplified setting depicted in Fig. 1A, deviations from the reference (flying straight) will inevitably accumulate unless the mechanical system works alongside neural feedback loops that can sense these deviations and make corrections. Thus, at an intermediate level, robust, *goal-directed* locomotion can be achieved by well-tuned sensory feedback and smart mechanical design. In this case, sensory feedback of multiple origins is integrated to maintain a reference state (e.g., flying straight by maintaining visual equilibrium) in the face of perturbations. At the highest level of neural organization, adaptive locomotion requires online learning, such as through an internal model (Fig. 1A).

Teasing out the relative contributions of feedback in this hierarchy—mechanical feedback, neural control, and learning—is of great relevance to understanding the flexibility of animal locomotion. However, this is challenging as these distinct strategies are layered and coupled in organisms. Fortunately, their individual contribution can be revealed by comparing task-level compensatory response speed and temporal features during perturbation recovery periods (Fig. 1B). Considering the case of sudden appendage damage (such as leg, wing, or fin loss), for a robust control system we would expect a near-instantaneous response mediated by passive mechanics and reflexive feedback. Specifically, passive mechanics would provide the fastest response (limited by physics), whereas local and more central reflexive feedback could act on the order of milliseconds (e.g., proprioceptive) or tens of milliseconds (visual, electrosense, or audition). As controller gains are fixed, this system may not recover optimal performance especially if appendage loss is significant. For an adaptive control system, we would expect a time-dependent recovery of performance through error-based learning (Van der Kooij et al. 2018; Krakauer et al. 2019; Shadmehr et al. 2010; Tseng et al. 2007). Canonically, task performance may improve exponentially over time as an animal calibrates motor output based on sensory prediction error (Fig. 1B). A defining feature of error-based learning is the presence of after-effects (Yang et al. 2021). Finally, an animal may learn a new controller entirely through *de novo* or reinforcement learning (Fig. 1B) (Krakauer et al. 2019; Sternad 2018; Telgen et al. 2014; Yang et al. 2021). This strategy is thought to be much slower than error-based learning as an animal may try out different limb movement strategies during a learning epoch to achieve acceptable task-level performance. Furthermore, this strategy may result in inefficient locomotor states during state exploration as animals may try out limb-coordinating strategies that

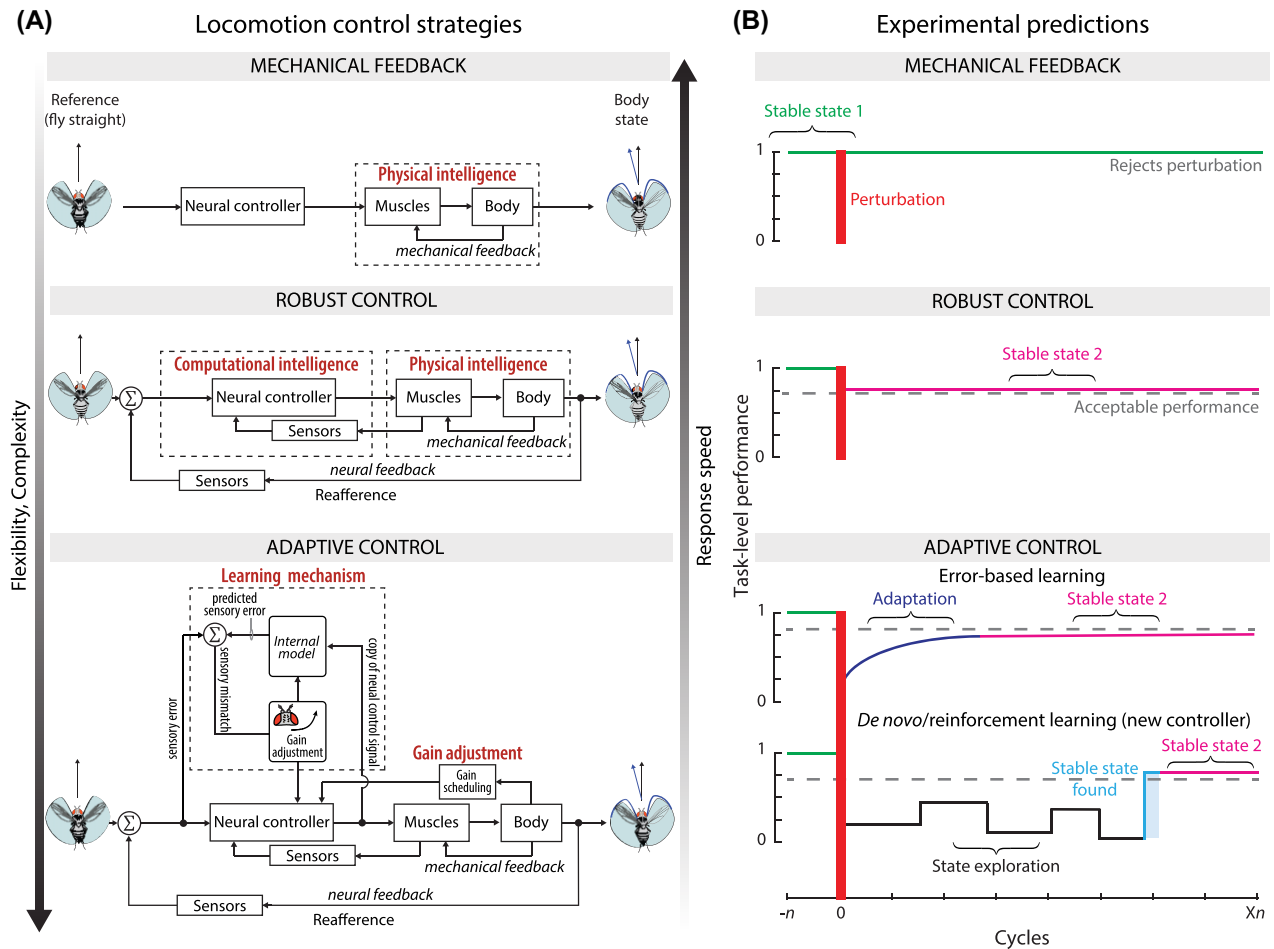


Fig. 1 (A) Hierarchy of locomotion control strategies using analogies from robust and adaptive control theory. Control strategies are classified according to flexibility, complexity, and response speed. (B) Time-domain signatures of mechanical feedback, robust, and adaptive compensation strategies. Following a perturbation (red line; e.g., appendage damage), an animal may recover via distinct control strategies that have distinct evolution in time. Such signatures can help identify feedback mechanisms of animal locomotion.

are ineffective. However, this strategy provides the most flexibility. Collectively, robust and adaptive control theory provide testable hypotheses to study animal locomotion.

In this review, we focus on emerging principles of robust and adaptive control of locomotion. To illustrate this, we organize this review into two broad and distinct (but far from exhaustive) classes of paradigms that can reveal principles of robust and adaptive locomotion: (1) compensation to appendage injury or loss (leg and wing) and (2) image stabilization and fixation. Internal perturbations such as appendage injury are particularly well suited to reveal where organisms are situated along the robust–adaptive axis because they are persistent perturbations that often destabilize locomotion. Further, visually active animals rely on image stabilization and fixation to stabilize a scene and identify features, respectively. Because these processes are thought to operate hierarchically and map to different motor

programs (Cellini and Mongeau 2020; Hardcastle and Krapp 2016)—with image stabilization at a low level and fixation at a higher level—studying their interactions using virtual or augmented reality paradigms can reveal how robust and adaptive control emerges from a putative hierarchy in the nervous system. We emphasize recent mechanistic descriptions of locomotion that employ mathematical frameworks combined with behavioral, physiological, mechanical, and/or robophysical data. We specifically focus our review on recent findings in non-human animals (vertebrates and invertebrates), which may provide compact and computationally efficient ways to control locomotion [advances in motor learning in primates and humans have been reviewed previously (e.g., Krakauer et al. 2019)]. In addition, small animals can benefit from their relatively small kinetic energy to assist in mechanically mediated control without severe injury, providing unique opportunities when moving in complex environments

(Jayaram et al. 2018b). Furthermore, small animals have to deal with unique challenges/opportunities as they may operate in a regime where gravitational, inertial, elastic, and viscous damping forces are important (Dickinson et al. 2000; Sutton et al. 2023). Finally, we conclude by highlighting exciting future directions and interdisciplinary collaborations that are needed to identify principles of motor control in biology.

Compensation to appendage injury

Animals often have to cope with injury to appendages (legs, fins, or wings) which impairs mobility and have dire consequences for survival and fitness. Appendage imperfections could result from birth defects (Angelini and Kaufman 2005), illness or disease (Hackney and Cherbas 2014), damage from repeated use (Parle et al. 2017), injury during prey capture (Rovner 1980), predator evasion (Edwards and Reddy 1986) fights for a mate (Emberts et al. 2019), regeneration limitations (Tanaka et al. 1992), or autotomy (Bateman and Fleming 2009; Maginnis 2006). It is estimated that voluntary autotomy as an effective defensive strategy has evolved at least nine times in the evolutionary history of the animal kingdom (Emberts et al. 2019). Consequently, the levels of appendage loss are high in animals. For instance, the incidence of bodily injury and the proportion of species able to perform autotomy are frequently above 50% in phyla such as Echinodermata and Arthropoda (Jobson et al. 2024). In the arachnid order of Opiliones, more than half of individuals (51%) across 19 species are found missing legs (Escalante and O'Brien 2024), and in one species of crickets (*Gryllus bimaculatus*) 40% of individuals are missing at least one whole appendage (Fleming and Bateman 2007). Therefore, for some animals, injury and appendage loss are prevailing. Consequently, we expect that locomoting organisms have evolved a suite of mechanisms to be robust and adaptive to such a change and maintain contextually appropriate behavior. Therefore, studying injury compensation can reveal the extent and the timescales for such control strategies.

Compensation to leg injury in invertebrates

A rich body of literature spanning the last five decades illustrates that sensorless mechanical feedback (Fig. 1A; lowest complexity, fastest response) generated through complex body/limb-environment interactions results in rapid, tuned viscoelastic responses capable of rejecting external perturbations (Full and Koditschek 1999; Holmes et al. 2006) enabling animals to run on a variety of complex surfaces. These studies have spurred

the development of bio-inspired robots with carefully tuned mechanics (e.g., Raibert 1986) and continue to be driven by recent innovations in multiscale fabrication such as tunable metamaterials (McClintock et al. 2021; McCracken et al. 2020).

As appendages are the primary means of interfacing with the environment, it would be natural to hypothesize that their sudden loss should detrimentally affect performance and therefore, appendage loss offers an ideal paradigm for understanding the hierarchy of motor control. However, observations that not all of an arthropod's legs are used equally for locomotor tasks accompanied by their frequent loss in natural habitats (Fleming and Bateman 2007) have led some to propose a spare leg hypothesis (Guffey 1998, 1999), which considers legs as redundant modules suggesting a robust framework for control of locomotion. While locomotion following leg loss has been studied in several arthropods, including centipedes (Minelli et al. 2000), crabs (Brown et al. 2018), spiders (Wilshin et al. 2018), scorpions (Bowerman 1975), stick insects (Bässler et al. 2007; Schmitz et al. 2015), etc., in this section, we describe recent progress in two specific organisms, cockroaches and Opiliones (known as harvestmen), where a more comprehensive understanding of their kinematics, energetics, and neuromechanics provides evidence of largely robust control of locomotion (Fig. 1A; intermediate speed, flexibility, and complexity) using both physical and computational intelligence.

Cockroaches are known for their high-speed performance running on level ground (Full and Tu 1991), locomoting across rough surfaces (Sponberg and Full 2008), climbing up vertical terrains (Goldman et al. 2006), squeezing through tight gaps (Jayaram and Full 2016), and performing rapid maneuvers to disappear under ledges (Mongeau et al. 2012) or transition onto walls (Jayaram et al. 2018b). During these rapid behaviors (typically induced by an escape response), studies have shown that *Blaberus discoidalis* do not seem to significantly change their speed, kinematics, or leg patterns (alternating tripod) despite the loss of one or two middle legs (Jayaram 2015) hinting at a robust control system. However, with the loss of both middle legs, a significant increase in roll oscillations was observed accompanied by a significant decrease in lateral ground reaction forces hinting at the potential loss of locomotion stability. Additionally, despite limited changes in kinematics, differences in energetic costs were associated with losing different pairs of legs, suggesting that their legs are not redundant (Saintings 2022). Similarly, reductions in endurance were recorded after middle and hind leg loss, but not after front leg loss. With increased leg loss resulting in a three- (a single tripod) or two-legged (two middle legs only) configurations,

running speed decreased but was still impressively over 50% of its intact condition indicating a loss of performance associated with robust control (Fig. 1B). However, at slower locomotion speeds (such as during walking), several wave gaits have been observed (Delcomyn 1971), but cockroaches usually rely on an alternating tripod gait at higher running speeds. The earliest studies on single-leg amputation during walking demonstrated marked changes in posture and rhythm of movement (Hughes 1952, 1957; Wilson 1966). These changes were often immediate so that the role of a missing leg was taken over by the remaining legs on the side of the lost leg. When one leg on each side was amputated, variable gait patterns were observed (Wilson 1966).

Similarly, *Prionostemma* sp.1 and *Nelima paessleri*, two slow-moving species of Opiliones, exhibit decreasing speed and endurance and increasing oxygen consumption with increasing loss of legs (one to three) immediately after ablation (Escalante et al. 2020, 2021). Notwithstanding these decreases in performance, Opiliones with two missing legs (six remaining legs) successfully locomote, demonstrating compensatory mechanisms such as a change of gait coordination. These changes in coordination post-ablation resemble an alternating tripod gait, suggesting an emphasis toward recovering stability, as described in spiders (Wilshin et al. 2018) and crabs (Pfeiffenberger and Hsieh 2021). Interestingly, with the unilateral loss of the second (sensory) or third legs, performance recovery approaching that of intact organisms was observed about 24 h post-ablation hinting at adaptive control mechanisms (Escalante et al. 2020). Despite the high prevalence of leg loss in multiple species of Opiliones (Escalante and O'Brien 2024), these arachnids have not shown negative fitness consequences of this defensive strategy. With field and lab experiments, researchers have found no effect of leg loss on two independent fitness components. As for survival, in Opiliones of *Prionostemma* sp. 5, the likelihood of being recaptured over several weeks—a proxy for survival—did not differ between intact and ablated individuals (Escalante and Elias 2021). In another arachnid, *Pardosa valens* wolf spiders, individuals missing one leg showed lower survival than intact eight-legged ones (Brown et al. 2018). Additionally, spiders experimentally induced to lose one leg paired with a predator in the lab showed lower survival rates than intact individuals. As for reproduction, the mating success of *Prionostemma* sp. 5 male Opiliones that had lost legs was similar to intact males (Escalante and Elias 2022). These findings suggest that leg loss has a minimal effect on fitness.

Neural plasticity (and more broadly, computational intelligence mechanisms) can aid in the recovery of lo-

comotor performance after leg loss. Studies in cockroaches have revealed that locomotion performance similar to pre-ablation can be realized by manipulating the thoracic ganglia (Noah et al. 2004), highlighting the contribution of local sensory feedback to the coordination of leg movement after leg loss (Delcomyn 1988). Additionally, amputation can affect both the frequency and timing of motor bursts during leg stepping cycles in the remaining stump of the amputated leg and its neighbors (Delcomyn 1991a, b). However, these effects are reduced at faster speeds resulting in movement more similar to that of walking in intact animals (Berendes et al. 2016; Delcomyn 1971). Exploration of the effects of leg loss on the neural anatomy of arachnids (Barth 2002, 2021) have informed the neurophysiological effects of this behavior. Recent advances have described the anatomy of brain regions of the central nervous system in arachnids and correlated changes in ganglia structure over ontogenetic processes (Steinhoff et al. 2018, 2020, 2023). For instance, in the ogre-faced spider *Deinopis spinosa*, ganglia associated with visual input (the mushroom bodies and optic nerves) decrease in volume when juvenile males molt to adulthood (Stafstrom et al. 2017). These changes correlate with a reduction in the size of the anterior median eyes and a decrease in foraging activity as these males mature. In *Marpissa muscosa* jumping spiders, differential enrichment during growth affects the volume of higher-order brain centers (Steinhoff et al. 2018). This was found in the arcuate body, a brain center involved in locomotor control, but not in the mushroom body, which is involved in learning and memory. Additionally, the histological processes associated with tissue regeneration after autotomy have been explored in echinoderms. In the sea star *Coscinasterias muricata*, the radial nerve cord exhibits rapid reorganization (Byrne 2020; Byrne et al. 2019), as the recently regenerated arm needs to be innervated and fully functional. Altogether, these findings suggest the presence of outstanding neural plasticity in invertebrate groups that experience voluntary bodily damage. Future work can then shed light on the role of centralized versus decentralized control when animals undergo voluntary limb loss.

In summary, recent work has provided critical insights into how animals deal with the potential negative consequences of bodily damage. While studies have focused on decrements in fitness in crabs (Brueseke et al. 2001) and spiders (Brown et al. 2018) after ablation, few have examined the effect on the dynamics of locomotion (Blickhan et al. 2013; Carrier et al. 2001), suggesting this as an area for future work. Similarly, while several investigations have detailed changes to inter-leg coordination (Cruse 1976; Schilling et al. 2013) and underlying neural modulation mechanisms (Bidaye et al.

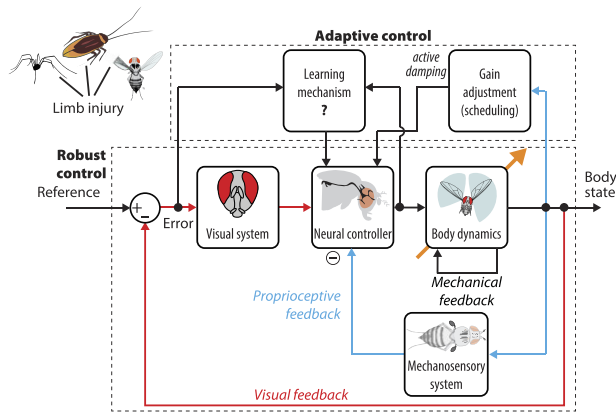


Fig. 2 Proposed control diagram for compensation to appendage injury in invertebrate locomotion. Robust control arises from the integration of neural and mechanical feedback. In the case of a fly with wing damage (orange arrow), nested visual and proprioceptive feedback could correct for changes in retinal image and body velocity, respectively, as a result of a torque imbalance between the left and right wing. Through a mechanism analogous to gain scheduling in adaptive control, flies actively increase damping to maintain stability following wing damage (Salem et al. 2022). Diagram adapted from Salem et al. (2022) and (2023).

2018; Ritzmann and Büschges 2007) during slow walking in amputated organisms such as in stick insects (Graham 1977), crickets (Shimizu and Masaki 1993), scorpions (Bowerman 1975), and tarantulas (Gorb et al. 2006), we found no strong evidence of error-based motor learning during legged locomotion. Instead, compensatory behaviors that include recovery after ablation appear mainly driven by hierarchical mechanosensory reflex loops and thus appear largely robust (Fig. 2) (Dallmann et al. 2023; Tuthill and Wilson 2016). Additional work is required to explore evidence for reinforcement learning in invertebrates, as they have proven to be effective compensatory strategies in robots (Cully et al. 2015).

Compensatory mechanisms to wing damage in flying insects

The response of flying insects to wing damage can provide fundamental insights into robust and adaptive flight control mechanisms as changes in aerodynamic surface translate to the alteration of forces and moments about the center of mass. Wing damage can arise from wear or predation and directly influences mortality, thereby insects have likely evolved a host of control mechanisms to maintain fitness (Rajabi et al. 2017). Importantly, insects, unlike birds and bats (Hedenström 2023), cannot repair wing damage and therefore require neuromechanical control strategies. In the case of bilateral wing damage, where the extent of damage of the left

and right wing is identical, insects can compensate for the loss in lift by increasing wingbeat amplitude, flapping frequency, and/or the rotation (pitch) angle of both wings symmetrically (Combes et al. 2010; Fernandez et al. 2012).

However, when a single wing is damaged, the situation is more challenging as asymmetrical aerodynamic forces can rapidly destabilize the body. In a magnetic tether system allowing free rotation about yaw, *Drosophila* compensate for unilateral damage, thus keeping them from spinning (Bender and Dickinson 2006), but it remained unclear how flies adjust 3D wing kinematics on a stroke-by-stroke basis. More recent work showed that unilateral wing damage causes freely flying flies to increase their overall wingbeat frequency, which appears sufficient for weight support but creates a net roll torque (Muijres et al. 2017). To compensate for this perturbation, flies increase the stroke angle amplitude (and therefore velocity) of the damaged wing. To further compensate for roll torque, flies advance wing rotation for the damaged wing, delay rotation of the intact wing, and generate more upward drag on the damaged wing at the start of the upstroke, further reducing roll torque. These adjustments in intact and damaged wings result in net sideways forces, which flies appear to compensate for by rolling their body toward the damaged wing (Muijres et al. 2017). Using a dynamically scaled robot model showed that adjustments of three kinematic parameters (stroke amplitude of both wings and wingbeat frequency) could be sufficient to compensate for wing damage and inspire control strategies for flapping-wing robots. Collectively, this study showed that flies compensate for unilateral wing damage through adjustments in both wing and body kinematics.

Using a control theoretic framework, a recent study showed that gaze stabilization performance in flies was modestly influenced by unilateral wing area loss of up to 60% (Salem et al. 2022). By combining an aeromechanical model, an insect-inspired resonant system, and animal experiments, the authors showed that both visual feedback and passive mechanics appear to modulate wing stroke angle and wingbeat frequency. Further, they identified a shift in abdomen position driven by a mechanosensory-based reflex loop between the wings and abdomen, which may serve to balance aerodynamic forces. Finally, using control theory, they demonstrated that flies actively increase damping in response to unilateral wing damage, which in turn enables injured flies to be as stable as intact-wing flies, i.e., similar closed-loop pole locations (Salem et al. 2022). Collectively, these studies suggest that flies are robust to wing damage, which emerges from passive mechanics and reflexive feedback. An increase in damping (active damp-

ing) may arise from a change in proprioceptive feedback gain (e.g., halteres) (Cellini and Mongeau 2022; Elzinga et al. 2012; Fuller et al. 2014; Rimnicanu et al. 2023; Salem et al. 2023) through a process perhaps akin to gain scheduling in adaptive control, whereby the proprioceptive (haltere) gain is modulated for distinct "operating points" (e.g. distinct wing damage levels or forward flight speed) (Elzinga et al. 2014, Salem et al., 2023). However to our knowledge the exact physiological mechanism remains elusive.

In the hawk moth *Manduca sexta*, asymmetrical wing damage causes an increase in the wingbeat amplitude of the damaged wing, which appears sufficient to restore symmetry in lift production (Fernandez et al. 2012). Interestingly, in moths, the increase in wingbeat frequency as a result of wing damage may arise passively from neuro-mechanical coupling with the thorax below 12% asymmetry in the wing second moment of area (Fernandez et al. 2012). For damage over 12%, moths appear to require active neural control. Interestingly, flower tracking performance in hawkmoths is not compromised by wing damage (Kihlström et al. 2021). Thus moths appear to be mechanically robust to small wing damage, but higher damage likely relies on sensory feedback that modulates neural control.

Taken together, studies in flies and hawk moths suggest that flying insects are robust and adaptive to wing damage, relying on passive mechanics, neural feedback and gain modulation (Fig. 2). Flying insects can compensate for wing damage by implementing distinct strategies, which may differ across taxa due to different body mass, wing-thorax mechanics, flight mode (asynchronous versus synchronous muscle-thorax drive), etc. Despite these advances, the strategies that flying insects implement for compensatory control remain poorly understood. For example, do insects adapt to changes in wing surface over time on a stroke-by-stroke basis, or is compensation mostly reflexive and facilitated by passive mechanics? What is the interplay between passive mechanics and active neural control? Answers to these questions could provide unique insights into how robustness arises from the hierarchical control organization of animals.

Image stabilization and fixation

To perform complex visuomotor tasks such as chasing prey, locomoting animals must stabilize images of the world onto their retina. Image stabilization is facilitated by optokinetic and vestibulo-ocular reflexes. Visually guided tasks such as driving a joystick have been the subject of many studies in the human motor control literature (reviewed in Krakauer et al. 2019), and these

tasks appear to exhibit considerable plasticity through error-based learning. Error-based learning is primarily driven by cerebellar computations that compare predictive and feedback signals. Such predictions can also help to compensate for sensorimotor delays (More and Donelan 2018). While there is substantial evidence for motor learning in vertebrates, it remains unclear to what extent animals without a cerebellum (e.g., arthropods) can do error-based motor learning. Here, we review image stabilization and fixation behavior in non-human animals, from insects to fish during visually guided locomotion.

Image stabilization and fixation in flies

Among flying insects, flies use a suite of reflexes to keep their gaze stable and level during flight. The optokinetic reflex, a.k.a. the optomotor response, has been studied extensively in insects. Classic work from the 1950s showed that a rotating drum elicits a co-directional turning response of a tethered beetle (Hassenstein and Reichardt 1956). These studies formed the basis of the highly influential Elementary Motion Detector model of vision, which provides a simple phenomenological model for directionally selective motion detection across an array of photoreceptors (Hassenstein and Reichardt 1956) and has provided testable hypotheses to probe motion vision computations in the brain (Borst and Groschner 2023). Subsequent work showed that flies *Musca domestica* could discriminate and fixate a "stripe" (a small-field visual feature) (Reichardt 1973). Classically, image stabilization and fixation in flies have been treated as distinct control systems, containing position- and velocity-dependent terms (Reichardt and Poggio 1976). More recent behavioral and physiological evidence supports the notion that the optomotor response and fixation response are parallel control systems that map onto different motor programs (Aptekar et al. 2012; Frighetto and Frye 2023; Mongeau and Frye 2017; Salem et al. 2020). In terms of control hierarchy, it has been suggested that the optomotor response sits at a lower level than goal-directed object fixation (Hardcastle and Krapp 2016). Within this framework, the optomotor response is an inner-loop stabilization reflex (and a prerequisite for a stable image), whereas stripe fixation is an outer-loop, goal-directed behavior. This distinction suggests that optomotor reflex is autonomous and that it must be modified by outer-loop goal-directed behavior to prevent maladaptive optomotor responses.

Over the last few decades, several groups have provided some evidence that flying insects have the ability to learn and adapt during visuomotor tasks. Work by Reichardt in the 1970s showed that *Musca domes-*

tica flies could fixate a stripe with a variety of different coupling gains, demonstrating the robustness of the fly feedback system (Reichardt 1973). Subsequent work by Wolf and Heisenberg suggested that *Drosophila* could learn to fixate a vertical stripe with a positive feedback gain in closed-loop virtual reality (i.e., when the fly turns clockwise the stimulus also turns clockwise), a feat that requires about 20–30 min (Heisenberg and Wolf 1986). The same group showed that flies could adapt to different coupling gains between yaw torque and movement of the stimulus in as little as 200 ms (Wolf and Heisenberg 1990). In a follow-up paper titled “Can a fly ride a bicycle?”, Wolf and Heisenberg showed that *Drosophila* could stabilize a vertical stripe by pushing a platform side-to-side with their legs, even under positive feedback (Wolf et al. 1992). From their work, Heisenberg and Wolf argued that flies have a highly flexible control architecture enabling the activation of a range of motor programs until one achieves a desired state (e.g., zero retinal slip in a visuomotor task) through operant or reinforcement learning. Collectively, there appears to be some evidence that stripe fixation has some flexibility, but the mechanisms remain unclear and to our knowledge these results have not been reproduced in other invertebrates.

Error-based motor learning would presumably require an internal prediction (Fig. 1A), such that gains can be recalibrated over time. Recent studies showed that saccades are associated with motor-related efference copies, whereas visually evoked smooth movement stabilizing turns (optomotor response) are not (Fenk et al. 2021; Kim et al. 2015). As an internal prediction could be associated with motor learning in invertebrates—although policy-based motor learning could occur without a model (Hadjiiosif et al. 2021)—it would appear that the optomotor response is less flexible, as it is primarily driven by smooth movement (Land 1973; Land and Collett 1974). Using an augmented reality yaw-free tether—which caused a constant visual error between expected and actual visual feedback—and control theory, recent work showed that the optomotor response is autonomous for flight bouts of up to 30 min and resembles a linear, time-invariant system (Cellini et al. 2024). Even under positive visual feedback, the optomotor response was autonomous, showing little flexibility. Collectively, these results suggest that the lower-level optomotor response in flies is inflexible compared to stripe fixation behavior.

Although these results support the notion that the optomotor response in flies is inflexible with respect to changes in visual feedback, optomotor gains can be modulated by non-visual cues. Indeed, different senses can act at different levels in the sensorimotor hierarchy (Merel et al. 2019) and over different spatiotem-

poral scales (Mongeau et al. 2021). For instance, both odor and proprioception appear to modulate optomotor gains. In flies, proprioceptive feedback (e.g., via halteres) can directly modulate optomotor gains via active damping (Cellini and Mongeau 2022; Elzinga et al. 2012; Fuller et al. 2014; Rimniceanu et al. 2023) and odor can modulate gains at both behavioral and physiological levels (Chow and Frye 2008; Chow et al. 2011; Wasserman et al. 2015). However, gain modulation of visuomotor reflexes via olfactory or proprioceptive inputs may emerge from reflexive loops, and therefore may be part of a robust rather than adaptive control architecture.

Image stabilization in weakly electric fish

Image stabilization is also integral to postural and gaze control in vertebrates. For instance, the weakly electric glass knifefish *Eigenmannia virescens* naturally maintains its position and moves back and forth to track a longitudinally moving refuge (Cowan and Fortune 2007; Roth et al. 2011). Such behavior is akin to stripe fixation in *Drosophila*, since fish tracks a certain target (i.e., the walls and edges of the refuge) in the task, relying on vision and their electrosense (Stamper et al. 2012; Sutton et al. 2016) under feedback control (Cowan et al. 2014; Cowan and Fortune 2007; Roth et al. 2011; Uyanik et al. 2020).

Yang et al. examined how *Eigenmannia* learned novel dynamics during refuge tracking under an augmented feedback paradigm (Yang et al. 2024) (Fig. 3). More specifically, they studied whether fish could learn to compensate for the destabilization of the refuge tracking system (Yang et al. 2024). Instead of directly reversing the gain in the feedback system like visual inversion (Yang et al. 2021) or “backward bikes” [with a set of gears making handlebars turn the front wheel in opposite directions, also see video in (Sandlin 2015)], Yang et al. designed a high-pass filter in the augmented feedback loop. The key crucial innovation of the high-pass filter approach is that *it does not alter the low-frequency dynamics* (i.e., below the high-pass-filter’s cut-off frequency), yet still can reverse the sign of the high-frequency feedback (i.e., above the filter cut-off frequency). With this unique experimental design, the system was gracefully (not abruptly) destabilized as the gain was increased. In their experiments, Yang et al. incrementally tuned up the augmented feedback gain (Yang et al. 2024). They discovered that *Eigenmannia* retuned its controller to adapt to the destabilizing dynamics during a single experimental session of about 30 min; the changes in the fish’s control system improved tracking performance as well as control-theoretic measures of robustness, including reduced sensitivity to

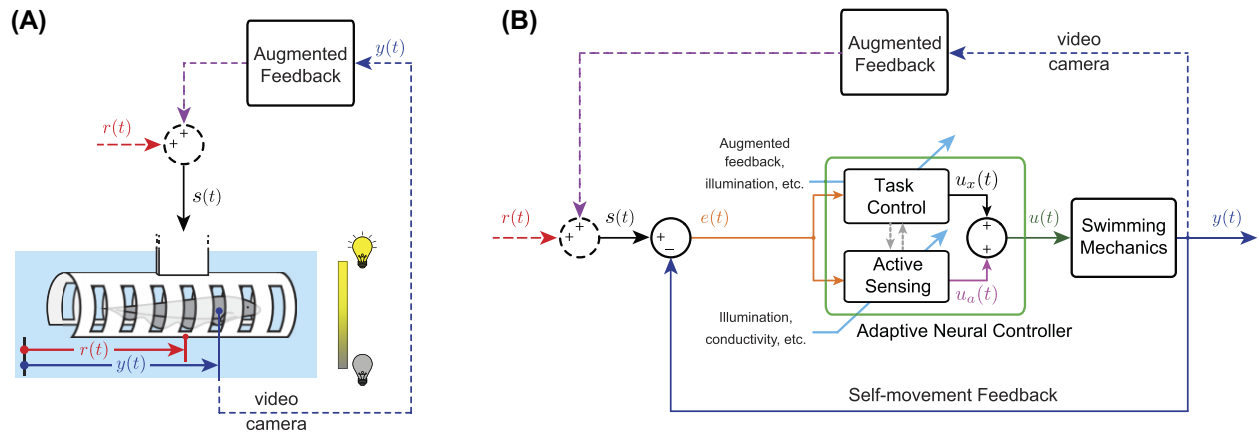


Fig. 3 Adaptation in weakly electric fish refuge tracking. Experimental feedback is indicated with a dashed line, whereas solid lines indicate “normal” (i.e., veridical) signals. (A) Schematic of refuge tracking system with augmented feedback. A fish tracks a longitudinal moving refuge in different luminance conditions (Biswas et al. 2018, 2023; Uyanik et al. 2019); electrical jamming (Chen et al. 2020) or changes in conductivity (Stamper et al. 2012) can also be used to modulate sensory conditions. The fish position $y(t)$ is captured by a video camera, fed through augmented feedback in real-time, and added to the external input $r(t)$ to control refuge motion $s(t)$. Various categories of augmented feedback (constant value gains, high-pass filter, etc.) can be used to garner insights into active sensing in an uncertain world (Biswas et al. 2018; Zerefa et al. 2023) and sensorimotor control adaptation to novel destabilizing dynamics (Yang et al. 2024). (B) Block diagram of refuge tracking system with augmented feedback. As in (A), refuge motion $s(t)$ is the summation of external reference stimulus $r(t)$ and augmented fish motion $y_f(t)$. The fish sense the difference $e(t)$ between refuge position $s(t)$ and the veridical self-movement feedback $y_f(t)$. Such difference, named as “sensory slip,” is passed through the neural controller and swimming mechanics, thereby adjusting the fish position, $y(t)$. The neural controller must continually balance the need for achieving a goal—using the task control for refuge tracking—with the requirements for gaining sensory information via active sensing (Biswas et al. 2023). The neural controller exhibits plasticity in response to the augmented feedback (Biswas et al. 2018; Yang et al. 2024; Zerefa et al. 2023) and changes in illumination (Biswas et al. 2018; Zerefa et al. 2023; Yeh et al. 2023) and conductivity (Stamper et al. 2012).

low frequency disturbances and improved phase margins. These changes in the fish’s neural control system were temporarily retained and finally washed out within about 10 min after the removal of augmented destabilizing feedback (Yang et al. 2024). These results imply that weakly electric fish adaptively retune their control system under augmented feedback for maintaining robust task-level control performance. Such sensorimotor adaptation observed in *Eigenmannia* may be mediated by cerebellum or cerebellum-like circuits (Bastian 1975, 1996; Bell et al. 1997; Huang et al. 2019). Further neurophysiological studies could reveal how retuning of sensorimotor gain in neural circuits of fish brains.

These studies with *Eigenmannia* are experimentally similar to those by Cellini et al. (2024) in *Drosophila*, but unlike in the fruit fly, *Eigenmannia* exhibited sensorimotor adaptation. A possible reason for this difference is that object tracking or stripe fixation (as in Yang et al. 2024) and the wide-field optomotor response (as in (Cellini et al. 2024)) are implemented by distinct, parallel neural pathways (Hardcastle and Krapp 2016; Frighetto and Frye 2023; Mongeau and Frye 2017). Another possibility is that sensorimotor gain adaptation under augmented feedback may require an internal prediction or internal model, thus

may require a cerebellum or cerebellum-like structure (Miall et al. 1993; Sawtell and Bell 2008; Wolpert et al. 1998) so that a mismatch between predicted and actual sensory feedback can be corrected over time. Interestingly, in contrast to the findings in weakly electric fish, Sperry found that *Triturus viridescens* (salamander) and *Sphaeroides spengleri* (puffer fish) did not adapt their optomotor response to a 180° rotation of the retinal field (Sperry 1943, 1950), the effect of which is equivalent to reversing the sensory feedback gain directly from -1 to 1 via augmented feedback. It might be the case that directly reversing a visual gain can bring about dramatic and abrupt changes in the stability of the system, and may require quite different learning mechanisms. In studies with weakly electric fish, the highest augmented feedback gain applied in preliminary experiments with a static gain (Zerefa et al. 2023) was still insufficient to reverse the sensory perception, while the gain manipulation of high-passed augmented feedback in Yang et al. (2024) gradually reversed the sign of high-frequency error feedback while leaving low-frequency feedback unchanged. As a comparison, humans appear to have more plasticity in adapting to gain reversal in their optomotor response. Humans are able to partially adapt to visual inversion within weeks (Kohler 1963; Lillicrap et al.

2013), suggesting a greater flexibility to adapt than other vertebrates.

One challenge in understanding image stabilization involves unraveling the trade-off animals face between moving in order to gain sensory information (“explore”) versus making small compensatory (“exploit”) movements to achieve the goal of image stabilization in uncertain environments. For example, *Eigenmannia* generate active sensing movements to gather information as they performed the refuge tracking task, particularly in lower light intensity environments which results in higher sensory uncertainties for their electrosense (Biswas et al. 2018, 2023; Chen et al. 2020; Stamper et al. 2012; Uyanik et al. 2019). To examine whether animals can dynamically tune their active sensing behavior, Biswas et al. introduced an augmented reality system to manipulate sensory feedback during this image stabilization task (Fig. 3) (Biswas et al. 2018). They found fish robustly regulated the “sensory slip,” i.e., the dynamic difference between the position of the refuge and the fish, through closed-loop control of active sensing. What drives the details of the temporal dynamics of active sensing movements? One theory is that exploratory active sensing movements are tuned to the physiological demands of sensory receptors (Stamper et al. 2012). For example, many sensory receptors are “adapting” or “phasic” in the sense that they respond more strongly to rapidly changing stimuli than to static, or persistent stimuli (Chen et al. 2020). A simplified model of such adapting sensors reveals a fundamental requirement to perform sensing movements during image stabilization because, without those movements, the state of the system would become “unobservable” to the fish (Kunaparedy and Cowan 2018; Sontag et al. 2022). In other words, if an animal were to fail to actively sense its surroundings in an uncertain world, properties of sensory receptors would cause an ever-increasing uncertainty about the animal’s relative position with the environment. Indeed, Biswas et al. discovered a state-uncertainty-based mode-switching strategy that seems to predict active sensing movements of a taxonomically diverse range of behavior (Biswas et al. 2023).

Discussion

Mapping robust and adaptive control of locomotion across animal groups

How do robust and adaptive features of locomotion control map across animal groups? Here, we propose a mapping of motor flexibility along the robust–adaptive axis (Fig. 4). At one extreme end in this simplified framework would lie purely robust systems, which are defined as reactive, more genetically determined, and putatively lower (and certainly far less well

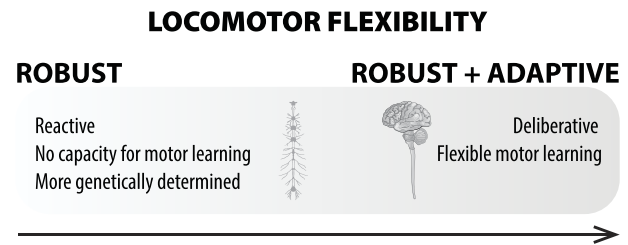


Fig. 4 Proposed mapping of motor flexibility along the robust–adaptive axis.

documented) capacity for motor learning. These animals tend to be small and have a decentralized nervous system without a cerebellum [although there may be cerebellar-like structures, e.g., the mushroom body (Farris 2011)]. At the other end of the axis are (demonstrably) highly adaptive systems—or, more precisely, both robust and adaptive—which are deliberative and possess highly flexible motor learning supported by the cerebellum, but face longer neural transmission delays. While there is unequivocal evidence for motor learning in animals with a cerebellum, evidence for motor learning in invertebrates remains controversial [with the possible exception of cephalopods (Shigeno et al. 2018)]. In particular, to our knowledge, it is unknown if/how animals without a cerebellum implement error-based motor learning as this process would presumably require a prediction of the sensory consequence of motor actions (e.g., internal model), although an internal model is not strictly necessary (Hadjiosif et al. 2021). While the presence of efferent copies or corollary discharges is well established in invertebrates (Crapse and Sommer 2008), it is unknown if/how these signals assist in motor learning. Generally, behavioral evidence in support of motor learning in invertebrates is sparse, whereas evidence for rich behavioral repertoires and associative learning in invertebrates is well established (Chittka and Niven 2009).

By taking a comparative approach, an exciting area of future research will be to determine where organisms across animal groups are situated along the robust–adaptive axis (Fig. 4). Such comparative analysis of adaptive–versus–robust locomotor behaviour could yield important insights into brain evolution and the neural control of movement. For instance, given the genetic tractability of invertebrate model systems (e.g., *D. melanogaster* and *C. elegans*), we can functionally characterize individual neural networks at the cellular levels (Venken et al. 2011). But first, it will be important to reveal whether animals like fruit flies can unequivocally implement error-based motor learning, or whether they have emergent robustness by relying on physical intelligence and a layered reflexive architecture that integrates

multi-modal sensory feedback (Merel et al. 2019). This effort will require novel behavioral assays that track behavior (e.g., response to appendage damage or across molting stages) over long periods of time.

The robust-adaptive axis can also be informative to situate the “phylogeny” of robots over the last few decades. Using terrestrial robots as an example, some of the earliest successful walking robots [e.g., Genghis (Angle 1989), Robot II (Espenschied et al. 1996), ASIMO (Sakagami et al. 2002), etc.] relied on reactive controllers using a simple architecture of nested feedback (Brooks 1986) inspired by invertebrates to ensure robust kinematics. These were followed by mechanically tuned robots [e.g., RHex (Altendorfer et al. 2001), Whegs (Quinn et al. 2022), BigDog (Raibert et al. 2008), DASH (Birkmeyer et al. 2009), HAMR (Goldberg et al. 2017), ANYMal (Hutter et al. 2016), CLARI (Kabutz and Jayaram 2023), etc.] across size scales [from meter (Raibert et al. 2008) to centimeter (Jayaram et al. 2020; Kabutz et al. 2023) lengths] that emulated the low-dimensional (template) dynamics (Full and Koditschek 1999) of animal locomotion (Dickinson et al. 2000; Holmes et al. 2006) to also realize robust running (Doshi et al. 2019; Kim et al. 2006) and climbing (Birkmeyer et al. 2012; De Rivaz et al. 2018) and in some cases without sensor-based feedback. With growing progress in computation (machine learning) and AI, recent versions of these robots use a combination of physical (McClintock et al. 2021) and computational intelligence to realize robust locomotion despite a variety of perturbations (Doshi et al. 2019; Hutter et al. 2017; Jayaram et al. 2018a). As they become more capable, such robots can serve as platforms to systematically explore and test hypotheses about different neural architectures commonly found in biological organisms (Ijspeert 2014, 2008; Ramdya and Ijspeert 2023). More recently, robotic systems are beginning to demonstrate an impressive capacity for motor learning that enables agile maneuvers over harsh (Hwangbo et al. 2019; Lee et al. 2020) and deformable natural terrains (Choi et al. 2023; Guizzo 2019) and even compensate for leg loss (Cully et al. 2015; Yang et al. 2020). The lessons learned from the DARPA Locomotion Grand Challenges (Johnson et al. 2015; Krotkov et al. 2018; Tranzatto et al. 2022) show both the excitement and promise for robots to improve significantly and achieve animal-like performance in the near future.

Conclusion

In this review, we highlighted recent progress in understanding the principles of robust and adaptive control of animal locomotion, with a particular focus on non-human animals (invertebrates and vertebrates). We pro-

vided definitions of robust and adaptive control drawn from control theory to classify how animals cope with uncertainty, such as the loss of an appendage. We highlighted that these distinct control schemes link to distinct behavioral outcomes, thus providing testable hypotheses for unraveling principles of animal locomotion control. Following appendage loss, our review suggests that invertebrates rely primarily on robust control from reflexive feedback, and that strong evidence for adaptive control, e.g., error-based learning, is lacking; however a change in active damping in response to wing damage may be analogous to gain scheduling in adaptive control. Thus, invertebrates could compensate for injury through gain adjustment via proprioception rather than through canonical error-based learning. With respect to image stabilization behavior, invertebrates and vertebrates (with the exception of humans) appear unable to correct for augmented feedback during optomotor responses but appear to adapt to augmented object tracking or stripe fixation behavior using error-based learning. This lends support to an existing hypothesis (Hardcastle and Krapp 2016) that the optomotor response and fixation may operate at different levels in the feedback control hierarchy.

Unraveling deep principles of robust and adaptive control will continue to require interdisciplinary teams with broad expertise bridging the disciplines of evolutionary and organismal biology, behavioral ecology, comparative physiology, genetics, biomechanics, and neuroscience with control theory, robotics, material science, and computer science. Undoubtedly, such teams will also be required to take on the “embodied Turing test” (Zador et al. 2023).

Author contributions

All authors wrote and reviewed the manuscript.

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Conflict of interest

No competing interest is declared.

Data availability

There are no new data associated with this article.

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