A leg to stand on: computational models of proprioception

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Dexterous motor control requires feedback from proprioceptors, internal mechanosensory neurons that sense the body's position and movement. An outstanding question in neuroscience is how diverse proprioceptive feedback signals contribute to flexible motor control. Genetic tools now enable targeted recording and perturbation of proprioceptive neurons in behaving animals; however, these experiments can be challenging to interpret, due to the tight coupling of proprioception and motor control. Here, we argue that understanding the role of proprioceptive feedback in controlling behavior will be aided by the development of multiscale models of sensorimotor loops. We review current phenomenological and structural models for proprioceptor encoding and discuss how they may be integrated with existing models of posture, movement, and body state estimation.

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Experimental perturbations probe the role of proprioceptive feedback in motor control

All animals possess specialized sensory neurons that monitor the mechanical consequences of their actions. These sensors, known as proprioceptors, are essential for coordinating body movement and maintaining body posture [1,2]. While it is possible for some isolated motor circuits to generate structured output in the absence of proprioceptive feedback, behaviors driven by purely feedforward motor signals are often clumsy and ineffectual [3]. Understanding how proprioceptive feedback interacts with motor circuits to control the body remains a fundamental problem in neuroscience.

An effective method to investigate the function of sensory circuits is to perturb neural activity and measure the effect on an animal's behavior. For example, activating or silencing neurons in the mammalian visual cortex [4] or insect optic glomeruli [5] has identified the circuitry and patterns of activity that underlie visually guided behaviors. However, due to the distributed nature of proprioceptive sensors and their tight coupling with motor control circuits, perturbations to the proprioceptive system can be difficult to execute and tricky to interpret.
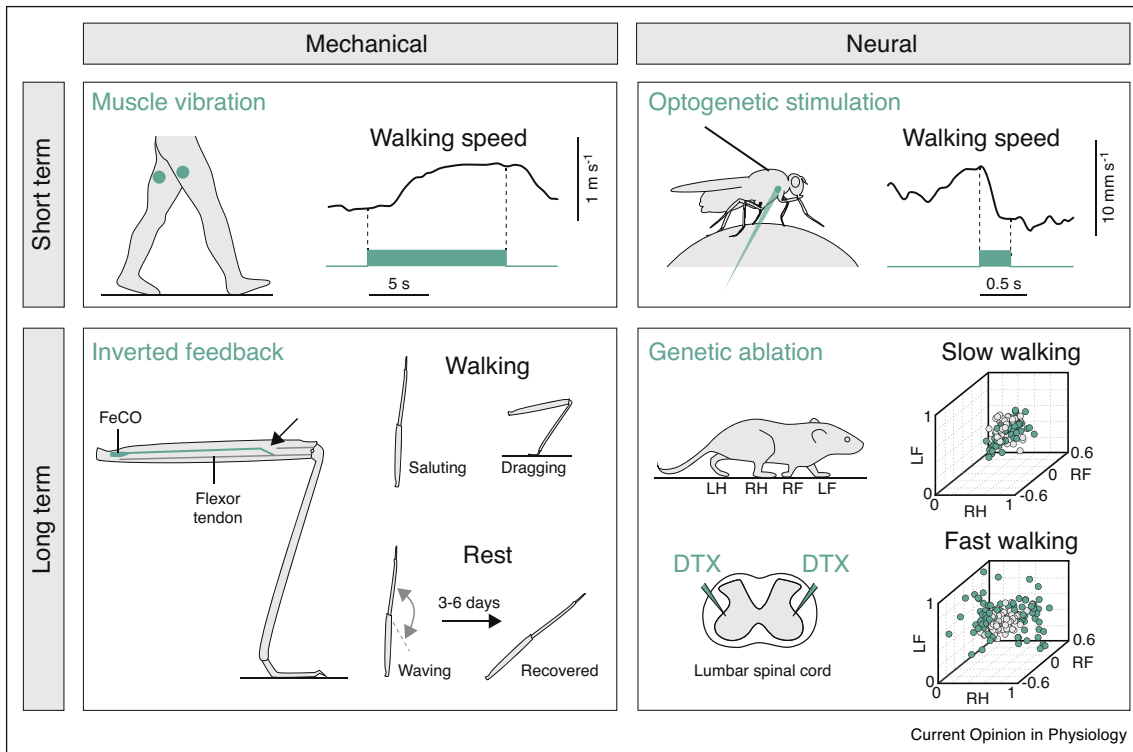
Mechanical perturbation experiments

Early efforts to understand the behavioral contributions of proprioceptive feedback relied on lesions and mechanical perturbations. A classic example of a proprioceptive perturbation experiment is the use of vibration to artificially excite primary muscle spindle afferents. In humans, muscle vibration creates the illusory perception that a muscle is being stretched [6]. If a person is walking, vibrating their hamstring produces an increase in forward walking speed, while vibrating their quadriceps has little effect on walking kinematics [7] (Figure 1, top left). During backward walking, however, these effects are reversed, suggesting that proprioceptive feedback acts in a context-dependent manner.

Longer-term mechanical perturbations have also been used to investigate the dynamics of sensorimotor adaptation. Bässler *et al.* [8] inverted the sign of feedback signals from the femoral chordotonal organ in the stick insect leg by surgically crossing the receptor tendon (Figure 1, bottom left). This manipulation causes a walking stick insect to either 'salute' or 'drag' her leg, and a standing stick insect to rhythmically wave her tibia. Over the course of a month, Bässler and colleagues observed that the walking salute and dragging remained unchanged, while the waving movements gradually decreased. This observation suggests that the postural feedback control system recovered, while the control system for leg movement did not.

These examples illustrate several hazards to consider when executing and interpreting proprioceptive perturbation experiments. First, the effects of proprioceptive feedback on motor output are often context-dependent, such as during forward and backward walking. Second, proprioceptive signals are typically used for controlling

Figure 1

Examples of experimental perturbations used to probe the role of proprioceptive feedback in motor control. Top left: Vibration of hamstring muscles in humans stimulated muscle spindles, leading to an increase in walking speed [7]. Bottom left: Inverting sensory feedback from the femoral chordotonal organ of a stick insect front leg by crossing the receptor tendon (arrow) led to saluting or dragging of the leg during walking and waving during rest (front leg in the air, other legs on the ground). The normal rest posture of the front leg (extended in air) recovered after a few days, but saluting and dragging during walking remained unchanged [8]. Top right: Optogenetic stimulation of second-order proprioceptive neurons in tethered *Drosophila* walking on a treadmill caused a decrease in walking speed. Trace shows mean of multiple animals [9•]. Bottom right: Genetic ablation of hindlimb muscle spindles in the mouse lumbar spinal cord caused inter-limb coordination deficits only during fast walking. 3D plots show timing (phase) of right hindlimb (RH), right forelimb (RF), and left forelimb (LF) relative to left hindlimb (LH) for gait cycles with (gray) and without (green) muscle spindles [10•].

both posture and movement, often at the same time. An additional challenge of mechanical perturbations is that they often lack specificity, leaving it unclear which specific proprioceptor neurons underlie the observed behavior.

Neural perturbation experiments

With the emergence of genetic tools to label and manipulate specific cell-types, it has recently become possible to genetically activate or silence specific proprioceptive neurons to assess their role in behavior. However, such manipulation experiments come with their own challenges [11]. For example, Agrawal *et al.* [9•] used optogenetics to study a population of second-order proprioceptive neurons in *Drosophila* that encode extension of the fly's tibia. Activation of these neurons caused walking flies to slow down, suggesting that they may participate in controlling walking speed (Figure 1, top right). However, fine-grained kinematic analysis of leg joints revealed that the same perturbation produced reflexive flexion of the

tibia whenever the leg was unloaded, not just during walking. Thus, the decrease in walking speed was likely driven by the fly's reaction to a perceived extension of her tibia, rather than a disruption to walking speed control.

Another recent study used intersectional genetic methods to test the role of local proprioceptive feedback in rodent locomotion. When Takeoka and Arber [10•] expressed Diphtheria toxin (DTX) in muscle spindles that innervate the front or rear legs of adult mice, they observed only subtle changes in spontaneous walking gait. The inter-limb coordination deficits produced by these ablations became apparent only when mice were forced to run at high speeds on a motorized treadmill (Figure 1, bottom right).

These examples illustrate how it can be misleading to infer a direct, causal relationship between neural activity and behavior when the perturbation impacts multiple feedback loops at different levels of the nervous system.

For example, activating or silencing proprioceptors may alter postural reflexes that interfere with an ongoing behavior, such as walking. In other cases, changes to motor output produced by genetic perturbations may only become visible in specific behavioral contexts. Finally, removing proprioceptive feedback can lead to general deficits to motor coordination that alter an animal's ability or desire to perform certain behavioral tasks.

How models can help
Our thesis is that the design and interpretation of such perturbation experiments would benefit from the integration of models for proprioceptive sensing with theoretical frameworks for motor control. Because of the tight feedback between proprioceptive and motor circuits at multiple levels, the emergent behavior of a sensorimotor system depends on how its components are integrated. Therefore, computational simulations are a means to generate specific, quantitative predictions about the roles of key parameters in the system, including sensory delay, gain modulation, and encoding nonlinearities. By formalizing how the components contribute to overall behavior, an integrated model can illustrate how different manipulations may produce similar results and aid in the design of experiments to disambiguate among multiple hypotheses.

Our overall goal is to guide the design and interpretation of experiments to understand the role of proprioceptive neurons in flexible control of behavior. We first review current approaches to model sensory coding in proprioceptive sensory neurons. Next, we discuss the role of proprioceptive feedback in existing models of posture, locomotion, skilled movements, and body state estimation. Although proprioception plays an important role in motor learning, here we focus on innate behaviors driven by movement of the limbs, such as walking. We conclude by discussing three obstacles to achieving a systems-level understanding of proprioception: firstly, the diversity of proprioceptive sensors; secondly, a lack of experimental separability between proprioceptive and motor circuits; and finally, context-dependent modulation of proprioceptive feedback for guiding behavior.

Computational models of sensory coding in proprioceptors
Proprioceptors are mechanosensory neurons located within muscles, tendons, and joints that convert mechanical forces in the body into patterns of neural activity. Proprioceptors can be classified into different functional subtypes that encode limb displacement, load, or their time derivatives [2]. For example, the proprioceptors innervating a muscle spindle encode either muscle length or a combination of muscle length and its rate of change (velocity) [12]. Similarly, proprioceptors in the insect femoral chordotonal organ encode distinct kinematic parameters, including position, velocity, and acceleration

[13,14]. Recent studies have begun to map these functional subtypes onto neuronal cell-types defined using genetic markers [13,15]. These tools now enable targeted perturbation experiments to investigate the role of proprioceptor subtypes in specific motor tasks.

Due to a combination of neural and mechanical properties [16,17], proprioceptors are tuned to biologically relevant stimuli. These same properties can make proprioceptor responses vary as a function of stimulus history and behavioral context. Such nonlinearities make proprioceptors different from most engineered sensors, which are designed to directly measure a physical quantity, such as a joint angle or torque. Because sensory neurons constrain the information available for other downstream computations in the nervous system, the construction of proprioceptor models is an essential first step in quantitative analysis of sensorimotor loops.

Current models of proprioceptors fall into two broad categories: phenomenological models and structural models. Phenomenological models reproduce the computational properties of a proprioceptor in abstraction, for instance by deriving a mathematical function, often a transfer function, from experimentally determined relations between mechanics and neural activity [18–23]. This function is often derived from recorded neural activity in response to simple ramp-and-hold or sinusoidal stimuli using linear systems theory or non-linear curve fitting.

Phenomenological models are compact and computationally efficient, which allows them to be integrated with models of the motor system. For example, the simple muscle spindle models by Prochazka and Gorassini [20,21] have been incorporated into musculoskeletal models of arms and legs [24–26,27••]. Similarly, the Golgi tendon organs models by Houk and Simon [23] and Rosenthal *et al.* [28] have been used in models of the stretch reflex [18,29]. A drawback of phenomenological models derived from ramp-and-hold or sinusoidal stimuli is that they might perform well for only a narrow subset of stimuli [20,30]. This overfitting is particularly problematic when proprioceptor activity is context-dependent, such as in muscle spindles. Measuring the responses of proprioceptors to more complex stimuli (e.g. white noise or naturalistic limb trajectories) and incorporating nonlinearities are both likely to produce more generalizable models of spiking responses to sensory stimuli [31,32].

Unlike abstract phenomenological models, structural models derive firing patterns of proprioceptors by approximating their anatomical structure [33,34••,35–39]. For example, structural models of muscle spindles simulate intrafusal muscle fibers and their interaction with the extrafusal muscle and tendon. In a recent muscle spindle model by Blum *et al.* [33,34••], the forces of intrafusal

muscle fibers are calculated based on measurements of cross-bridge kinetics. Importantly, this knowledge of mechanics allows the model to predict varied and complex spindle firing patterns, including history-dependent features. Structural models are more computationally demanding and make more assumptions about parameters than phenomenological models, but they tend to generalize better across conditions because firing patterns are emergent rather than built-in. Thus, structural models can be particularly effective for proprioceptors with non-linear tuning, such as muscle spindles.

Behavioral functions of proprioceptive feedback

Proprioceptive information is involved in nearly all aspects of motor control, from rapid recovery after a stumble to searching for a light switch with your toes in a dark room while your hands are bound tightly behind your back. When trying to investigate the role of proprioceptive feedback in a specific motor task, it is important to consider the impact of perturbing proprioceptive sensors at different levels of the sensorimotor hierarchy. Below, we delineate the multiple levels of motor function for which proprioceptive feedback plays an essential role. Although we discuss posture and movement separately, we note that they are ultimately integrated behaviors that are not necessarily controlled independently [40].

Reflexive control of body posture

Proprioceptors from the limbs project to the spinal cord (in vertebrates) and the ventral nerve cord (in invertebrates), where they provide excitatory synaptic input to populations of projection neurons, local interneurons, and motor neurons (Figure 2, left). The architecture of these circuits has been extensively studied [41,42], although only recently have genetic tools begun to reveal the connectivity of identified cell types [9•,43].

Behaviors mediated by direct (monosynaptic) or nearly direct feedback from proprioceptors are typically characterized as 'reflexive' because they occur with a shorter latency than voluntary movements [44]. In their simplest form, proprioceptive reflexes rapidly (<50 ms) stabilize body posture against external perturbations. For example, when a physician taps the tendon near your knee cap, muscle spindles elicit a compensatory reaction by activating the quadriceps and inhibiting the antagonistic hamstring. Similarly, when a grasshopper's tibia is flexed, proprioceptive feedback from the femoral chordotonal organ activates the extensor muscle and inhibits the flexor muscle.

Such stabilization reflexes can be modeled as negative feedback controllers, which produce corrective motor output to minimize the error between the sensed posture and a reference posture. These controllers may act locally to stabilize individual joints, or they may act across joints to produce a coordinated response that stabilizes a task-level variable, such as the position of the hand while grasping an object [45] or the position of the body's center of mass while standing [46].

A key parameter to achieve stability in negative feedback controllers is the ratio of motor output to sensory input, known as feedback gain. Tuning feedback gains can be accomplished in modeling studies by identifying the range of parameters in which the model is stable or by fitting model predictions to experimental data. In rare cases, gains have also been measured experimentally. In one such experiment, Weiland et al. [47] measured the gain of the feedback loop that controls the posture of the stick insect femur–tibia joint. This experiment was only possible because the anatomy of the stretch receptor (femoral chordotonal organ) allowed its mechanical stimulation without affecting the surrounding muscles. Today, optogenetic stimulation may enable equivalent analyses of reflex loops that cannot be manipulated mechanically.

In addition to their established function in basic postural control, elementary reflex loops also participate in more complex behaviors that involve multiple joints or limbs [44]. Understanding the context-dependent role and tuning of reflexes remains an important direction for future research, and computational models will likely be useful in exploring the underlying circuits and algorithms [48,49••].

Feedback control of locomotion

Walking and other forms of locomotion are characterized by rhythmic movements of the body and limbs. The rhythmic pattern of these movements can, in some cases, be generated without feedback by intrinsically rhythmic circuits in the spinal cord and ventral nerve cord, referred to as central pattern generators (CPGs) [50,51]. However, proprioceptive feedback has long been known to regulate phase transitions, stabilize ongoing movements, and adjust locomotion to changes in the environment [52,53].

Several recent models of locomotion control combine feedforward motor commands from CPGs with proprioceptive feedback. Such models have been useful in testing the contribution of each control pathway in producing coordinated movements. For example, in a CPG model of cat walking, Markin et al. [26] found that the integration of feedback from muscle spindles and Golgi tendon organs is critical for providing body weight support and coordinating the legs' transitions between stance and swing phases. Proctor and Holmes [54] modeled cockroach running and found that the integration of feedback from leg joints (roughly corresponding to load feedback from campaniform sensilla) with a CPG model helps recover the heading direction after a lateral perturbation. Similarly, feedback from body stretch receptors

Figure 2
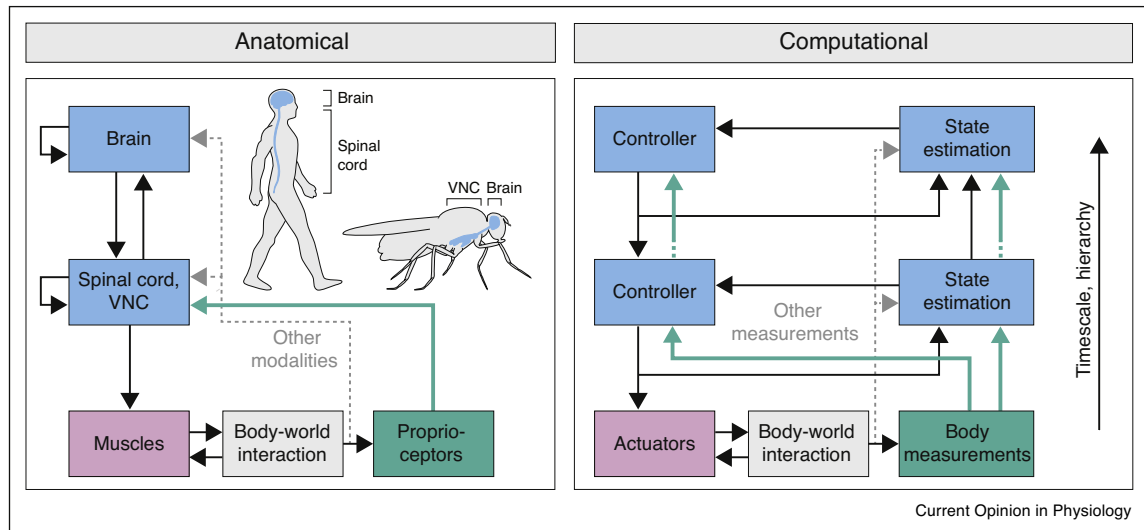
Anatomical and computational view of proprioceptive feedback in motor control. Left: Proprioceptors from the limbs project to the spinal cord (in vertebrates) and the ventral nerve cord (VNC, in invertebrates), where they transmit sensory signals to distributed circuits for posture and movement control. Right: Proprioceptive signals affect motor control on different timescales through multiple nested feedback loops. Proprioceptive signals are integrated in low-level and high-level controllers for posture, movement, and planning. They may also be used to estimate the state of the body. Note that each box represents a computation, not necessarily an anatomically confined circuit. Computations higher up in the hierarchy are more abstract and operate at longer timescales.

effectively tunes rhythmic CPG patterns for swimming and crawling [55•,56]. In fact, locomotion can be successfully modeled without CPGs [57••,58–60], emphasizing the functional importance of integrating proprioceptive feedback in low-level motor circuits. In high-level motor circuits, proprioceptive information may be used for planning movement on a longer timescale. For instance, during walking, a high-level controller may use proprioceptive feedback to plan desired foot placements, which then serve as target inputs to a low-level controller [57••,59].

The use of proprioceptive feedback to drive or fine-tune motor control of locomotion is ultimately constrained by neural conduction delays and muscle kinetics. During fast running, for example, proprioceptive feedback might not be fast enough to modulate muscle activity on a step-by-step basis [61]. In such situations, stable locomotion can arise from interactions between feedforward control and passive body mechanics [62,63]. Using direct experimental perturbations of proprioceptive neurons has the potential to disambiguate the relative contributions of feedforward and feedback signals in locomotion control, but interpreting these experiments may require careful modeling of inputs and outputs at multiple scales.

Feedback control of skilled limb movements
The control of non-rhythmic movements, such as putting on a sock or dodging a projectile, also critically depends on proprioceptive feedback. A particularly useful framework for modeling such goal-directed movements is optimal feedback control [64,65]. Optimal control posits that the motor system attempts to minimize a set of cost functions that describe the performance criteria of a given task — for example, movement effort or accuracy. The role of proprioception in this framework is to help generate and update an accurate estimate of the state of the body, which in turn determines how the controller initiates and refines movements. Unlike the simple negative feedback controllers discussed above, optimal feedback controllers correct for perturbations only to the degree that they interfere with task success. For example, when throwing a ball to a target, an optimal feedback controller minimizes the variability of hand trajectories only around the time of release while allowing variability at other times [64].

Although optimal feedback control can predict many common features of goal-directed movement, it remains unclear how this strategy may be implemented in the nervous system. It is typically assumed that feedback control of skilled movements is mediated by higher-order regions, such as cortex in vertebrates, but recent experiments suggest that even fast spinal reflexes can produce sophisticated control reminiscent of optimal feedback [45,66]. In humans and other primates, there is a strong tradition of combining mechanical perturbations with computational models to understand the sensory inputs and algorithms that underlie feedback control of reaching [67,68]. Recent studies of primate motor cortex have

revealed that neural activity during skilled movements exhibits rotational dynamics that lie on a low-dimensional manifold [69]. The role of proprioceptive signals in constructing these representations is currently unclear, although a recent modeling study showed that recurrent neural network models trained to control a limb exhibited similar rotational dynamics [70]. These activity patterns have also been modeled using an implementation of a feedback controller in a spiking neural network [71]. Going forward, these modeling frameworks may also help understand the results of genetic perturbations to neural circuits that underlie skilled motor behavior. As optimal feedback control models generally have few parameters, they may prove particularly useful for providing experimental predictions of behavior when combined with models of proprioceptors.

Body state estimation

Natural proprioceptive signals are noisy and subject to conduction delays, creating problems for continuous feedback control. To quantify and manage the uncertainty introduced by noise and delays, the central nervous system may implement a form of state estimation (Figure 2, right), where sensory feedback is combined with a prediction of the body's state from an internal model — a neural representation of the system that is being controlled [72]. This comparison of sensory feedback against an internal prediction can compensate for sensory delays and make control more robust to sensory noise. Robustness to noise makes state estimation a useful strategy for controlling motor tasks, including posture [73], reaching [74], and locomotion [75]. For example, in a dynamical simulation of posture control during standing, both feedback and state-estimation controllers were found to be stable against external perturbations without noise, but in the presence of proprioceptive noise, only state-estimation-based control was stable [73].

It is typically assumed that state estimation occurs in higher-level circuits, such as the cerebellum and parietal cortex in vertebrates [72], or the mushroom bodies in insects [76]. But an intriguing idea is that locomotor CPGs perform computations equivalent to state estimation and can thus be understood as observers of feedback control rather than just generators of limb motion [77•]. This idea suggests that a form of state estimation may occur at multiple timescales and levels of the sensorimotor hierarchy (Figure 2, right). Indeed, signals from different proprioceptor subtypes can converge as early as in second-order neurons [9•,42,78,79]. However, little is known about how circuits at different levels represent the body and to what degree they combine signals from the diverse proprioceptor subtypes. Going forward, one useful role of computational models could be to predict the proprioceptive information available during natural movement, for example by combining models of proprioceptors with realistic models of the muscles and limbs [27••].

State estimates enabled by proprioceptive feedback are also used beyond the motor system. Recent work in the *Drosophila* central complex has revealed circuits that encode the body in both self-centered and world-centered coordinates [80–82]. Neural encoding of several key quantities that guide spatial navigation during walking, including heading in allocentric coordinates and velocity in egocentric coordinates, persist in darkness [83], which suggests that they rely on proprioceptive signals from the legs. However, it remains unknown precisely which proprioceptive signals are used to compute these signals. Computational models that predict the proprioceptive information available during fly walking by simulating both proprioceptors and the mechanics of the limbs could help explore which signals are suited to extract key quantities like heading and velocity.

Approaches for systems-level modeling of proprioception

We propose that developing multiscale computational models that span proprioceptive sensing and motor control will make it easier to understand how neural circuits flexibly control the body. Below, we outline several possible approaches, including developing tractable models that grapple with proprioceptor diversity, integrating across levels of the sensorimotor hierarchy, and accounting for the roles of sensory delay, noise, and contextual modulation of proprioceptive signals.

Diversity of proprioceptive sensors and their models

A major challenge in modeling proprioceptors is the diversity of sensory neuron subtypes. Unlike sensory systems that are concentrated into specialized organs (e.g. the eye, nose, and ear), proprioceptors are distributed throughout the body. Furthermore, the receptive field of each proprioceptor is idiosyncratic to the tissue in which it is embedded and how that tissue moves through and interacts with the environment. Therefore, a model that describes the input-output function of a muscle spindle in a leg muscle may have little in common with a muscle spindle in a jaw muscle. Existing models may be tuned to match the properties of different proprioceptors (e.g. [84]), but in most cases, additional physiological data is needed. In addition, there remain many proprioceptors for which models do not currently exist. Historically, there has been a strong focus on modeling the activity of mammalian muscle spindles and Golgi tendon organs [18–21,33,34••,35–39]. In contrast, computational models of invertebrate proprioceptors are only beginning to emerge (e.g. [22,85•]), despite the growing literature characterizing encoding properties of chordotonal organs, campaniform sensilla, slit sensilla, and other proprioceptors [86–88]. Models of insect proprioceptors would be particularly useful to complement the available genetic tools to experimentally manipulate specific proprioceptive neurons during behavior [86].

Even where precise proprioceptor models are available, many recent neuromechanical simulations rely on simplified phenomenological proprioceptor models [24,26,27••,84,89,90]. Whether such simplifications are appropriate may depend on the level of system being modeled, and further experimental and computational analyses are needed to identify constraints on useful approximations. One attractive possibility is that a transformation of coordinates in the input and output variables may help simplify proprioceptor models, as in the case of using force instead of fiber length to model muscle spindle responses [34••] or transforming signals between eye, head, or body reference frames to model proprioceptive encoding in the cerebellar nuclei [91]. More generally, a powerful modeling framework would capture diverse proprioceptors with a tractable number of tunable parameters, such as location on body, hysteresis, and maximum firing rate. Of course, simulation parameters and code should be openly shared to facilitate reproducibility and reuse.

Integration of models for proprioception and motor control

A major challenge in understanding the behavioral functions of proprioceptive feedback is the lack of experimental separability between proprioceptive and motor circuits across the sensorimotor hierarchy. An integration of models across levels can provide unique insights into the control of posture, movement, and state estimation that only emerge when considering these systems as a whole.

To study how specific proprioceptive signals contribute to posture control, Prochazka *et al.* [48] integrated models of muscle spindles and Golgi tendon organs into a feedback-controlled stimulation of arm and leg muscles. The authors found that positive force feedback from Golgi tendon organs, which is generally considered unstable, can actually stabilize a muscle's response to increased load if one also incorporates sensory delays and natural filtering properties of mammalian muscle. The conclusion that positive force feedback is a stable means to control load-bearing motor tasks would not have been clear in studying the controller or proprioceptors alone.

Several recent neuromechanical models of movement control have also simulated the dynamic activity of proprioceptors [24,26,89,90,92]. For example, Goldsmith *et al.* [89] integrated models of proprioceptors into a simulation and robotic model of a walking fruit fly. Using feedback signals inspired by the tuning properties of insect femoral chordotonal neurons and campaniform sensilla enabled the robot to adapt to continuous changes in load. These models could eventually be used to study the effects of conduction delays, noise, and modulation of specific proprioceptive signals on locomotion and skilled limb movements, and to generate testable predictions for perturbation experiments. We hope that emerging

methods for neuromechanical modeling will make these models easier to construct and use [93–95].

Systems-level models can also provide insights into how proprioceptive circuits represent the body and suggest potential roles for feedback in motor control. For example, Hamlet *et al.* [55•] used a multiscale model of lamprey swimming to investigate how different proprioceptive signals, encoding the direction and magnitude of body curvature, may exert different effects on locomotor speed and energy consumption. In another example, Sandbrink *et al.* [27••] recently showed that some proprioceptive representations naturally arise in a deep neural network trained to recognize characters from arm motions given a biologically realistic model of a human arm. Finally, Ache and Dürr [85•] modeled the proprioceptive hairs of an insect antenna to predict how downstream neurons encode antennal movements. These studies illustrate how systems-level models provide a useful framework to investigate the role of proprioceptive feedback in guiding natural movements.

Context-dependent modulation

An important characteristic of proprioception is that its effects on motor control are not fixed, but can be tuned by the nervous system under different behavioral contexts. Modeling experimental results with such context-dependent changes requires information about interactions across multiple levels, further motivating systems-level models.

A clear example of such a top-down modulation is the case of reflex reversal, in which a reflex changes sign depending on the behavioral state of the animal. For instance, stimulating neurons in the femoral chordotonal organ in the stick insect leads to either extension or flexion of the tibia depending on whether the leg is in stance or swing [96]. Although there have been detailed studies of the circuits that mediate reflex reversal [97], this phenomenon is not commonly built into models for sensorimotor control. One notable exception is the recent model by Goldsmith *et al.* [49••], which investigated different perturbations in a neuromechanical model and found that reflex reversal may be due to inhibition of the flexion-tuned position-sensitive and velocity-sensitive neurons. In another example, Bacqué-Cazenave *et al.* [98] built a neuromechanical model of the crayfish leg circuitry which was able to reproduce state-dependent reflex reversal observed during locomotion [99].

Reflex modulation may also play an important role in steering, possibly via descending input which modulates sensory feedback depending on the steering direction. For example, Schilling and Cruse [57••] proposed a fully decentralized model of walking control that produces curved walking by adjusting the setpoint of local control loops in each leg. Ultimately, we expect that most

behaviors will involve not only a unique set of descending motor commands, but also bespoke tuning of proprioceptive feedback pathways.

Conclusion

Due to advances in genetic targeting of neuronal cell-types, our ability to perform targeted perturbations in proprioceptive and motor circuits is rapidly expanding. As the space of possible experiments grows, there is a pressing need for computational frameworks to help guide experimental design and interpretation. Models developed for proprioceptors and motor control at different scales can be integrated to yield new insights about how proprioception interacts with motor control to support dexterous and flexible movements. These biological principles may also inspire the design of novel robotic systems and contribute to our understanding and treatment of movement disorders.

Conflict of interest statement

Nothing declared.

Acknowledgments

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Papers of particular interest, published within the period of review, have been highlighted as:

- of special interest
- •• of outstanding interest

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