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REVIEW

CENTENARY ARTICLE

# Integration of feedforward and feedback control in the neuromechanics of vertebrate locomotion: a review of experimental, simulation and robotic studies

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## ABSTRACT

Animal locomotion is the result of complex and multi-layered interactions between the nervous system, the musculo-skeletal system and the environment. Decoding the underlying mechanisms requires an integrative approach. Comparative experimental biology has allowed researchers to study the underlying components and some of their interactions across diverse animals. These studies have shown that locomotor neural circuits are distributed in the spinal cord, the midbrain and higher brain regions in vertebrates. The spinal cord plays a key role in locomotor control because it contains central pattern generators (CPGs) – systems of coupled neuronal oscillators that provide coordinated rhythmic control of muscle activation that can be viewed as feedforward controllers – and multiple reflex loops that provide feedback mechanisms. These circuits are activated and modulated by descending pathways from the brain. The relative contributions of CPGs, feedback loops and descending modulation, and how these vary between species and locomotor conditions, remain poorly understood. Robots and neuromechanical simulations can complement experimental approaches by testing specific hypotheses and performing what-if scenarios. This Review will give an overview of key knowledge gained from comparative vertebrate experiments, and insights obtained from neuromechanical simulations and robotic approaches. We suggest that the roles of CPGs, feedback loops and descending modulation vary among animals depending on body size, intrinsic mechanical stability, time required to reach locomotor maturity and speed effects. We also hypothesize that distal joints rely more on feedback control compared with proximal joints. Finally, we highlight important opportunities to address fundamental biological questions through continued collaboration between experimentalists and engineers.

**KEY WORDS: Neural oscillators, Spinal circuits, Nervous system, Movement, Sensorimotor control, Central pattern generation, Reflexes**

## Introduction

Animal locomotion arises from complex and rich interactions between the nervous system, the musculoskeletal system and the environment (Dickinson et al., 2000; Nishikawa et al., 2007). Animal sensorimotor control involves multi-layered and distributed systems, with central networks, reflexes and mechanics all contributing to sensorimotor responses on varied time scales (Büschges, 2005; Buschmann et al., 2015; Bidaye et al., 2018; Grillner, 1985; Grillner and El Manira, 2019; Loeb et al., 1999; Nirody, 2023; Pearson, 1995; Pearson and Gramlich, 2010; Rossignol et al., 2006). Because of this inherent complexity, it has been a longstanding challenge in biology to rigorously understand the structure, function and integration of animal sensorimotor systems. Integrative approaches are needed to address this challenge. Exchange between biology, physics and engineering disciplines can be particularly useful for generating and rigorously testing hypotheses about how mechanics and control interact to produce agile locomotion. In this Review, we discuss how the exchange between comparative experimental biology, physics and engineering can provide fundamental insights into the neuromechanics (see Glossary) of vertebrate locomotion.

Historically, comparative approaches have been essential for providing mechanistic understanding of the control of movement, and Journal of Experimental Biology (JEB) has been an important venue for comparative studies across diverse taxa. In the 1930s–1940s, Gray and co-authors published numerous papers on animal movement in JEB, characterizing the locomotor movements, reflex responses and locomotor pattern generation in the eel, dogfish, toad, leech and earthworm (Gray, 1933; 1936; Gray et al., 1938; Gray and Lissmann, 1938; 1940; Gray and Sand, 1936). Subsequent studies continued to expand on this diversity and contribute to mechanistic understanding of sensorimotor control (e.g. Hughes, 1952, 1957; Wilson, 1965, 1967). Many of the early studies were foundational for understanding both the basic biomechanics and neural control circuitry for movement. At that time, it was often necessary to study movement mechanics and neural control together, because so little was known about both.

In recent decades, the fields of comparative biomechanics and sensorimotor physiology have been relatively isolated, as each field focused on more detailed mechanistic understanding of specific subsystems. Simultaneously, studies of sensorimotor control have increasingly focused on a few genetic animal models, such as the mouse, zebrafish, fruit fly and *Caenorhabditis elegans*, which enable the use of the most richly developed genetic and molecular tools (Bidaye et al., 2018; Fetcho and McLean, 2010; Fouad et al., 2018; Kiehn, 2011; Lewis and Eisen, 2003; Zhong et al., 2012; Mantziaris et al., 2020). Nonetheless, this narrow focus has its drawbacks, and important questions remain about the diversity and specialization of sensorimotor control across species. We suggest that it is important to continue to expand studies beyond the classic genetic animal models, because comparative approaches provide opportunities to address fundamental questions about the evolution and diversity of neuromechanical integration. Critical gaps in understanding remain in how the different elements of the sensorimotor system are integrated with each other, and how this

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## Glossary

**Altricial**
Animals that take extended time after birth to reach locomotor maturity.

**Central pattern generator (CPG)**
Neural circuits that can generate the basic rhythmic motor patterns for movement and breathing without any sensory inputs. These circuits produce periodic signals that are often mathematically modeled as oscillators (see below). A defining feature of a CPG is that it can generate a periodic motor output without a periodic input.

**Compliance**
Elastic deformation of a mechanical system. Compliance can be viewed as the opposite of stiffness.

**Control theory**
Field of applied mathematics that deals with the control of dynamical and engineered systems.

**Decerebrate preparation**
An experimental manipulation in which cerebral brain function is eliminated by transection or removal of the cerebrum. The extent to which longer-latency feedback pathways remain intact or eliminated depends on the specific location of the transection.

**Dynamic stability**
Stability of a gait that requires movement to prevent falling (as opposed to static stability, see below). Typically, a dynamically stable gait exhibits convergence to a limit cycle behavior, namely periodic behavior that is robust against (small) perturbations.

**Efferent copy**
A copy of the motor signals that are used as inputs to internal models to predict dynamics and sensory feedback.

**Entrainment**
Synchronization of oscillatory dynamical systems such that they converge to the same frequency and therefore to constant phase differences. Two dynamical systems can mutually entrain each other (and converge to a frequency that is typically an average of their intrinsic frequencies), or one dynamical system can entrain another (and impose its intrinsic frequency on the other).

**Feedback control**
A control pathway in which sensory signals are returned back to generate an error signal that regulates the input commands towards desired output dynamics.

**Feedforward control**
A control pathway that generates a predefined command signal based on the anticipated load and dynamics of the system. In this Review, we discuss two types of feedforward control mechanisms: spinal CPGs and supraspinal internal models.

**Fictive locomotion**
The generation of the basic rhythmic muscle activation patterns required for locomotion in isolated spinal cords, such as the alternating activation of flexors and extensors in the leg of walking animals or the transmission of an undulatory wave down the body in swimming animals.

**Internal models**
Internal neural representations that can predict the interactions between the nervous system, the musculoskeletal system and the environment. Forward internal models can predict causal relationships between actions and their consequences. Inverse internal models can predict which actions are needed to reach particular consequences.

**Model-based control**
Control architecture that uses internal models for performing anticipatory (as opposed to reactive) movements. An example of model-based control in robotics is model-predictive control, which uses a model of the robot and an optimization criterion to define motor commands over a finite-time horizon.

**Neuromechanics**
The scientific field focused on the interactions between biomechanics of the musculoskeletal system and sensorimotor control and their integration for robust and agile movement.

**Oscillators**
Dynamical systems or neural networks that exhibit stable limit cycle behavior, i.e. that produce stable periodic signals.

**Precocial**
Animals that locomote effectively shortly after birth.

**Preflexes**
The intrinsic dynamic properties of the musculoskeletal system in its activated state that automatically stabilize movements through visco-elastic properties. These form a kind of zero-delay feedback stabilizing movement.

**Sensorimotor delay**
The time lag between the onset of a mechanical perturbation and its reception by a sensory organ to the development of peak muscle force in response to the perturbation. It includes sensing delay, nerve conduction delay, synaptic delay, neuromuscular junction delay, electromechanical delay and muscle force development delay.

**Spinal preparation**
An experimental manipulation in which the brain and brainstem function are completely removed by transection of the spinal cord, typically in the thoracic region.

**Static stability**
Stability of a posture or a gait in which the center of mass is always maintained above the (possibly time-varying) support polygons formed by the contacts between the limbs (or any body parts) and the ground. An animal that is statically stable will not fall when it freezes its posture.

integration varies with body size and among animals adapted for different locomotor environments.

The interdisciplinary field of comparative neuromechanics has emerged over the last 15 years or so (Nishikawa et al., 2007; Ting and McKay, 2007), focusing on the study of mechanics and control of movement in a comparative framework. In this Review, we highlight principles and hypotheses that have emerged from this field, with a specific focus on sensorimotor and neuromechanical integration in vertebrates. We discuss current conceptualization of the role of central pattern generators (CPGs; see Glossary) and their integration with reflexes and limb mechanics, and the interactions between feedforward and feedback control mechanisms (see Glossary). In the sections below, we first summarize current understanding in biology based on both historical and recent

Journal of Experimental Biology (2023) 226, jeb245784. doi:10.1242/jeb.245784

experimental evidence, then discuss contributions from bio-inspired robotics and simulations, and highlight current open questions and future directions that are enabled through direct integration of engineering and experimental biology. Our Review focuses mainly on vertebrate locomotion; however, we note that many principles of locomotor control have parallels between vertebrates and invertebrates, and readers are directed to recent reviews of invertebrate systems (Nirody, 2023; Mantziaris et al., 2020; Bidaye et al., 2018).

## Biology: historical experimental evidence, current understanding and new hypotheses

### Integration of CPGs and sensory feedback in the spinal cord

The spinal cord plays a key role in integrating predictive and reactive elements of vertebrate locomotor control (Grillner and El Manira, 2019; Rossignol et al., 2006). Animal control involves inherently long sensorimotor delays (see Glossary; More et al., 2010; More and Donelan, 2018). Because of these delays, animals cannot rely entirely on reactive, feedback-driven control, but must instead use a combination of predictive and reactive control mechanisms for stable movement (Fig. 1). The spinal cord contains neural circuits involved in integrating CPGs (see Box 1), reflex responses, and descending and ascending pathways to the brain (Grillner and El Manira, 2019; Pearson, 1995; Rossignol et al., 2006). CPGs in the spinal cord provide a type of predictive, feedforward controller for locomotion that helps to overcome delays. CPGs are activated by a descending ‘drive’ signal and produce predetermined motor outputs for locomotion. These outputs provide complex muscle activation for the anticipated mechanical demands, resulting in, for instance, traveling waves for undulatory locomotion and alternation of stance and swing phases for legged locomotion. Therefore, CPGs resemble feedforward controllers in control theory (see Glossary), because they produce complex and detailed motor commands given a simpler high-level descending signal for the desired behavior, such as movement at a specific speed. However, CPGs do not act in isolation. The CPG receives continuous modulation through descending drive commands and reflex feedback (Grillner et al., 2008; Rossignol et al., 2006). Consequently, the CPG can be thought of as a type of feedforward controller nested within a feedback control system (Holmes et al., 2006).

Current evidence suggests that animal locomotion makes use of a nested, multi-layered control architecture that organizes sensing and action (Grillner and El Manira, 2019; McLean and Dougherty, 2015; Pearson, 1995; Rossignol et al., 2006). A nested architecture enables separation of task selection (starting, stopping, gait and speed), task coordination (e.g. generation of coordinated rhythmic leg movements) and stabilization in response to disturbances. As a first approximation of the hierarchical organization, CPGs generate rhythmic commands that act as feedforward signals for task coordination, whereas descending commands activate and modulate CPGs for task selection, and reflexes provide stabilizing responses to perturbations (Fig. 1). We will later see that neuromechanical models suggest more complexity, with sensory feedback also contributing to task coordination (Owaki et al., 2013; Thandiackal et al., 2021). Sensorimotor delays give rise to temporal scaling of control responses based on the spatial distribution of system elements (Fig. 1). Inner loops deal locally with perturbations, relying on fast peripheral mechanisms, including intrinsic mechanics (Brown and Loeb, 2000; Daley et al., 2007; Dickinson et al., 2000; Full and Koditschek, 1999; Jindrich and Full, 2002) and short-latency reflexes (Af Klint et al., 2010; Daley et al., 2009; Hiebert and Pearson, 1999; Moritz and Farley, 2004).

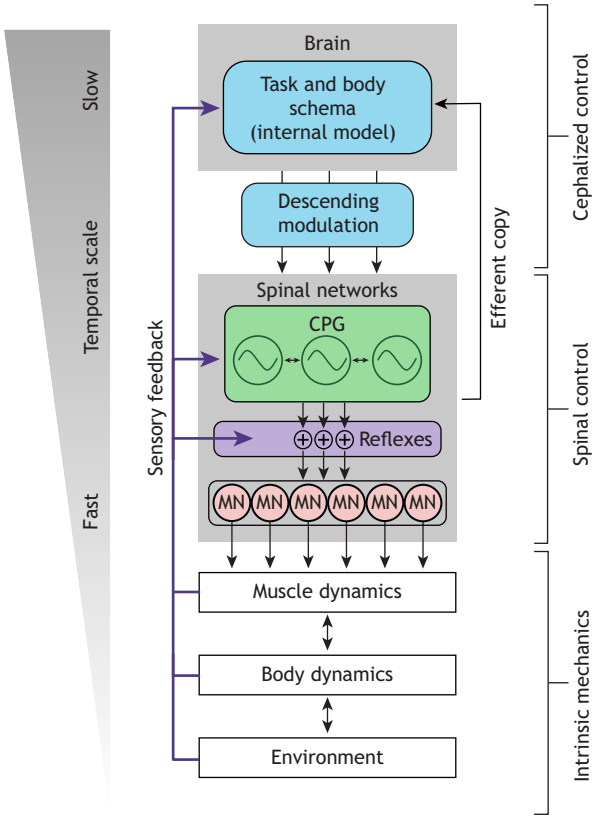


**Fig. 1. Schematic of the neuromechanical system of vertebrates, including the brain, descending drive, spinal networks and intrinsic musculoskeletal mechanics.** Temporal scaling of control arises from the spatial distribution of the system components and delays inherent to animal sensorimotor systems. Central pattern generators (CPGs) in the spinal column receive relatively simple descending signals and generate complex rhythmic motor outputs. The CPG rhythm is entrained by sensory feedback in intact animals but generates fictive locomotor patterns in the absence of feedback. Sensory feedback acts in multiple layers, through (1) short-latency monosynaptic reflexes, (2) entraining CPGs, (3) longer-latency multi-synaptic sensory feedback, and (4) ascending pathways that contribute to internal models, task planning and modulation of descending commands. Efferent copy from the spinal networks also contributes input into internal models, enabling prediction of sensory signals that are compared with sensory feedback. The plus symbol indicates summation of multiple signal paths to the motor neurons (MN).

Intermediate loops modify task-level variables, such as joint and leg stiffness, and outer loops integrate sensorimotor information in the brain to select and switch among different tasks and update internal models (see Glossary; Pearson and Gramlich, 2010). However, many uncertainties remain in how different control layers are integrated and modulated based on experience, learning and different locomotor contexts.

There was a longstanding historical debate about the relative importance of feedforward and feedback in control of animal locomotion. Sherrington’s work on reduced animal preparations revealed that reflex actions could generate the component motions necessary for rhythmic walking (Sherrington, 1910). Thus, Sherrington argued that locomotion could be viewed as the result of a chain of reflexes (Sherrington, 1900, 1906, 1910). Subsequent work by Graham Brown demonstrated that motor patterns for locomotion could be generated in deafferented preparations and did not require sensory input. Graham Brown (1911, 1914) argued that ‘spinal centers’ (later named CPGs) acted as the primary unit of

Journal of Experimental Biology (2023) 226, jeb245784. doi:10.1242/jeb.245784

**Box 1. Central pattern generators (CPGs)**

CPGs play important roles in the generation of coordinated motor patterns for both vertebrate and invertebrate locomotion. CPGs are neural circuits that can generate the basic rhythmic motor patterns for movement and breathing without any sensory inputs. Locomotor CPG circuits are located in the spinal cord of vertebrates (Grillner and El Manira, 2019), and in the ventral nerve cord of invertebrates (Mantziaris et al., 2020). The existence of CPGs has been demonstrated across diverse vertebrate species through the observation of fictive locomotion in spinal preparations, with all inputs from the brain and periphery transected (Gray, 1936; Gray and Lissmann, 1940; Grillner and Wallén, 1982; Ho and O'Donovan, 1993; Sholomenko et al., 1991; Sholomenko and Steeves, 1987; Ten Cate, 1964, 1965). The CPG circuits in the isolated spinal cord generate fictive swimming in aquatic species (e.g. lamprey, zebrafish), fictive walking in terrestrial species (birds, mammals), and both fictive swimming and fictive walking in amphibious species (e.g. salamanders) (Chevallier et al., 2008; Fetcho and McLean, 2010; Grillner and El Manira, 2019; Grillner and Wallen, 1985; Ryczko et al., 2010; Whelan, 1996). Genetic studies have identified specific subpopulations of interneurons involved in rhythm generation that are conserved across vertebrates (Grillner and El Manira, 2019; Kiehn, 2016; Rybak et al., 2015). Locomotor CPGs are distributed segmentally along the spinal cord as interconnected rhythmic units (Grillner et al., 1995; Kiehn, 2016; McLean and Dougherty, 2015; Rybak et al., 2015), typically one per pair of antagonist muscles or even one per muscle (Cheng et al., 1998). Specific ventrolateral regions of the spinal cord generate flexor/extensor alternation, and specific ventromedial interneurons generate left/right coordination (Kiehn, 2016; McLean and Dougherty, 2015). Note that although there is no direct evidence of CPG circuits in humans, there is ample indirect evidence that humans possess CPG circuits similar to those of other vertebrate species (Minassian et al., 2017).

motor activity, not the reflex. He suggested that the reflexes regulate rather than generate motor activity (Graham Brown, 1911). To this day, the relative roles of central and reflex-generated contributions to locomotion remain somewhat controversial; however, it has become clear that both mechanisms co-exist and provide redundancy and flexibility in the system.

Subsequent work has confirmed the existence and shared features of spinal CPGs across vertebrates (see Box 1). Vertebrates also share a common mechanism for descending drive to CPGs to control gait speed and initiation. Stimulation of the mesencephalic locomotor region invokes gait initiation and gait transitions across species, inducing swimming in fish and walking in terrestrial animals (Cabelguen et al., 2003; Grillner and Wallen, 1985; Shik et al., 1966; Steeves et al., 1987). As the strength of the stimulation increases, swimming speed increases in the fish, and a quadruped increases speed and transitions between gaits from a walk to trot to gallop (Shik et al., 1966; Wallén, 1982).

In vertebrates, sensory feedback plays an essential role in entraining CPG rhythms to the mechanics of the body and the interaction with the environment. In the lamprey, periodic bending of the spinal cord results in entrainment (see Glossary) of the patterns of fictive locomotion (see Glossary), through sensory feedback from mechanosensitive edge cells in the spinal cord (Grillner et al., 1981; Grillner and Wallén, 1984). Similarly, proprioceptive feedback entrains gait rhythm and the timing of stance–swing transitions in quadrupedal gait (Pearson, 2008; Whelan, 1996). In decerebrate and spinal preparations (see Glossary), increasing belt speed leads to gait transitions from walk to trot and gallop, suggesting a role for sensory feedback entrainment in gait transitions (Barbeau and Rossignol, 1987; Forssberg et al., 1980; Kriellaars et al., 1994; Pearson, 2008; Whelan, 1996; Yanagihara et al., 1993). With increasing knowledge of the interneuronal networks and cellular mechanisms underlying sensorimotor control, it has become clear that sensory feedback is integrated at multiple levels: as distinct reflexes, as modulators of central pattern generation, and integrating with longer-latency feedback loops to regulate navigation and task selection (Grillner and El Manira, 2019; Rossignol et al., 2006) (Fig. 1).

### Diversity in the integration of feedforward, feedback and model-based neural control

Recent evidence and modeling studies (see below) suggest that the relative contributions of feedforward and feedback control can vary depending on size of the animal, speed, terrain and risks of falling. Below, we discuss emerging hypotheses about specialization and diversification of control components among vertebrates. Loosely speaking, we suggest two types of feedforward control, one in the spinal cord, based on CPGs, and one in higher brain centers, based on internal models, which we will here call (cephalized) model-based neural control (see Glossary). We call them both feedforward because they represent an anticipatory component as opposed to the reactive nature of feedback.

#### Body size and scaling of neuromechanical delays

Body size is one important source of diversity in control mechanisms for locomotion (Fig. 2, Table 1). Sensorimotor loop delay increases with body size ($M$), in proportion to $M^{0.21}$ (More et al., 2010, 2013; More and Donelan, 2018). Large animals experience longer sensorimotor delays relative to movement durations compared with the same ratio in small animals. For example, at speeds near the trot–gallop transition, a shrew has a total delay of 10 ms, 25% of its stance duration, but an elephant has a total delay of approximately 180 ms, 60% of its stance duration (More and Donelan, 2018). Delay relative to stance duration is important because this determines the time available to apply force for a corrective response to a disturbance. If an animal cannot respond to a disturbance within the stance phase, the response requires coordination of multi-step and multi-legged strategies, which involve longer-latency feedback loops. Delays therefore challenge the ability of large animals to respond effectively to perturbations, even though they have slower dynamics and step cycles compared with smaller animals (Mohamed Thangal and Donelan, 2020; More and Donelan, 2018).

To compensate for the relatively longer delays, it is expected that larger animals rely more on model-based control, using sensory feedback and internal models in the brain to generate state estimates for stable movement. Internal models can allow animals to compensate for delayed and noisy sensory feedback to predict future states, enabling generation of appropriate motor outputs for stable movement (Todorov, 2004; Todorov and Jordan, 2002; Wolpert and Ghahramani, 2000). The synaptic delays associated with internal model computations are a higher fraction of the total sensorimotor delay in very small animals (Mohamed Thangal and Donelan, 2020; More and Donelan, 2018). Consequently, the benefits of model-based control may not outweigh the costs of increased computation times in small animals (Thangal and Donelan, 2020; More and Donelan, 2018). Thus, overall, it is expected that larger animals are likely to have more cephalized model-based control, with higher brain involvement compared with small animals (Fig. 2, Table 1), whereas small animals can achieve agile and robustly stable movement through more spinalized control

Journal of Experimental Biology (2023) 226, jeb245784. doi:10.1242/jeb.245784

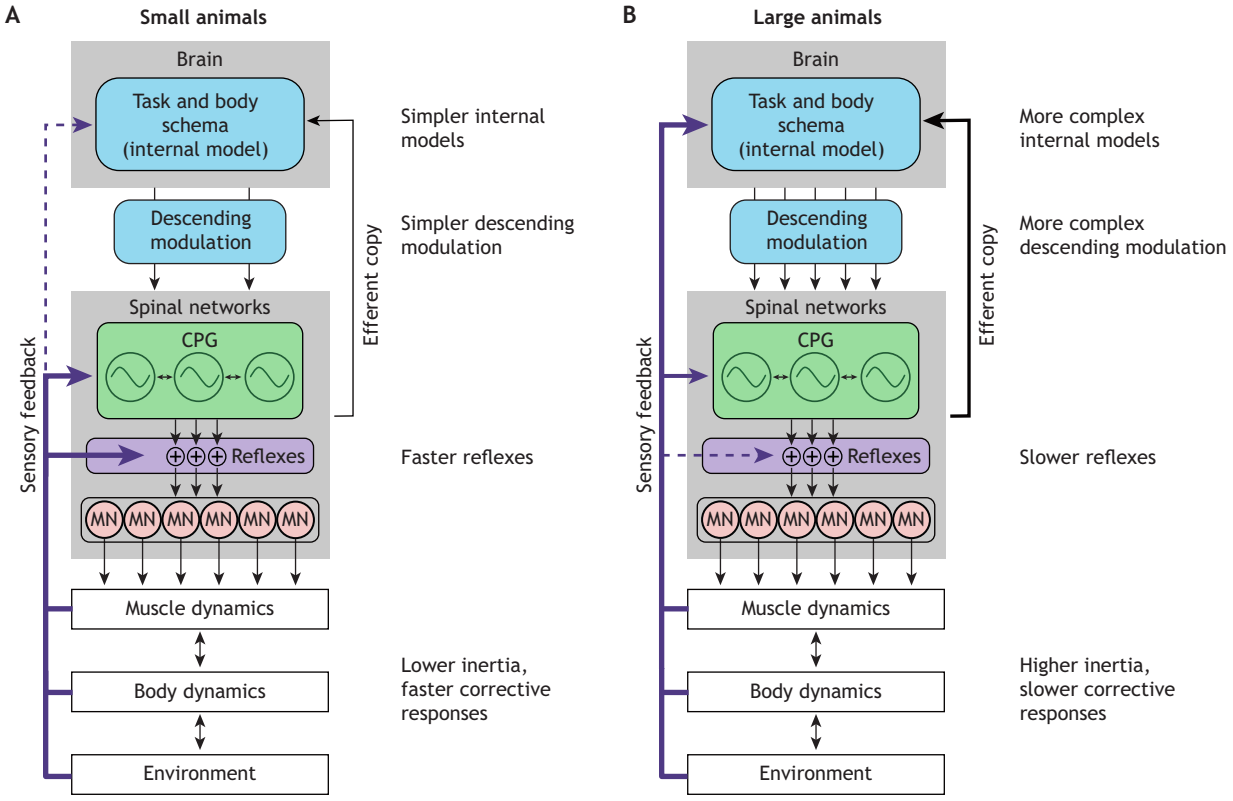


**Fig. 2. Hypothesized differences in the integration of mechanics and control between small and large animals.** (A) Differences in delays between small and large animals (see Table 1) may lead small animals to rely more on reflex feedback, with higher-gain short-latency reflexes (indicated by thicker arrows in A) and intrinsic mechanical preflexes for corrective responses. (B) In contrast, inertial delays exceed reflex delays in the largest animals, suggesting that reflexes and intrinsic mechanics may not be sufficient to allow stable corrective responses. Consequently, it is expected that large animals must rely more on higher-gain sensory input to internal models for predictive control (indicated by thicker arrows in B). Predictive control is enabled by computations in the brain involving many synapses. The ratio of reflex delay to synaptic delay is much greater in large animals compared with small animals, suggesting a lower penalty for increased computational complexity.

mechanisms coupled to intrinsic mechanical preflexes (see Glossary).

### Spinalization versus cephalization of feedforward control may relate to mechanical stability and the time to locomotor maturity

Although all vertebrates share similar component systems for locomotor control, a source of diversity among vertebrates is the degree of involvement of the brain and the complexity of descending drive modulation (Fig. 3). This distinction may be related to different developmental demands between precocial and altricial species (see Glossary). Precocial species tend to have relatively small brains as adults, whereas altricial species tend to have larger adult brain size (Bennett and Harvey, 1985; Garwicz et al., 2009). We hypothesize that these developmental differences may also be related to the relative degree of 'spinalization' versus 'cephalization' of locomotor control. That is, precocial species have more spinalized locomotor control, relying mainly on spinal CPG networks as a feedforward controller, coupled to intrinsic mechanics of the body, with short-latency reflexes. In contrast, altricial species have more cephalized control, relying more on model-based control in the brain, with longer-latency reflexes updating internal models. Through experience and optimization, animals can optimize the use of efference copy (see Glossary) and sensory feedback to estimate current states and predict future states to determine desired motor outputs (Todorov, 2004; Todorov and Jordan, 2002; Wolpert and Ghahramani, 2000). Multiple brain regions may be involved in the generation, maintenance and updating of internal models, including the cerebellum and the posterior parietal cortex (Ito, 2008; McVea et al., 2009; Pearson and Gramlich, 2010). Multi-layered model-based control can overcome delays by predicting mechanical conditions over a wide range of contexts and adjusting feedforward commands through descending pathways (Nakahira et al., 2021).

The contrast between precocial and altricial species can be appreciated when comparing large ground birds (such as ostriches and rheas) with humans. Although birds and humans have

**Table 1. Estimated differences in delays between a shrew and an elephant (More and Donelan, 2018; Thangal and Donelan, 2020)**

| | Delay estimate | |
|---|---|---|
| | Shrew | Elephant |
| Synaptic (ms) | 0.7 | 0.7 |
| Monosynaptic reflex (ms) | 10 | 180 |
| Inertial delays (ms) | 3–5 | 200–400 |
| Ratio of reflex: inertial | 2–3.3 | 0.5–0.9 |
| Ratio of reflex: synaptic | 14 | 260 |
| Ratio of reflex: stance duration | 0.25 | 0.6 |

Small animals have faster reflex responses relative to movement durations, but synaptic delays are a larger fraction of reflex delays (More and Donelan, 2018). Large animals have relatively longer inertial delays (Thangal and Donelan, 2020).

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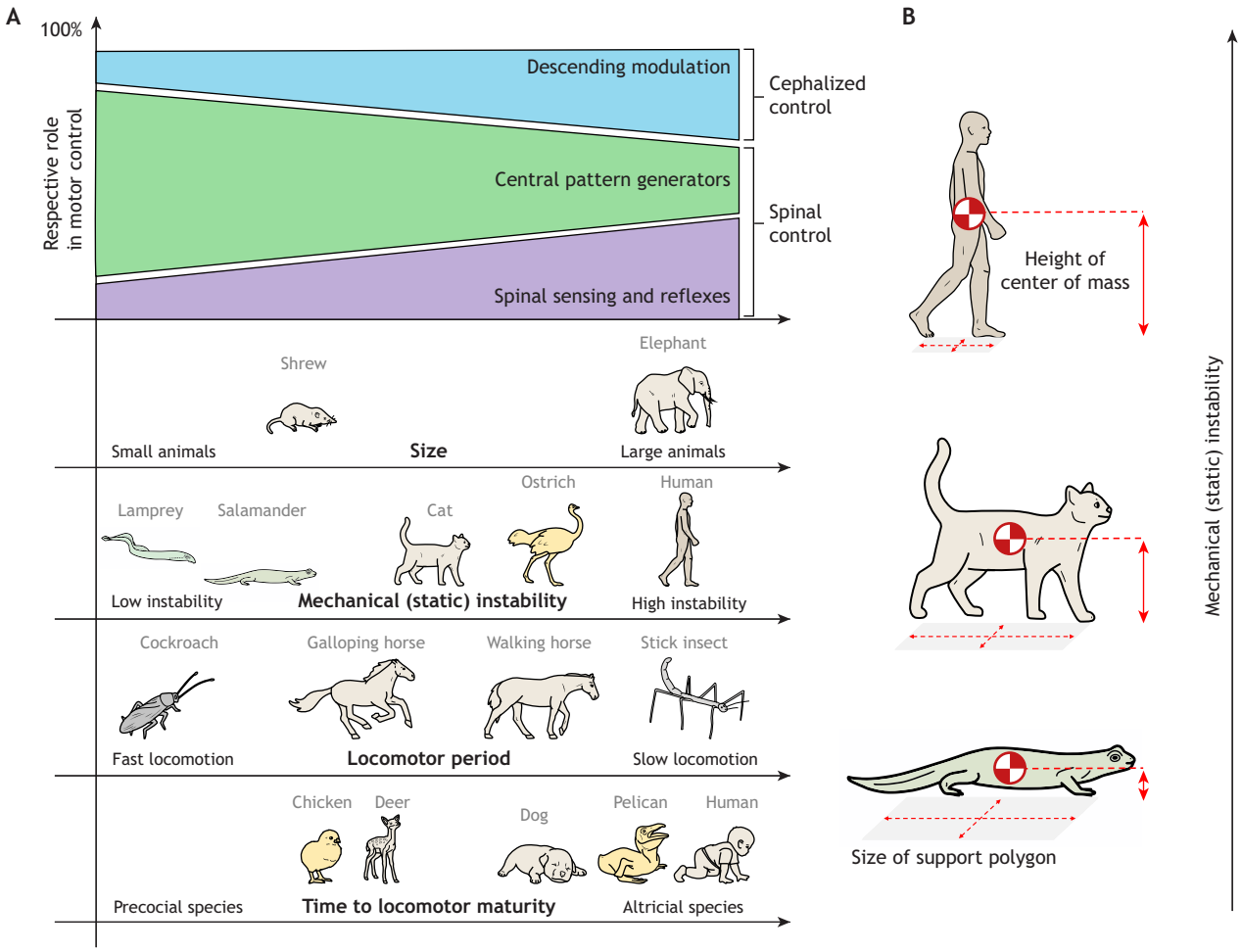


**Fig. 3. Hypothesized control gradients in the diversity of animal locomotion.** (A) We hypothesize that the relative roles of spinal sensing and reflexes, CPGs and descending modulation vary among species and between gaits depending on several factors: size, static mechanical stability/instability (estimated based on the ratio between the height of the center of mass and the size of the support polygon), cycle period (which decreases with speed) and time to locomotor maturity (which varies substantially between precocial and altricial species). Animals on the left of these axes rely more on CPGs, whereas animals on the right rely more on spinal sensing and reflex, and on descending modulation. We hypothesize that the functional gradients shown exist across taxa; nonetheless, phylogenetic differences are not represented here, and the contributions of descending control likely vary substantially among taxa. The gradients should be interpreted conceptually rather than as an absolute scaling. (B) Static mechanical instability is related to the ratio of the height of the center of mass compared with the size of the support polygon.

independently evolved bipedalism, they have converged upon walking and running gaits with similar mechanical and energetic demands (Gatesy and Biewener, 1991; Roberts et al., 1998; Rubenson et al., 2004; Watson et al., 2011). Yet, they exhibit important differences in development and sensorimotor control features. Ground birds are precocial, able to walk and run very shortly after hatching (Muir et al., 1996; Muir and Chu, 2002; Ryu and Bradley, 2009; Smith et al., 2010), whereas humans are exceptionally altricial, requiring many months of practice to walk without falling. We suggest that these developmental differences also reflect differences in spinalization versus cephalization of locomotor control. Birds have relatively more spinalized locomotor control compared with more cephalized control in mammals, including humans. Neurophysiological studies have demonstrated that spinal circuits are sufficient to generate complete locomotor patterns for self-supported walking in birds (Ho and O'Donovan, 1993; Sholomenko et al., 1991; Sholomenko and Steeves, 1987; Ten Cate, 1960). Birds do possess a common descending pathway with other vertebrates, from the mesencephalic locomotor region to the spinal CPGs, but lack a direct telencephalic–spinal projection analogous to the mammalian corticospinal tract (Sholomenko and O'Donovan, 1995; Sholomenko and Steeves, 1987; Steeves et al., 1987; Webster and Steeves, 1988). A recent study genetically silenced interneurons in the dorsal spinal tract in chicks, which increased kinematic variability in walking (Haimson et al., 2021), suggesting that sensory feedback and descending modulation contribute to stability of walking in birds. Nonetheless, locomotor control appears to be relatively more spinalized in birds compared with the more cephalized sensorimotor control observed in mammals.

The relatively spinalized versus cephalized locomotor control in ground birds versus mammals, respectively, might represent different solutions to the problem of neural delays. Cephalization allows more sophisticated internal models and model-based control; this allows delays to be overcome by predicting mechanical conditions over a wide range of learned contexts and adjusting descending commands accordingly. In contrast, spinalization relies on simpler CPG-based feedforward control, with the feedback-entrained rhythm providing estimates of current state and generation of motor output. We hypothesize that animals with more spinalized

control also tend to have more intrinsically stable biomechanics (Fig. 3). Among bipeds, birds have a relatively flexed limb posture compared with humans, a forward horizontal position of the body and high elasticity in the distal leg muscles, features that increase mechanical stability (Badri-Spröwitz et al., 2022; Daley, 2018; Daley et al., 2009; Daley and Biewener, 2011; Daley and Birn-Jeffery, 2018). Humans, in contrast, have a straight leg posture with the body vertically balanced over the hips, which is highly unstable without active control.

Among quadrupeds, there is also diversity in intrinsic mechanical stability that may relate to degree of cephalization versus spinalization of control. Large ungulates have parasagittal limb posture with relatively straight legs, a high body center of mass and a relatively narrow base of support. These features benefit locomotor economy by minimizing the active muscle force required to support body weight against gravity (Biewener, 1989). However, upright postures are relatively unstable compared with the sprawled posture and wide base of support typical of many amphibians and lizards (Alexander, 2002; Ijspeert, 2020). Note that here we mainly refer to static stability (see Glossary) rather than dynamic stability. At least at slow speeds, static stability in quadrupeds is proportional to the size of the support polygon, and inversely proportional to the ratio of body height to stance width (Alexander, 2002). We hypothesize that there is a control gradient in which mechanical stability enables spine-localized feedforward control, whereas mechanical instability is associated with brain-dominated feedforward control (Fig. 2). We also hypothesize that unstable animals require better proprioception for monitoring their posture and loads on limbs, and hence have a larger role for spinal sensing than mechanically stable animals. A similar hypothesis has been proposed in Ryczko et al. (2020).

#### Proximo-distal differentiation in control

Across diverse tetrapod animals, limbs have a proximo-distal distribution in muscle–tendon morphology, which may also result in differentiation in control mechanisms (Daley et al., 2007). The largest, most powerful muscles are proximal, concentrating mass near the body. Distal muscles have lower mass and high mass-specific force owing to their short, pennate muscle fiber arrangement and high in-series compliance (see Glossary). The pennate architecture of distal muscles leads to a load-sensitive architectural gear ratio (Azizi et al., 2008; Eng et al., 2018; Roberts et al., 2019), which is likely to make them sensitive to external perturbations. In contrast, the high inertia and lower compliance of the proximal muscles is likely to make them less sensitive to external perturbations. Based on these mechanical differences between proximal and distal muscles, we hypothesize that proximal muscles use higher-gain feedforward control, with length and position feedback entraining CPG rhythm, whereas distal muscles rely more on intrinsic mechanics (i.e. preflexes) and short-latency load and stretch reflexes (Fig. 4). Indeed, evidence from cats suggests that proximal muscles at the hip contribute to regulation of stance–swing transitions, whereas the distal ankle extensors use force feedback to regulate stance load bearing (Donelan and Pearson, 2004; Gorassini et al., 1994; Hiebert et al., 1994; Pearson et al., 1998). Modeling studies also support this hypothesis (Dzeladini et al., 2014; see below).

## Using neuromechanical simulations and biorobots to investigate animal motor control

One theme that has emerged from neuromechanical studies is the importance of effective tuning of control to the biomechanical properties of the system and to physical interactions with the environment. However, the multi-layered, distributed and redundant nature of animal sensorimotor systems makes it challenging to rigorously understand the relationships and connections among the component systems through experiments alone. Neuromechanical simulations (i.e. numerical simulations of both neural circuits and bodies interacting with a virtual environment) can be useful tools to tackle these challenges and test hypotheses about animal motor control. Additionally, simulated neural circuits can also be tested in the real world with biomimetic robots used as physical models of animal bodies.

Because the modeler is in control of all components, models are ideally suited to study motor control in animals with an integrative perspective, following Richard Feynman's famous quote: 'What I cannot create, I do not understand'. Neuromechanical simulations and biorobots present multiple interesting properties: (i) they allow the modeler to explicitly determine, implement and modify different components (e.g. feedback loops, CPGs, muscle models); (ii) they provide access to many internal states, including quantities which are impossible to measure in moving animals; (iii) they offer the option to systematically change some properties (e.g. sizes and masses); (iv) they allow for repeatable experiments; (v) they allow 'what-if' scenarios and testing of motor behaviors not observed in nature; and (vi) they allow for multiple types of perturbations and lesion studies. Modeling experiments benefit from an iterative approach, with iterations between animal studies, hypothesis design, model design, (numerical) experiments and predictions (Webb, 2001). They are particularly useful for experiments that cannot be performed on real animals for practical, financial and/or ethical reasons.

The use of neuromechanical simulations and robots to investigate animal behavior has a fairly long history and finds its roots in early work in cybernetics (Ashby, 1957; Wiener, 2019) and in robotics, for instance, with Grey Walter's tortoise robots (Walter, 1950, 1951). Other reviews have addressed the use of simulations and robots to investigate animal behavior (Dickinson et al., 2000; Floreano et al., 2014; Holmes et al., 2006; Ijspeert, 2014; Pearson et al., 2006; Webb, 2001; 2020; Ramdya and Ijspeert, 2023). Here, we focus in particular on locomotion and on how simulations and robots can help in the investigation of the interactions between CPGs, sensory feedback loops and descending modulation, and more specifically on interactions between feedforward and feedback control.

### Models of lamprey swimming highlight the importance of the CPG in mechanically stable locomotion

The lamprey represents a good example of how numerical modeling has contributed to decoding how neural circuits interact with the body to generate swimming. A first contribution of numerical modeling has been to decipher the neuronal and network properties of rhythm generation in the local segmental circuits. The lamprey spinal cord is composed of approximately 100 segments and each segment contains neural oscillators (see Glossary) that are part of the locomotor CPG. Biophysical models of these segmental circuits have shown that several mechanisms play a role in rhythm generation, including contralateral inhibition, frequency adaptation and stretch-sensitive cells (Ekeberg et al., 1991; Hellgren et al., 1992; Traven et al., 1993; Wallén et al., 1992). The relative importance of these mechanisms likely depends on the cycle frequency, which varies extensively in the lamprey (Traven et al., 1993; Wallén et al., 1992).

Numerical and mathematical models have also investigated the complete CPG circuits, and how traveling waves of neural activity are generated along the 100 segments of the spinal cord to produce

Journal of Experimental Biology (2023) 226, jeb245784. doi:10.1242/jeb.245784

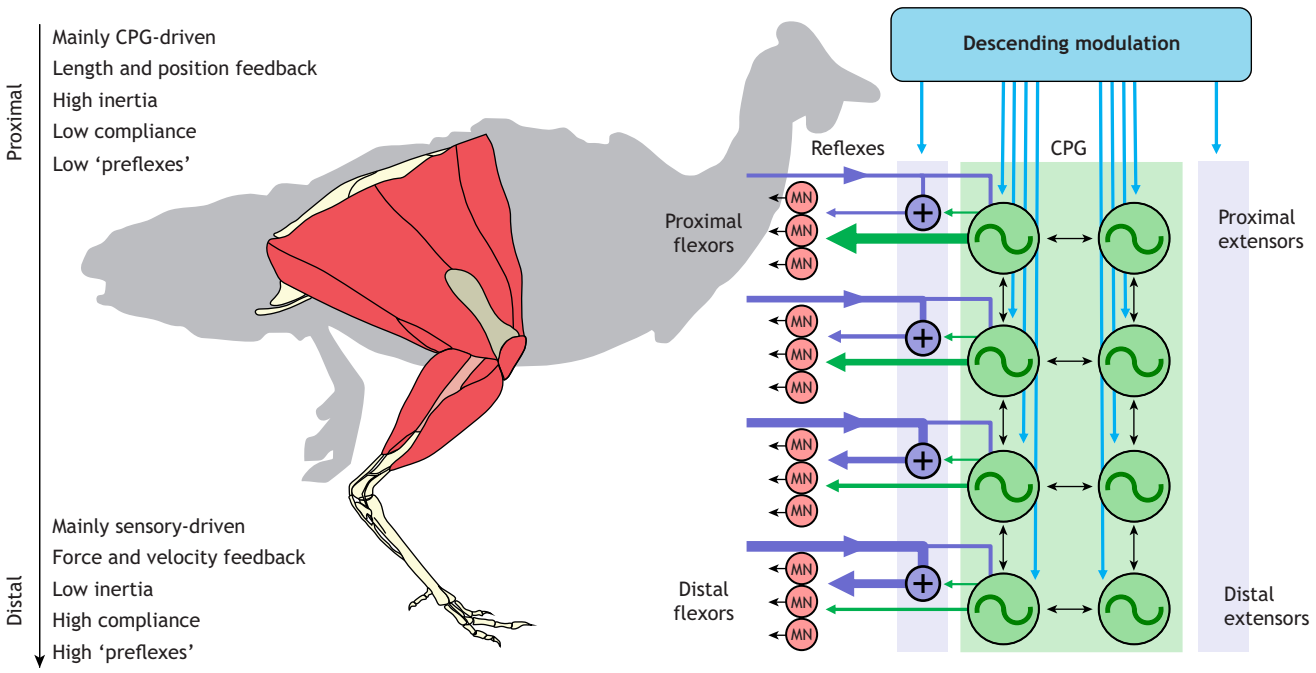


**Fig. 4. Hypothesized proximo-distal differentiation in the balance of feedforward and feedback control of limb muscles.** Owing to differences in muscle–tendon architecture and inertia of the proximal versus distal limb, it is expected that proximal muscles exhibit higher-gain feedforward control, with length and position feedback entraining the rhythm of the CPG oscillators, influencing stance and swing frequencies. In contrast, distal muscles, with higher compliance and lower inertia, are expected to have higher-gain short-latency reflexes, and higher contributions from intrinsic mechanics ('preflexes'). The width of the arrows showing the reflexes (purple) and CPG (green) is proportional to the hypothesized gains. For clarity, the peripheral circuits are drawn only for the flexors, but similar connections exist for the extensors. The plus symbol indicates summation of multiple signal paths to the motor neurons (MN).

forward swimming (Buchanan, 1992; Ekeberg, 1993; Ekeberg et al., 1995; Ijspeert, 1996; Williams, 1992a,b; Cohen et al., 1982; Kopell et al., 1991; Kopell and Ermentrout, 1988; Williams et al., 1990). It is known that neurons in the local segmental oscillators project up and down the spinal cord, thus creating couplings between oscillators. The models have shown that the most likely mechanisms to explain the phase lags between oscillators are asymmetries of inter-oscillator couplings, and that other potential explanations such as gradients of intrinsic frequencies and conduction delays are less likely.

Finally, models of the lamprey spinal cord have also been connected to simulated bodies in the water, i.e. to form complete neuromechanical simulations (Fig. 5A) and relate CPG activity to actual swimming behavior (Ekeberg, 1993; Ekeberg et al., 1995; Ekeberg and Grillner, 1999; Ijspeert, 1996; Thandiackal et al., 2021; Williams and McMillen, 2015). These neuromechanical simulations have demonstrated that the traveling waves of neural activity indeed generate forward swimming, and that modulating the descending drive signals applied to the CPG models can change the speed of swimming as well as induce turning, when symmetric and asymmetric left–right descending pathways are activated (Ekeberg, 1993). These simulations and robotic experiments (Ijspeert and Crespi, 2007) have shown that lamprey-like swimming can be obtained using CPG models without sensory feedback, supporting our hypothesis that CPGs play an important role in mechanically stable locomotion (Fig. 3). In this case, the surrounding water provides a kind of mechanical stability (i.e. by preventing large accelerations).

Note that sensory feedback still plays a useful role in lamprey swimming. Sensory feedback is necessary for handling perturbations in the water, and neuromechanical simulations have shown the role of stretch receptors (that provide feedback about curvature to the CPG) in coping with changes of flow velocity in the water (Ekeberg et al., 1995; Ijspeert et al., 1999). Thus, there are specific environments that can only be crossed when sensory feedback is included, and cannot be crossed with the CPG in open-loop.

Remarkably, a lamprey-like robot (Fig. 5B) (Thandiackal et al., 2021) has furthermore shown that local sensory feedback alone (in this case from pressure-sensitive cells in the lamprey skin) could synchronize the oscillators that comprise the CPG when direct coupling is removed. See Hamlet et al. (2023) for a similar finding in a neuromechanical simulation with stretch feedback. In other words, sensory feedback presents an alternative and redundant mechanism for traveling wave generation, separate from direct CPG coupling. This offers a high robustness against lesions, similar to that seen in eels, which can continue swimming despite full transection of the spinal cord (Wallén, 1982). It also suggests that inter-oscillator couplings might be less strong than previously thought (see discussion below).

### Models show that CPGs can induce transitions between swimming and walking in amphibians

The transition between swimming and walking has been studied in the salamander using neuromechanical simulations and robots (Fig. 5C) (Bicanski et al., 2013; Ijspeert, 2001; Ijspeert et al., 2007; Karakasiliotis et al., 2013, 2016; Knüsel et al., 2020). Because of its amphibious locomotion, the salamander represents an interesting animal to study the transition from water to ground locomotion and to create a bridge between aquatic and terrestrial vertebrate studies (Ryczko et al., 2020).

Modeling studies in salamanders have demonstrated that the transition from swimming to ground locomotion can, in principle, be obtained by extending an undulatory swimming circuit with

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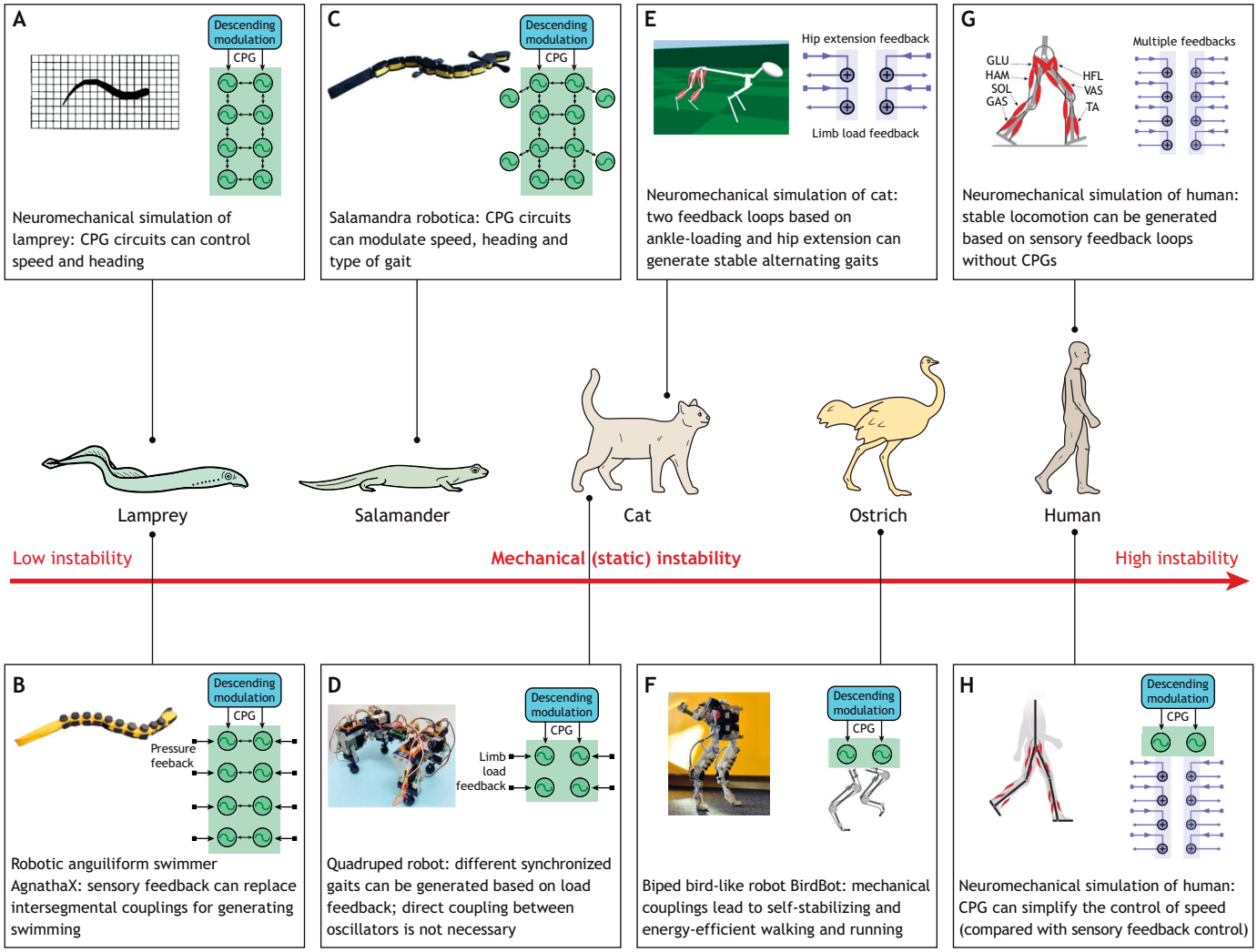


**Fig. 5. Robots and neuromechanical simulations.** Multiple robots and neuromechanical simulations have been used to investigate the roles of CPGs, sensory feedback and mechanical properties in the generation of animal locomotion. (A) Ekeberg (1993), image used with permission from Springer Nature. (B) Thandiackal et al. (2021). (C) Ijspeert et al. (2007) and Crespi et al. (2013), image used with permission from IEEE. (D) Owaki et al. (2013), image used with permission from The Royal Society Publishing. (E) Ekeberg and Pearson (2005), image used with permission from the American Physiological Society. (F) Badri-Spröwitz et al. (2022), image reprinted with permission from AAAS. (G) Geyer and Herr (2010), image used with permission from IEEE. (H) Dzeladini et al. (2014).

neural oscillators for the limbs, rather than by creating a completely new locomotor circuit for ground locomotion (Ijspeert, 2001; Ijspeert et al., 2007). Modeling reveals that the modulation of two descending drives applied to the left and right sides of the simulated circuits can vary speed, heading and even the type of gait in the simulated and robotic bodies. Thus, the patterns generated by CPGs are not rigidly fixed but can be modulated extensively for adaptive locomotion. Modeling also shows that for simple environments, locomotion can be generated purely in open-loop, i.e. using CPG models without sensory feedback (Ijspeert et al., 2007). This is due to the high mechanical stability of the sprawling posture of salamanders, with a large support polygon and a low center of mass. This therefore supports our hypothesis that mechanically stable locomotion can largely be CPG-driven (Fig. 3). But sensory feedback loops also play an important role. Local proprioceptive (stretch) feedback can reduce the variability of intersegmental phase lags toward values appropriate for locomotion and can simplify the generation of different motor behaviors (Knüsel et al., 2020). Furthermore, sensory feedback could, in principle, also replace direct coupling of CPG oscillators (Suzuki et al., 2021), similarly to what has been found for lamprey-like swimming (Thandiackal et al., 2021).

### Models of mammalian legged locomotion inform our understanding of sensory feedback and task coordination

The importance of sensory feedback in mammalian legged locomotion has been investigated by Ekeberg and Pearson (2005), who developed a neuromechanical simulation of the cat (Fig. 5E) with a focus on hindlimbs. They studied two types of feedback involved in determining the duration of the stance in a leg: one proportional to limb loading and the other proportional to hip extension. Their model did not include a CPG. The study showed that these two types of sensory feedback can generate interlimb coordination corresponding to an alternating gait and can handle irregular terrain. The findings also suggested that limb loading is more important than hip extension in providing sensory feedback. A related study investigated the role of hip extension feedback and CPGs in rat locomotor adaptation to split-belt conditions, in which

the right and left legs are on belts with different speeds (Fujiki et al., 2018). Under these conditions, hip extension could be used as a phase-resetting signal to keep the CPG entrained with the mechanical movements of the legs, such as to adapt to the split-belt conditions. These findings are consistent with the hypothesized proximo-distal differentiation in control mechanisms summarized in Fig. 4.

Controllers inspired by animal CPGs and reflex loops have become popular for the control of legged robots and have also provided new scientific insights (Aoi et al., 2017; Bellegarda and Ijspeert, 2022; Fukuoka et al., 2003; Manoonpong et al., 2007). For instance, load feedback similar to that of Ekeberg and Pearson was used to generate different gaits on a quadruped robot (Fig. 5D) (Owaki et al., 2013; Owaki and Ishiguro, 2017). Each limb was driven by a local oscillator without direct coupling to other oscillators, representing CPGs without direct couplings. Local loading feedback was sufficient to generate stable gaits, showing the importance of the body and physical interactions as mechanisms for synchronizing CPGs. Interestingly, transitions between walking, trotting and galloping gaits could be produced by simply increasing the frequency of the oscillators, as previously shown in decerebrated cats (Shik et al., 1966). This shows the potential role of sensory feedback as a task coordination mechanism (in addition to a role in perturbation responses). Similar principles have been shown in insect models, for instance, for the stick insect (Cruse, 1990; Cruse et al., 1995; Daun-Gruhn, 2011; Schilling et al., 2013).

More detailed models of mammalian CPGs have been developed by Rybak and colleagues (Danner et al., 2016, 2017; Markin et al., 2016; Rybak et al., 2015). These models reveal how CPG circuits with two layers, one for rhythm generation and the other for pattern formation, can produce several features of quadruped locomotion in open loop (without a body); even gait transitions can be produced by the activation of specific descending pathways (Danner et al., 2017). Thus, it appears that multiple mechanisms could explain gait transition (consistent with our view that animal neuromechanical systems show high redundancy); some transitions are mainly induced through descending modulation, whereas others are mainly driven by sensory feedback. The development of new full-body models of mammalian musculoskeletal systems (e.g. see Tata Ramalingasetty et al., 2021) will allow the community to investigate gait generation and modulation in more detail. Overall, evidence suggests that CPGs and sensory feedback are equally important in gait generation in quadruped mammals. It is likely that gaits in complex environments require more complex modulation of descending pathways than in simple environments, and therefore involve more cephalized, rather than spinalized, control. Similarly, slow gaits might require more descending modulation than fast gaits, to allow the animal to maintain posture and balance (Fig. 3).

### Numerical models suggest that biped locomotion relies more on sensory feedback than on CPGs

Some of the first neuromechanical simulations of biped locomotion were developed by Taga and colleagues (Taga, 1995, 1998; Taga et al., 1991). These simulations of human walking demonstrated how robust locomotion could emerge from the interaction of CPGs and reflexes. Multiple studies have since explored the interplay of CPGs and reflexes in biped locomotion with simulations and robots (Aoi et al., 2019; Fujiki et al., 2015; Geyer and Herr, 2010; Ryu and Kuo, 2021; Van der Noot et al., 2018, 2019). A particularly influential neuromechanical model developed by Geyer and Herr (2010) demonstrated that a limited number of reflexes can generate stable locomotion without the need for CPG circuits (Fig. 5G). The simulated gaits closely match human gait recordings in terms of joint kinematics, ground reaction forces and muscle activities. Although the model did not include a CPG, it did depend on a finite-state machine that selectively activates and deactivates reflexes, so that they are only active at particular phases of the locomotor cycle. One could argue such a gating mechanism represents a similar function as a CPG and could in fact be implemented in a CPG circuit.

The Geyer and Herr model has inspired several follow-up models to investigate gait modulation (Dzeladini et al., 2014; Ramadan et al., 2022; Russo et al., 2021; Song and Geyer, 2015), 3D walking and running (Wang et al., 2012), and locomotor pathologies (Bruel et al., 2022; Ong et al., 2019; Song and Geyer, 2018). Control of speed is difficult to achieve with a purely sensory-driven circuit, as it requires the modulation of multiple reflex gains with non-linear functions. Dzeladini et al. (2014) demonstrated that adding CPG circuits to the sensory-driven model of Geyer and Herr (2010) could simplify the control of speed (Fig. 5H). They achieved speed regulation over a large range using simple drive signals that modulated the frequencies and amplitudes of the CPG oscillations. Interestingly, they obtained the best speed control by adding oscillators only to the muscles controlling the hip joints. These simulations support the hypothesis proposed by Daley et al. (2007) – based on perturbations to running gaits of birds – that proximal joints are controlled with higher-gain feedforward (CPG) signals and distal joints are controlled by higher-gain feedback signals (Fig. 4).

Overall, it is clear from these simulation studies that sensory-feedback loops are essential for human locomotion, supporting our hypothesis that mechanically unstable locomotion is more sensory driven than CPG driven (Fig. 3). CPGs are likely to contribute mainly to speed and gait modulation. Interestingly, the simulations of Geyer and Herr (2010) and most follow-up simulations are not capable of producing slow and very slow walking, because the simulated models simply fall. This suggests more sophisticated balance control mechanisms are missing in the models, and hence these models do not yet properly implement the more important role of descending modulation that we hypothesize for unstable locomotion (Fig. 3).

The neuromechanics of bipedal locomotion of birds has been less commonly modeled than human locomotion. One neuromechanical simulation study demonstrated that the sensory-driven control architectures of Geyer and Herr (2010) and Wang et al. (2012) could be adapted to control an ostrich-like body (Geijtenbeek et al., 2013). A number of bird-like robots have also been developed (Apgar et al., 2018; Badri-Spröwitz et al., 2022; Pratt et al., 2001). Among these, BirdBot is particularly interesting, because it implements a bird-inspired tendon system that uses mechanical coupling to control leg stiffness in the stance and swing phases (Fig. 5F). The mechanically coupled design provides self-stable and energy-efficient walking and running with simple CPG-based control and no sensory feedback, highlighting intrinsically stable features of the avian distal limb. Therefore, this represents another source of redundancy, in which the intrinsic musculoskeletal mechanics contributes to intralimb coordination and balance, aspects that are often considered to be pure control problems.

## Open questions

Here, we have reviewed historical and current perspectives on the organization of locomotor circuits based on experimental and modeling evidence. Although there are shared features of the component elements across vertebrates, there is also diversity in the

relative contributions of these components. We have proposed several hypotheses about how the respective roles of CPGs, reflexes and descending modulation vary across vertebrates: depending on body size, the mechanical instability of gaits, the speed of locomotion and the developmental time to locomotor maturity. We have also hypothesized that these roles can vary within the body, between proximal to distal joints, and depending on the speed and gait. However, to rigorously confirm or reject these hypotheses, we need further integration of animal experiments and neuromechanical simulations.

Numerical models can be particularly useful to test some of these hypotheses. For instance, neuromechanical simulations of a pendulum (which can be viewed as a very simple model of a leg) have shown that periodic behaviors can be obtained by either purely feedback or purely feedforward (CPG-based) mechanisms; however, circuits that combine both feedback and feedforward contributions are more robust against unexpected disturbances and sensorimotor noise (Kuo, 2002). Similar results are obtained with a simulation of biped locomotion (Ryu and Kuo, 2021). An interesting proposition from Kuo and colleagues is that CPGs can be viewed as 'state estimators' that predict the state of limbs (and therefore sensory signals). Based on this, a CPG could be viewed as a 'filter for processing sensory information rather than as a generator of commands' (Kuo, 2002). In our view, this perspective underestimates the role of CPGs in coordinating and modulating locomotion (e.g. for regulating speed, gait and heading), but it has the merit of analyzing the trade-off between feedforward and feedback control using rigorous optimal estimation principles. Importantly, the potential roles of the CPG as a pattern generator and a state estimator are not necessarily mutually exclusive – CPGs may act as a type of internal model that filters sensory inputs, estimates current state and generates rhythmic outputs based on current state estimates.

Another important open question is related to the degree of centralization of locomotion control and the strength of inter-oscillator couplings within and across animals (Aoi et al., 2017; Holmes et al., 2006; Neveln et al., 2019; Revzen et al., 2009). Historically, fictive locomotion experiments gave the impression that locomotor patterns were mainly generated by CPGs, and that inter-oscillator couplings serve as the mechanism for inter-joint coordination. However, as presented above, modeling has shown that sensory feedback is another mechanism for synchronization that can replace inter-oscillator couplings (Cruse et al., 1995; Owaki et al., 2013; Thandiackal et al., 2021; Suzuki et al., 2021). Biological evidence also shows that local sensory feedback is directly integrated into segmentally distributed CPGs (Grillner et al., 1981; Grillner and Wallén, 1984; Pearson, 2008; Rossignol et al., 2006; Whelan, 1996). Inter-oscillator couplings might therefore be weaker than previously thought. This relatively decentralized control organization would allow for flexible motor patterns to be adapted to environmental constraints, through sensing and modulation of descending pathways.

Neveln et al. (2019) have proposed an interesting framework based on mutual information to quantify centralization in animal locomotion, which could help systematically investigate the degree of centralization across species and conditions. They suggest that locomotor coordination 'could either be achieved through strong, global coupling with dense connections between components', representing high centralization, or 'through weak, local coupling with sparse connections', representing low centralization. Furthermore, centralization can also be affected by the strength of mechanical coupling and the organization of sensory feedback, regardless of whether it is processed centrally or locally (Holmes et al., 2006). Neveln and colleagues (2019) tested their approach in simulation, with robots, and in cockroach experiments. This model-free, empirical method of quantifying centralization will be useful for analyzing future neuromechanical models and animal experiments. It is likely that the level of centralization depends on the morphology and stability of locomotion, as well as on environmental conditions (speed of locomotion and complexity of the environment). Consistent with this, the strength of coupling between legs appears to be speed-dependent in invertebrates (*Drosophila*), with no coupling at low speeds of walking and high coupling at high speeds (Berendes et al., 2016). Further research is needed to clarify the mechanisms that enable variation in coupling strength with speed, and to understand the diversity of oscillator coupling strengths across species with varying locomotor demands.

Concerning descending modulation, we do not yet know exactly how many independent descending pathways exist, how many local spinal locomotor circuits they project to (global versus local joint-specific projections), and their effect (activating oscillators, changing a joint offset or modulating reflexes, for instance). From several studies (Arber and Costa, 2022; Ferreira-Pinto et al., 2018; Rossignol et al., 2006), we know that descending projections present a mix of these properties. Modeling studies have started exploring how different aspects of legged locomotion (e.g. frequency, step size, ground clearance and others) can be modulated by descending pathways (Song and Geyer, 2015; Bellegarda and Ijspeert, 2022; Ramadan et al., 2022). But more studies are needed to investigate the diversity of descending pathways across species and how they relate to motor behaviors and mechanical features of the body. Decoding descending pathways will be particularly important in allowing us to understand what types of voluntary movements an animal can perform (for instance, for gait transitions and for limb placement in visually guided locomotion). Animals can smoothly switch between steady-state locomotion and highly modulated locomotion as needed when crossing a complex terrain. It is likely that this is done by switching from activating a small number of descending pathways to more complex time-varying activations of multiple descending pathways. This is related to the concept of relatively spinalized versus cephalized control, discussed above. Also, some animals appear to be better than others at performing fine-tuned movements, and this may reflect a higher number of descending pathways and a larger role of descending modulation in mammals than in amphibians, for example (Fig. 3). Integration of experimental and modeling work is needed to test these ideas.

## Conclusions and outlook

We envision a bright future for the next 100 years of research in this area, with exciting opportunities to integrate experiments and modeling to address open questions about the neuromechanical control of locomotion. Thanks to new imaging techniques and genetic identification methods, future full atlases and connectomes of spinal circuits and descending and ascending pathways will be tremendously useful to improve our understanding of the underlying circuits involved in vertebrate locomotion. For instance, by quantifying the proportion of sensory neurons within the spinal cord and the number of independent descending pathways (Arber and Costa, 2022; Ferreira-Pinto et al., 2018), it will be possible to more quantitatively estimate the respective roles of sensory feedback, CPGs and descending modulation across different vertebrate animals. We hope that these techniques will not be limited to classic genetic model animals (e.g. zebrafish and

mice), but also used extensively across diverse species to allow comparison between different morphologies and locomotor modes. In particular, compared with the rich literature on terrestrial locomotion, there has been relatively little research on the diversity of sensorimotor control mechanisms among flying vertebrates, which is an important area for further study.

Additionally, advances in optogenetic and chemogenetic techniques represent a tremendous opportunity to selectively activate or deactivate specific cell types, performing experiments that were previously possible only in simulation. There are exciting opportunities for new 'virtual twin' experiments that combine experimental technologies and computing power for simulations; for example, by creating neuromechanical simulations that replicate animal behavior in real-time, it could become feasible to conduct state-dependent animal experiments, in which a perturbation is applied when a modeled internal state from the simulation (e.g. tension in a tendon or phase of an oscillator) reaches a specific threshold (see Ramdya and Ijspeert 2023 for additional ideas). It might also become possible to create hybrid experiments in which a spinal cord preparation is connected in closed loop with a musculoskeletal simulation moving in a virtual physics-based environment. In such an experiment, recorded activity from ventral roots would be used to activate simulated muscles, and virtual sensory signals from the simulated moving body would be used to stimulate sensory neurons. Such preparations would allow one to record and investigate spinal cord circuits with all the technologies available for controlled bench experiments while still approximating *in vivo* conditions of unconstrained locomotion. These kinds of integrative studies will be essential for testing hypotheses about of the fundamental principles of locomotion in vertebrates, understanding how control varies among species, and for guiding functional restoration and therapeutic approaches such as electric epidural stimulation (van den Brand et al., 2012; Wagner et al., 2018).

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#### References
**Af Klint, R., Mazzaro, N., Nielsen, J. B., Sinkjaer, T. and Grey, M. J.** (2010). Load rather than length sensitive feedback contributes to soleus muscle activity during human treadmill walking. *J. Neurophysiol.* **103**, 2747-2756. doi:10.1152/jn.00547.2009

**Alexander, R. M.** (2002). Stability and manoeuvrability of terrestrial vertebrates. *Integr. Comp. Biol.* **42**, 158-164. doi:10.1093/icb/42.1.158

**Aoi, S., Manoonpong, P., Ambe, Y., Matsuno, F. and Wörgötter, F.** (2017). Adaptive control strategies for interlimb coordination in legged robots: a review. *Front. Neurorobot.* **11**, 39. doi:10.3389/fnbot.2017.00039

**Aoi, S., Ohashi, T., Bamba, R., Fujiki, S., Tamura, D., Funato, T., Senda, K., Ivanenko, Y. and Tsuchiya, K.** (2019). Neuromusculoskeletal model that walks and runs across a speed range with a few motor control parameter changes based on the muscle synergy hypothesis. *Sci. Rep.* **9**, 369. doi:10.1038/s41598-018-37460-3

**Apgar, T., Clary, P., Green, K., Fern, A. and Hurst, J. W.** (2018). *Fast Online Trajectory Optimization for the Bipedal Robot Cassie*. Robotics: Science and Systems.

**Arber, S. and Costa, R. M.** (2022). Networking brainstem and basal ganglia circuits for movement. *Nat. Rev. Neurosci.* **23**, 6. doi:10.1038/s41583-022-00581-w

**Ashby, W. R.** (1957). *An Introduction to Cybernetics*. Chapman & Hall Ltd.

**Azizi, E., Brainerd, E. L. and Roberts, T. J.** (2008). Variable gearing in pennate muscles. *Proc. Natl. Acad. Sci. USA* **105**, 1745-1750. doi:10.1073/pnas.0709212105

**Badri-Spröwitz, A., Aghamaleki Sarvestani, A., Sitti, M. and Daley, M. A.** (2022). BirdBot achieves energy-efficient gait with minimal control using avian-inspired leg clutching. *Sci. Robot.* **7**, eabg4055. doi:10.1126/scirobotics.abg4055

**Barbeau, H. and Rossignol, S.** (1987). Recovery of locomotion after chronic spinalization in the adult cat. *Brain Res.* **412**, 84-95. doi:10.1016/0006-8993(87)91442-9

**Bellegarda, G. and Ijspeert, A.** (2022). CPG-RL: learning central pattern generators for quadruped locomotion. *IEEE Robot. Autom. Lett.* **7**, 12547-12554. doi:10.1109/LRA.2022.3218167

**Bennett, P. M. and Harvey, P. H.** (1985). Brain size, development and metabolism in birds and mammals. *J. Zool.* **207**, 491-509. doi:10.1111/j.1469-7998.1985.tb04946.x

**Berendes, V., Zill, S. N., Büschges, A. and Bockemühl, T.** (2016). Speed-dependent interplay between local pattern-generating activity and sensory signals during walking in *Drosophila*. *J. Exp. Biol.* **219**, 3781-3793. doi:10.1242/jeb.146720

**Bicanski, A., Ryczko, D., Knuesel, J., Harischandra, N., Charrier, V., Ekeberg, Ö., Cabelguen, J.-M. and Ijspeert, A. J.** (2013). Decoding the mechanisms of gait generation in salamanders by combining neurobiology, modeling and robotics. *Biol. Cybern.* **107**, 545-564. doi:10.1007/s00422-012-0543-1

**Bidaye, S. S., Bockemühl, T. and Büschges, A.** (2018). Six-legged walking in insects: how CPGs, peripheral feedback, and descending signals generate coordinated and adaptive motor rhythms. *J. Neurophysiol.* **119**, 459-475. doi:10.1152/jn.00658.2017

**Biewener, A. A.** (1989). Scaling body support in mammals: limb posture and muscle mechanics. *Science* **245**, 45-48. doi:10.1126/science.2740914

**Brown, I. E. and Loeb, G. E.** (2000). A reductionist approach to creating and using neuromusculoskeletal models. In *Biomechanics and Neural Control of Posture and Movement*, (ed. J. M. Winters and P. E. Crago), pp. 148-163. Springer.

**Bruel, A., Ghorbel, S. B., Di Russo, A., Stanev, D., Armand, S., Courtine, G. and Ijspeert, A.** (2022). Investigation of neural and biomechanical impairments leading to pathological toe and heel gaits using neuromusculoskeletal modelling. *J. Physiol.* **600**, 2691-2712. doi:10.1113/JP282609

**Buchanan, J. T.** (1992). Neural network simulations of coupled locomotor oscillators in the lamprey spinal cord. *Biol. Cybern.* **66**, 367-374. doi:10.1007/BF00203673

**Buschmann, T., Ewald, A., von Twickel, A. and Buesches, A.** (2015). Controlling legs for locomotion—Insights from robotics and neurobiology. *Bioinspir. Biomim.* **10**, 041001. doi:10.1088/1748-3190/10/4/041001

**Büschges, A.** (2005). Sensory control and organization of neural networks mediating coordination of multisegmental organs for locomotion. *J. Neurophysiol.* **93**, 1127-1135. doi:10.1152/jn.00615.2004

**Cabelguen, J. M., Bourcier-Lucas, C. and Dubuc, R.** (2003). Bimodal locomotion elicited by electrical stimulation of the midbrain in the salamander Notophthalmus viridesecens. *J. Neurosci.* **23**, 2434-2439. doi:10.1523/JNEUROSCI.23-06-02434.2003

**Cheng, J., Stein, R. B., Jovanovic, K., Yoshida, K., Bennett, D. J. and Han, Y.** (1998). Identification, localization, and modulation of neural networks for walking in the mudpuppy (*Necturus maculatus*) spinal cord. *J. Neurosci.* **18**, 4295-4304. doi:10.1523/JNEUROSCI.18-11-04295.1998

**Chevallier, S., Ijspeert, A. J., Ryczko, D., Nagy, F. and Cabelguen, J.-M.** (2008). Organisation of the spinal central pattern generators for locomotion in the salamander: biology and modelling. *Brain Res. Rev.* **57**, 147-161. doi:10.1016/j.brainresrev.2007.07.006

**Cohen, A. H., Holmes, P. J. and Rand, R.** (1982). The nature of coupling between segmented oscillations and the lamprey spinal generator for locomotion: a mathematical model. *J. Math. Biol.* **13**, 345-369. doi:10.1007/BF00276069

**Crespi, A., Karakasiliotis, K., Guignard, A. and Ijspeert, A. J.** (2013). Salamandra Robotica II: an amphibious robot to study salamander-like swimming and walking gaits. *IEEE Trans. Robot.* **29**, 308-320. doi:10.1109/TRO.2012.2234311

**Cruse, H.** (1990). What mechanisms coordinate leg movement in walking arthropods? *Trends Neurosci.* **13**, 15-21. doi:10.1016/0166-2236(90)90057-H

**Cruse, H., Brunn, D. E., Bartling, C., Dean, J., Dreifert, M., Kindermann, T. and Schmitz, J.** (1995). Walking: a complex behavior controlled by simple networks. *Adapt. Behav.* **3**, 385-418. doi:10.1177/105971239500300403

**Daley, M. A.** (2018). Understanding the agility of running birds: sensorimotor and mechanical factors in avian bipedal locomotion. *Integr. Comp. Biol.* **58**, 884-893.

**Daley, M. A. and Biewener, A. A.** (2011). Leg muscles that mediate stability: mechanics and control of two distal extensor muscles during obstacle negotiation in the guinea fowl. *Philos. Trans. R. Soc. B Biol. Sci.* **366**, 1580-1591. doi:10.1098/rstb.2010.0338

**Daley, M. A. and Birn-Jeffery, A.** (2018). Scaling of avian bipedal locomotion reveals independent effects of body mass and leg posture on gait. *J. Exp. Biol.* **221**, jeb152538. doi:10.1242/jeb.152538
**Daley, M. A., Felix, G. and Biewener, A. A.** (2007). Running stability is enhanced by a proximo-distal gradient in joint neuromechanical control. *J. Exp. Biol.* **210**, 383-394. doi:10.1242/jeb.02668
**Daley, M. A., Voloshina, A. and Biewener, A. A.** (2009). The role of intrinsic muscle mechanics in the neuromuscular control of stable running in the guinea fowl. *J. Physiol.* **587**, 2693-2707. doi:10.1113/jphysiol.2009.171017
**Danner, S. M., Wilshin, S. D., Shevtsova, N. A. and Rybak, I. A.** (2016). Central control of interlimb coordination and speed-dependent gait expression in quadrupeds. *J. Physiol.* **594**, 6947-6967. doi:10.1113/JP272787
**Danner, S. M., Shevtsova, N. A., Frigon, A. and Rybak, I. A.** (2017). Computational modeling of spinal circuits controlling limb coordination and gaits in quadrupeds. *eLife* **6**, e31050. doi:10.7554/eLife.31050
**Daun-Gruhn, S.** (2011). A mathematical modeling study of inter-segmental coordination during stick insect walking. *J. Comput. Neurosci.* **30**, 255-278. doi:10.1007/s10827-010-0254-3
**Dickinson, M. H., Farley, C. T., Full, R. J., Koehl, M. A. R., Kram, R. and Lehman, S.** (2000). How animals move: an integrative view. *Science* **288**, 100-106. doi:10.1126/science.288.5463.100
**Donelan, J. M. and Pearson, K. G.** (2004). Contribution of force feedback to ankle extensor activity in decerebrate walking cats. *J. Neurophysiol.* **92**, 2093-2104. doi:10.1152/jn.00325.2004
**Dzeladini, F., van den Kieboom, J. and Ijspeert, A.** (2014). The contribution of a central pattern generator in a reflex-based neuromuscular model. *Front. Hum. Neurosci.* **8**, 371. doi:10.3389/fnhum.2014.00371
**Ekeberg, Ö.** (1993). A combined neuronal and mechanical model of fish swimming. *Biol. Cybern.* **69**, 363-374. doi:10.1007/BF01185408
**Ekeberg, Ö. and Grillner, S.** (1999). Simulations of neuromuscular control in lamprey swimming. *Philos. Trans. R. Soc. B Biol. Sci.* **354**, 895-902. doi:10.1098/rstb.1999.0441
**Ekeberg, Ö. and Pearson, K.** (2005). Computer simulation of stepping in the hind legs of the cat: an examination of mechanisms regulating the stance-to-swing transition. *J. Neurophysiol.* **94**, 4256-4268. doi:10.1152/jn.00065.2005
**Ekeberg, Ö., Lansner, A. and Grillner, S.** (1995). The neural control of fish swimming studied through numerical simulations. *Adapt. Behav.* **3**, 363-384. doi:10.1177/105971239500300402
**Ekeberg, Ö., Wallén, P., Lansner, A., Traven, H., Brodin, L. and Grillner, S.** (1991). A computer-based model for realistic simulations of neural networks I: the single neuron and synaptic interaction. *Biol. Cybern.* **65**, 81-90. doi:10.1007/BF00202382
**Eng, C. M., Azizi, E. and Roberts, T. J.** (2018). Structural determinants of muscle gearing during dynamic contractions. *Integr. Comp. Biol.* **58**, 207-218. doi:10.1093/icb/icy054
**Ferreira-Pinto, M. J., Ruder, L., Capelli, P. and Arber, S.** (2018). Connecting circuits for supraspinal control of locomotion. *Neuron* **100**, 361-374. doi:10.1016/j.neuron.2018.09.015
**Fetcho, J. R. and McLean, D. L.** (2010). Some principles of organization of spinal neurons underlying locomotion in zebrafish and their implications. *Ann. N. Y. Acad. Sci.* **1198**, 94-104. doi:10.1111/j.1749-6632.2010.05539.x
**Floreano, D., Ijspeert, A. J. and Schaal, S.** (2014). Robotics and neuroscience. *Curr. Biol.* **24**, R910-R920. doi:10.1016/j.cub.2014.07.058
**Forssberg, H., Grillner, S., Halbertsma, J. and Rossignol, S.** (1980). The locomotion of the low spinal cat. II. Interlimb coordination. *Acta Physiol. Scand.* **108**, 283-295. doi:10.1111/j.1748-1716.1980.tb06534.x
**Fouad, A. D., Teng, S., Mark, J. R., Liu, A., Alvarez-Illera, P., Ji, H., Du, A., Bhirgoo, P. D., Cornblath, E., Guan, S. A. et al.** (2018). Distributed rhythm generators underlie *Caenorhabditis elegans* forward locomotion. *ELife* **7**, e29913. doi:10.7554/eLife.29913
**Fujiki, S., Aoi, S., Funato, T., Tomita, N., Senda, K. and Tsuchiya, K.** (2015). Adaptation mechanism of interlimb coordination in human split-belt treadmill walking through learning of foot contact timing: a robotics study. *J. R. Soc. Interface* **12**, 20150542. doi:10.1098/rsif.2015.0542
**Fujiki, S., Aoi, S., Funato, T., Sato, Y., Tsuchiya, K. and Yanagihara, D.** (2018). Adaptive hindlimb split-belt treadmill walking in rats by controlling basic muscle activation patterns via phase resetting. *Sci. Rep.* **8**, 17341. doi:10.1038/s41598-018-35714-8
**Fukuoka, Y., Kimura, H. and Cohen, A. H.** (2003). Adaptive dynamic walking of a quadruped robot on irregular terrain based on biological concepts. *Int. J. Robot. Res.* **22**, 187-202. doi:10.1177/0278364903022003004
**Full, R. J. and Koditschek, D. E.** (1999). Templates and anchors: neuromechanical hypotheses of legged locomotion on land. *J. Exp. Biol.* **202**, 3325-3332. doi:10.1242/jeb.202.23.3325
**Garwicz, M., Christensson, M. and Psouni, E.** (2009). A unifying model for timing of walking onset in humans and other mammals. *Proc. Natl. Acad. Sci. USA* **106**, 21889-21893. doi:10.1073/pnas.0905777106
**Gatesy, S. M. and Biewener, A. A.** (1991). Bipedal locomotion: effects of speed, size and limb posture in birds and humans. *J. Zool.* **224**, 127-147. doi:10.1111/j.1469-7998.1991.tb04794.x
**Geijtenbeek, T., van de Panne, M. and van der Stappen, A. F.** (2013). Flexible muscle-based locomotion for bipedal creatures. *ACM Trans. Graph.* **32**, 206. doi:10.1145/2508363.2508399
**Geyer, H. and Herr, H.** (2010). A muscle-reflex model that encodes principles of legged mechanics produces human walking dynamics and muscle activities. *IEEE Trans. Neural Syst. Rehabil. Eng.* **18**, 263-273. doi:10.1109/TNSRE.2010.2047592
**Gorassini, M. A., Prochazka, A., Hiebert, G. W. and Gauthier, M. J.** (1994). Corrective responses to loss of ground support during walking. I. Intact cats. *J. Neurophysiol.* **71**, 603-610. doi:10.1152/jn.1994.71.2.603
**Graham Brown, T.** (1911). The intrinsic factors in the act of progression in the mammal. *Proc. R. Soc. Lond. Ser. B* **84**, 308-319.
**Graham Brown, T.** (1914). On the nature of the fundamental activity of the nervous centres; together with an analysis of the conditioning of rhythmic activity in progression, and a theory of the evolution of function in the nervous system. *J. Physiol.* **48**, 18-46. doi:10.1113/jphysiol.1914.sp001646
**Gray, J.** (1933). Studies in animal locomotion: I. The movement of fish with special reference to the eel. *J. Exp. Biol.* **10**, 88-104. doi:10.1242/jeb.10.1.88
**Gray, J.** (1936). Studies in animal locomotion: V. Resistance reflexes in the eel. *J. Exp. Biol.* **13**, 181-191. doi:10.1242/jeb.13.2.181
**Gray, J. and Lissmann, H. W.** (1938). Studies in animal locomotion: VII. Locomotory reflexes in the earthworm. *J. Exp. Biol.* **15**, 506-517. doi:10.1242/jeb.15.4.506
**Gray, J. and Lissmann, H. W.** (1940). Ambulatory reflexes in spinal amphibians. *J. Exp. Biol.* **17**, 237-251. doi:10.1242/jeb.17.2.237
**Gray, J. and Sand, A.** (1936). The locomotory rhythm of the dogfish (*Scyllium canicula*). *J. Exp. Biol.* **13**, 200-209. doi:10.1242/jeb.13.2.200
**Gray, J., Lissmann, H. W. and Pumphrey, R. J.** (1938). The mechanism of locomotion in the leech (*Hirudo medicinalis* Ray). *J. Exp. Biol.* **15**, 408-430. doi:10.1242/jeb.15.3.408
**Grillner, S.** (1985). Neural control of vertebrate locomotion – central mechanisms and reflex interaction with special reference to the cat. In *Feedback and Motor Control in Invertebrates and Vertebrates*, (ed. W. J. P. Barnes and M. H. Gladden), pp. 35-56. Croom Helm.
**Grillner, S. and El Manira, A.** (2019). Current principles of motor control, with special reference to vertebrate locomotion. *Physiol. Rev.* **100**, 271-320. doi:10.1152/physrev.00015.2019
**Grillner, S. and Wallén, P.** (1982). On peripheral control mechanisms acting on the central pattern generators for swimming in the dogfish. *J. Exp. Biol.* **98**, 1-22. doi:10.1242/jeb.98.1.1
**Grillner, S. and Wallén, P.** (1984). How does the lamprey central nervous system make the lamprey swim? *J. Exp. Biol.* **112**, 337-357. doi:10.1242/jeb.112.1.337
**Grillner, S. and Wallen, P.** (1985). Central pattern generators for locomotion, with special reference to vertebrates. *Annu. Rev. Neurosci.* **8**, 233-261. doi:10.1146/annurev.ne.08.030185.001313
**Grillner, S., McClellan, A. and Perret, C.** (1981). Entrainment of the spinal pattern generators for swimming by mechano-sensitive elements in the lamprey spinal cord *in vitro*. *Brain Res.* **217**, 380-386. doi:10.1016/0006-8993(81)90015-9
**Grillner, S., Degliana, T., Ekeberg, Ö., El Marina, A., Lansner, A., Orlovsky, G. N. and Wallén, P.** (1995). Neural networks that co-ordinate locomotion and body orientation in lamprey. *Trends Neurosci.* **18**, 270-279. doi:10.1016/0166-2236(95)80008-P
**Grillner, S., Wallén, P., Saitoh, K., Kozlov, A. and Robertson, B.** (2008). Neural bases of goal-directed locomotion in vertebrates—An overview. *Brain Res. Rev.* **57**, 2-12. doi:10.1016/j.brainresrev.2007.06.027
**Hamlet, C., Fauci, L., Morgan, J. R. and Tytell, E. D.** (2023). Proprioceptive feedback amplification restores effective locomotion in a neuromechanical model of lampreys with spinal injuries. *Proc. Natl. Acad. Sci. USA* **120**, e2213302120. doi:10.1073/pnas.2213302120
**Haimson, B., Hadas, Y., Bernat, N., Kania, A., Daley, M. A., Cinnamon, Y., Lev-Tov, A. and Klar, A.** (2021). Spinal lumbar dI2 interneurons contribute to stability of bipedal stepping. *eLife* **10**, e62001. doi:10.7554/eLife.62001
**Hellgren, J., Grillner, S. and Lansner, A.** (1992). Computer simulation of the segmental neural network generating locomotion in lamprey by using populations of network interneurons. *Biol. Cybern.* **68**, 1-13. doi:10.1007/BF00203132
**Hiebert, G. W. and Pearson, K. G.** (1999). Contribution of sensory feedback to the generation of extensor activity during walking in the decerebrate cat. *J. Neurophysiol.* **81**, 758-770. doi:10.1152/jn.1999.81.2.758
**Hiebert, G. W., Gorassini, M. A., Jiang, W., Prochazka, A. and Pearson, K. G.** (1994). Corrective responses to loss of ground support during walking. II. Comparison of intact and chronic spinal cats. *J. Neurophysiol.* **71**, 611-622. doi:10.1152/jn.1994.71.2.611
**Ho, S. and O'Donovan, M. J.** (1993). Regionalization and intersegmental coordination of rhythm-generating networks in the spinal cord of the chick embryo. *J. Neurosci.* **13**, 1354-1371. doi:10.1523/JNEUROSCI.13-04-01354.1993
**Holmes, P., Full, R. J., Koditschek, D. and Guckenheimer, J.** (2006). The dynamics of legged locomotion: models, analyses, and challenges. *SIAM Rev.* **48**, 207-304. doi:10.1137/S0036144504445133

**Hughes, G. M.** (1952). The co-ordination of insect movements: I. The walking movements of insects. *J. Exp. Biol.* **29**, 267-285. doi:10.1242/jeb.29.2.267
**Hughes, G. M.** (1957). The co-ordination of insect movements: II. The effect of limb amputation and the cutting of commissures in the cockroach (*Blatta orientalis*). *J. Exp. Biol.***34**, 306-333. doi:10.1242/jeb.34.3.306
**Ijspeert, A. J.** (1996). Modelling the neural controller of a swimming lamprey: a comparison of naturally and artificially evolved networks. MSc thesis, University of Edinburgh.
**Ijspeert, A. J.** (2001). A connectionist central pattern generator for the aquatic and terrestrial gaits of a simulated salamander. *Biol. Cybern.* **84**, 331-348. doi:10.1007/s004220000211
**Ijspeert, A. J.** (2014). Biorobotics: using robots to emulate and investigate agile locomotion. *Science* **346**, 196-203. doi:10.1126/science.1254486
**Ijspeert, A. J.** (2020). Amphibious and sprawling locomotion: from biology to robotics and back. *Ann. Rev. Control Robot. Auton. Syst.* **3**, 173-193. doi:10.1146/annurev-control-091919-095731
**Ijspeert, A. J. and Crespi, A.** (2007). Online trajectory generation in an amphibious snake robot using a lamprey-like central pattern generator model. In Proceedings - IEEE International Conference on Robotics and Automation, 262-268. doi:10.1109/ROBOT.2007.363797
**Ijspeert, A. J., Hallam, J. and Willshaw, D.** (1999). Evolving swimming controllers for a simulated lamprey with inspiration from neurobiology. *Adapt. Behav.* **7**, 151-172. doi:10.1177/105971239900700202
**Ijspeert, A. J., Crespi, A., Ryczko, D. and Cabelguen, J.-M.** (2007). From swimming to walking with a salamander robot driven by a spinal cord model. *Science* **315**, 1416-1420. doi:10.1126/science.1138353
**Ito, M.** (2008). Control of mental activities by internal models in the cerebellum. *Nat. Rev. Neurosci.* **9**, 304-313. doi:10.1038/nrn2332
**Jindrich, D. L. and Full, R. J.** (2002). Dynamic stabilization of rapid hexapedal locomotion. *J. Exp. Biol.* **205**, 2803-2823. doi:10.1242/jeb.205.18.2803
**Karakasiliotis, K., Schilling, N., Cabelguen, J.-M. and Ijspeert, A. J.** (2013). Where are we in understanding salamander locomotion: biological and robotic perspectives on kinematics. *Biol. Cybern.* **107**, 529-544. doi:10.1007/s00422-012-0540-4
**Karakasiliotis, K., Thandiackal, R., Melo, K., Horvat, T., Mahabadi, N. K., Tsitkov, S., Cabelguen, J. M. and Ijspeert, A. J.** (2016). From cineradiography to biorobots: an approach for designing robots to emulate and study animal locomotion. *J. R. Soc. Interface* **13**, 20151089. doi:10.1098/rsif.2015.1089
**Kiehn, O.** (2011). Development and functional organization of spinal locomotor circuits. *Curr. Opin. Neurobiol.* **21**, 100-109. doi:10.1016/j.conb.2010.09.004
**Kiehn, O.** (2016). Decoding the organization of spinal circuits that control locomotion. *Nat. Rev. Neurosci.* **17**, 224-238. doi:10.1038/nrn.2016.9
**Knüsel, J., Crespi, A., Cabelguen, J.-M., Ijspeert, A. J. and Ryczko, D.** (2020). Reproducing five motor behaviors in a salamander robot with virtual muscles and a distributed CPG controller regulated by drive signals and proprioceptive feedback. *Front. Neurorobot.* **14**, 604426. doi:10.3389/fnbot.2020.604426
**Kopell, N. and Ermentrout, G. B.** (1988). Coupled oscillators and the design of central pattern generators. *Math. Biosci.* **90**, 87-109. doi:10.1016/0025-5564(88)90059-4
**Kopell, N., Ermentrout, G. B. and Williams, T. L.** (1991). On chains of oscillators forced at one end. *SIAM J. Appl. Math.* **51**, 1397-1417. doi:10.1137/0151070
**Kriellaars, D. J., Brownstone, R. M., Noga, B. R. and Jordan, L. M.** (1994). Mechanical entrainment of fictive locomotion in the decerebrate cat. *J. Neurophysiol.* **71**, 2074-2086. doi:10.1152/jn.1994.71.6.2074
**Kuo, A. D.** (2002). The relative roles of feedforward and feedback in the control of rhythmic movements. *Motor Control* **6**, 129-145. doi:10.1123/mcj.6.2.129
**Lewis, K. E. and Eisen, J. S.** (2003). From cells to circuits: development of the zebrafish spinal cord. *Prog. Neurobiol.* **69**, 419-449. doi:10.1016/S0301-0082(03)00052-2
**Loeb, G. E., Brown, I. E. and Cheng, E. J.** (1999). A hierarchical foundation for models of sensorimotor control. *Exp. Brain Res.* **126**, 1-18. doi:10.1007/s002210050712
**Manoonpong, P., Pasemann, F. and Roth, H.** (2007). Modular reactive neurocontrol for biologically inspired walking machines. *Int. J. Robot. Res.* **26**, 301-331. doi:10.1177/0278364906076263
**Mantziaris, C., Till, B. and Ansgar, B.** (2020). Central pattern generating networks in insect locomotion. *Dev. Neurobiol.* **80**, 16-30. doi:10.1002/dneu.22738
**Markin, S. N., Klishko, A. N., Shevtsova, N. A., Lemay, M. A., Prilutsky, B. I. and Rybak, I. A.** (2016). A neuromechanical model of spinal control of locomotion. In *Neuromechanical Modeling of Posture and Locomotion* (ed. B. I. Prilutsky and D. H. Edwards), pp. 21-65. Springer New York. doi:10.1007/978-1-4939-3267-2_2
**McLean, D. L. and Dougherty, K. J.** (2015). Peeling back the layers of locomotor control in the spinal cord. *Curr. Opin. Neurobiol.* **33**, 63-70. doi:10.1016/j.conb.2015.03.001
**McVea, D. A., Taylor, A. J. and Pearson, K. G.** (2009). Long-lasting working memories of obstacles established by foreleg stepping in walking cats require area 5 of the posterior parietal cortex. *J. Neurosci.* **29**, 9396-9404. doi:10.1523/JNEUROSCI.0746-09.2009
**Minassian, K., Hofstoetter, U. S., Dzeladini, F., Guertin, P. A. and Ijspeert, A.** (2017). The human central pattern generator for locomotion: does it exist and contribute to walking? *Neuroscientist* **23**, 649-663. doi:10.1177/1073858417699790
**Mohamed Thangal, S. N. and Donelan, J. M.** (2020). Scaling of inertial delays in terrestrial mammals. *PLoS One* **15**, e0217188. doi:10.1371/journal.pone.0217188
**More, H. L. and Donelan, J. M.** (2018). Scaling of sensorimotor delays in terrestrial mammals. *Proc. R. Soc. B* **285**, 20180613. doi:10.1098/rspb.2018.0613
**More, H. L., Hutchinson, J. R., Collins, D. F., Weber, D. J., Aung, S. K. H. and Donelan, J. M.** (2010). Scaling of sensorimotor control in terrestrial mammals. *Proc. R. Soc. B* **277**, 3563-3568. doi:10.1098/rspb.2010.0898
**More, H. L., O'Connor, S. M., Brøndum, E., Wang, T., Bertelsen, M. F., Grøndahl, C., Kastberg, K., Hørlyck, A., Funder, J. and Donelan, J. M.** (2013). Sensorimotor responsiveness and resolution in the giraffe. *J. Exp. Biol.* **216**, 1003-1011. doi:10.1242/jeb.067231
**Moritz, C. T. and Farley, C. T.** (2004). Passive dynamics change leg mechanics for an unexpected surface during human hopping. *J. Appl. Physiol.* **97**, 1313-1322. doi:10.1152/japplphysiol.00393.2004
**Muir, G. D. and Chu, T. K.** (2002). Posthatching locomotor experience alters locomotor development in chicks. *J. Neurophysiol.* **88**, 117-123. doi:10.1152/jn.2002.88.1.117
**Muir, G. D., Gosline, J. M. and Steeves, J. D.** (1996). Ontogeny of bipedal locomotion: walking and running in the chick. *J. Physiol.* **493**, 589-601. doi:10.1113/jphysiol.1996.sp021406
**Nakahira, Y., Liu, Q., Sejnowski, T. J. and Doyle, J. C.** (2021). Diversity-enabled sweet spots in layered architectures and speed–accuracy trade-offs in sensorimotor control. *Proc. Natl. Acad. Sci. USA* **118**, e1916367118. doi:10.1073/pnas.1916367118
**Neveln, I. D., Tirumalai, A. and Sponberg, S.** (2019). Information-based centralization of locomotion in animals and robots. *Nat. Commun.* **10**, 1-11. doi:10.1038/s41467-019-11613-y
**Nishikawa, K., Biewener, A. A., Aerts, P., Ahn, A. N., Chiel, H. J., Daley, M. A., Daniel, T. L., Full, R. J., Hale, M. E., Hedrick, T. L. et al.** (2007). Neuromechanics: an integrative approach for understanding motor control. *Integr. Comp. Biol.* **47**, 16-54. doi:10.1093/icb/icm024
**Nirody, J. A.** (2023). Flexible locomotion in complex environments: the influence of species, speed and sensory feedback on panarthropod inter-leg coordination. *J. Exp. Biol.* **226**, jeb245111. doi:10.1242/jeb.245111
**Ong, C. F., Geijtenbeek, T., Hicks, J. L. and Delp, S. L.** (2019). Predicting gait adaptations due to ankle plantarflexor muscle weakness and contracture using physics-based musculoskeletal simulations. *PLoS Comput. Biol.* **15**, e1006993. doi:10.1371/journal.pcbi.1006993
**Owaki, D. and Ishiguro, A.** (2017). A quadruped robot exhibiting spontaneous gait transitions from walking to trotting to galloping. *Sci. Rep.* **7**, 277. doi:10.1038/s41598-017-00348-9
**Owaki, D., Kano, T., Nagasawa, K., Tero, A. and Ishiguro, A.** (2013). Simple robot suggests physical interlimb communication is essential for quadruped walking. *J. R. Soc. Interface* **10**, 20120669. doi:10.1098/rsif.2012.0669
**Pearson, K. G.** (1995). Proprioceptive regulation of locomotion. *Curr. Opin. Neurobiol.* **5**, 786-791. doi:10.1016/0959-4388(95)80107-3
**Pearson, K. G.** (2008). Role of sensory feedback in the control of stance duration in walking cats. *Brain Res. Rev.* **57**, 222-227. doi:10.1016/j.brainresrev.2007.06.014
**Pearson, K. G. and Gramlich, R.** (2010). Updating neural representations of objects during walking. *Ann. N. Y. Acad. Sci.* **1198**, 1-9. doi:10.1111/j.1749-6632.2009.05422.x
**Pearson, K. G., Misiaszek, J. E. and Fouad, K.** (1998). Enhancement and resetting of locomotor activity by muscle afferentsa. *Ann. N. Y. Acad. Sci.* **860**, 203-215. doi:10.1111/j.1749-6632.1998.tb09050.x
**Pearson, K. G., Ekeberg, Ö. and Büschges, A.** (2006). Assessing sensory function in locomotor systems using neuro-mechanical simulations. *Trends Neurosci.* **29**, 625-631. doi:10.1016/j.tins.2006.08.007
**Pratt, J., Chew, C. M., Torres, A., Dilworth, P. and Pratt, G.** (2001). Virtual model control: an intuitive approach for bipedal locomotion. *Int. J. Robot. Res.* **20**, 129-143. doi:10.1177/02783640122067309
**Ramadan, R., Geyer, H., Jeka, J., Schöner, G. and Reimann, H.** (2022). A neuromuscular model of human locomotion combines spinal reflex circuits with voluntary movements. *Sci. Rep.* **12**, 8189. doi:10.1038/s41598-022-11102-1
**Ramdya, P. and Ijspeert, A. J.** (2023). The neuromechanics of animal locomotion: from biology to robotics and back. *Sci. Robot.* **8**, eadg0279. doi:10.1126/scirobotics.adg0279
**Revzen, S., Koditschek, D. E. and Full, R. J.** (2009). Towards testable neuromechanical control architectures for running. In *Progress in Motor Control: A Multidisciplinary Perspective* (ed. D. Sternad), pp. 25-55. Springer US. doi:10.1007/978-0-387-77064-2_3
**Roberts, T. J., Kram, R., Weyand, P. G. and Taylor, C. R.** (1998). Energetics of bipedal running. I. Metabolic cost of generating force. *J. Exp. Biol.* **201**, 2745-2751. doi:10.1242/jeb.201.19.2745
**Roberts, T. J., Eng, C. M., Sleboda, D. A., Holt, N. C., Brainerd, E. L., Stover, K. K., Marsh, R. L. and Azizi, E.** (2019). The multi-scale, three-dimensional nature of skeletal muscle contraction. *Physiology* **34**, 402-408. doi:10.1152/physiol.00023.2019

**Rossignol, S., Dubuc, R. and Gossard, J.-P.** (2006). Dynamic sensorimotor interactions in locomotion. *Physiol. Rev.* **86**, 89-154. doi:10.1152/physrev.00028.2005

**Rubenson, J., Heliams, D. B., Lloyd, D. G. and Fournier, P. A.** (2004). Gait selection in the ostrich: mechanical and metabolic characteristics of walking and running with and without an aerial phase. *Proc. R. Soc. Lond. Ser. B: Biol. Sci.* **271**, 1091-1099. doi:10.1098/rspb.2004.2702

**Russo, A. D., Stanev, D., Armand, S. and Ijspeert, A.** (2021). Sensory modulation of gait characteristics in human locomotion: a neuromusculoskeletal modeling study. *PLoS Comput. Biol.* **17**, e1008594. doi:10.1371/journal.pcbi.1008594

**Rybak, I. A., Dougherty, K. J. and Shevtsova, N. A.** (2015). Organization of the mammalian locomotor CPG: review of computational model and circuit architectures based on genetically identified spinal interneurons. *ENeuro* **2**, ENEURO.0069-15.2015. doi:10.1523/ENEURO.0069-15.2015

**Ryczko, D., Charrier, V., Ijspeert, A. and Cabelguen, J.-M.** (2010). Segmental oscillators in axial motor circuits of the salamander: distribution and bursting mechanisms. *J. Neurophysiol.* **104**, 2677-2692. doi:10.1152/jn.00479.2010

**Ryczko, D., Simon, A. and Ijspeert, A. J.** (2020). Walking with salamanders: from molecules to biorobotics. *Trends Neurosci.* **43**, 916-930. doi:10.1016/j.tins.2020.08.006

**Ryu, Y. U. and Bradley, N. S.** (2009). Precocious locomotor behavior begins in the egg: development of leg muscle patterns for stepping in the chick. *PLoS One* **4**, e6111. doi:10.1371/journal.pone.0006111

**Ryu, H. X. and Kuo, A. D.** (2021). An optimality principle for locomotor central pattern generators. *Sci. Rep.* **11**, 13140. doi:10.1038/s41598-021-91714-1

**Schilling, M., Hoinville, T., Schmitz, J. and Cruse, H.** (2013). Walknet, a bio-inspired controller for hexapod walking. *Biol. Cybern.* **107**, 397-419. doi:10.1007/s00422-013-0563-5

**Sherrington, C. S.** (1900). On the innervation of antagonistic muscles. Sixth note. *Proc. R. Soc. Lond.* **66**, 66-67. doi:10.1098/rspl.1899.0075

**Sherrington, C. S.** (1906). Observations on the scratch-reflex in the spinal dog. *J. Physiol.* **34**, 1-50. doi:10.1113/jphysiol.1906.sp001139

**Sherrington, C. S.** (1910). Remarks on the reflex mechanism of the step1. *Brain* **33**, 1-25. doi:10.1093/brain/33.1.1

**Shik, M. L., Severin, F. V. and Orlovsky, G. N.** (1966). Control of walking by means of electrical stimulation of the mid-brain. *Biophys.* **11**, 756-765.

**Sholomenko, G. N. and O'Donovan, M. J.** (1995). Development and characterization of pathways descending to the spinal cord in the embryonic chick. *J. Neurophysiol.* **73**, 1223-1233. doi:10.1152/jn.1995.73.3.1223

**Sholomenko, G. N. and Steeves, J. D.** (1987). Effects of selective spinal cord lesions on hind limb locomotion in birds. *Exp. Neurol.* **95**, 403-418. doi:10.1016/0014-4886(87)90148-8

**Sholomenko, G. N., Funk, G. D. and Steeves, J. D.** (1991). Locomotor activities in the decerebrate bird without phasic afferent input. *Neuroscience* **40**, 257-266. doi:10.1016/0306-4522(91)90188-T

**Smith, N. C., Jespers, K. J. and Wilson, A. M.** (2010). Ontogenetic scaling of locomotor kinetics and kinematics of the ostrich (Struthio camelus). *J. Exp. Biol.* **213**, 1347-1355. doi:10.1242/jeb.020271

**Song, S. and Geyer, H.** (2015). A neural circuitry that emphasizes spinal feedback generates diverse behaviours of human locomotion. *J. Physiol.* **593**, 3493-3511. doi:10.1113/JP270228

**Song, S. and Geyer, H.** (2018). Predictive neuromechanical simulations indicate why walking performance declines with ageing. *J. Physiol.* **596**, 1199-1210. doi:10.1113/JP275166

**Steeves, J. D., Sholomenko, G. N. and Webster, D. M. S.** (1987). Stimulation of the pontomedullary reticular formation initiates locomotion in decerebrate birds. *Brain Res.* **401**, 205-212. doi:10.1016/0006-8993(87)91406-5

**Suzuki, S., Kano, T., Ijspeert, A. J. and Ishiguro, A.** (2021). Spontaneous gait transitions of sprawling quadruped locomotion by sensory-driven body–limb coordination mechanisms. *Front. Neurorobot.* **15**, 92. doi:10.3389/fnbot.2021.645731

**Taga, G.** (1995). A model of the neuro-musculo-skeletal system for human locomotion. *Biol. Cybern.* **73**, 97-111. doi:10.1007/BF00204048

**Taga, G.** (1998). A model of the neuro-musculo-skeletal system for anticipatory adjustment of human locomotion during obstacle avoidance. *Biol. Cybern.* **78**, 9-17. doi:10.1007/s004220050408

**Taga, G., Yamaguchi, Y. and Shimizu, H.** (1991). Self-organized control of bipedal locomotion by neural oscillators in unpredictable environment. *Biol. Cybern.* **65**, 147-159. doi:10.1007/BF00198086

**Tata Ramalingasetty, S., Danner, S. M., Arreguit, J., Markin, S. N., Rodarie, D., Kathe, C., Courtine, G., Rybak, I. A. and Ijspeert, A. J.** (2021). A whole-body musculoskeletal model of the mouse. *IEEE Access* **9**, 163861-163881. doi:10.1109/ACCESS.2021.3133078

**Ten Cate, J.** (1960). Locomotor movements in the spinal pigeon. *J. Exp. Biol.* **37**, 609-613. doi:10.1242/jeb.37.3.609

**Ten Cate, J.** (1964). Locomotory movements of the hind limbs in rabbits after isolation of the lumbosacral cord. *J. Exp. Biol.* **41**, 359-362. doi:10.1242/jeb.41.2.359

**Ten Cate, J.** (1965). Automatic activity of the locomotor centres of the lumbar cord in lizards. *J. Exp. Biol.* **43**, 181-184. doi:10.1242/jeb.43.1.181

**Thandiackal, R., Melo, K., Paez, L., Herault, J., Kano, T., Akiyama, K., Boyer, F., Ryczko, D., Ishiguro, A. and Ijspeert, A. J.** (2021). Emergence of robust self-organized undulatory swimming based on local hydrodynamic force sensing. *Sci. Robot.* **6**, eabf6354. doi:10.1126/scirobotics.abf6354

**Ting, L. H. and McKay, J. L.** (2007). Neuromechanics of muscle synergies for posture and movement. *Curr. Opin. Neurobiol.* **17**, 622-628. doi:10.1016/j.conb.2008.01.002

**Todorov, E.** (2004). Optimality principles in sensorimotor control. *Nat. Neurosci.* **7**, 907-915. doi:10.1038/nn1309

**Todorov, E. and Jordan, M. I.** (2002). Optimal feedback control as a theory of motor coordination. *Nat. Neurosci.* **5**, 11. doi:10.1038/nn963

**Traven, H., Brodin, L., Lansner, A., Ekeberg, Ö., Wallén, P. and Grillner, S.** (1993). Computer simulations of NMDA and non-NMDA receptors mediated synaptic drive: sensory and supraspinal modulation of neurons and small networks. *J. Neurophysiol.* **70**, 695-709. doi:10.1152/jn.1993.70.2.695

**van den Brand, R., Heutschi, J., Barraud, Q., DiGiovanna, J., Bartholdi, K., Huerlimann, M., Friedli, L., Vollenweider, I., Moraud, E. M., Duis, S. et al.** (2012). Restoring voluntary control of locomotion after paralyzing spinal cord injury. *Science* **336**, 1182-1185. doi:10.1126/science.1217416

**Van der Noot, N., Ijspeert, A. J. and Ronsse, R.** (2018). Bio-inspired controller achieving forward speed modulation with a 3D bipedal walker. *Int. J. Robot. Res.* **37**, 168-196. doi:10.1177/0278364917743320

**Van der Noot, N., Ijspeert, A. J. and Ronsse, R.** (2019). Neuromuscular model achieving speed control and steering with a 3D bipedal walker. *Auton. Robots* **43**, 1537-1554. doi:10.1007/s10514-018-9814-6

**Wagner, F. B., Mignardot, J.-B., Le Goff-Mignardot, C. G., Demesmaeker, R., Komi, S., Capogrosso, M., Rowald, A., Seáñez, I., Caban, M., Pirondini, E. et al.** (2018). Targeted neurotechnology restores walking in humans with spinal cord injury. *Nature* **563**, 7729. doi:10.1038/s41586-018-0649-2

**Wallén, P.** (1982). Spinal mechanisms controlling locomotion in dogfish and lamprey. *Acta Physiol. Scand. Suppl.* **503**, 1-45.

**Wallén, P., Ekeberg, Ö., Lansner, A., Brodin, L., Traven, H. and Grillner, S.** (1992). A computer-based model for realistic simulations of neural networks II: the segmental network generating locomotor rhythmicity in the lamprey. *J. Neurophysiol.* **68**, 1939-1950. doi:10.1152/jn.1992.68.6.1939

**Walter, W. G.** (1950). An electro-mechanical 'animal'. *Dialectica* **4**, 206-213. doi:10.1111/j.1746-8361.1950.tb01020.x

**Walter, W. G.** (1951). A machine that learns. *Sci. Am.* **185**, 60-64. doi:10.1038/scientificamerican0851-60

**Wang, J. M., Hamner, S. R., Delp, S. L. and Koltun, V.** (2012). Optimizing locomotion controllers using biologically-based actuators and objectives. *ACM Trans. Graph.* **31**, 25. doi:10.1145/2185520.2185521

**Watson, R. R., Rubenson, J., Coder, L., Hoyt, D. F., Propert, M. W. and Marsh, R. L.** (2011). Gait-specific energetics contributes to economical walking and running in emus and ostriches. *Proc. R. Soc. B* **278**, 2040-2046. doi:10.1098/rspb.2010.2022

**Webb, B.** (2001). Can robots make good models of biological behaviour? *Behav. Brain Sci.* **24**, 1033-50; discussion 1050-94. doi:10.1017/s0140525x01000127

**Webb, B.** (2020). Robots with insect brains. *Science* **368**, 244-245. doi:10.1126/science.aaz6869

**Webster, D. M. and Steeves, J. D.** (1988). Origins of brainstem-spinal projections in the duck and goose. *J. Comp. Neurol.* **273**, 573-583. doi:10.1002/cne.902730411

**Whelan, P. J.** (1996). Control of Locomotion in the decebrate cat. *Prog. Neurobiol.* **49**, 481-515. doi:10.1016/0301-0082(96)00028-7

**Wiener, N.** (2019). *Cybernetics or Control and Communication in the Animal and the Machine, Reissue of the 1961*, 2nd edn. MIT Press.

**Williams, T. L.** (1992a). Phase coupling by synaptic spread in chains of coupled neuronal oscillators. *Science* **258**, 662-665. doi:10.1126/science.1411575

**Williams, T. L.** (1992b). Phase coupling in simulated chains of coupled neuronal oscillators representing the lamprey spinal cord. *Neural Comput.* **4**, 546-558. doi:10.1162/neco.1992.4.4.546

**Williams, T. L. and McMillen, T.** (2015). Strategies for swimming: explorations of the behaviour of a neuro-musculo-mechanical model of the lamprey. *Biol. Open* **4**, 253-258. doi:10.1242/bio.20149621

**Williams, T. L., Sigvardt, K. A., Kopell, N., Ermentrout, G. B. and Rempler, M. P.** (1990). Forcing of coupled nonlinear oscillators: studies of intersegmental coordination in the lamprey locomotor central pattern generator. *J. Neurophysiol.* **64**, 862-871. doi:10.1152/jn.1990.64.3.862

**Wilson, D. M.** (1965). Proprioceptive leg reflexes in cockroaches. *J. Exp. Biol.* **43**, 397-409. doi:10.1242/jeb.43.3.397

**Wilson, D. M.** (1967). Stepping patterns in tarantula spiders. *J. Exp. Biol.* **47**, 133-151. doi:10.1242/jeb.47.1.133

**Wolpert, D. M. and Ghahramani, Z.** (2000). Computational principles of movement neuroscience. *Nat. Neurosci.* **3**, 1212. doi:10.1038/81497

**Yanagihara, D., Udo, M., Kondo, I. and Yoshida, T.** (1993). A new learning paradigm: adaptive changes in interlimb coordination during perturbed locomotion in decerebrate cats. *Neurosci. Res.* **18**, 241-244. doi:10.1016/0168-0102(93)90060-4

**Zhong, G., Shevtsova, N. A., Rybak, I. A. and Harris-Warrick, R. M.** (2012). Neuronal activity in the isolated mouse spinal cord during spontaneous deletions in fictive locomotion: Insights into locomotor central pattern generator organization. *J. Physiol.* **590**, 4735-4759. doi:10.1113/jphysiol.2012.240895