COMPREHENSIVE PHYSIOLOGY

Behavioral Motor Performance

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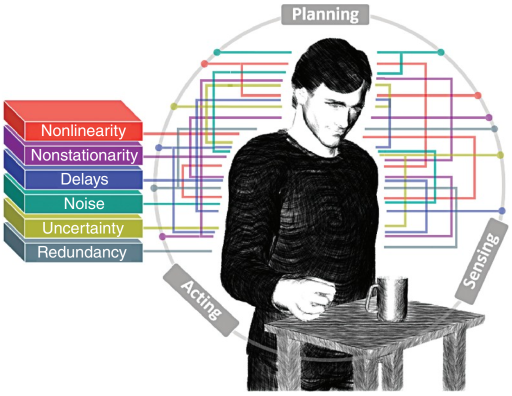
ABSTRACT

The human sensorimotor control system has exceptional abilities to perform skillful actions. We easily switch between strenuous tasks that involve brute force, such as lifting a heavy sewing machine, and delicate movements such as threading a needle in the same machine. Using a structure with different control architectures, the motor system is capable of updating its ability to perform through our daily interaction with the fluctuating environment. However, there are issues that make this a difficult computational problem for the brain to solve. The brain needs to control a nonlinear, nonstationary neuromuscular system, with redundant and occasionally undesired degrees of freedom, in an uncertain environment using a body in which information transmission is subject to delays and noise. To gain insight into the mechanisms of motor control, here we survey movement laws and invariances that shape our everyday motion. We then examine the major solutions to each of these problems in the three parts of the sensorimotor control system, sensing, planning, and acting. We focus on how the sensory system, the control architectures, and the structure and operation of the muscles serve as complementary mechanisms to overcome deviations and disturbances to motor behavior and give rise to skillful motor performance. We conclude with possible future research directions based on suggested links between the operation of the sensorimotor system across the movement stages. © 2023 American Physiological Society. *Compr Physiol* vol number: page range, year.

GRAPHICAL ABSTRACT

The human motor control system has exceptional abilities to perform skillful actions. However, factors such as nonlinearity, nonstationarity, delays, noise, uncertainty, and redundancy make this a difficult computational problem for the brain to solve. Here, we go over the major solutions to each of these problems in the three parts of the motor performance cycle namely, sensing, planning, and acting.



Didactic Synopsis

Major teaching points

- Movements can be characterized by a range of trajectory invariances including the speed-accuracy trade-off, smoothness, and the production of bell-shaped velocity profiles.
- The idea is that the brain produces movements with such invariances as they are a solution to the optimization of task goals, such as ensuring stability, reducing error, minimizing energy usage, and maximizing rewards.
- The goal of research in this area is to reverse motor performance and use the trajectory invariances to work out the computations and task goals that govern sensorimotor control.

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- Skillful motor performance is limited due to the problems of motor control: delays, nonstationarity, redundancy, nonlinearity, noise, and uncertainty.
- Solutions to these problems can be found at all three levels of the sensorimotor loop: sensing, planning, and acting.
- Within sensing, a variety of computational approaches are used to maximize the sensory information, obtain overlapping or complementary information from multiple sensory modalities, and combine these to obtain accurate estimations of the state of the body and world.
- The sensory information is then acted upon in the planning stage using computational approaches that combine multiple task goals in a complex cost function.
- All actions are subject to the mechanics of the musculoskeletal system.
- The intrinsic stiffness and damping of muscle stabilizes the body against perturbations, while the time dynamics of muscle help to smooth movements.
- The sensorimotor control system uses the mechanics of the body to solve many of the task goals through variations in body posture, muscle mechanics, and feedback loops.
- Failure in any aspect of the sensing, planning, and acting stages of the sensorimotor loop can produce a significant decline or complete failure in motor performance.
- Understanding the neural control can only proceed if we consider the neural circuits acting along with the sensors, actuators, and the motor behavior and task goals that connect all three.

Introduction

Movement is the only manner (apart from sweating) in which we influence and interact with our environment, be it through speech, manipulation, locomotion, or tool use. However, to influence the world around us as we desire, we need to constrain our movements such that the task goal—which varies depending on the specific task—is achieved. For example, in speech, the task is communication with the person we are talking with, whereas in golf, the task is to get the golf ball into the hole with the fewest number of strokes. Due to the large variation in possible task goals and movement behaviors, understanding behavioral performance can be complex. To understand how the sensorimotor control system functions and how it selects and achieves a particular movement at each moment in time, we need to extract computational principles that govern, or at least predictively explain, these behaviors.

We cannot fully understand motor performance without also considering the sensory input and planning necessary to perform the actions. Together, sensation, planning, and action create a complex structure in which information is flowing between the different systems that are required to generate movements. For example, muscle spindles provide information regarding the state of the limb for movement planning, and this plan is also used to control the state of the spindles to enhance movement performance by, for example, suppressing the stretch reflex in the direction of the movement. The mechanisms that are present in each of the three stages of movement help the motor system to produce the movement and overcome many issues that arise from the controlled system and the way information is transferred.

We can identify six main problems that need to be solved to ensure successful motor performance: redundancy, uncertainties, noise, delays, nonstationarity, and nonlinearity. To generate any movement, the central nervous system needs to decide on one motor plan out of an infinite number of possibilities (redundancy) while taking into account the probabilistic state of the environment due to uncertainties in the state of the world and our own body. This motor plan is then transformed into motor commands that are sent to the muscles. This neural transmission is corrupted by noise and introduces a time delay. The muscles themselves exhibit high nonlinearity in force production and strong history dependence. Feedback signals arise from the periphery of the body from sensors that are both nonlinear and nonstationary. These signals are again corrupted by noise while traveling back to the brain and arrive at a range of different times depending on the different transmission delays arising from their different neural pathways. Thus, in general, there are issues of nonlinearity, nonstationarity, delays, noise, uncertainties, and redundancy, all of which can affect the sensing, planning, and acting stages of movement.

We discuss these problems and focus on the main known mechanisms that can explain motor performance across the three stages (Figure 1) of sensing, planning, and acting. We suggest that the body and brain work in concert to satisfy task constraints and goals. Together, these two structures create a sensorimotor loop in which task goals set the next movement and can be updated based on the state of the body and environment.

Movement Laws and Invariances

Observation and theory

Speed and accuracy

Early studies of human movement, such as those by the psychologist Woodsworth, demonstrated that there was an interaction between the speed of movements and their accuracy (406). That is, faster movements produce larger variability in the endpoint of the movement, whereas slower movements exhibit higher accuracy. In Woodsworth's study, participants were asked to move between two targets according to the pace set by a metronome. When the metronome frequency set a slow movement between targets, Woodsworth

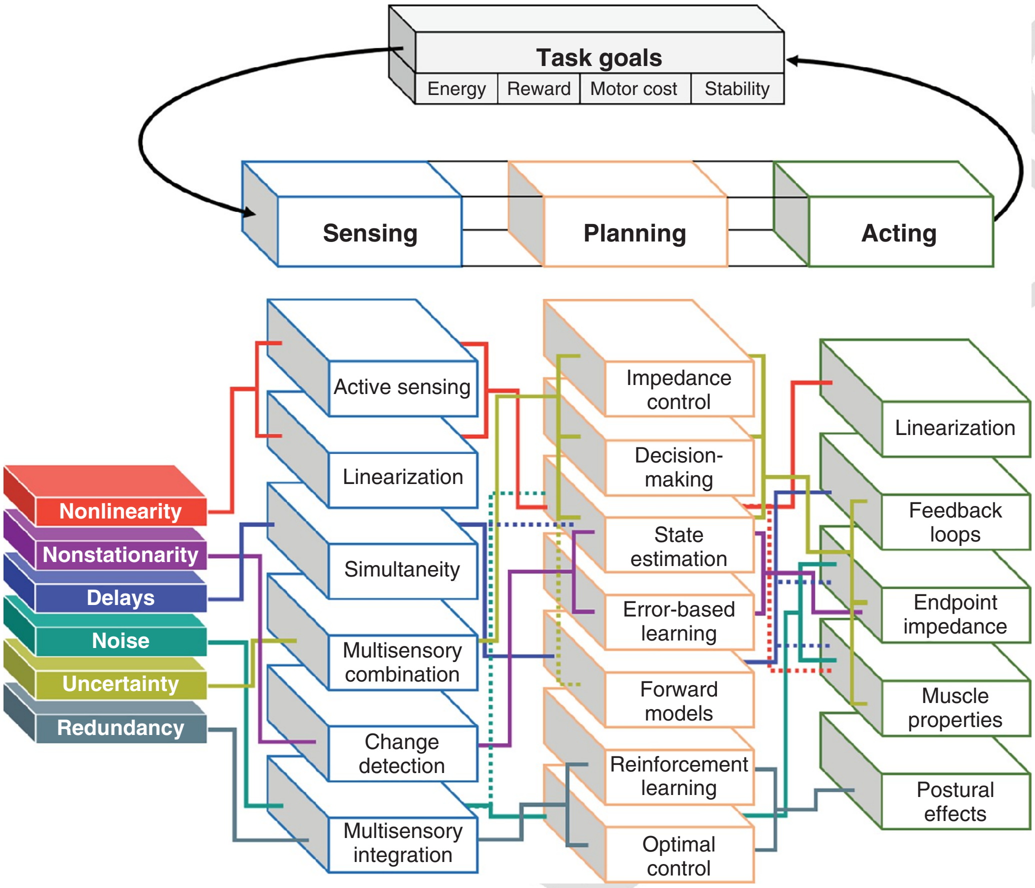

Figure 1 All interactions with the environment require us to generate movement. However, different behavioral observations, such as movement smoothness or trajectory invariances, have motivated a view of the sensorimotor system in which we have multiple interactions between different factors that govern the way we choose our motor task and the means we use to accomplish this task. In this review, we discuss the fundamental aspects of setting a task goal and three phases of motor performance: sensing, planning, and acting. Within each of these stages, we focus on six issues: nonlinearity, nonstationarity, delays, noise, uncertainty, and redundancy. The sensorimotor system has to handle these six issues, each of which can lead to a deterioration in performance. We identify different mechanisms which can provide solutions to these issues and suggest different ways of implementation. Colored solid lines connect between each issue and the possible mechanisms for reducing its effect. Colored dashed lines connect to other supporting mechanisms that may also be involved in providing adequate solutions.

observed a two-phase movement in which the purpose of the initial primary movement was to get the hand close to the target, while the secondary movement was used to correct the hand position so that it would hit the target. When movement frequency increased, correspondingly increasing the required movement velocity, the secondary phase was abolished, and the participants relied solely on their initial planned movement. To explain this result, Woodsworth suggested that the secondary corrective movement is based on visual feedback that allowed participants to estimate the error and correct for it using the secondary movement. To test this, Woodworth repeated this experiment while participants were asked to close their eyes not allowing any visual feedback. The results showed that the rapid movement trials and the eyes-closed trials had similarly large amounts of error. This result indicated the minimum amount of time required for visual feedback to be utilized for error correction.

This work led toward the formation of Fitts' law (102), which describes the specific relation among the amplitude, duration, and accuracy of a movement. In the original study, Fitts had subjects move a stylus as quickly as possible back and forth between two targets that could have different target widths (Figure 2A). He found that the duration of movement chosen by each subject was related logarithmically to the target width and distance between the two targets. As the speed of the movement depends directly on the duration and the distance of the movement, the relation describes the speed-accuracy trade-off. That is, the faster you wish to go, the less accurate you will be, or the more accurate you need to be, the slower you will move.

This relation between speed and accuracy makes sense when we consider the presence of noise throughout the sensory, neural, and muscular systems that make up the sensorimotor control system. In particular, the motor command is characterized by signal-dependent noise, noise that has

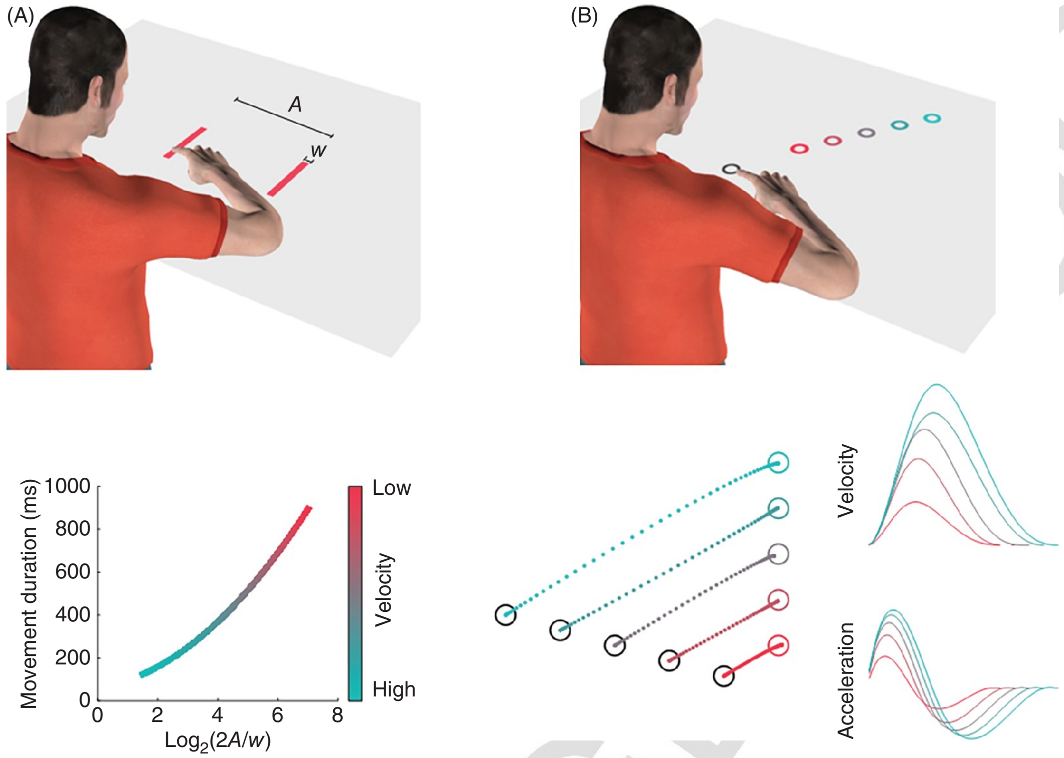

Figure 2 Temporal and spatial characteristics of point-to-point hand-reaching movements. (A) The reciprocal tapping task. In his experiment, Fitts had participants move between two rectangles, with a width *w*, located at a distance *A*. Participants were asked to move as fast as possible between the targets while trying to finish the movement within the boundaries of the rectangle. By changing the width of the rectangle, he showed that this accuracy demand increased the movement duration, which meant that participants decreased their general movement speed. The movement duration was roughly changed linearly with the increased accuracy demand, measured as log2(2*A*/*w*). (B) Despite the endless possibilities, we normally exhibit similar temporal and spatial movement characteristics when moving. For example, during a hand-reaching task between a start point (black circle) and a target point, we observe a roughly straight line path with a bell-shaped velocity profile and double-peak acceleration profile. These invariant features characterize most of the hand-reaching movements with simple scaling due to differences in movement length or duration. Here, we simulated five different movements (marked using different colors) that demonstrate participants' trajectories.

a constant coefficient of variation and therefore increases as the motor command increases. A faster movement, one with higher acceleration, requires higher muscular forces and therefore has correspondingly higher level of motor noise. Given that a faster movement also requires a shorter duration for the same amplitude, this also means that there would be less time for any sensory-based error corrections to take place to adjust the accuracy. Thus, the presence of motor noise produces limitations in the accuracy of movements that can be produced for a given speed requirement.

Smoothness

Natural hand movement, despite being affected by neural noise, is frequently described as being smooth. Measurements describing the hand trajectory, that is, hand position, velocity, and acceleration, are usually continuous in nature, without exhibiting abrupt changes in position or its temporal derivatives (12, 255). However, the source of this smooth hand trajectory is still a matter of debate. On one hand, observations regarding muscle properties and their nonlinear, almost discontinuous, activation pattern suggest that movement smoothness is a result of low pass filtering of the activation signals due to the mechanical structure and properties of the limb (316). On the other hand, it has also been suggested that smoothness is a desired feature of movement generated by the sensorimotor system when planning and executing movements, and hence smoothness is planned (325). While these two views propose different explanations for the origin of movement smoothness, one a passive feature and one an active feature, it is possible that movement smoothness is simply a result of a combination of these two factors.

To support the idea that the musculoskeletal dynamics of the arm contribute to movement smoothness, it was proposed that the intrinsic mechanical muscle properties account for transforming the pulsed spiking neural control signal activating the muscles into a smooth movement (31, 208). Moreover, different levels of arm impedance, that is, different levels of inertia, damping, and stiffness, which automatically occurs when we move different joints, can reduce the movement smoothness. For example, movements performed with the shoulder joint are smoother than those of the wrist joint (316), which are in turn smoother than the finger movements that can even exhibit discontinuities in velocity profiles (375).

In addition to the contribution of musculoskeletal dynamics to movement smoothness, the sensorimotor control system itself might set movement smoothness as a desired goal. It was suggested that smooth movements are more predictable and thus reduce the computational processing effort needed for movement control (325). Smooth trajectories also frequently occur during biological motion because animals appear to pay attention to energetic cost of motion (170, 198, 416) and the forces these movements require (96). Since smooth trajectories are associated with lower accelerations, and thus lower muscular forces, practiced movements like reaching are typically very smooth (105, 255). During locomotion, ground contact forces can influence animals to choose movements that reduce ground forces, by smoothly making contact with the ground, at the expense of efficiency (96). In addition, there is an increase in movement smoothness during early development (21) or after experiencing medical conditions, such as stroke (207), where movements are more intermittent but shift to a smoother nature over time. Overall, smoothness appears to be a fundamental characteristic of movement.

Trajectory invariance

Movements, in addition to being smooth, are characterized by other invariant features. Hand-reaching movements in the horizontal plane are characterized by a straight line path between start and end points (105, 255) with a symmetrical bell-shaped velocity profile (2, 255), features that are consistently observed across different movement durations or lengths (Figure 2B). While keeping the same temporal shape, movement velocity also tends to be scaled with the movement length. This isochrony principle suggests that movement duration is kept roughly constant by increasing or decreasing the velocity for longer or shorter distance, respectively (380, 382). Another invariant principle that appears in more complex movements involving curved motions, such as drawing (381), suggests that the hand velocity is related to path curvature. This relation was originally described mathematically as the two-thirds power law (214) and was later adapted to a variety of movements by changing its mathematical formulation (106). These features appear during unconstrained movement but also after adaptation to external perturbations. In the example of force field adaptation, the hand is perturbed from the original straight path. However, after an adaptation period, in which the motor system learns to produce compensating forces, the movements are restored so that they again follow a straight line path with bell-shaped velocity profile (334). It has been suggested that all these principles might provide the brain the means to find a solution to the redundancy problem in motor planning in which there are many movement alternatives available, but the appropriate one needs to be found to complete a task (397). In addition, movements tend to exhibit differences in their variability in task-relevant dimensions compared to task-irrelevant dimensions. That is, we find much lower movement variability in dimensions that directly affect the task performance and higher variability in dimensions that are unrelated to task success (321).

While hand trajectories appear to follow these principles, the joint trajectories depend on the spatiotemporal characteristics of the movement. To produce a straight hand path, the arm joint trajectories need to vary significantly as a function of the points in space between which we move (255). However, even in these variable joint trajectories we can still find repeated features, such as the timing of the maximum angular velocities of the shoulder and elbow joints, suggesting that the joint trajectories are planned according to invariant principles. Other studies reported that invariant characteristics of hand movement are usually evident for movements performed in the center of the reachable workspace, whereas movements done between points at the boundaries of the workspace (160, 372) or without visual feedback (374) will tend to be curved. Moreover, hand-reaching movements in 3D can exhibit more curvature than horizontal movements (68). While such curvature can be explained using more complex but accurate models of the arm, which include many muscles (101), it does not necessarily mean that the curvature is a movement goal. Instead, if we examine other movement variables, such as the arm center of mass, we can again observe straight path and bell-shaped velocity profiles, even for large and extreme movements (221, 357). Thus, curved movements can serve as indicators for potential controlled state variables and planning objectives (281). Overall, it is apparent that the motor system is planning movements according to a defined set of principles, in a coordinate system the nature of which is yet to be fully determined.

Task goals

To understand behavioral performance and the sensorimotor control system that governs it, scientists have continually looked for the invariant characteristics that describe movements. The idea is that through understanding the regularity of the movements that we perform, the key goal of the motor system could be uncovered, allowing us to understand and explain the sensorimotor control system. More recent theories, such as optimal feedback control, have suggested a more complex interaction between task goals and the movement characteristics. That is, through specifying multiple task goals or costs that vary for each task, the invariant characteristics of movements arise as a by-product of the simultaneous optimization of each of these goals. For example, in speech, the movements of the lips, tongue, and vocal tract are unlikely to be governed by specific desired trajectories of each of these motor effectors. Instead, the movements work together to solve a more complex task of producing sounds that encode a message that can be decoded by the listener. Indeed, experiments have shown that when speakers are provided with a distorted auditory feedback of their own voice, they rapidly change the movements of their vocal system to adjust the perceived utterances toward their original desired auditory targets (163). Nonetheless, understanding the characteristics of movement still provides important information about the limitations that can be expected in behavioral performance.

Stability

Successful movements require stable control of the body. If the overall system, where the system comprises the interaction and possibly coupling of the body with the environment, is unstable, then any small variations in initial conditions, noise, or additional perturbations will in general lead to unpredictable and often undesired motions. However, a stable system will be well behaved, and even small variations in the motor commands will typically produce similar and predictable motions. Alongside planning how to achieve task goals such as energy minimization or error reduction, any movement plan must also ensure the system's stability. In this manner, one could also consider stability as a complex constraint (29) that must be satisfied by the sensorimotor control system. However, there are usually trade-offs between the level of stability and other task goals such as energy minimization or accuracy, such that it often functions more like a cost (or task goal) than a constraint.

Although stability can be defined in terms of dynamical systems theory, in the field of human motor control, we can consider stability in two different ways. The first is that a system is considered stable if an additional small perturbation during a movement is counteracted such that the motion returns to the mean unperturbed trajectory (112). The second is simply to examine the variability in the movements. These are bounded if the system is stable, and increase with time if the system is unstable (33). Although we can roughly connect both of these definitions to the notion of Lyapunov stability, behaviors observed during human movements go well beyond this simple definition. For example, in walking and running, the body is continually thrown out of balance in the forward direction and then arrested with the leg (156, 328), which can be considered within the framework of bounded stability.

Stability is important for several reasons. First, stability means that the movement outcome can be predictable and therefore can be planned. That is, for a given desired outcome, the sensorimotor system is able to plan a particular, repeatable, set of motor commands that will be able to perform the action with some bounded variability. Secondly, many theories of motor learning actually require the system to be stable prior to learning (261, 342). Although there are several learning algorithms that can learn stability as part of the adaptation process (109, 188, 362), most theories require stability to be guaranteed. This is due to the fact that if the system is unstable, adaptation produces different errors on each trial, such that no adaptation occurs (33).

While the reaching movements studied experimentally are usually inherently stable, the full range of human tasks involves many that are unstable such as balancing upright, walking, and most examples of tool use (e.g., using a screwdriver, chisel, or drilling) (300). During these tasks, any small variations on the motor command from one moment to another, or material discrepancies (such as a nail in the wood during drilling), could produce disturbances of the system causing the task to fail. The sensorimotor control system is able to generate stability during these tasks by increasing the impedance of the musculoskeletal system, through modifications of cocontraction, posture or feedback gains, such that the net impedance of the human and the environment is nonnegative. If the system is stable, then the effect of small perturbations will be limited.

Errors

Within the laboratory environment, we often consider fairly straightforward task goals which typically involve moving toward a specific target. In such cases, the experimenter has set up some predefined task goals that might also specify the amount of accuracy to which the task should be performed. Similarly, there may be other constraints, such as the speed of the movement, how quickly it should be finished, or a particular obstacle that needs to be avoided. Any difference between the task performance and the specific goal can be considered as a task error. For example, the task error might be the distance from the final target, difference in the peak speed, or whether contact occurred with an object. Any of these task goals may also be relevant for everyday life. If we would like to drink from a glass of water on our desk, we need to ensure that our fingers are able to grasp the glass securely without dropping it and bring the rim of the glass accurately to our mouth without spilling the water on the way. A required speed of the movement may not exist, but moving too quickly could easily spill the water or impact the accuracy that the glass reaches our mouth. There are a whole range of possible task goals that could be set for different movements, some of which may compete with one another. Even a simple example of moving between two lines as accurately and quickly as possible shows a trade-off between the speed of the movement and the accuracy that it can be achieved by, as described by Fitts's law (102).

When we expand to look at more complex, real-world tasks, such competing task errors become even more apparent. In the long jump, to maximize the distance of the jump, the athletes must be sprinting close to top speed (around 10 m/s just before the jump) but still step as close to the takeoff point without overstepping and failing the jump. Professional jumpers will be running at around 10 m/s and will step on the final board with an accuracy of around 4 cm (220). Errors in either the speed of movement or the accuracy of the takeoff foot placement have a huge effect on the success of the overall task. Skilled serves in table tennis or pitches in baseball also try to minimize any differences in the motion of the server or pitcher while maximizing the differences in the motion of the ball once it is released. That is, the goal here is deception in the release, where errors are both any small differences in the initial movement that might give rise to a prediction by their opponent of the future motion of the ball but also in the specific motion and spin of the ball after the release. Errors in a task are often a complex combination of the specific placement, timing, speed, path, or other features representing the movement of the person and objects involved.

Motor costs and energetics

It is clear that metabolic cost is such an important consideration in motor performance that movement patterns are continuously updated in the pursuit of efficiency (331). Many models assume that the sensorimotor control system chooses particular movements that minimize the energetic cost and are thereby able to replicate many kinematic features of human movement (6, 271). In each model the specific function that is used to model the energetic cost is slightly different: motor command, muscle activity, neural effort, and mechanical energy. However, each of these functions is usually assumed to be representing the actual metabolic cost. In locomotion, many studies have shown that within a gait pattern, humans choose to optimize their speed (416) and step lengths and step widths (85) such that they move with minimum metabolic cost (243). Moreover, changes in these parameters away from the preferred pattern increase the metabolic cost of performing the locomotion (415). While there are a range of possible energetics to consider, we can roughly consider that one goal is to minimize the amount of energy (ATP) that is used for a movement, and that this energy is the sum of both the neural and muscular costs. One important open question is to think about how such costs are measured by the sensorimotor control system for feedback into the learning system to reduce the energy expenditure on subsequent attempts. Whether the brain simply tries to reduce motor commands, directly uses measures of the oxygen consumption, or relies on other sensory signals is still not clear (405).

A second important point to consider here is the question of whether energy reduction is one of the task goals or is it a consequence of optimization of other movement aspects (85). Huang et al. (172) showed that during adaptation to a force field, participants reduced their metabolic cost (as measured by oxygen and carbon dioxide exchange) after initial learning when movement kinematics and muscle activity were stabilized. They suggested that this reduction consists of reducing the amount of energy needed for the movement as well as optimizing the neural activity during such adaptation. However, Kistemaker et al. (201) suggested that energy cost might be a secondary goal when generating movement, specifically while adapting to novel dynamics. To support this, the authors had participants move in a force field in which a straight trajectory between initial and target points required a larger amount of counterreactive force to overcome forces generated by the force field compared with other curved paths in which the required forces were kept at a low value. Despite having options for paths in which the required energy, measured as generated endpoint forces, was kept low, participants adapted to the force field by generating forces that allowed them to maintain a straight line path between start and target points. This might indicate that energy is optimized at the level of muscle activation, making the activation pattern more efficient (e.g., reducing coactivation), but not changing the specific movement path. Instead, the optimal path plan might be a result of optimizing other kinematic variables (e.g., hand jerk) or maximizing efficient sensory feedback through producing straighter movements that allow visual information to be more efficiently used (104, 409). However, recently, it has been shown that if we also consider the energy cost of calcium transport to activate and deactivate muscles, in addition to the mechanical cost of movement, then energy cost predicts the smooth discrete reaching movements that were previously only explained through accuracy constraints (404). That is, minimizing energy might also explain the smooth kinematics. To further untangle this issue, future studies will need to focus on experimental designs that could dissociate the contribution of the movement plan from that of the movement execution to the overall energy cost. This can be achieved, for example, in the form of finding clear ways to measure energy expenditure for each one of these stages.

Reward

Another extremely important category of task goals is reward, or more generally, both reward and punishment. That is, we would like to perform movements or behaviors that maximize rewards and limit punishments as much as possible. Rewards are the presence of positive reinforcements (or the removal of negative reinforcements) that increase the likelihood of a behavior being performed again. In general, positive reinforcements can be broken down into primary reinforcements (e.g., food, water, and sex) that are necessary to carry on the life of the species and do not need to be learned and secondary rewards in which we have learned to associate specific items with a value. For example, we have learned to associate money as a reward due to its connection with primary rewards. Punishment (or negative reinforcements) can range from primary aversive stimuli such as pain or disgusting tastes to secondary (or learned) aversive stimuli such as a decrease in points or a specific noise. It can be seen how specific movements might be chosen to both maximize reward and minimize punishment. In the example of drinking a glass of water, avoiding dropping the glass both provides a reward (the water) and avoids punishment (breaking the glass). In laboratory experiments, the rewards range from water or juice drops in animal studies to money, points, or other pleasant stimuli in human studies. Rewards are often paired (in both real life and laboratory experiments) with sufficiently low errors (e.g., reached the target with high accuracy), but there is evidence that errors and rewards play different roles in learning and motor performance (1, 123, 274). Rewards are thought to influence movements and learning through reward prediction errors (323, 324). Once a reward is paired with a specific action, the brain predicts that the reward will be provided at the time of the action, long before the reward is provided. When the reward is then provided, the amount and quality of the reward is compared to the previously predicted reward, generating this reward prediction error. If the reward is greater than predicted, this action is strengthened, whereas if the reward was not provided, this action may be avoided due to the negative reward prediction error.

Cost functions

Despite the presence of redundancy (and indeed all of the problems in motor control detailed above) many movements tend to exhibit very repeatable trajectories. Reaching trajectories tend to have bell-shaped velocity profiles and straight-line paths in external space. The regularity of these actions motivated scientists to examine whether these arose through the specific optimizations occurring within the sensorimotor control system. That is, they asked whether the brain perhaps simplified the control problem by choosing movements that solved a specific function or minimized a cost. Flash and Hogan suggested that the optimization was performed for minimum jerk (the third derivative of position), a function that provides a good fit to most of the point-to-point and via-point movements tested in a plane (105), although it did not well capture the curved movements that occur during large three-dimensional reaching motions (12). Similarly, the minimum torque change model (372) suggests that the brain instead cares about minimizing the rate of change of the torques at the joints. The library of cost functions has expanded to make it possible to simulate not just reaching but also walking and running: the sum of muscle stresses raised to a power (62), metabolic energy (170), the cost of transport (350), and a combination of both joint and muscle stress (73). Many of these cost functions have been applied not just to human movement but also to simplified models of mammals, birds, insects, and arthropods (162). Although these models are able to capture many of the characteristics of movement (Table 1), each has distinct limitations in terms of their ability to explain the whole range of observations seen in motor behavior. For example, it is not clear why the sensorimotor control system should care specifically about a cost such as hand jerkiness, or how it would integrate this across the whole movement. Nor is it clear how cost functions based on joint kinematics or muscle stress could generalize to more complex movements such as a basketball jump shot.

To get around these issues, a model was proposed that attempted to explain motor control using the minimization of a cost that the sensorimotor control system might actually care about—that of the accuracy of the endpoint of a movement (147). Harris and Wolpert proposed that if movements are governed by signal-dependent noise (69, 186), where more rapid or forceful movements are subject to larger noise, then optimizing the accuracy of movements automatically considers the entire trajectory that is used to get to the endpoint. That is, every possible trajectory that could be used to fulfill a specific movement—get to a target in a specific time—is associated with a specific torque profile and therefore torque profile variability. Thus, each movement trajectory will produce a specific variability of possible endpoints around each movement. The goal of the motor control system is therefore to choose the specific movement trajectory that produces the minimal variability in the endpoint. Therefore, the goal of the motor system could be thought of as finding the specific trajectory that minimizes the effects of noise while simultaneously fulfilling the specific requirements of the movement, such as the endpoint accuracy. This model was able to accurately predict movement profiles for both the hand and eye (Table 1) (147). This model was an important step forward as it proposed a single cost function that can be applied to many tasks, can resolve muscle redundancy, and is easily measured: accuracy of the endpoint. It deals with redundancy because the noise occurs at the muscle level, meaning that every different possible action produces a different error pattern and therefore cost. Redundancy is therefore both solved and exploited using the specific motion that minimizes the cost function. Perhaps most important for generalization, this model can be easily extended to deal with more complex tasks, such as a jump shot. Under this framework, the optimal movement is one that maximizes the chances that the ball falls into the basketball hoop. However, both this and the previous optimization models provide a feedforward solution to the problem: an optimal desired trajectory that should be performed to maximize the chances of achieving the task. However, the motor control system is composed of both feedforward and feedback systems, and the incorporation of feedback required major extensions to the theory of movement optimization.

Complex cost functions

When we try to explain how people choose specific patterns of movements, for example, specific types of kinematic invariance such as bell-shaped velocity profiles, we can consider the brain to be solving a cost function. That is, it tries to find the specific movement pattern that minimizes something akin to a mathematical function. For example, as mentioned above, one early model of arm movements suggests that the brain attempts to minimize the sum of squared jerk (derivative of acceleration) (105). If we accelerate earlier or decelerate later (non-bell-shaped velocity profiles), then the jerk increases, resulting in a movement to be avoided. Although focusing on one aspect of motion for the cost function, for example, a kinematic or dynamic variable, can explain some of the invariant movement characteristics, it is more likely that the motor system compromises between multiple costs.

It has become more and more clear that the characteristics of each movement depend on, and can be affected by, multiple

Table 1 Overview of computational theories used to explain movement invariances and address motor control problems

Theory		Cost function	Level	Addressed problems	Predicted invariance	References
Optimization	Kinematic variables	Minimum acceleration $\min_{\dddot{x}}(\ddot{x}^{\mathrm{T}}\ddot{x})$	Endpoint	Redundancy	Two-third power law Smoothness Hand trajectory	Ben Itzhak and Karniel (14)
		Minimum jerk $\min_{x^{(4)}}(\dddot{x}^{\mathrm{T}}\dddot{x})$				Flash and Hogan (105)
		Minimum snap $\min_{x^{(5)}}(x^{(4)\mathrm{T}}x^{(4)})$				Richardson and Flash (305)
		Minimum crackle $\min_{x^{(6)}}(x^{(5)\mathrm{T}}x^{(5)})$				Dingwell et al. (83)
	Dynamic variables	Minimum energy $\min_{u}(f^{\mathrm{T}}f)$	Muscles	Redundancy	Two-third power law Smoothness Hand trajectory	Nelson (271)
		Minimum torque change $\min_{u}(\dot{\tau}^{\mathrm{T}}\dot{\tau})$	Joints			Uno et al. (372)
	Minimum time	$\min_{u}(T)$	Endpoint	Redundancy	Smoothness Hand trajectory	Nelson (271)
Minimum variability		$\min_{u}(\mathrm{diag}(\mathrm{Cov}[x(T)]))$	Endpoint	Redundancy Noise Variability	Fitts' law Hand trajectory	Harris and Wolpert (147)
Minimum intervention		$\min_{u}(\mathrm{Err}(x,t)+u^{\mathrm{T}}R(x,t)u)$	Muscles/joints/ endpoint	Redundancy Noise Variability	Two-third power law Smoothness Hand trajectory	Todorov and Jordan (365)
Bayesian integration (state estimation and sensory integration)		$\min_{\hat{x}}(\mathrm{diag}(\mathrm{Cov}[x-\hat{x}]))$		Uncertainty Noise Variability		Kording and Wolpert (205), Ernst and Banks (91)
Error-based learning		$\min_{u}((x-x^{\mathrm{desired}})^{\mathrm{T}}(x-x^{\mathrm{desired}}))$	Muscles/joints/ endpoint	Nonstationarity		Kawato et al. (193)
Reinforcement learning		$\max_{A}(Q[s,A])$	Muscles/joints/ endpoint	Redundancy		Watkins and Dayan (385)

u, control signal; x, state vector; f, applied force; $^{(n)}$, the nth derivative; T, movement duration.

costs. The motor system needs to consider the duration of the movement, how much energy will be invested, what is important with regard to task performance, and so on. For different movements, some of these requirements can be optimized simultaneously. For example, fast movements may result in the ability to perform more tasks in a fixed time (maximizing some reward) while simultaneously minimizing the duration for each movement. However, this is not the case for all requirements, as movements that are optimal with regard to one requirement might be suboptimal for other requirements. For example, in walking, smaller durations between steps will require more energy compared with self-paced walking (331). In general, the complex cost function can be thought of as a surface, spanned by multiple dimensions such as duration, smoothness, or energy, in which each point will set the movement characteristics. The optimum behavior will relate to finding a minimum on this multidimensional surface.

Depending on the task, task constraints, and other requirements, the sensorimotor system can choose which aspect of the movement gets a higher priority or greater weight in the overall combination of costs. That is, the motor system can decide to prioritize one cost, while overlooking other costs. For example, when movement stability (111) or accuracy (141) is more important for the task, we can elevate the cocontraction around different joints with the penalty of higher energy expenditure and probably greater fatigue. Contrary to this, we can calculate trajectories by optimizing a cost function that includes two or more affecting factors, which will represent a midway solution between individual optimal solutions. For example, two major contributors that affect movement profiles, especially the movement duration, are effort, which we want to minimize, and reward, which we want to maximize (307, 332, 335). Changing the movement duration can allow us to change the cost and benefits of each of these factors. That is, we prefer to get a reward in a short time and thus elevate our desire to move as fast as possible (collecting more rewards in a fixed time interval). However, fast movements with short durations increase the required energy and thus increase the cost for such movements. By simultaneously taking into consideration these two factors in the cost function, it can allow us to predict the optimal movement duration that provides the best solution for both reward and energy requirements but not optimal for either of them.

Alternatively, we could also examine a two-level solution to explain invariant movement properties, each of which puts emphasis on different movement aspects. For example, Biess et al. (22) suggested that the optimal path and joints configuration for 3D movements is a result of minimizing the arc length of the geodesics in possible arm configuration space, while the velocity profile can be calculated using the minimum hand jerk model. Together, these two levels can predict movement trajectories that correspond to trajectories in which we achieve a minimum peak kinetic energy for the joints. However, this last example also raises a problem of lacking the ability to distinguish between trajectories predicted by different complex cost functions. As discussed previously, for hand-reaching movement, calculating the hand trajectory based on optimization of different cost functions results in predictions that are similar to each other and to the trajectories exhibited by humans. If indeed movement planning is based on optimizing a cost function, these similarities between trajectory predictions make it hard to differentiate which cost function underlies such a process. In such cases, we can consider a cost function that is a linear-weighted sum of different cost functions, such as kinematic based (105), dynamics based (372), or energy based (20), and try to fit the experimental trajectory by minimizing the cost of this general cost function. By assuming such a linear combination of costs, we can find the individual contribution of each cost, using an inverse optimal control approach, while achieving an almost perfect fit to the behavioral data. While this was shown to account for simple reaching movements (19) or jumping (390), in other cases such as object manipulation, where the hand trajectory can have a more complex pattern, different costs in the overall sum may not be relevant, which questions such ideas of combining costs using a linear combination.

Achieving motor goals—exploration and exploitation

Following specifying task goals, such as rewards or minimizing motion cost or a combination of them, we need to find one or several movement plans that allow us to achieve them. For this purpose, movement errors, and more generally motor variability, allow us to explore the motor space for any given task. These deviations (or variations) in movements can also be used to collect additional information about the environment, for example, about the presence of additional rewards or simply to provide more accurate sensory information. Deviation from the movement plan, especially during initial exposure to a new task or environment, can help us discover new preferred or more beneficial plans that can help us maximize reward or minimize errors. For example, when trying to hit a target by throwing a ball tethered to a center pole, we can observe initially elevated variability in the ball trajectory (50). Once a solution space is found, we can observe that participants are trying to exploit this solution by reducing the movement variability so as to reduce error or increase reward. However, since not all aspects of motion are relevant to performance, there is an open question regarding how relevant and irrelevant motion variabilities change between exploration and exploitation.

General movement variability can be decomposed into relevant variability that directly affects the task performance and irrelevant variability that does not affect the success or failure of the task. For movement dimensions relevant to task performance, elevated variability can increase errors and decrease reward, while for irrelevant dimensions, increasing or decreasing the variability will not affect performance. For example, when typing on a keyboard, we focus on controlling the spatial location of our fingers so that they will hit the desired key, while the power with which we hit the key can be more varied as long as it is above a certain threshold. Thus, task-relevant variability should be reduced to ensure a successful task, while task-irrelevant variability can be unattenuated since it has little to no effect on task success. If we need to learn a new task, we may increase task-relevant variability, allowing us to explore the solution space and obtain more detailed information about the environment. Indeed, there are many examples, such as in reaching movements (286, 407), finger movements (124), standing balance (203), or during walking (35), where participants initially increased task-relevant variability to explore possible solutions or increase their reward. Once a solution is found, to exploit it, participants usually try to reduce variability to avoid any deviation from the rewarding strategy. Irrelevant-task variability can be less affected by the change between exploration and exploitation (260). Recently, this view on variability behavior was challenged by more complex tasks (66, 339). For example, providing feedback that includes both reward and failure compared to only reward or no reward produces an increase in both task-relevant and -irrelevant variability to allow for better exploration of the solution space (377). While changes in intentional variabilities for exploration and exploitation can be observed in many tasks, the factors contributing to this process still need to be fully understood.

Problems in motor control

To discuss motor performance, it is critical to understand the problems involved in motor control and the limitations these place on skillful performance. It has been proposed (117) that there are six critical issues that the sensorimotor control system must solve: delays, noise, uncertainty, redundancy, nonlinearity, and nonstationarity. Each of these issues affects the three stages of motor control: sensation, control, and action.

Delays

The sensorimotor control system contains significant delays in all stages of information processing, from the delay in receiving afferent sensory information in the brain to the delay in acting upon the efferent output (257). Taken across the different stages, these delays can range from 50 ms for the fastest monosynaptic stretch reflex response to more than 500 ms for complex responses that require extensive processing or complex decisions. These delays therefore place limits on maximum human motor performance—although many aspects can be mitigated through different computational mechanisms.

Nonstationarity

Nonstationarity in the motor system refers to the fact that the properties of both the sensorimotor system and the external environment change over time. Further complicating this issue, these properties change on different timescales. On short timescales, this could be as simple as the rapid changes in sensory signals even with a constant input (rapidly adapting receptors), short-term plasticity of the nervous system, or the fatigue of our muscles under continued activity (23).

Redundancy

The sensorimotor system receives information from multiple sensory modalities and uses this information to control approximately 600 muscles that move 200 joints in one particular way, chosen out of an infinite number of possible different ways so that it can perform the task (18). Even within the highly constrained task of reaching between two fixed points in space, there are infinite paths and hand speeds along each path, infinite joint angle trajectories that achieve each hand trajectories, and infinite combinations of muscle activations that achieve such joint trajectories with variations in the muscles used and the level of cocontraction or stiffness. While some of these solutions will have a higher accuracy, a lower metabolic cost, or achieve some other important measure better than other solutions, it is not entirely clear how the sensorimotor system deals with redundancy even for this simple movement task, although models of optimal control go some way to providing an explanation.

Nonlinearity

All stages of the sensorimotor loop are nonlinear. Nonlinearities are present throughout the control system, due to the all or nothing principle of action potential firing in the neurons, which has a minimum threshold of depolarization at the soma before any action potential is produced. Moreover, the musculoskeletal system is highly nonlinear, from the movement of the joints to the force production of muscle, which depends on the length, velocity, activation history, and prior state in a complex nonlinear manner. Such nonlinearity throughout the system complicates our mathematical understanding of the control and prediction of our bodies.

Noise

Noise limits our ability to accurately perceive both our environment and the state of our own bodies and to precisely act upon the environment (95). At all levels of processing in our motor system, the effect of noise can be thought of as generating fluctuations around the desired output when the same stimulus is used. For example, the firing rate of any particular sensory neuron will have some fluctuation in its output, even if it receives the exact same stimulus (306). In a similar way, the force output of muscle fibers will be different even for the same input from the motor neurons. Perhaps the main reason for this variability is the state of neurons and other cells that change stochastically over time.

With respect to motor behavior, noise produces variability from one movement to the next even when performing the same action repeatedly, regardless of the amount of training. No matter the desire to perform the same action, noise within the system induces variability that affects the performance.

Uncertainty

Uncertainty is unknown information or the incomplete knowledge of the state of our body, the state of the world, the task, or the rewards that we might receive. Although uncertainty can arise through delays and noise, it also arises through many other sources. We can roughly separate uncertainty into three types: uncertainty due to inherent ambiguity, uncertainty due to signal imprecision (including that due to data compression and decompression), and uncertainty due to unpredictability. These factors affect motor performance through different pathways. First, there are clear limitations on the accuracy of a movement, as we will have limited information about the precise location of a target, or indeed the precise location of our own limbs. Secondly, unpredictability means that we cannot guarantee a successful action every time we perform a task: someone may bump us, or instability may induce variations in our movements. There are techniques that the sensorimotor system can use to deal with these issues such as forward models or impedance control (117), but each of these consumes higher energy costs, be it from neural or motor costs.

Solutions in Motor Control

Sensing

The sensory system consists of different modalities in which different forms of energy or states are being transformed into a neural signal that travels back to the brain. Our sensory system can capture and convert a great number of physical signals into neural signals including light, sounds, forces, and temperature. The number of sensory systems can differ between animals; for example, contrary to humans and other animals, some fish can sense electricity coming from other prey animals and act according to this sensory input. Moreover, within each modality, different animals can be sensitive to a different range of the physical stimulus. For example, humans have three types of color-detecting cones, while dogs have only two types, which limit their ability to distinguish between different colors in the environment. However, in addition, dogs can “see” thermal radiation with their nose (13). Both the number of sensory modalities and the detectable range within each sensory modality can impact the way we perceive and estimate different aspects in the environment. Particularly, for motor behavior, these sensory inputs make it possible to identify task goals and provide feedback about performance once the movement is finished.

Active sensing

The vast majority of our movements are goal oriented. Whether we interact with the environment, such as manipulating objects, or interacting with others, such as greeting another person with a handshake, we usually set multiple movement goals that will eventually allow us to complete the desired task. To perform the task we initially need to gather information about the state of the environment and to understand the options and constraints that we have for achieving task goals. The sensorimotor system must solve the difficult problem of extracting out task-relevant information from a large amount of extraneous data using limited sensory and processing resources. For example, when we see and reach for an object, we must identify the object and ignore the background using eyes (327) that see with a high resolution in only a narrow visual range (the fovea) and process this information without interrupting other tasks such as walking and talking.

One solution characterizing the human as well as other animals’ sensorimotor system is the ability to actively change the sensing strategy. In such an active sensing strategy, the environment is sampled at sparse times and/or at specific spatial locations by changing the focus point of the different senses (Figure 3). For example, people will gaze in the direction of objects to grasp. Diving raptors, constrained by aerodynamic forces and eyes that have limited mobility, adopt logarithmic flight patterns when diving to keep the image of the prey fixed on the fovea (371). Another example can be seen in sperm whales which train their auditory gaze by pointing their noses at prey items while hunting (368). Similarly, there is evidence that the gamma drive to the muscle spindles is controlled to change the proprioceptive feedback during specific tasks (80, 81, 90). While we can observe different sensory mechanisms that can direct our senses to relevant information for our task, the computational principles that are responsible for generating these sequences of active changes to the senses are still unknown.

A possible framework to explain such a strategy is based on the idea of Bayesian inference (267). According to this principle, we direct our sensors to maximize the information that will allow us to distinguish between possible states of our own body or states of the environment. For example, when trying to classify an unknown object that is partially hidden in the environment, we are trying to relate this unknown object to known objects based on prior information regarding color, shape, surface pattern, and so on. To do so, our visual scanning pattern will move between points on the object that could allow the greatest reduction in categorization error (408). However, this cannot explain the entire gazing pattern. Some gazing locations within the pattern do not maximize information regarding the task we need to perform. This can be explained by considering another scheme in which we are tuning our gaze to informative locations while considering the energy costs of the movement, such as in the case of gazing where the movement is eye saccades (42). Interestingly, this idea is also supported during simple reaching movements

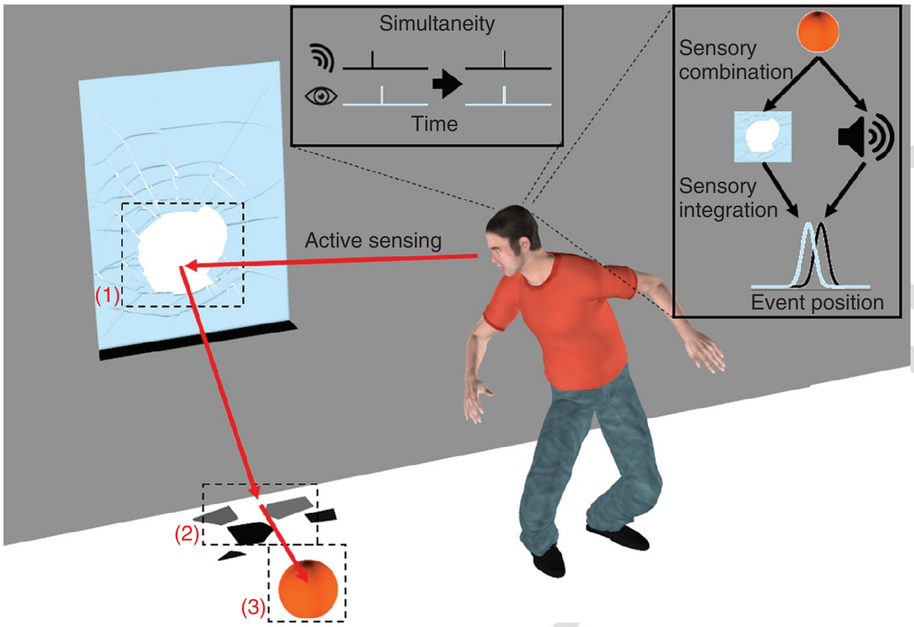

Figure 3 Sensing: prediction and integration. Usually, we can anticipate the events in the environment. For example, when we bounce a ball, we expect to see the ball hitting the ground and hear the bouncing sound. However, due to different delays in the transmission of the signals, the information arrives at different times to the brain, which needs to compensate for the delays, so we will experience this as a single, simultaneous event. Since we know that these signals originated from a single event, we integrate them to better estimate the event characteristics, such as the distance between our hand bouncing the ball and the ground. During unexpected events, we initially have limited sensory information, as most, if not all, of our sensors are not attentive to the event. For example, when a window is unexpectedly shuttered behind us, we hear the loud noise but do not directly see the event. If we want to understand what happened, we initially focus our gaze on an estimated position of the broken glass based on sound information. The visual and auditory signals are combined so we understand that the two types of information represent the same event, that is, the ball broke the window. Once we understand that the two signals represent the same event, we can again integrate the sensory information to understand better what exactly happened, for example, the velocity at which the ball broke the window. This initial understanding allows us to gather information more efficiently through active sensing as it will be used to calculate the next probable location in space in which we can find the most useful information, for example, the position in which we expect to see the broken glass. Similarly, the spread of the broken glass provides us with the probable path for the ball, so we do not need to search for it in the entire environment.

in which participants were willing to spend more energy to maximize information (409).

Linearization

Nonlinearities in the sensing system arise from individual receptors requiring a large enough input signal before they start to transmit action potentials and saturating their firing beyond a specific level of sensory input. The simplest way to reduce system nonlinearities is to linearize the system around an operating point. Since sensors with linear characteristics are easier to control through the superposition principle and are invertible, which can allow retrieving transformed information, it is reasonable that sensing systems will be linearized. We can find evidence of linearization in the proprioceptive information processing of muscle spindles that, under some conditions, can tune their firing rate so that it will be proportional to changes in muscle length (80). Other evidence for linearization can be found in the auditory system in which A1 neurons exhibit an approximate linear response during detection of sound source direction (320). In addition, we can observe linearization of sensory information in the somatosensory system of animals such as in the example of principal whisker movements in Wistar rats that provides tactile information (253). However, despite the advantages of linearization, it demands that the sensors work around the operating point that limits the range of measurement and is subject to less-accurate results if the parameters in the nonlinear system change unexpectedly.

Another possibility is to take advantage of the nonlinear characteristics of the different sensory systems. Specifically, for nonlinear sensory systems, neural noise at specific intensity can improve information processing and detect subthreshold stimuli. This phenomenon of stochastic resonance appears in many different sensory modalities (242, 259). For the sensorimotor system this includes increased sensitivity of muscle spindles (54), enhanced tactile sensation (51, 389), or enhanced sensitivity to luminance information (202). It still remains an open question whether the sensorimotor system can change the parameters of nonlinear sensors so that this phenomenon of stochastic resonance will appear at different levels of neural noise.

Finally, some sensors provide a linear readout of a highly nonlinear physiological relationship. For example, the relation between muscle activation and muscle force depends nonlinearly on the force-length curve, force-velocity curve, muscle history, and activation history (31), in addition to other effects such as fatigue. This means that it is difficult to predict the exact muscle force given by a specific muscle activation pattern. However, the Golgi tendon organs provide a linear readout of the muscle force (57), allowing for a measurement of the muscle tension achieved.

Simultaneity

Sensing the external environment or our internal state requires the use of sensory receptors such as rods and cones in our visual system or muscle spindles and Golgi tendon organs in our musculotendon complex. Delays result both from the receptor dynamics and more significantly from the transmission of the action potentials from the receptor to the central nervous system (axon conduction delays and synaptic transmission) and scale with the size of the animal (257). The magnitude of these delays varies significantly, depending on the sensory modality (proprioception is faster than vision) and the complexity of processing (visual orientation is faster than face perception). These delays mean that our central nervous system only has access to sensory information from the past, normally on the order of 100 ms out of date, with specific delays varying with the sensory modality.

Despite this temporal latency between incoming signals, the sensorimotor system can infer that these signals represent the same event (Figure 3). The trivial solution to overcome such temporal difference between signals is to implement temporal recalibration by estimating the delay value and shifting the signals according to this estimation (222). However, the mechanism of temporal recalibration at the level of sensory signals used for motor control is not well known. Most of the evidence that supports different possible recalibration and synchronization mechanisms originated from results of perceptual tasks. Since sensory information might be handled differently for perception and action (103), these proposed mechanisms still require further testing to be generalized to motor control. Nonetheless, it is important to consider that these concepts might underlie the processes the central nervous system (CNS) uses to synchronize signals. We can identify two main principles that classify these models into two groups.

In the first group, there are models that suggest that the brain estimates the temporal difference between signals and either uses this estimation to infer that the two sensory signals describe the same event or uses the delay estimation to recalibrate the signals and compensate for the delay (384). For example, we can consider a neural mechanism which estimates the time that is required for the signal in each modality to travel and be processed. By knowing the speed of each physical signal together with an estimation of distance each signal needs to travel, we can estimate the time delay between signals to test whether the sensed delay matches the estimated delay and therefore likely originated from the same event (76, 130, 131, 304). A different approach would suggest that this estimation of the time delay can be used to temporally shift the signals so that they will realign (97, 258, 348). Examples for this realignment can be found mostly in rapid recalibration processes, that is, without the need of prolonged exposure to signals misalignments, for visuoauditory (74) and visuotactile (218) signals. Interestingly, this recalibration might be achieved by changes in attentional distribution across the different sensory modalities as this was shown to increase the processing speed and thus shorten the overall delay (337).

In the second group we find models that change the processing of the signals so that they will be perceived as originated by the same event since perception of sensory simultaneity can be achieved when the different event times, as marked by multiple sensory modalities, fall within an integration time window (348). As the delay between signals increases, the possibility that the times of these markers to fall outside of the integration window increases and thus reduces the sense of simultaneity. In contrast, small delay values between signals are unnoticeable since the times of event markers are within the window. By changing the characteristics of this signal processing procedure, we can restore the sense of simultaneity. For example, increasing the duration of the integration time window can allow for two signals with noticeable delays to fall within the window and be perceived as simultaneous (348, 384). Another option is to change when we set the event detection time. To detect an event, we accumulate sensory evidence until a set threshold is crossed, which marks the event time. By changing the threshold value for a specific modality, we can change the event time marked by this modality and match it with the event time detected by other modalities (384). Although these mechanisms for coping with delay are more relevant for the perceptual domain, they can also help in understanding the ways the brain might overcome sensory delays for motor control, where sensory differences become even more apparent (and relevant) in tasks such as teleoperated systems.

Change detection

Nonstationarity characterizes both the physical signals captured by the sensory system and the sensors used to capture them. Physical signals can have complex time-dependent characteristics such as in the case of speech sound waves that can change due to articulatory mechanisms (314) or brightness changes due to changes in light source. In addition, random noise that distorts the signals makes it difficult to capture these changes in the statistical characteristics of the sensed signals. Sensors also exhibit changes in performance, which depend on activation history (272). For example, during sound source localization using the auditory system, Hofman and Van Opstal found that nonstationary sound signals affected the perception of vertical but not horizontal position of a sound source (157). To overcome the nonstationary effects in the sensory system, it was suggested that the brain might implement different solutions such as signal processing techniques or Bayesian inference schemes.

The classic signal processing solution involves analyzing data in small time windows. By dividing the entire data into small intervals, we can focus on an interval in which the statistical properties of the information are kept constant (157, 383). Analyzing multiple windows can provide general information regarding the environment as well as the times of the changes occurring. For example, for vertical localization of a sound source, it was suggested that the sensory system uses spectral analysis in a time window of several tens of milliseconds (383). The brain can also use designated signals that aimed at detecting changes, such as in the case of the FA-II afferent information originating from the Pacinian corpuscles mechanoreceptors, which act as high-pass filters and thus allow for detecting changes in the stretch of the skin (230). A different way of finding changes in environmental parameters is using an adaptive Kalman filter that estimates the information variance so it can tune the contribution of past sensory information that might be irrelevant when the environment changed (268). Another mechanism for handling nonstationary environments is based on Bayesian inference. These types of models allow us to detect the time points where the environmental statistics changed and thus change the weight of past sensory information in light of new sensory information (4, 17, 275, 412). By detecting changes in sensory information, the sensorimotor system can have both better representation of the current state and better understanding of how past information should be handled for planning future actions.

Multisensory combination

Sensory inputs can lead to uncertainty about the state of the body and the environment due to ambiguous information or limited sensor capabilities. Uncertainty due to inherent ambiguity arises through the information that we receive about the environment. The external world exists in three dimensions, and yet the only visual information we receive is on the back of the two-dimensional retina (197). This means that the three-dimensional objects are mapped onto a two-dimensional image containing only partial object information. There are theoretically an infinite number of objects that could map onto the same two-dimensional image at the back of the eye. Similarly, inherent ambiguity occurs because of the aperture problem. That is, we only receive partial information about something in the environment, for example, the movement of part of an object viewed through an aperture. In this case, we may only perceive lateral motion, although the object could also be moving upward or toward us. Uncertainty also arises due to signal imprecision, that is, through the structural constraints of our sensory systems and the digital representation (neural firing) of the analog world. For example, visual acuity decreases away from the fovea (391).

One possible way of solving these issues is by combining multiple sensory inputs to get a better understanding about the state (Figure 3) (75, 92). Additional sensory modalities provide complementary information regarding the state that can be different from the uncertain information provided by a single sensory channel. For example, when seeing the projection of an emergency vehicle headlights on the walls of a building, we might be uncertain of the vehicle's movement direction until we combine it with the siren sound which can provide a more clear indication for the movement direction. When the sensorimotor system combines multiple sensory inputs, we can observe different phenomena such as gain modulation, increased accuracy, or faster reaction time, serving as a clear indication of the reduction in uncertainty.

Gain modulation suggests that combination of sensory inputs can cause enhancement or suppression of the stimulus perception compared to the unisensory reaction. Such modulation is evident, for example, in detection of light sources (351) or enhanced visual cortex excitability using auditory (312) or tactile stimulation (299). In addition, it was suggested that a combination of sensory information decreases the response time to various stimuli. That is, the system identifies and reacts faster to a stimulus if it is accompanied by a stimulus in a different, perhaps redundant, sensory modality. For example, combining visual and auditory stimulus resulted in faster reaction times than a visual stimulus alone (87, 152, 322). Similarly, an auditory stimulus reduced the reaction time to a movement cue (250). Moreover, perceptual identification of a stimulus during combination of tactile and auditory information (262), or tactile and visual information (108), was also speeded up when both sensory inputs were present. This faster reaction time does not necessarily produce a reduction in accuracy (87). For example, multisensory combination was suggested to facilitate more accurate target matching using visual and proprioceptive information (28, 376) or during object recognition using visual and auditory inputs (254). Interestingly, even by providing irrelevant information via different sensory modalities, we can reduce the uncertainty of relevant sensory information, such as in the case of touch sensation (196), light detection (122, 232), visual pattern frequency detection (93), or sound detection (132).

Possible explanations for the mechanism that allows for multisensory combination were examined at the behavioral and neuronal levels. On the behavioral level, Clark and Yuille suggested that multisensory combination might be formalized using a Bayesian approach (strong coupling) in which we combine a prior assumption regarding the estimated property with a combined likelihood function of the sensory inputs (16, 46, 413). In addition to behavioral explanation, neural recording of neurons that receive multisensory inputs allows us to understand the fundamental principles underlying sensory combination (88). Multisensory neurons exhibit enhanced response when receiving inputs from multiple sensory modalities, which is also known as the superadditivity. That is, the response to multiple sensory inputs is higher than the response of each of the contributing unisensory inputs and can also be higher than their sum (245, 352). This usually occurs when the stimuli are aligned or in close proximity in space, known as the spatial principle, and in time known as the temporal principle. Such response enhancement is even greater for weak stimuli, known as the inverse effectiveness principle, which allows detection of low-intensity events if they can be sensed with multiple sensory modalities (317) allowing for a reduction in uncertainty regarding events in the environment.

Multisensory integration

Multiple sensory modalities allow for detecting events or object properties based on different measurements of physical energy. However, when the same event or property can be perceived via more than one sensor, the sensorimotor system might encounter a situation of information redundancy. When two or more sensory modalities provide different estimations for the internal or external state, the brain needs to decide which sensory source is more reliable. Reliability is usually measured by the variability of the signal due to noise. The external stimuli are intrinsically noisy (95), for example, vision results from the absorption of photons that are inherently binary in nature. This binary information is then converted into an analogue receptor potential. However this can only be conveyed to the central nervous system by converting it to the digital code of action potential firing in which only the frequency of firing conveys the signal to the brain. Moreover, low levels of signals may not cross the threshold for generating an action potential, thereby introducing differences between the external world and our internal representation. These conversions from analogue to digital information or vice versa introduce variability or noise into the signals. Since one possible aim for the brain is to reduce variability, it might rely differently on each sensory modality when integrating the redundant sensory information. To do so, it was suggested that the brain uses a Bayesian approach that can generate a more reliable state estimation based on the sensory inputs.

The Bayesian integration scheme can explain both the initial processing of the sensory information and how we integrate between modalities (Table 1). The initial processing involves identifying the structure of the system and information, that is, Bayesian inference. At this stage, we need to understand the origin and interactions between sensory inputs. For example, if there is a small temporal difference between light and sound, the brain needs to decide whether they originated from the same event, or that each of them originates from a different source (204). Understanding the information structure is a crucial part of integration since we want to avoid integration in cases where information originated from different events. In addition, after deciding that the signals originated from a single source, representation of the source structure is needed for different assumptions for integration such as the uncertainty that we have in each sensory modality. Following this stage, the Bayesian framework aims to solve the conditional probability $p(x|y)$, where x is the property we need to estimate, and y is a vector of the sensory information we received from multiple sensors. To solve this, we can use Bayes' rule that suggests that this conditional probability, the posterior probability, is proportional to the conditional probability $p(y|x)$ multiplied by the probability $p(x)$. According to this rule, we need to combine the prior knowledge, the belief $p(x)$, about the probability of the estimated property with the likelihood function, $p(y|x)$, that represents the probability to get the sensory inputs that we received, given a value of the environmental property. In other words, this framework suggests that if the brain has some knowledge about the probability of the estimated property in the environment and how sensory signals are generated by different values of the property, it can estimate the property value.

Considering this framework, if we assume that the sensory information vector is assembled from independent sensory inputs, and that both this vector and the estimated property can be described by Gaussian distributions, the integration between senses is identical to the maximum-likelihood estimator (MLE) (91, 217). There are many examples for integration that follow this principle such as integration between vision and proprioceptive information (91) or visual and auditory information (5). However, the MLE cannot explain some aspects of sensory integration such as in the case where assumptions regarding the prior cannot describe the estimated property distribution (217). Moreover, while the Bayesian sensory integration concept can explain different behavioral results and reveal the optimality in integration, other studies provided evidence, suggesting suboptimal integration, which questions the idea of an optimal sensory integrator (298). Importantly, when we are considering integrating sensory information for rapid decisions or movement, the delay at which such information transfers also becomes critical. Indeed it has been shown that the speed of somatosensory information is weighted much more than the more accurate but delayed visual feedback during reaching (59). Nonetheless, the Bayesian integration idea serves as an important tool in understanding ways to deal with redundant, noisy, and uncertain information and can serve as a competitive model for future more sophisticated integration schemes.

Planning and control

The sensorimotor system needs to generate appropriately coordinated movements, which requires taking into account the kinematics (motion) and dynamics (forces) of our bodies as well as those of the tools and objects we may wish to manipulate. Consider the generation of a visually guided voluntary movement of the hand toward a goal, such as reaching out to grab an apple. We first need to generate an estimate of the target, relative to our body, based on visual information. This target location needs to be transformed from the coordinate system of our eyes into the coordinate frame of the arm, which will then be used to generate a motor plan of the movement. From the motor plan, a pattern of neural motor signals are generated, which lead to muscle activation and force generation within the limbs (as well as stabilization of the body) that will lead to movement of the hand toward the apple. Multiple feedback signals from proprioception and vision provide a means to estimate the limb state, which can be used as feedback to ensure that the hand reaches the goal. Within this process, we can identify different control strategies, each of which can dominate or act in parallel with other control strategies.

Feedforward control

To gain more understanding of the processes involved, and human sensorimotor control in general, we consider the control of movement from a control engineering perspective. The field of control engineering is concerned with getting dynamical systems—termed the "plant"—to perform specific goals or actions, through the application of a suitable controller. One of the simplest architectures that can generate a control signal is the open-loop control architecture. Here, the output (e.g., motion of the plant) has no effect on the control action (Figure 4A). That is, open-loop controllers operate without feedback. However, to operate effectively, the input goal needs to be transformed into an appropriate feed-forward motor command. More precisely, feedforward control requires that we preprocess the input goal with the inverse model of the plant. To better illustrate this point, we consider a linear or linearized system, $p(t)$, we wish to control. If we provide an input signal $x(t)$ to this system, the resulted output signal, $y(t)$, can be calculated using a mathematical operation called convolution and is marked as $y(t) = x(t) * p(t)$. If we also include a controller, $c(t)$, that receives the input signal and generates a control signal that will serve as the input to the system, we can calculate the output signal as $y(t) = x(t) * c(t) * p(t)$, where $x(t) * c(t)$ is the control signal that will be the input to the plant $p(t)$. To get the system to follow the desired goal, the output (e.g., motion) should equal the input (e.g., desired motion), that is, $y(t) = x(t)$. In such case, the above equation turns into $x(t) = x(t) * c(t) * p(t)$, which is possible if $c(t) * p(t) = \delta(t)$, where $\delta(t)$ is an impulse function (which can be interpreted as a 1). In such a case, the controller, $c(t)$, needs to be the precise inverse function of the plant $p(t)$ (118).

Usually, in such a control scheme, we use a trajectory generator to produce a signal specifying the desired path for the plant, such as the trajectories in joint space of the arm needed to reach the goal. This desired trajectory is then fed into the controller that ensures that the joints follow that trajectory irrespective of dynamic forces within the plant and under internal and external perturbations (Figure 4B). Such desired trajectories can be obtained by fitting power series curves through a set of desired via points or by minimizing a cost function such as the minimum hand jerk trajectory. Although feedforward schemes may work satisfactorily in some cases, they have their limitations. First, the controller has to be a highly accurate inverse model of the plant since, if it is inaccurate, the appropriate control input to the plant will not be generated. That is, any imprecision or noise in either the system or the inverse model would result in failure to reach the target motion. A second limitation of a feedforward scheme is that the controller is unable to compensate for unpredictable disturbances to the plant.

Feedback control

To overcome limitations of feedforward control (inaccuracies in the inverse model and disturbances to the plant), we can make use of feedback from the output of the plant (118). In this architecture, we specify target goal and compare it to the plant output to calculate an error (Figure 4C). This error is fed into a controller block to generate motor commands such that the system output moves toward the goal until the error is ideally reduced to zero. In the design of a simple feedback controller, the main task is to find the appropriate controller gain or gains. In practice, the controller could range from a simple linear amplifier to something much more sophisticated. For example, in PID control, the controller block consists of three parallel pathways which calculate proportional, integral, and derivatives of the input. These are individually weighted by three corresponding gain terms, and the outputs summed to generate the motor command. To operate effectively, the feedback gain term needs to be set sufficiently high to achieve good performance, for example, to implement fast movements to targets and good compensation to disturbances. However, the feedback gain term also needs to be chosen without the system going unstable since change in gain magnitude can cause system instability. Other factors also influence the choice of the gain, such as the performance of the system. For example, how fast do we want the system to respond to changes in the input value. Overall, feedback controllers are generally more robust than feedforward controllers because they do not need a precise model of the plant and can compensate for disturbances.

Feedforward and feedback control schemes can be designed using different methods such as root locus analysis. However, these approaches are generally limited to systems with a single input and output and struggle when there are multiple inputs and outputs that need to be controlled. In addition, they only apply to linear systems. An alternative approach is to use state space representation that can address these limitations (10, 342). In state space representation, the system, or linearized version of it, is represented as linear matrix equations, using vectors and matrices to capture system dynamics and input-output relationships. Describing dynamical systems in this way allows powerful linear algebra techniques to be used to analyze dynamical systems and

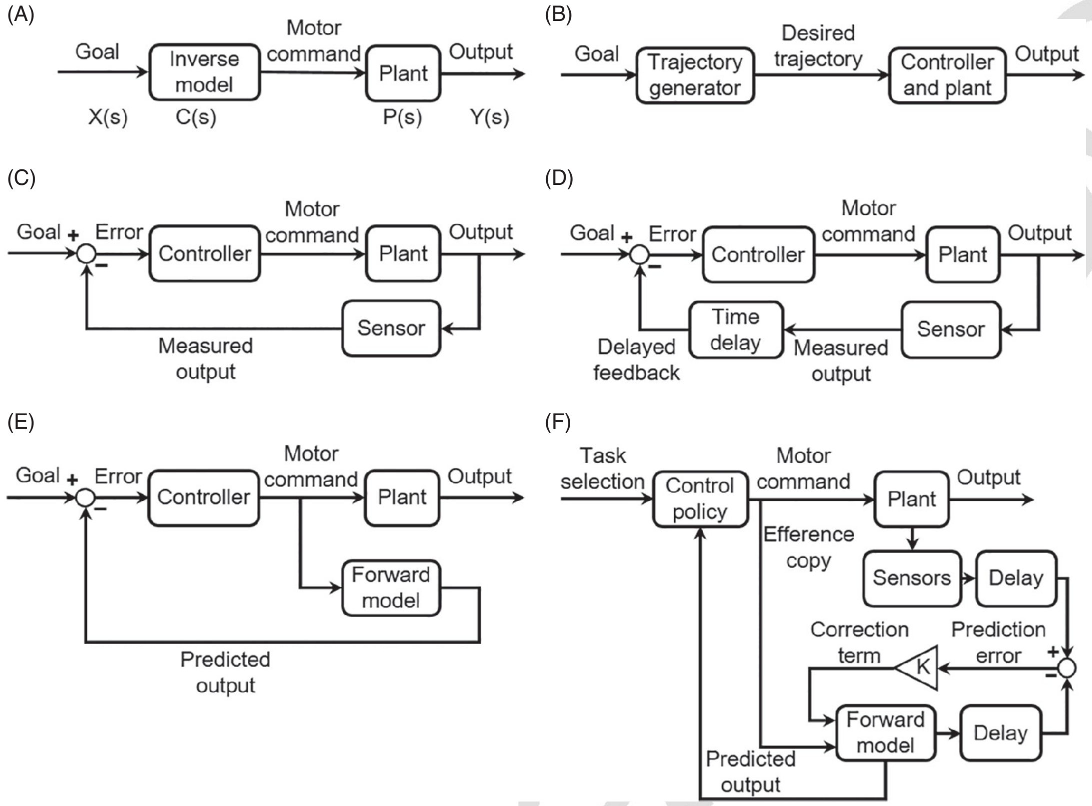

Figure 4 Models of control. (A) Open-loop feedforward control. An inverse model maps the input goal to the signal needed to control the plant. (B) Trajectory generation. A separate module is often used to generate a feed-forward movement trajectory. In this scheme, although the controller can use feedback from the plant and its measured output, no feedback is used to generate the goal trajectory. (C) Output feedback control. Output measurements are used to modify the control input by subtracting it from the input signal to calculate error. The error is fed to the controller to generate motor commands. In a functioning system, the output then moves toward the goal. This scheme will also have the ability to compensate for disturbances. (D) A scenario when feedback delay is significant. Although direct feedback can sometimes be very effective, problems with system stability can arise if the sensory feedback signal is delayed in time. (E) The forward model estimates the output, which is then used in the feedback loop, rather than having to wait until actual direct feedback is received. (F) Optimal controller making use of an observer, dealing with time delay and implementing online updates.

applied to control problems. The two main state space model equations are:

$$\dot{X} = AX + BU$$

$$Y = CX + DU$$

The first equation indicates how the change in system state is affected by its current state, X, and system input, U. The second equation is the output equation that indicates how the system output, Y, depends on the system state and the system input. A, B, C, and D are matrices that set the system behavior.

One aspect of the state space approach is that it does not just represent the output of the system. That is, the full dynamical state of the system is captured within the state space model. For example, in the case of control of hand position, the state vector could contain the endpoint velocity and acceleration, joint angles, and even internal states of the force-generation actuators (motors or muscles). The state space equations can also be used to establish whether a system is fully controllable (whether the control input influences all state variables). It can also be seen whether a system is fully observable (this is only the case if there are no hidden dynamics inside it that are not visible at the output).

While simple output feedback control makes use of only the observable output from the plant, in general, it is better to make use of the full state of the system. Direct state feedback control simply uses the full system state and feeds back a weighted version of it to the input comparator. Similar to the design of PID controllers, to implement state feedback control, the state vector needs to be scaled using a gain that is fed back and compared to the input goal. This is represented by the expression $U = -KX$, where the feedback matrix K represents the feedback gain vector of the system state. In general, it is not trivial to determine K, since there are various important aspects of the dynamic system performance that must be taken into consideration in determining the feedback gain. It is important that when we apply control to a plant, it remains stable. However, control design generally involves more issues than just the overall system stability, such as requirements on response fall times, ensuring internal states are bounded, and other important factors. One approach formulates the task of finding feedback gain K as an optimization problem, which minimizes a cost function. The latter can be used to select desirable controller properties and is discussed in a later section.

The state space approach would appear to be complete to both model and control a musculoskeletal system, but it ignores one phenomena common to all biological systems: time delays. Nerve conduction delays, processing delays, and muscle activation delays can be substantial in all but the smallest animals (257) and often cannot be ignored without compromising the accuracy of the model. The Pade approximation is one of the most common approaches to represent delays, though this approach is not exact and can introduce instabilities into the model that do not exist in the real system (338). If the system has a single constant feedback delay, the Lambert W function provides an analytic method for modeling the system as an infinite series of state space systems (410). The general case, in which variable delays appear throughout the system, is an active area of research (191).

Forward models

Finding an appropriate control strategy becomes increasingly challenging with increasing time delays. If the sensory feedback is delayed (through conduction pathways) when it is compared to the desired state, then the error does not correspond to the present but rather what has happened in the past (Figure 4D). In addition, when this error is used for corrections, these are further delayed through the neural conduction and muscle mechanics. Time delays can therefore lead to a system that would have been stable becoming unstable (401). For example, if the input goal in a rhythmic activity is represented as a sine wave, then when the time delay in the system corresponds to half its period, we end up with positive rather than negative feedback from the sensor measurement. When the gain is high enough, the system will become unstable. Consequently, effective feedback correction cannot be directly applied in systems with a significant time delay. Indeed, as delays become larger, the feedback gains must be reduced accordingly to still maintain a stable movement. It is important to note that delays do not only arise from the detection and transport of the information but also from the processing of the information for the control.

While simple monosynaptic reflex loops may only require the processing time of one synapse in the spinal cord (5 ms), most motor tasks involve much more complicated decisions relying on a multitude of uncertain information, which can result in much more significant delays. For example, even in the relatively simple random-dot decision task in which one of two possible actions needs to be taken based on visual inputs (133), the decision time alone can vary between 120 and 250 ms (302). To reduce time delays, neurons could have larger myelinated axons to increase the velocity conductance (288). However, there are limits of this effect, due to the brain size, energy consumption elements, and spatial organization, both within the brain and across the body.

A different approach to deal with time delays in the control loop is to adopt an architecture that involves using immediate feedback from the output of a forward model of the plant rather than using sensory feedback from the body directly (344). According to the forward model concept, neural circuits in the brain use a copy of the motor command, an efference copy, to predict the sensory consequences of motion (Figure 4E). By doing so, we can immediately use the information for planning and control (400).

Forward models contribute to improvements of motor performance in multiple ways. First, they can be used to modify perception. That is, they can predict the sensory consequences of our own actions to subtract this from the total sensory feedback received. An accurate prediction allows for sensory cancellation of our actions, making us more sensitive to unpredicted events or external disturbances, both of which are much more relevant for control. Second, they can be used for correcting errors in our motor commands even before such errors have influenced our movements. An efference copy of the sent motor command through an accurate forward model of the dynamics can predict future errors in the movements, which could already be partially corrected with feedback responses prior to the initial motor command reaching the muscles. Forward models can therefore improve the accuracy of both our sensory feedback and our movements, reducing the effect of delays and contributing to improved motor performance.

Evidence supporting the existence of a forward model comes from both neurophysiological and behavioral studies, although direct proof of the existence of forward models in the sensorimotor control system is difficult to obtain (117). In a series of papers, Sommer and Wurtz (346, 347) provided evidence that the efference copy of the saccadic motor command was used to update predictions for control of future saccades and updates to the receptive fields of neurons in the visual system. The use of this efference copy could update the control before any feedback could have been received so as to adjust future saccade plans and ensure the stability in image perception following a saccade. Behavioral studies have examined the delay compensation based on a forward model in tasks that involve motor adaptation. For example, during balancing an unstable object, such as balancing a pole, the motor system relies on predictions by a forward model that needs to overcome large delays as sensory information regarding the pole state comes mostly from the visual system (244). There are further studies providing evidence of the use of forward models in preparatory muscle activity: the adjustment of grip force to delayed load force (222, 395), adaptation to delayed visual feedback during reaching movement (25), saccade adaptation to target jump (44), or during tracking motion (311). For hand movements, the cerebellum has been proposed as a candidate area to host the forward model (180, 361). While without corrections forward model-based predictions will likely diverge from the true state as time passes, these predictions provide a fast internal feedback loop that can assist the motor system to overcome delays.

Optimal control

Redundancy is present throughout the biomechanical and neuromuscular systems. That is, when we move our body, we have many more degrees of freedom (DOF) to be controlled than is necessary for the task. For example, while our arm has at least seven DOF in the joints, neglecting those of the hand, fingers, and scapula, reaching out to touch an object may only require three DOF (localization in 3D space). This means that we have more DOF than necessary to perform the task (kinematic redundancy); there are many possible sets of joint angles of the limb that achieve the goal of the hand at the desired location. This implies that there are infinite possibilities to perform the task, an issue termed the DOF problem by Bernstein (18). Moreover, if we consider the whole body, the degrees of kinematic redundancy are exceptionally large. However, the issue of redundancy is much larger than this. For each movement to a location, one trajectory needs to be chosen from one of infinite possible trajectories. For each path, the speed and timing of the movement can be chosen from one of infinite possible movements. Even the specific muscles used or the amount of coactivation of the muscles needs to be determined from a wealth of possibilities. Although every movement must obey the laws of physics, this still allows for infinite solutions from which the brain must select one movement to perform. Despite this abundance of possible solutions, human movements are often stereotyped, suggesting that the sensorimotor control system might use a system to determine an ideal movement for each task. One of the main goals in sensorimotor control has been to determine why one particular solution is chosen from the infinite possibilities.

One possible explanation for the way the motor system chooses a particular movement suggests that movement is chosen by an optimization process of a particular set of costs. For example, minimizing the hand jerk along the movement path, minimizing the variability of the end position around the target location, or a combination of such cost functions (19) can explain different characteristics of simple reaching movements (see section titled "Cost functions"). However, if indeed movements are based on this optimization process, it implies that the motor system relies on a feedforward control architecture in which the plant movement is driven by the desired optimal trajectory. Contrary to this idea, observed trajectories are directly affected by sensory feedback (sometimes changing the entire movement and goal), suggesting that feedforward control cannot fully explain the nature of the chosen movement.

To get around the problem of desired trajectories, optimal feedback control or OFC (365), built upon the ideas of optimal control from control theory (8), was proposed as a model of human movement. In this model, optimization is combined with feedback control tuned to task demands. OFC finds the best possible series of feedback control laws for each task that minimizes a mixed cost function involving components such as accuracy and energy costs. Therefore, it solves for the series of time-varying feedback gains throughout the movement that minimize the expected cost of the movement. Importantly, OFC does not solve for a specific trajectory or state of the body at each moment in time. Instead, the time-varying feedback gains are used with the current estimate of the state of the body to determine the next motor command. Therefore, these feedback control laws do not correct for any deviation in the movement but only correct for those deviations that would impact upon the cost of the movement: the task-relevant deviations. This is a critical feature of OFC, that of the minimum intervention principle in which the control system will only correct deviations that impact upon the successful completion of the movement. Therefore, feedback should not necessarily act to return the system back to an unperturbed movement but instead act to reduce any effects of the disturbance only upon the task goal. Overall, OFC combines trajectory formation, noise reduction, and energetic costs, all within a single framework to explain motor control, by specifying a mixed cost function to be optimized, and predicting the time-varying feedback gains and resulting trajectories (Table 1 and Figure 5). The redundancy of any movement is therefore solved by the cost function. Specific muscles, paths, velocities, and joints are selected because they minimize this cost function, for example, by reducing the needed energy or increasing the accuracy of the movement.

As introduced above, the feedback gains for a general state-dependent controller can be determined by setting the values of the desired eigenvalues of the system. However, a more principled approach to determine the feedback gains K for a specific task is to design an optimal controller. This approach uses performance criteria that depend on aspects of the control task, such as the magnitude of the control signal (energy use), the endpoint error, and the duration of movement. The optimal control approach can also compute gains online so that they change during the task (39, 40, 82). However, the structure of the state feedback controller is essentially the same in both cases, and it is only the way that the feedback gains are computed that changes depending on whether the controller is designed using pole placement or optimal control.

Thus, instead of direct pole placement, optimal feedback control makes use of a performance criterion. To do so, we define a "cost function" J, which lets us minimize some quantity of the control process. For example, if we are speaking to someone, we could minimize the time required to move an articulator from position A to B

$$J = \int_0^{\mathrm{finalTime}} (1)\, \mathrm{d}t$$

Or, we could minimize the muscle activation used to go from A to B

$$J = \int_0^{\mathrm{finalLocation}} (\mathrm{muscleActivation})\, \mathrm{d}x$$

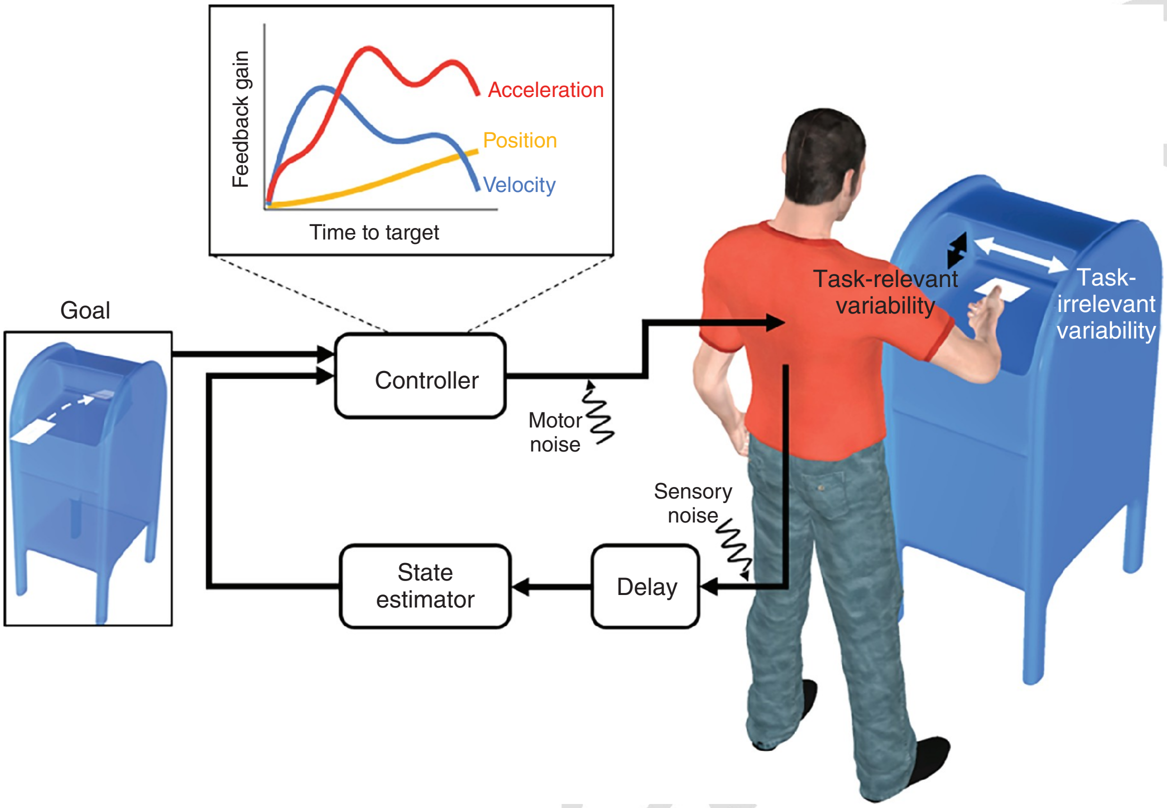

Figure 5 Optimal feedback control scheme. During daily activities, such as trying to insert a letter into a mailbox, we want to generate accurate movements so as not to miss the mailbox slot while keeping the control effort to a minimum. Since open-loop control cannot satisfy these demands due to internal noise or unexpected external perturbations, such as wind perturbing the hand, we can instead use feedback control. In optimal feedback control, the control signal generated by the controller is based on time-varying feedback gains, each multiplied by the different state variables describing the system, for example, the hand position or velocity. These state variables are estimated using a state estimator that uses sensory predictions from a forward model and true delayed sensory feedback. In this example, the resulting trajectory may differ between the times we try to mail the letter. However, the controller always drives to minimize the variability along the vertical axis, where we need to be very accurate (task-relevant variability) compared to the horizontal axis in which we have more room to be variable (task-irrelevant variability).

To make analysis easier mathematically, often a quadratic performance measure is adopted, which leads to well-behaved solutions. For example, we can choose costs in terms of tracking and control input characteristics (although many other criteria are also possible). Writing the cost more formally in terms of a weighted quadratic deviation of system state to its goal value and weighted quadratic control inputs, we have

$$J = \int_0^\infty (X^TQX + U^TRU)\,dt$$

Here, the term

$$X^TQX$$

is the weighted square distance of state from its origin, and it affects convergence rate if the system achieves its target values—that is if it affects system rise time and settling time. A large value of Q therefore biases the control to achieve good tracking but at the expense of requiring a large control input. The term

$$U^TRU$$

represents the weighted square of control input term. It penalizes large and aggressive inputs. Therefore, a large value of R biases the control to use little input but at the expense of poor state tracking. We now need to find a controller with the optimal gain K that optimizes the performance index for the given state space system, given its expression of cost. That is, we want to find the corresponding gain K that minimizes J

$$J = \int_0^\infty (X^TQX + U^TRU)\,dt \quad \text{subject to}$$

$$\dot{X} = AX + BU \quad \text{and} \quad U = -KX$$

Solving this integral leads to the expression for the optimal gain

$$K = R^{-1}B^TP$$

where R is invertible, and P is symmetric and satisfies the algebraic Riccati equation

$$A^TP + PA - PBR^{-1}B^TP + Q = 0$$

In this particular example, the optimal control design procedure results in a static gain vector K, which can be used within the OFC framework. However, it is also possible to design controllers where this gain varies as a function of time, which is often necessary to better explain the characteristics of human movements.

Optimal feedback control (365) appears to currently represent the best way to model many observations made in human motor control (26, 60, 79, 326, 364, 365). When motor planning is coupled with the appropriate cost function for movement such as endpoint movement variance based on signal-dependent noise (147), it can generate the necessary control to move the plant to its endpoint goal without the need of a precomputed trajectory. The OFC framework has now been used to explain or predict characteristics of a huge number of human motor behaviors including straight point-to-point movements, bell-shaped velocity profiles seen in arm and speech articulator movements, pointing and grasping movements in 3D (143), manipulating objects with internal degrees of freedom (266), bimanual control (78), full body balance (209), and task-relevant feedback gains (41, 58, 269), to name a few.

Within the broad topic of optimal control, there are many variations, each of which may better represent different aspects of human sensorimotor control. For example, we can specify the different control horizons of each controller. The control horizon refers to the look-ahead time window over which a controller's performance criteria are optimized with respect to the cost function. This horizon could be given a finite time, for example, specified over a particular time for a movement (227). In contrast, to avoid specifying a particular time or duration for a movement to take place, the control horizon could either be receding (continually reoptimized over the next short time period) (144), or it could extend indefinitely into the future as in the case of infinite-horizon control (296). As each control horizon produces different predictions, only some of which match human movement (39), a mixed-horizon controller has also been proposed that combines the best features of each of these different control horizons (40). Another approach to designing controllers is robust control. Robust control builds controllers capable of maintaining performance across a range of uncertainties or disturbances in a system's parameters, its environment, or the plant itself. This method ensures that the controller delivers satisfactory performance even when the actual system deviates from the mathematical model used in the design process. It has been suggested that human sensorimotor control may span the range between robust and stochastic optimal control, with a trade-off between efficiency and stability to perturbations (48, 61).

However, optimal control models also have their limitations (229). For example, it appears that habit plays a critical role in motor action recall, rather than computing an optimal policy (72). In addition, this framework suggests that the mixture of costs could be different for every movement where the relative weighting of these costs is a free parameter that can be used to fit the data. Therefore, almost any movement could be fit with an optimal feedback control model, given the range of free parameters. The question is whether these cost functions and parameters make coherent sense with the expected costs of the tasks being performed.

State estimation

Within OFC, as well as other state-dependent control frameworks, the feedback or motor command at each moment in time depends on the current state estimate of the body during the movement. Therefore, a critical component of such control systems is the state estimator, which generates an online estimation of the current state (location, velocity, and other important parameters) of the motor system. For example, it could be an estimation of the current joint angle and joint velocity of a joint during a reach. State estimation is needed primarily due to three of the problems in motor control discussed previously: noise, delays, and uncertainty. Even when stationary, there exists some uncertainty in our current position due to receptor imprecision and noise. Once a motor command is sent, this will also be subject to noise, and differences in the motor commands are further enhanced by nonlinearities in the musculoskeletal system. While the sensorimotor control system receives multiple modalities of sensory feedback, all of these are subject to both significant delays and noise (Figure 4D). Thus, the control system is always working with out-of-date sensory information—on the order of 50 to 100 ms, depending on the modality.

One possible way to overcome these problems is by constructing an observer that is based on a forward model which can approximate the full state vector by predicting sensory consequences, given the motor command (Figure 4E). The idea of this observer is based on an open-loop estimate of that state using a model of the plant, which has the same matrices A and B as the real system, $\frac{\mathrm{d}}{\mathrm{d}t}\hat{X} = A\hat{X} + BU$, where $\hat{X}$ is the estimated state. Implementing a forward model within a feedback control system (Figure 4F) allows the system to operate without actual feedback from the plant. The actual output (sensory feedback) measurement is only needed to deal with unpredicted disturbances. That is, any disturbance that will result in a deviation of the true output from that which is expected will be used to correct the state estimate. This correction mechanism will operate as fast as sensory feedback delays and the dynamics of the observer and the state feedback controller will permit. Therefore, in the case of proprioceptive feedback, this could be as fast as 50 ms (60), but auditory or visual feedback might exceed 150 ms.

Although state estimation processing could be achieved using a pure forward model of the plant, providing reliable estimation strongly depends on the stability of the plant, as represented by the state space model matrices. For example, if A is unstable, then the estimate will diverge from the true state. In addition, if there are any inaccuracies in the model of the plant, the predicted state will rapidly diverge from the real state of the system. This means that we require a closed-loop correction to help solve this problem. Thus, the output of the actual system (sensory feedback) is normally used to correct the state estimate from the forward model.

One such observer that operates in a closed-loop fashion is the Luenberger observer. It generates the state estimate according to the dynamical equation $\frac{\mathrm{d}}{\mathrm{d}t}\hat{X} = A\hat{X} + BU + L(Y - C\hat{X})$. For this observer, the state estimate is updated based on the actual output of the plant, where the gain vector L can be chosen in such a way that even for unstable system A matrix, the state estimation error will decay over time. However, sensory delay will still affect the estimated correction. More sophisticated approaches to state estimation can also be adopted, including the Kalman filter (190). The Kalman filter calculates the optimal state estimates accounting for the level of noise in the system and also generates online updates of the system gains. In the human motor system, a Kalman filter-based state estimator can integrate the efference copy of the motor command with a correction term based on the delayed sensory feedback (399).

Both the Luenberger observer (designed based on stability criteria) and the Kalman filter are designed to provide state estimation for linear systems. However, since the sensorimotor system is nonlinear, the approach requires modifications to estimate the state of nonlinear systems. For the nonlinear case, the extended Kalman filter (EKF), which is based on linearization at operating points, or a modified Luenberger observer (345) can be used. Other state estimation techniques also exist, for example, ones based on particle filtering (9) or nonlinear contraction theory (417). Although we do not know what kind of state estimator the sensorimotor control system uses, there is extensive evidence that such a system is critical for motor control.

Within the sensorimotor control system, there is evidence that state estimation is implemented within, or at least requires input from, the cerebellum (246, 285, 360). Extensive lines of support have implicated the cerebellum as a location of forward models, which are a necessary part of state estimation (246, 276, 402). One possibility is that the output of these forward models is combined with sensory feedback for state estimation within the parietal cortex, with Shadmehr and Krakauer (333) suggesting that state estimation is distributed throughout the central nervous system. Regardless, both the cerebellum in vertebrates and similar brain areas in sharks and other fishes have been conserved through millions of years of evolution and across a whole range of body structures and functions, suggesting a key function in sensorimotor control—such as state estimation (285).

Error-based learning

Properties of the motor system and our bodies are not constant but change on multiple timescales. In everyday activities, as we pick up a new object with our hand, the effective inertia and mass of our limb immediately change. This means that to produce the same motion, a different set of motor commands are needed. Our motor system must also deal with other changes in the characteristics of the motor system. For example, there are changes in muscular strength due to neural and muscular fatigue, which take place over timescales of minutes to hours. On longer timescales, there are dramatic changes that occur throughout growth and aging: nerve conduction delays (94), muscle strength (225), and sensory acuity (282). The presence of changing parameters of our physiological system places demands on the sensorimotor control system, which needs to accurately model and account for these changes, since any errors in such estimates will affect the accuracy and overall performance that can be achieved. This means that the sensorimotor control system must adapt the parameters of the controller to account for changes in both the internal (body) and external (environment) dynamics.

If we make a movement after our limb dynamics are suddenly changed (for example, by adding a mass (206) or applying forces with a robotic device (334)), we will initially generate movements that exhibit large kinematic errors. While these errors will elicit feedback corrections on the current movement limiting the effect of the overall disturbance, the motor memory or model of the dynamics will need to be updated for skilled action to take place on subsequent movements. One type of motor learning makes use of these errors as training signals to change the feedforward control. Movement-specific iterative learning uses the errors to shape the pattern of feedback muscle activation, but only for a specific movement, but does not transfer to other movements or tasks. However, it is known that humans rapidly adapt to novel external dynamics (213, 334), but this learning also generalizes to other similar movements (53). This demonstrates that humans do not simply rote-learn a pattern of feedforward muscle activation for each specific movement but instead form a model of the task dynamics.

Instead of adopting iterative control, evidence suggests that we learn the parameters of the dynamics such that we can generalize learning over a range of movements, a concept termed nonlinear adaptive control (342) or feedback error learning (192, 193). These learned parameters could reflect the limb lengths and inertial parameters of the body or the dynamics of the external environment. If they were learned accurately enough, this model would be able to generalize the appropriate pattern of muscle activation for any movement with little to no errors. The idea is that the sensory feedback of errors is used to adapt the parameters of the model or motor memory (Table 1). There are extensive studies showing generalization to untrained movements (15, 166, 185, 239), but this generalization is also partially local, decaying away from the trained states (84, 164, 165, 363). This decay may arise through one of three possibilities. First, there is imperfection in the adaptive control model; either the parameters are not accurate enough, or the model itself is incorrectly specified. Second, the learned model is combined with our body model in a weighted sum that discounts the learned model as we move further away from the trained state space (a type of Bayesian discounting). Third, we learn a local basis function of the model, similar to a neural network model. Such a model approximates the real dynamics near the training state space but decays away, depending on the size of the basis functions. Most research suggests this third option—local neural basis function adaptation approximating nonlinear adaptive control over the trained state space (185, 188, 289).

Importantly, we do not just need an accurate motor memory (or model) of the dynamics for the current task, but we need to be able to learn and switch between multiple motor memories as we change tasks. This switching between memories occurs quickly when there are appropriate contextual cues for each of the dynamics (107, 155, 167, 169, 277, 336, 411). The idea is that the contextual signal is combined with model predictions to determine which motor memory is selected for the current task. Finally, we also need to decide when to form a new motor memory for a task, and when to simply adjust existing motor memories (278). One suggestion is that this is done through inferring the context under which the different sensory information arises (150). Determining the specific context and motor memory to be used for a task is critical to achieving optimal performance within that task.

Reinforcement learning

Reinforcement learning (RL) provides a very different framework to approach the understanding of how the sensorimotor system decides on a particular control solution out of an infinite number of possible solutions and learns to adapt to changing body and environmental dynamics. We previously considered that the movement redundancy can be solved for a task by searching for solutions that optimize specific costs related to the movements. However, an alternative approach—reinforcement learning—considers a control approach in which an agent interacts with the environment and can learn to generate appropriate state-dependent actions to maximize cumulative reward and thereby achieve a goal (Table 1 and Figure 6).

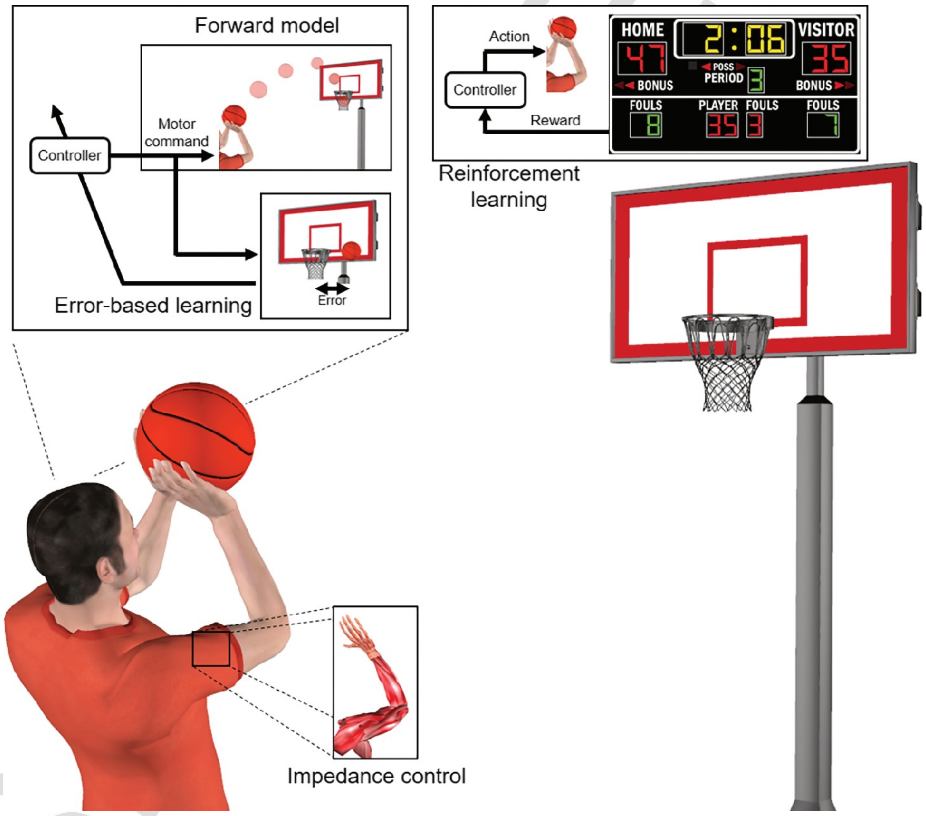

Figure 6 Complementary control strategies during movement and object manipulation. When we shoot a basketball, the forward model can predict the trajectory of the ball based on a copy of the motor command if it has a good representation of the arm, the ball, and the environment. This prediction allows us to know ahead of time if we will make the basket and if there are any unpredictable changes in the controlled system by comparing the predicted and actual outcomes. Any errors in predictions can then be used to adapt our internal representation of the system and the controller so it will generate appropriate commands. Alternatively, in reinforcement learning, the control update mechanism uses task reward, for example, whether we increased the score count to update the controller policy. In parallel to the feed-forward adaptation process, to stabilize the arm while holding the ball, and reduce the effects of noise, we can increase the muscles' cocontraction around different joints, changing the limb stiffness throughout the shot.

Stated formally, at time t, when an RL agent is in state S_t, the agent generates an action A_t. This action results in a reward from the environment R_t and leads to an observation of the environment O_t which the agent can use to update its state. In this framework, no supervisor is required to drive learning in this process, only reward from the environment. For the agent to operate effectively, it is important that the agent's state adequately describes the environment (or circumstances) the agent acts in, so it has enough information about the environment to appropriately generate future behavior. The reward is used to change the actions that might be performed when in a specific state.

Computationally, there are many approaches to reinforcement learning. For example, in Monte Carlo, dynamic programming, and temporal difference learning schemes, a value function is used to indicate the long-term expected gain or value of a given state. After the value of states has been estimated, it is then possible to choose the next reachable state that has a higher value than the current one. Alternatively, there are policy gradient methods that try to learn the optimal policy $\boldsymbol{\pi}$ directly. Finally, there are actor-critic approaches that use both value functions and policy learning simultaneously ((356); see Ref. (24) for a recent overview of the field).

The policy $\boldsymbol{\pi}$ defines how the agent behaves. It is the agent's probability of choosing a given action in a given state. In the case of Q-learning (385), which was inspired by behavioral learning in animals, learning policy $\boldsymbol{\pi}$ involves learning a state-action pair function $Q(S, A)$ to specify its behavior. The Q value indicates how good actions are in a given state. Initially, an RL agent will not know the policy π and consequently will not know which actions to generate in a particular state. RL agents can learn to behave optimally by exploring possible actions in a given state to find their long-term cumulative reward. After the agent has learned the policy $\boldsymbol{\pi}$, it can then simply follow and exploit it to generate the optimum behavior and maximize reward. Thus, reinforcement learning generally operates in two modes. In the first mode, the agent randomly explores its environment, generally only with a small probability, and learns the value of its actions by making use of a reward signal relating to the values of the actions. Using the information gained from the environment by exploration, in the second mode of operation, it can exploit this and generate the optimal action for a given state. Thus, action exploration is inherently a part of the RL framework, and the exploration mechanism plays an important part in learning. Conversely, exploitation is the way to make use of the learned policy to behave optimally.

In simple tasks, a lookup table can be used to map between state and value, or indeed to represent policy directly. However, as the number of states increases, it rapidly becomes intractable to directly model value or policy in this way. Therefore, to avoid the curse of dimensionality in real-world RL tasks, it becomes necessary to make use of generalization functions to implement policy. Indeed a recent impressive application of RL was a recent Atari game-playing system (252). The latter application deals with high-dimensional sensory inputs using deep learning strategies implemented in multilayered feedforward convolutional networks and learned to play video games to a better-than-human level of performance. One issue in RL is that most current methods focus on learning policies that generate discrete actions such as in simple decision-making (219). However, many problems, particularly the control of dynamical systems, such as our bodies, require continuous control. Fortunately, recent work indicates that progress in continuous control is now also being made by RL methodologies (224).

Although derived from mathematical principles, the framework of RL also aligns with the operation of mechanisms in the brain. It is believed that in the brain the reward prediction error is signaled by dopamine (86, 100, 323), highlighting the involvement of the basal ganglia within reinforcement learning in biological systems. Although it is difficult to purely separate reinforcement learning from more error-based learning processes in understanding human movement and performance, several studies have shown that the presentation of additional explicit rewards affects motor performance and motor memories (1, 123, 182, 274). Moreover, it has been shown that the sensorimotor control system uses distinct loss functions for error- and reinforcement-based learning (38) using a reaching task involving a random cursor offset, sampled from a skewed probability distribution. When error feedback was provided, participants adjusted their actions based on the mean of the noise, but when reinforcement feedback was used, they compensated based on the mode of the noise. When both reinforcement learning and error feedback were present, error feedback dominated the learning behavior.

Impedance control

There is often uncertainty in our interaction with the environment, arising from its unpredictable nature or due to inherent instability in the tasks we perform. For example, if we are walking a dog on a leash, the dog may suddenly pull in any direction depending on what grabs its attention. We cannot predict ahead of time exactly with which motion or force the dog will pull. Instability in some of the tasks we perform also makes prediction impossible. For example, when balancing an object, or even our own body upright, small deviations can cause the system to fall in any direction. Such unpredictable situations often occur, for example, standing upright (231, 256) or using tools such as a screwdriver or drill (300).

During such control tasks, one way in which the stability can be obtained is through regulating the impedance of the limbs or impedance control (Figure 6). Two properties that contribute to the limb impedance are stiffness and damping. Each of these can be controlled by changing the muscle activation (112, 137, 388), muscle coactivation (37, 137), body posture (265), or reflex gains (273). The main idea behind impedance control is that the sensorimotor control system regulates the impedance of the neuromuscular system to stabilize the interaction with the environment (158, 159), either through cocontraction of muscles or through posture manipulation. Simply increasing muscle cocontraction globally, for example, by cocontracting all your arm muscles, will increase endpoint stiffness in all directions (265), but at a high metabolic cost. However, it has been shown that the endpoint stiffness can be tuned appropriately to deal with the environmental instability, increasing endpoint stiffness only in the directions of the instability (32, 111, 115, 189). That is, we learn to activate specific pairs of antagonistic muscles that increase stiffness in the needed direction while keeping other muscles relaxed. Moreover, this increase in stiffness scales with the level of the instability, such that the net stiffness of the interaction between limb and the environment remains constant (115). This suggests that the sensorimotor control system selectively tunes the stiffness, maintaining stability, while limiting the metabolic cost. Increased limb impedance not only stabilizes the body but has also been shown to increase the speed of learning to novel dynamics (149).

One proposal for the way in which the endpoint impedance is gradually learned and tuned to the environment is through a mechanism that exhibits a V-shaped error-learning characteristic (109). Each time a task or movement is performed in an unstable or unpredictable environment, the sensorimotor control system will receive an error signal specifically from those muscles that were stretched by this error. The control system will then increase the activation of both this muscle and, to a lesser degree, its antagonistic pair at this specific state of the movement, producing both a change in the joint torque to correct the error and an increase in stiffness to stabilize the system. As errors are reduced close to zero, the overall muscle activation is correspondingly reduced. This learning mechanism predicts both the trial-by-trial changes in muscle activation (112) and changes in endpoint impedance (111) as we adapt to novel dynamics. It also simultaneously optimizes among stability, accuracy, and metabolic cost, producing appropriate impedance adaptation and learning over a large range of both stable and unstable environments (109, 188, 362). We note too that there have also been other approaches that embed the learning of impedance control within an optimal control framework that is able to learn the impedance to minimize the internal model uncertainty (251).

Decision-making

Most of our daily activities involve complex goals that we tend to break down into several small tasks that allow for a successful completion of our desired activity. Throughout this sequence of actions, we encounter uncertainties about the state of the environment, which are especially important if we want to manipulate objects in the environment. For example, when waiters are clearing dishes from a table, they need to choose and plan the order of items that will go on the tray and where will be the appropriate place to put these items that will allow for the other hand holding the tray to keep the balance. This is performed even though there is some uncertainty in the state of the objects due to ambiguity (an empty or half-full beer bottle might look the same but has different weight) or uncertain sensory inputs (objects in the visual field periphery have lower visual precision) as well as environmental unpredictability (someone took the next item on the waiter's planned list of actions). In addition, the timing of these uncertainties within the planning-acting sequence might change. While ambiguity usually appears during the planning stage, unpredictability usually manifests itself during the generation of action.

One possible way to deal with uncertainties is using a decision-making process that weighs the different sources of sensory information and then combines them to develop a better estimate of the state of the environment. By considering different possibilities, the system can decide which state is more likely based on sensory information or prior memory. During this process, the system uses the given information, normally accumulated over time, until a decision is made. After a decision has been made, the movement can be tuned for better performance of the task. While it is still not exactly clear how motor-related decisions are made, some of what is known about this mechanism can be used to explain how we move under these uncertainties.

Ambiguous information can appear before or during a movement, which leads to two different problems for the sensorimotor system. When the ambiguity appears before movement initiation, such as the appearance of multiple targets, from which we need to select just one, we might expect that the decision is made before computing the necessary motor command. This sets a serial cascade of events of planning followed by acting. For example, in a random dot motion task, in which we need to perform a saccade in the direction of a set of consistently moving dots that are blended in a group of random moving dots, we need to make a decision about the movement direction. In such cases, it was suggested that the decision can be predicted by a drift-diffusion model (301). Here, the abundant information is transformed into a value that moves between two thresholds representing the two decision alternatives, until one of the thresholds is crossed (394). Another formulation of decision-making is the urgency gating model (45) in which multiple alternatives are evaluated in parallel within the neural circuitry. However, in this model, the accumulating evidence in favor of each option over time is not simply due to sensory temporal integration but instead is attributable to a growing signal related to the urgency to respond, which modulates the continuously updated estimates of sensory evidence. After the decision is made, we can move to the next stage of acting according to the decision.

However, such a serial mechanism cannot explain some behavioral results when the state of the environment is ambiguous. For tasks that need movement initiation under target ambiguity, we need to compute multiple motor plans in parallel with the decision-making process. For example, if the movement must be initiated before the selection of one of the multiple possible targets is determined, participants move along the average path of the multiple competing paths until the target ambiguity is resolved by eliminating the redundant targets (355, 403). Moreover, even for tasks in which ambiguity is resolved before movement initiation, there is evidence of the computation and use of multiple motor plans, suggesting that planning occurs for multiple movements and occurs in parallel with the decision-making process (125, 126). While there has been a debate about whether the sensorimotor system averages multiple parallel plans or uses a single flexible plan (125, 126, 403), recent studies have argued against motor averaging of parallel plans and instead provided evidence that the action reflects the best single action available, given the uncertainty of the environment (7, 270).

This parallel planning and decision-making process for multiple movements or outcomes has also been suggested as a mechanism for handling motor plans for unpredictable environments. When there is a change in the state of the environment, or our body, we can quickly adjust the movement based on preplanned motor actions that allow us to complete the task. For example, when reaching toward a target while trying to avoid obstacles along the way, we initially decide on a motor plan that will allow us to bypass the obstacles in a particular path. If the hand is perturbed from this original plan by an unpredictable external load, participants resist the perturbation or switch to another motor plan, depending on the magnitude of the perturbation (269). To explain this behavior, it was suggested that the decision process continually receives and accumulates sensory information in parallel to generating movements. Similar to drift diffusion models, the accumulated information is used to decide between competing plans, but this process continues after an initial decision is made. This creates situations in which unpredictable events will make the initial decision irrelevant or inappropriate for completing the task, causing the decision process to change to a different motor plan (302).

Acting

The last stage of movement generation is producing action according to the motor plan. To do so, the sensory and control processes must act through the complex dynamics of the musculoskeletal system and peripheral neural pathways. The muscle is responsible for generating virtually all biological motion, from the beat of a butterfly's wings to the spring in a sprinter's step. However, muscle acts on the body through the kinematics and dynamics of the skeletal system and is controlled and assisted by the neural system to give rise to the impressive repertoire of our daily lives. Here, we start by focusing on the structure and function of muscle and present muscle models that attempt to capture the important mechanics of muscle that are critical for understanding behavioral performance. We then explore how the body structure, neural feedback loops, and the musculoskeletal dynamics help to solve the problems of motor control.

Muscle structure

Although muscles differ dramatically in size and shape, at its smallest scales, muscle is built by a regular hexagonal lattice of sarcomeres, geometrically structured like a crystal. Whole muscle (Figure 7A) is composed of packed bundles of myofibrils, which are in turn composed of finer filaments called myofilaments, which are composed of sarcomeres, the smallest contractile elements. Sarcomeres at rest are typically between 2 and 3 μm long in mammalian muscle tissue and are in turn composed of a number of smaller filaments that interact to produce both passive and active forces: myosin (thick filament), actin (thin filament), and titin. Sarcomeres are packed in a hexagonal structure (Figure 7B) within a myofilament so that each end of the myosin filament is surrounded by six actin filaments. Myosin is elastically suspended by titin filaments (236) that attach near the base of each actin filament and to the middle of the myosin filament. All of these filaments are suspended in water, which has the consequence that muscle maintains a constant volume during contraction (358): during shortening, muscles and sarcomeres become thicker; during lengthening, muscles and sarcomeres become thinner. This hierarchical structure is so consistent that many of the active and passive physical properties of sarcomeres scale to myofibrils, muscle fibers, and even to whole muscle.

The microstructure of the muscle sarcomere gradually revealed itself as technical methods, including the electron microscope, were developed. These advances made it possible to examine the striated patterns of myofibrils under passive and active tension (174), image the structure of the striated patterns (146), reveal the hexagonal pattern of thick and thin filaments (Figure 7D) (146), and even observe the appearance of "bridges" that appear to span between the thick and thin filaments (Figures 7C and 7D). In 1954, A.F. Huxley (174) and H. Huxley (176) independently proposed the sliding filament theory that the myosin filaments slide relative to the surrounding actin filaments, and that during activation, the tension is generated at the region of actin-myosin overlap. Experiments confirmed that the active force developed by sarcomeres is proportional to actin-myosin overlap (139). While the plateau and descending limb of the force-length curve (Figure 7E, lengths 1-5) are well explained using the sliding filament theory (139), the ascending limb (Figure 7E, lengths 5-6) is assumed to be caused by mechanical interference between myosin and the Z-lines (the network of filaments on the ends) of the sarcomere. Recently, it has been proposed (310) that, instead, myosin and actin filaments are able to pass through the tightly woven filaments that form the z-line predicting the small bump in the active force-length curve that occurs at short lengths (Figure 7E). In addition, it has been shown that the shape of the active force-length curve is skewed to the right with decreasing activation (354), phenomena that can only be explained when additional physical phenomena beyond the sliding filament theory (308) are included.

Once the sliding filament theory was proposed, the challenging work of determining how this structure interacts with the previously discovered (237) adenosine triphosphate (ATP, the fuel of muscle contraction) began and continues to this day (349). Although the chemical-mechanical interactions of the cross-bridge cycle are not fully known,

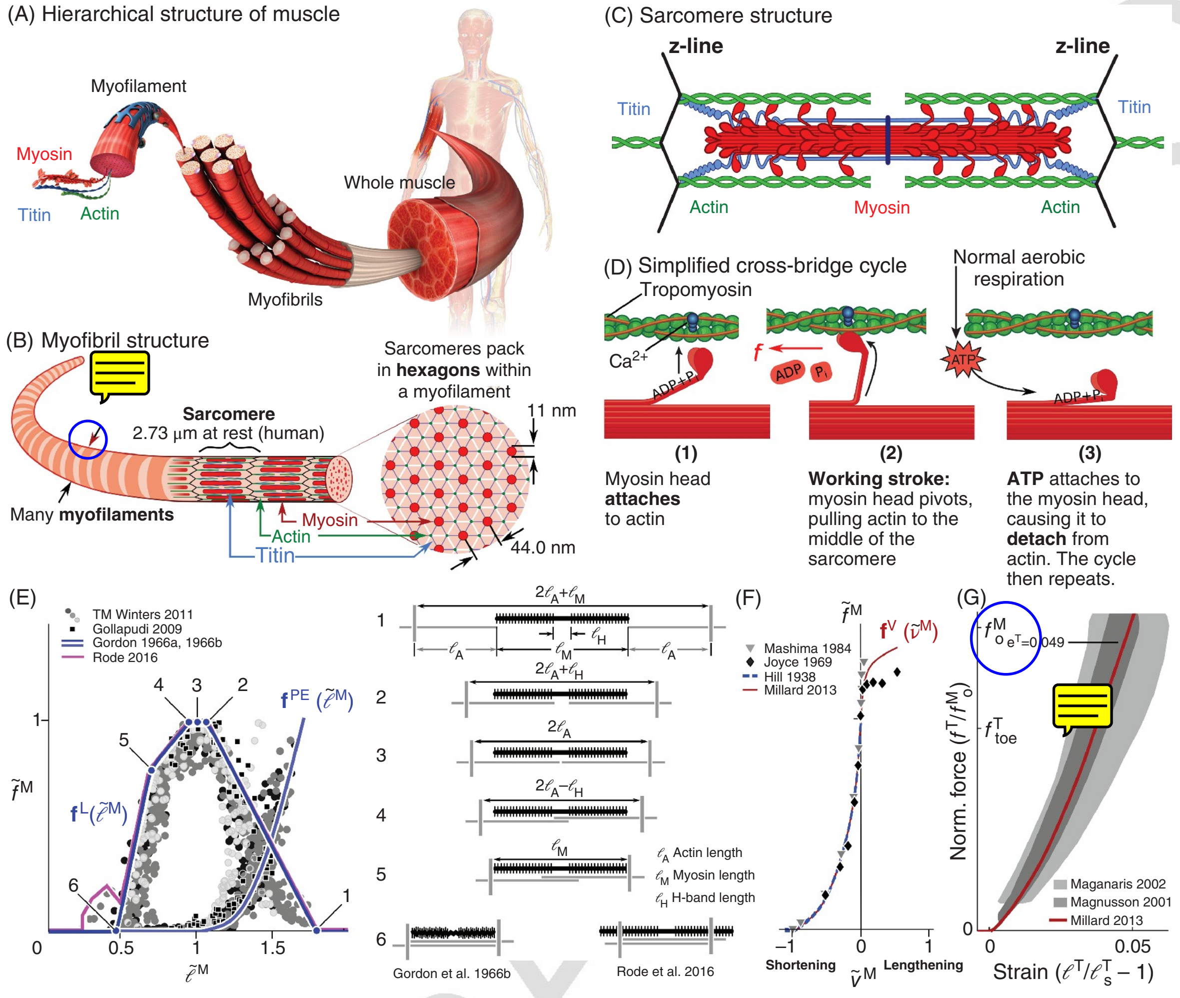

Figure 7 All of the active forces generated by muscle are developed among myosin, actin, and titin filaments (A), each of which are on the order of 1 µm. These filaments are packed into sarcomeres, the smallest contractile element. A myofilament is composed of many sarcomeres and the sarcoplasmic reticulum. The sarcoplasmic reticulum releases Ca^{2+} ions when stimulated by electrical impulses from the nervous system, and it is the rise of Ca^{2+} ions in the sarcomere that begins a cascade of micromechanical actions that ultimately result in force development. Within a myofibril, sarcomeres are packed in a highly structured hexagonal lattice (B). Sarcomeres are skinny (44 nm) relative to their resting length (2.72 µm in humans). We will magnify the thickness of a sarcomere in our illustrations so that the inner details are clearly visible. Image is based on work by 7activestudio©123rf.com and hfsimaging©123rf.com. Myosin is not a single filament but is composed of a regular array of myosin hexamers or cross-bridges that give the thick filament a feather-like structure (C). Tension is generated when the head of the cross-bridge (D1) attaches to actin (D2) and pulls on it. Once the myosin head encounters an ATP molecule (adenosine triphosphate), it can release from actin (D3), and the process can repeat. Image is based on work by hfsimaging ©123rf.com. Gordon et al. (139) measured the maximum isometric tension that can be developed by single muscle fibers (frog) and found that passive tension increases with length, while active tension can only be generated within a certain region (E). When the force is normalized by the maximum isometric force (f_o^{CE}) and length is normalized by the length (ℓ_o^{CE}) of the muscle at f_o^{CE}, the active-force-length profiles of muscle fibers look similar and have shapes that are largely explained by the sliding filament theory (173). When A.V. Hill (154) measured the shortening velocity of the sartorius muscle of an English frog, he observed a hyperbolic relationship between the force the muscle could generate and the velocity that it could pull the weight (F). While Hill's hyperbola (154) during shortening has been replicated in many others (187, 238), the force profile developed by actively lengthened muscle does not follow such a stereotypical pattern. In most muscles, the tension developed by the CE is transmitted through tendon (G) before being applied to the skeleton. The force development of tendon is nonlinear within the toe region ($f < f_{toe}^T$) but becomes linear beyond the toe region ($f > f_{toe}^T$).

Lymn and Taylor (233) proposed a simple four-step cross-bridge cycle that still forms the basic template for how this process unfolds (Figure 7D). Before the cycle begins, electrical activity from the nervous system causes Ca^{2+} ions to be pumped into a fibril and ultimately into the body of the sarcomeres within the fibril. These Ca^{2+} ions interact with the strands of actin to expose tropomyosin (a strand within actin), starting the beginning of the cross-bridge cycle. With tropomyosin exposed, a nearby "charged" cross-bridge can attach to the actin filament (Figure 7D1). Here, a "charged" cross-bridge has adenosine diphosphate (ADP) and an inorganic phosphate (P_i) bound to it. Upon attaching to actin, the cross-bridge's power stroke occurs with it, exerting a force of 3 to 4 pN over a stroke of 11 nm (99) to actin. A 0.8-μm half-myosin has a pair of cross-bridges over 0.7 μm of its length every 14.3 nm, which amounts to 97.9 per half-myosin (175). Assuming a duty cycle of 25% (values between 5% and 90% have been reported (99)), we arrive at a value of 73 to 98 pN of tension that can be generated per sarcomere. In the process of the power stroke, the bond to ADP and P_i is broken (Figure 7D2), and ADP and P_i are released, only to be recycled into fresh ATP moments later within the sarcomere.

The cross-bridge remains attached to actin until an ATP molecule comes close enough to attach to it, releasing it from actin and resetting it into a "charged" state (Figure 7D3). The cross-bridge cycle continues until the sarcomere becomes fatigued (309), or the electrical stimulation from the nervous system ceases. In this case, Ca^{2+} ions are pumped out of the fibril, and tropomyosin is once again isolated from myosin. Even though whole muscle can generate seemingly constant tensions, the underlying processes are anything but constant: individual fibers produce twitches of force rather than a constant output; muscle fibers are constantly fatiguing to be replaced with the recruitment of new fibers; and force is produced discretely within a sarcomere every time a cross-bridge completes a cycle.

While the cross-bridge cycle occurs at nanometer scales (99), the forces, movement, and heat generated by this work cycle were first measured in whole muscle by Hill in 1938 (154). Although Hill's primary focus was to provide a clear picture of the energy relations while muscles perform positive (or negative) work, in the process, he discovered that muscle has a consistent hyperbolic relationship between shortening velocity and tension (Figure 7F). The maximum shortening velocity of a muscle can be increased when it is connected to a long elastic tendon, such as an Achilles tendon (Figure 7G), because a tendon can recoil at a much higher rate than muscle. In addition, tendon compliance can also influence slow deliberate movements, since the length of the musculotendon path now depends on both the length of the muscle fibers and the strain of the tendon. However, unless the tendon is longer than the muscle (249), the maximum rate of contraction of a musculotendon is dominated by the muscle and well described by Hill's force-velocity curve.

There are at least four phenomena that influence the peak force, peak velocity, and shape of Hill's force-velocity curve: the length of each cross-bridge, the rate of cross-bridge cycling, the ratio of attached to unattached cross-bridges (duty cycle), and the phase differences between cross-bridge cycling. Since cross-bridges act as tiny levers, much like oars in a row boat, the length of the lever matters. By carefully tracking the sliding velocity of actin filaments across an artificially made surface coated in cycling cross-bridges, it was shown *in vitro* that longer cross-bridges lead to faster sliding velocities (373). The second rate-determining phenomenon is how quickly each cross-bridge can be driven through its cycle. While these *in vitro* experiments (373) suggested that a cross-bridge can complete a cycle at a rate of approximately 30 Hz, *in vivo* cycling rates are likely much faster: the *in vitro* sliding velocities are on the order of 0.5 to 1.2 lengths/s (1.6–3 μm/s), while *in situ* the rat extensor digitorum longus (one of the fastest mammalian skeletal muscles) can contract at nearly 20 lengths/s (47) (equivalently 43.7 μm/s for a sarcomere from human skeletal muscle). The duty cycle or the ratio of attached to the total number of cross-bridges will affect both the force and velocity that a sarcomere can develop. While duty cycles of between 5% and 90% have been reported (99), it is unclear how velocity affects the duty cycle of the cross-bridges within a sarcomere. Finally, while rowers in a boat are well coordinated by a coxswain, there is nothing to coordinate cross-bridges: a cross-bridge releases from actin when it happens to encounter an ATP molecule, which is a random event that is made more likely to happen with a higher ATP concentration. Thus, it can happen that one cross-bridge will begin its power stroke, but its neighbor, having not encountered an ATP molecule, is still attached to actin, and so the work done by one cross-bridge is absorbed and wasted by its neighbor.

Muscle mechanics

In addition to producing muscular force and muscle shortening, muscle exhibits stiffness and damping properties. Such stiffness and damping can be explained by observing the passive and active properties of the muscle. Previous studies considered the foundations provided by the sliding filament theory (174, 176), the force-length relation (139), and the force-velocity relation (154) to construct computational models that could explain the stiffness and damping properties of the muscle. The two most enduring families of mathematical muscle models created were Hill-type phenomenological muscle models (249, 414) and A.F. Huxley's mechanistic muscle models (173). Although Hill did not derive the Hill muscle model, this type of model bears his name because his hyperbolic force-velocity relationship is a key physiological and mathematical component to the formulation. Hill-type muscle models (Figure 8A) assume that the force (f^{CE}) produced by the contractile element (CE) is given by the relationship

$$f^{\mathrm{CE}} = a\mathbf{f}^{\mathrm{L}}(\tilde{\ell}^{\mathrm{CE}})\mathbf{f}^{\mathrm{V}}(\tilde{v}^{\mathrm{CE}}) + \mathbf{f}^{\mathrm{PE}}(\tilde{\ell}^{\mathrm{CE}})$$

which is the product of the chemical activation (e.g., from (392)) of the muscle (a), Hill's force-velocity curve (154) ($\mathbf{f}^{\mathrm{V}}(\tilde{v}^{\mathrm{CE}})$), and Gordon et al.'s active force-length curve (139) ($\mathbf{f}^{\mathrm{L}}(\tilde{\ell}^{\mathrm{CE}})$) summed with the passive force-length curve (138) ($\mathbf{f}^{\mathrm{PE}}(\tilde{\ell}^{\mathrm{CE}})$). By construction, a Hill model is able to replicate the experiments of Hill (154) and Gordon et al. (139, 138). In contrast, Huxley muscle models (173) instead construct the muscle model from the bottom up, beginning with an elastic cross-bridge model that can switch between attached and detached states (Figure 8B, left). The force developed by the CE in a Huxley model is, compared to a Hill model, easy

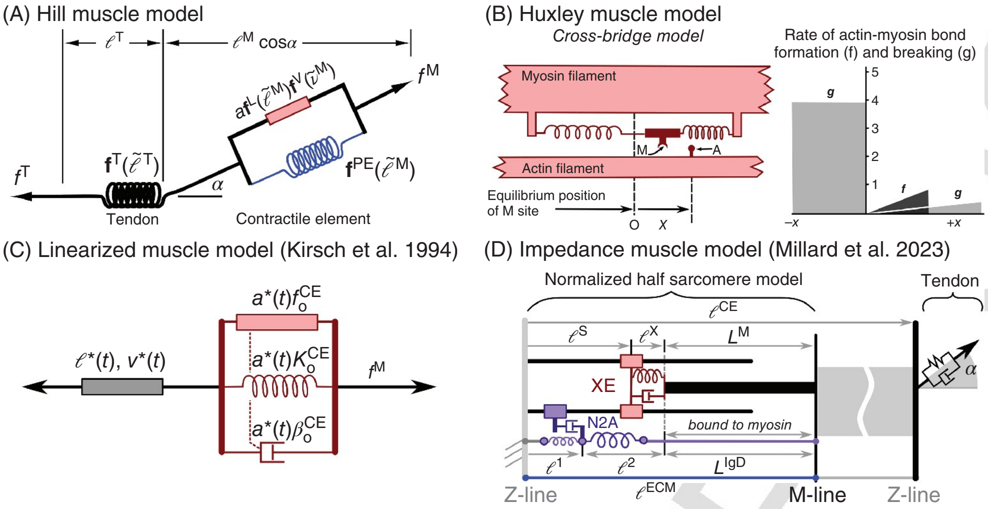

Figure 8 The Hill muscle model. The Hill muscle model is created by first assuming that the muscle and tendon always maintain a perfect force equilibrium and next using the force-velocity curve to define an ordinary differential equation (A). The Huxley model was created by modeling the active and elastic force developed by each cross-bridge when attached to actin as well as the timing and speed of cross-bridge cycling between attachments (B). A linearized muscle model typical of those used in motor control simulations (C). A recently developed regularized model (248) that has a response similar to the linearized model over short time spans but develops forces consistent with Hill and Gordon et al.'s experiments which occur over longer time spans (D).

to evaluate: simply sum up the elastic forces (Kx_i) developed by all of the N_A attached cross-bridges

$$f^{CE} = \sum_{i}^{N_A} Kx_i$$

The key assumption in Huxley's model (173) is that the rates of cross-bridge attachment ($f(x)$) and detachment ($g(x)$) follow piecewise-continuous functions that depend on cross-bridge strain (Figure 8B, right) and velocity (not shown, but appear in Figure 7 of (173)), functions that have not yet been experimentally evaluated. By carefully choosing these attachment and detachment functions, it is possible to make Huxley's model replicate Hill's force-velocity experiment (173). While thousands of Huxley's cross-bridge models can be used to construct and simulate whole muscle (378), this incurs a computational cost that is around 100 times higher than an equivalent Hill-type muscle model.

Although Hill (414) and Huxley (173) muscle models have been extraordinarily influential, there are results from two classes of experiments that both models have difficulties replicating: active lengthening experiments (153, 223) (Figure 9A) and experiments that depend on the stiffness and damping (impedance) of muscle (200) (Figure 9B). The active lengthening experiments (153, 223) depend on the forces developed by the titin filament, a filament that was discovered in 1976 (236) well after the Hill and Huxley models were first formulated. Since the discovery of titin, an enormous amount of research (226) has been done to characterize how titin varies between muscle tissues, across organisms, and functions in active and passive muscle tissue. Importantly, titin has been shown to account for a significant amount of the passive elasticity of muscle (290) and provides enhanced tension during long (approximately >10% ℓ_o^{CE}) active stretches (153, 223) of skeletal muscle (367) by interacting with actin (194). Since neither a Hill model (249, 414) nor a Huxley model (173) accounts for titin, both of these models perform poorly when replicating the active lengthening experiments across modest (153) and large (223) length changes. However, since titin has an insignificant stiffness (0.01 pN/nm (195)) when compared to even a single attached cross-bridge (0.69 ± 0.47 pN/nm (379)), and since cross-bridges significantly outnumber titin filaments (approximately 16:1), titin's contributions can probably be largely ignored by any motor control simulation that does not involve sudden length changes of 10% ℓ_o^{CE} or more. Note that this means that titin's effects may be ignored during swimming and bicycling (287), but activities such as walking or running (11) and certainly landing from a jump would include active contributions from titin. In contrast, the impedance provided by cross-bridges is substantial for any active movement within actin-myosin overlap and plays an important role in nearly all movement.

Muscle impedance

The impedance of muscle has received significant attention from the motor control community ever since the landmark experiments of Mussa-Ivaldi and colleagues (265), which showed that the planar impedance of the human arm is well described by an ellipse that changes shape with posture. Since these initial experiments, others have gone on to show that people adopt task-specific postures to improve performance (370) and reduce the effects of noise (330) of

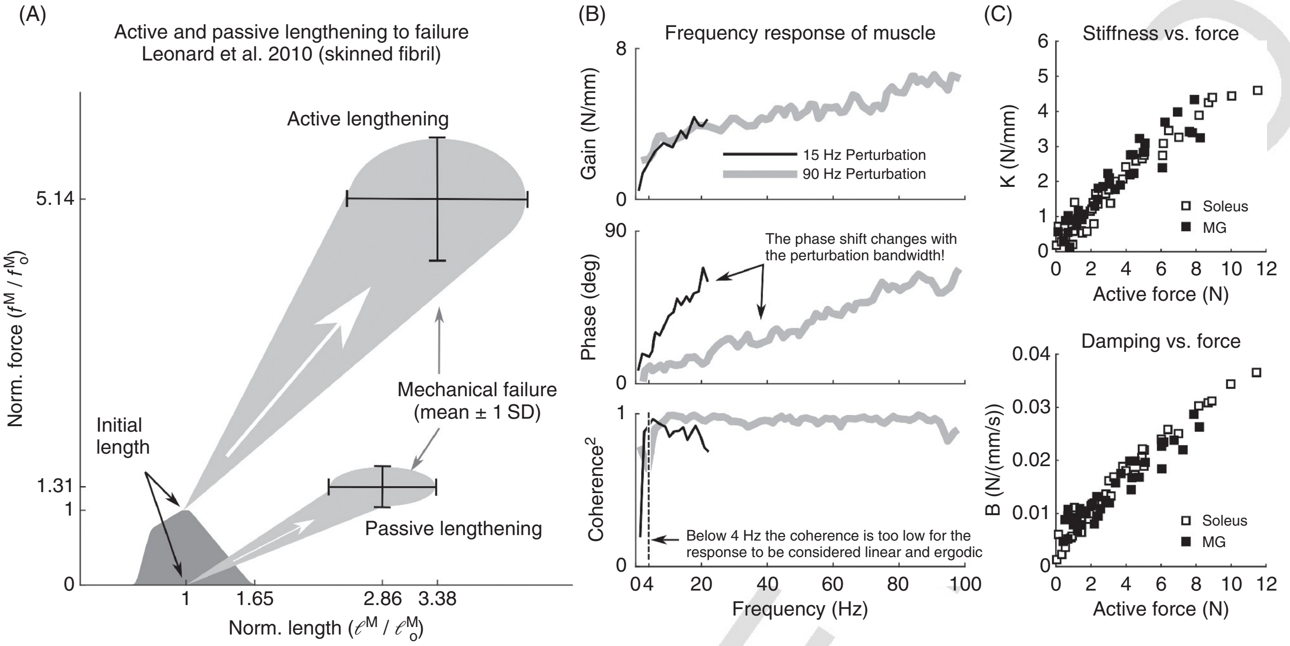

Figure 9 Active fibrils can develop forces that far exceed passive fibrils beyond actin-myosin overlap (223). Leonard et al. (223) established that these enormous active forces are being produced by the large elastic protein titin, and that somehow cross-bridge cycling is required within actin-myosin overlap to produce these large forces beyond actin-myosin overlap (A). Since neither Hill (414) nor Huxley (175) muscle models have a titin element, thus, neither of these models can replicate Leonard et al.'s experiment (223). Muscle also behaves in interesting ways when subjected to small perturbations within actin-myosin overlap: Kirsch et al.'s (200) experiment and analysis showed that the frequency response of muscle between 4 and 90 Hz is well described as a parallel spring-damper. Interestingly, the stiffness and damping of muscle is not constant but appears to vary linearly with the active force of the muscle (C). Neither Hill (414) nor Huxley (173) muscle models are likely to exhibit the same properties: a Hill muscle model's stiffness varies with the slope of the force-length curve and can become negative, while a Huxley model (173) lacks a source of damping that can produce the phase shift observed by Kirsch et al. (200) (B, middle).

the neuromuscular system. Impedance also appears to be an indicator of motor learning, since impedance becomes reduced as a novel task is learned with practice (32, 115). Thus, overall, impedance is of fundamental importance to both muscle physiology and motor control.

Studying experimentally the impedance of muscle is challenging using conventional experimental techniques (in which the muscle undergoes a length change following a simple ramp or sinusoid), because it is possible to construct an infinite number of spring-damper networks that replicate these experiments in the time domain. Kirsch and colleagues (200) realized that the force response of muscle to small length changes (1–3.8% optimal length) can be assumed to be linear functions of the change in length. Instead of using a simple ramp or sinusoid length change profile, they applied a pseudorandom length waveform to the muscle and measured the output force waveform. By applying the linear system and signals methods (279), Kirsch and colleagues (200) transformed the length and force waveforms into the frequency domain. In the frequency domain, the way that muscle transforms an input length waveform into an output force waveform can be described in terms of three diagrams: a gain plot, which shows how the ratio of the magnitude of the output to the input changes as a function of frequency (Figure 9B, top); a phase plot, which shows how the phase differs between the output and input as a function of frequency (Figure 9B, middle); and a coherence plot, which shows how well the signals meet the linearity assumption of the method (Figure 9B, bottom). As long as the system can be considered linear, the gain and phase response of a system is unique and can be used to identify a network of springs and dampers that best fits the data. The picture painted by their analysis is clear: for small perturbations, a parallel spring damper model can explain between 88% and 99% of the force variation of a muscle that is at a constant level of stimulation, and these stiffness and damping coefficients increase linearly with stimulation (Figure 9C).

The *in vivo* experimental measurements (265) and the *in situ* experiments (200) led to the development of linearized muscle models (Figure 8C) for use in motor control simulations (31). Typically linearized models decompose the force contribution of the muscles into two components (Figure 8C): the feed-forward component that is valid for a specific trajectory of length ($\ell^*(t)$, where * indicates feed-forward), velocity ($\upsilon^*(t)$), and activation ($a^*(t)$) and the intrinsic spring-damper forces ($a^*(t)K^M(\ell(t)-\ell^*(t))+a^*(t)\beta^M(\upsilon(t)-\upsilon^*(t))$) generated by the muscle when it is perturbed away from this feed-forward trajectory. By construction, linearized muscle models (Figures 8B and 8C) can replicate Kirsch et al.'s experiments (200) and as such will produce a realistic force response for small perturbations away from the learned feedforward trajectory. The model's force response will degrade in accuracy as the nonlinearities of muscle (139, 154) begin to dominate as perturbations become larger.

Millard et al. (248) have recently produced a model that has the advantages of both the linearized models and that of a Hill-type model (Figure 8D). Here, the impedance of the muscle is explicitly included by making a lumped model of the cross-bridge (XE) as an active force element attached to actin (at a distance ℓ^S from the z-line) in series with a spring-damper element that is attached to myosin. By carefully formulating the equation for $\dot{v}^S$, it is possible to arrive an XE model that can behave like a spring-damper for small perturbations (200) but will, given sufficient time, converge to the forces observed by Hill (154) and Gordon et al. (139) when subject to large length changes. While many aspects of titin remain unclear, the experiments of Trombitás et al. (369) and Leonard et al. (223) can be replicated by introducing a model of titin that is composed of two nonlinear springs separated by an activation-dependent viscous damper that interacts with actin. Although this model offers the possibility to simulate motor learning tasks that involve larger perturbations than were possible with the linearized model, it should be clear that are likely many models that will follow this one in the future: from the force-length curve to titin, there are still many unanswered mysteries behind the linearized mechanics of muscle contraction.

When muscle is stretched over a small range, the force increases as the cross-bridges are stretched, producing a rapid change in force, which is often termed short-range stiffness (297). Once the stretch of the muscle exceeds a certain amount, the rate of force increase is slowed as the stretch causes the actin-myosin bond to break. Depending on the fiber type and the rate of cross-bridge cycling (reattachment of cross-bridges), the force developed by the muscle decreases for larger stretches (366). However, larger active stretches will also stretch the elastic titin molecule, producing high forces for large perturbations of the muscle or limb (153, 223) which are captured in recent muscle models (248).

Muscle and limb properties

One consequence of the randomness in the cross-bridges mechanism is the increase in the variability of the motor output production as muscle activation increases. It has been shown that the variability in the muscle force scales with the level of these motor commands (186, 341), a feature termed signal-dependent noise. In particular, the standard deviation of the noise linearly increases with the applied force. It has been suggested that this effect arises through the mechanism of motor unit recruitment (186). That is, as the level of descending drive to the muscle increases, the level of activation in the motor unit pool increases. However, there is an orderly recruitment of motor units, depending on the size of the neurons (151). As the size of the neurons is strongly related to the force output of each motor unit, and the motor unit output is binary (produces either a twitch or not), any variability in the neural firing results in noise in force output that depends directly on the level of muscle activation. Therefore, the motor noise scales with muscle activation. When we consider that this motor noise interacts with the dependence of muscle force of length change history and current muscle state (muscle length and muscle velocity), this leads to the situation whereby the sensorimotor control system is unable to accurately predict the motor output that it generates.

The effect of noise is reduced because the motor system filters muscular force signals, leading to it becoming more predictable. Indeed, the nature of transformation between the electrical and mechanical response of muscle resembles a low-pass filtering process (284). The recruitment order of motor units also contributes to the efficiency of the filtering strategy since first units to be recruited have the lowest cut-off frequency to minimize the effect of noise (77). In addition, the inertial properties of the limbs and body provide a filtering-like smoothing of the motion. Finally, the stiffness (and damping) of the limbs also compensates for the effects of noise. For example, after adaptation to an unstable divergent force field, the variability of the movements in the null field was lower than prior to the increase in stiffness (32). This effect has been seen in a variety of studies (141, 215, 280), which show that increasing stiffness results in a decrease in variability of the movements and an increase in the endpoint accuracy. This is because as activation rises, stiffness increases faster than signal-dependent noise, and consequently, movement variability is reduced as cocontraction increases (329).

Dealing with noise through stiffness adaptation has also been examined in an object manipulation task that produced contact instability as two circular objects interact (330). As these two circular objects decrease in size, the level of instability increases. Although arm endpoint stiffness increased as the size of the object decreased, this did not necessarily occur along the direction of instability. Instead, a model of the arm with signal-dependent noise showed that the results agreed with an optimal change in endpoint stiffness that produced the required stability of the interaction with the minimal level of muscle activation. The results demonstrate that there is a complex interaction between the level of the noise and stiffness in the complex geometry of a multiple joint, multiple muscle limb, or body. Each muscle will contribute differently to the noise, force, and stiffness at the endpoint of the limb, and these contributions will vary as the geometry of the limb changes. It appears that the sensorimotor control system optimizes the trade-offs among task completion, noise, metabolic cost, and stability. Moreover, the geometry of the limb allows the control system to manipulate kinematic variability such that it predominantly occurs in a task-irrelevant direction. Therefore, the sensorimotor control system should be considered as optimally tuning the stiffness and impedance to the task, increasing the stiffness not in the direction of instability but in a direction that optimizes between task success and metabolic cost (330).

Figure 10 Our ability to stabilize and effectively move our limbs depends, among other factors, on mechanisms at the musculoskeletal level. This is especially evident during the operation of marginally stable objects, which by nature increase the control complexity. For example, when we operate a drill, we apply a large amount of force on the drill pivot point where any small deviations from the vertical axis due to noise can result in loss of stability. While the transformation between the electrical and mechanical signals in the muscle filters some of the noise, to resist any unpredictable perturbations, we increase the impedance of our hands in directions in which it is more likely to experience instabilities (blue ellipse marks the impedance magnitude in different directions). To do so, we can choose a posture for our arms which will generate the greatest increase in impedance once we elevate the cocontraction of muscle pairs. Together, with these noise filtering and stabilization mechanisms, if we unexpectedly lose our original posture, fast feedback loops generate an immediate response, such as the stretch reflex, that resists this sudden change. Such reflexive responses provide the initial solution to losing stability, which will later, due to delay, be complete with additional corrective responses.

Feedback loops

Sending motor commands from the cortex of the brain to the body involves significant delays in the transmission from a desired action (output of the motor command) to the actual physical movement. In addition to the delays from neural transmission (conduction and synapses), there is also a significant delay between the onset of electrical activity at the muscle and force development within the muscle. This electromechanical delay is on the order of 25 ms (181). In addition to a delay, the major effect of this electromechanical coupling is a low-pass filtering effect, whereby the peak force produced by an action potential occurs between 30 and 50 ms after the activation signal. Such low-pass filtering places limits on the bandwidth of the control system.

As discussed above, motor control does not occur purely through feedforward control. In addition to using sensory information for planning, it is used constantly for online state estimation and corrective motor control through feedback loops (Figure 10). Indeed, one of the critical control methods in the motor system is the use of sensorimotor feedback loops, whereby motor actions are modified by changes in sensory inputs. Although stretch reflexes are the classic feedback system that we often think about in terms of motor control, they are just one of the many feedback loops used within sensorimotor control. In general, feedback loops can take input from a variety of sensory modalities, proprioception, vision, tactile, pain, and auditory or vestibular stimuli, and can range from very rapid responses only involving a single synapse (monosynaptic reflexes) to more complex responses that rely on many sensory inputs, multiple computations, and control via descending commands from the brain. Indeed, at the extreme limit, we can think of the whole sensorimotor control system as an extended feedback loop, such as within an optimal feedback control framework (326). As such, these feedback loops span the range from simple involuntary reflex responses, through complex involuntary long-loop feedback responses, all the way to including voluntary correction. For simplicity, here we focus primarily on two of these feedback loops (stretch reflexes and visuomotor feedback responses), but the overall behavioral performance depends on all of these systems working together to produce motor behavior. For example, effectively grasping an object also heavily depends on tactile feedback responses to ensure successful grasp of the object and maintenance of the grip. Tactile sensors in the fingertips detect tiny microslips of the object and reactively increase the grip force to ensure that the object does not fall (89, 184). Similarly, any locomotory activity such as walking, or almost any sport with movements of the head, requires the interaction of vestibular feedback loops, both to ensure upright posture of the body and adjusting eye movements for movement of the head (64, 65). These feedback loops do not function independently for a specific task; instead, we should consider them as a series of nested feedback loops providing rapid control over our motor behavior.

Stretch reflexes. The classical view of a stretch reflex is an increase in the muscle activation in response to the stretch of a muscle. In its simplest construct, the stretch is sensed by the muscle spindles within the muscle, causing an increased firing of the Ia sensory fibers, which synapse directly onto the alpha motor neuron producing increased activation of the stretched muscle. This is often combined with inhibition of an antagonist muscle through a disynaptic pathway. These rapid changes in muscle activation usually occur within 20 to 50 ms of the onset of the stretch of the muscle, with the actual time depending on the distance away from the spinal cord (larger delays for stretch reflexes within the foot or hand compared to those within the spinal muscles), and are referred to as the short latency stretch reflexes. The short latency reflexes generally scale with the background load of the muscle (gain scaling) as well as the velocity and magnitude of the stretch (291). At a slightly longer delay (from 50 to around 105 ms), there is a second increase in activation, the long latency stretch reflex that results both from spinal pathways and higher levels (e.g., brain stem or cortical pathways) (240, 294). The further processing that can be done with increases in time provides further opportunities for more complex stimuli-response pairings. These long latency reflexes also exhibit gain scaling and are affected by the kinematics of the stretch but can also produce responses within muscles or joints that were unperturbed by the stretch (heteronymous reflexes) (343). It has been shown that while the short latency reflexes tend to reflect only the local information (e.g., stretch within a specific joint), the long latency reflexes reflect the overall task goals and consider information regarding multiple joints (see Ref. (295) for a review). For example, it has been shown that the long latency reflexes act to resist the underlying disturbance to the whole limb rather than the specific stretch that occurred in a manner that suggests that the limb dynamics are taken into consideration (210, 211, 292).

Visuomotor feedback responses. It is quite apparent that we use visual feedback to help guide our movements. We extract the location of objects in our environment that we might want to grasp. We also use it to localize our body's position, for example, where our hand is in relation to the object, and we use it to regulate the aperture size of our fingers as we grasp. However, the use of visual feedback is not limited to voluntary corrections or planning. The visual system can also induce rapid feedback responses in our motor system that are faster than those produced by voluntary action (67, 116). The movement of a target toward which we are reaching produces a motor response in arm muscles to correct this action (67, 128). Similarly, if the visual location of our hand suddenly shifts away from our planned movement, rapid increases in muscle activation will act to restore the movement back toward the path (27, 318). This is true even if the hand itself does not move (a purely visual perturbation of the hand's representation). These responses, termed visuomotor feedback responses, produce muscular activation with a 100-ms delay from the visual input (150 ms delay to force production). The response magnitude increases with error size for small errors but gradually saturates for larger visual errors (113).

Unlike stretch reflex responses, in which the correction normally occurs within the stretched muscle, the visual system has no obvious information about the specific muscles that would produce the appropriate corrective movement. This means that the visuomotor feedback response must have access to information regarding both the structure/dynamics of the limbs and its current state to produce the appropriate response. In addition, unlike stretch reflexes, there is evidence to suggest that these responses do not exhibit gain scaling (120, 121). That is, the response magnitude does not appear to depend on the background muscle activity level. However, the delays of the visuomotor feedback responses are much longer than those of stretch reflexes, on the order of 100 ms from visual stimuli to corrective muscle activation (116).

There are also two further visuomotor feedback systems that appear to be related—the manual following response (315) and stimulus-locked response (55, 56). The manual following response produces motor actions when the visual background of a scene shifts laterally during a movement (315), perhaps compensating for shifts in the visual field during either head or body motion (136). The stimulus-locked response is the time-locked muscle activity that is produced prior to the start of a movement by the appearance of a visual target (56). All four of these visuomotor feedback responses produce motor actions with identical delays relative to visual stimuli (100 ms) and similar characteristics. Given current evidence that some of these responses may be mediated through the superior colliculus (56, 142, 303), this may be the rapid pathway for all four of these responses. However, it is almost certain that further delayed (slower) visuomotor feedback loops through the cortex are also involved in the visual control of movement.

Feedback gain modulation. All feedback loops produce corrective action to an error signal at a short delay. This means that they can be used to correct for an unexpected disturbance and rapidly limit the error through changes in the muscle activity. This activity both changes the muscle force, by producing a corrective action, and the muscle stiffness, that is, reflexive stiffness that reduces the effect of the perturbation. Sometimes these errors are predictable, such as when repeating the same task multiple times, or sometimes, the task might itself provide incentives to avoid certain errors more than others, such as when we do not want to knock over a cup of coffee while reaching for some papers on the desk. In such cases, we can also learn to modulate the gain of these feedback responses.

While it has long been known that short latency stretch reflex responses can be modulated with long-term reinforcement training (396), recent work has shown that this can occur on faster timescales as well. Changes in the wrist posture produced strong changes in the short latency stretch reflex magnitude of the triceps during elbow perturbations (386, 387). Moreover, short latency reflexes produce different responses when perturbed just before reaching toward two different targets (283). The idea is that movement preparation sets up different tuning of the muscle spindles (preparatory set of the muscle spindles through changes in the gamma motor neuron drive) that results in different stretch reflexes even within the short latency interval. Longer latency stretch reflexes show a wide range of modulation according to the tasks (295), again through adaptation of the gamma motor neuron drive (81). For example, it has been shown to modulate according to task goals or target locations (293), the presence of objects in the environments (269), and the limb dynamics (211). Visuomotor feedback responses have shown similar ability to be modulated according to the task, scaling with the environmental dynamics (121) and the task relevance of the visual feedback (110, 116). Both stretch reflexes and visuomotor feedback responses modulate during the learning of novel dynamics (49, 52, 119, 120). These feedback gains rapidly increase early in learning to correct rapidly for the large errors, reducing the disturbance of the unknown dynamics. However, as learning progresses, they gradually decrease until they are tuned appropriately for the external dynamics. This has been used to suggest that changes in feedback gains during adaptation reflect two major components: a reactive component that upregulates in the presence of errors and a predictive component that is learned during adaptation and tunes to the task dynamics (119).

Postural effects

Performing any given task requires the sensorimotor system to choose a particular solution out of an infinite number of possibilities. For example, any of a number of trajectories with different joint postures could be chosen to produce a specific movement. Even once the trajectory has been selected, there are many combinations of muscle activations that could produce the same trajectory. Despite this redundancy, it appears that humans repeat the same muscle activation patterns and generate movements using the same joints, neglecting most of the possible patterns that are available and that will achieve the task. While the reason for such repeatability is still unclear, some studies suggested that the pattern is chosen so as to avoid limb postures in which the joints will reach their motion limits (63). Such an activation pattern will be a result of optimizing a cost function, in this case a cost about joint state. However, it has also been suggested that muscle activation patterns are more habitual than optimal (72). Another solution to reduce redundancy is the organization between muscles and joints, which creates a simple way for the CNS to control the output force of the muscles. For example, changing the posture of the arm has a similar effect on multiple muscles' output force, which means that the CNS can avoid complex computation by representing the changes instead of output computations (30, 71). In addition, the available activation patterns will be chosen based on the posture so as to complete the motor task but also to maintain other important aspects such as keeping the limb stable (115).

Limb posture modulates the endpoint impedance of limbs with little energy expenditure. As the limbs become more extended, the stiffness along the limb increases, but the stiffness orthogonal to this decreases. Simple extension of the limb, for example, holding your arm out straight in front of you, can be an energy-efficient manner to increase stiffness if it is only needed in a single direction. On the other hand, as the limb becomes more flexed, the stiffness becomes more isotropic—that is more equal in all directions. Similarly, the body and limb posture also affects the inertial properties of the body through changes in geometry (159). Changes in inertia arise through the relationship of the mechanical linkages of the skeleton and the distribution of mass of the body. It has been shown that one of the reasons that humans choose particular postures during tasks is to tune the limb impedance to the task, for example, endpoint stiffness according to directions of the environmental instabilities (Figure 10) (114, 300, 370).

Endpoint impedance

Many motor tasks have unpredictable elements that arise either from an inability to fully characterize the system or from the presence of noise. For example, when we are holding the hand of a small child, we cannot completely predict the direction in which he/she may suddenly pull as an object attracts him/her. Similarly, the presence of noise has a strong effect in a system with inherent instability. When we attempt to slice an apple with a knife, noise in the system can cause the knife to slip in one direction or the other, making the outcome unpredictable (300). Although feedback responses can be used to correct for many errors, their delay limits their use in some tasks. For example, in an unpredictable task (Figure 10), responses during such a situation may be delayed to the point that the task fails (244), especially in an unstable environment (32). In such cases, we must consider the instantaneous responses produced by the impedance of the musculoskeletal system, and how these might be regulated to ensure controlled motion.

In both unpredictable (359) and unstable (32, 111) environments, humans increase the endpoint impedance of their limbs through cocontraction. During reaching in unstable environments, this endpoint impedance is tuned precisely to the instability in the environment (32, 111, 115) so as to ensure stability while keeping metabolic costs low. The selective control over the direction of increases in endpoint stiffness occurs through control over the muscle pairs used in the cocontraction (111, 112). If we consider a two-joint arm model, there are three major sets of muscles that can produce changes in the endpoint stiffness of the arm: the single joint elbow muscles, the single joint shoulder muscles, and the biarticular muscles—muscles that cross both joints. Each of these muscle groups is able to increase the stiffness at the endpoint of the limb in a different direction (111), although this effect is governed strongly by the geometry of the limb posture and the musculoskeletal dynamics (114, 171). These three muscle groups allow the increase of the endpoint stiffness in three directions, but increasing the stiffness in any other directions requires cocontraction of multiple muscle pairs, thereby making the stiffness increase less directionally specific.

The endpoint impedance is not only important for stabilizing the system (32, 33) and reducing the effects of noise (141, 215, 280) but also is critical for determining the way in which we react when we impact the environment. For example, when running, the motion of the leg when each foot impacts the ground is governed by the impedance of the leg. It has been shown that the leg impedance is rapidly tuned to the running surface, increasing as the running surface becomes more compliant (98). One possibility is that the sensorimotor control system is performing a type of mechanical impedance matching, whereby the impedance of the interaction is controlled to maximize the power transfer and minimize the energy consumption during repeated movements. Such effects of the control over endpoint impedance during interaction are not specific to leg movements. Each time we tap our computer keyboard, play the piano, or hit a volleyball, the impedance of our bodies governs the interaction, sound, or movement of these objects.

Linearization

The acting part of the sensorimotor loop has significant nonlinearities throughout the system. For example, as the motor command is converted to muscular force, the force depends strongly on both the length of the muscle (139) and the velocity of shortening (154) in a nonlinear fashion. In addition, the moment arms of each muscle, which govern how muscular force is converted into joint torques, vary as the joint angle changes (263, 264). Muscle tendons add to this effect, as they exhibit both nonlinearity and hysteresis (414). The skeletal system itself has strong nonlinearities due to the rotational nature of the joints: even the simplified two-joint arm has complex nonlinear dynamics (161).

One popular approach to deal with strongly nonlinear control problems is to use controllers based on reinforcement learning or implement them directly using neural networks. However, there is still much insight to be gained using state space approaches, as they also lead to solutions that can be well understood and validated. Fortunately, we can often find linear approximations to nonlinear models. This is frequently done around their equilibrium points, which are often regions of desired operation. For example, the muscle spindle mechanism inherently provides linearization of the velocity and position feedback around the current configuration (80). Another example for linearized properties of muscle can be seen in muscle's impedance. Nichols and Houk (273) showed that for active muscles of cats, the inherent stiffness exhibits high nonlinearities (yield) which can be compensated by stretch reflex response, resulting in linearized stiffness. That is, the reflexive response contributes to the generated force in a nonlinear fashion, which together with the nonlinear muscle stiffness generates a constant ratio between force and displacement (273). This linear property of muscle stiffness can simplify the control as the control system can represent it using a single value that varies depending on factors such as activation levels (177, 340). However, regardless of the possible advantages that linearization may have on our understanding of the control, this does not mean that the sensorimotor control system requires linearization. Indeed most biomechanical models of the musculoskeletal system require the inclusion of nonlinearities in their simulations to accurately predict human behavior and kinetics (70, 201).

Sensing-Planning-Acting Composition

Each of the three movement stages—sensing, planning, and acting—is critical to generate efficient and effective motor performance. While within each stage we identified multiple mechanisms which aim to solve common problems, computation or execution failures in any of the stages will result in dramatic decline in the overall motor performance. This highlights the importance of considering how all three stages interact in producing skillful motor behavior.

There are many different examples for such decline, especially when we consider different neurophysiological conditions. For example, deafferented individuals lack proprioceptive feedback but still have full use of other sensory feedback, planning, and control of the muscular system. These individuals have difficulty in standing and walking, and even visually guided reaching movements show higher variability (129), different motion characteristics (319), and require attention (178). Although adaptation to changes in the environment such as force field adaptation (247) or visual perturbation (178) can still occur through compensation with visual inputs and predictive mechanisms, the overall motor performance is clearly affected, likely because proprioception is critical for state estimation. Here, the other sensory signals, such as vision, are used to provide important complementary information, but the effect is limited, both due to the reduction in internal state information (e.g., muscle force) and the longer delays for vision compared to proprioception. Using complementary sensory signals occurs in many other cases. For example, blind individuals rely more on proprioceptive information to compensate for the loss of visual inputs (43, 140). Loss of one sensory modality can be compensated by other sensory modalities or with other predictive mechanisms that can provide predicted sensory feedback in place of the sensory feedback for use in further processing during the planning stage.

Upper limb apraxia patients provide another example for a decline in motor performance when one of the movement stages is affected. In this case, motor weakness or sensory impairment is not responsible for the deficit (228), but patients do experience difficulties recalling motor memories or generating complex movements. For example, when being told to use a familiar object or generate some hand gestures, patients struggle or completely fail to generate appropriate movements. Since this failure is not related to receiving information or movement execution, the problem likely originates from the planning and control of movements, particularly in task and motor memory selection (34, 134).

Finally, when muscles or motor units are affected, movement performance will be strongly influenced even if the sensory or control systems are unaffected, as these are necessary for the final movement of our body. This is most evident in amyotrophic lateral sclerosis (ALS) patients who suffer from loss of motor neurons, which leads to decline in motor performance of both voluntary and nonvoluntary motion and eventually death (199). In such cases, during early stages of the disease, patients might exhibit mild motor deficiencies, such as muscle cramps or abnormal electromyography (EMG) patterns, which will turn more severe with the disease progress. Overall, these and other clinical syndromes such as Alzheimer's disease, Parkinson's disease, or Huntington's disease serve as examples for the decline in motor performance due to loss or decreased functionality in any of the three motor stages. This decline is evident despite the fact that we have multiple complementary mechanisms across the different stages that should assist with overcoming many motor-related problems.

Here, we have treated the six problems of motor control as unwanted issues the system needs to overcome. However, we do not suggest that these issues threaten the performance of the sensorimotor system in all cases. Instead, we suggest possible mechanisms that can help overcome these issues in cases when a solution is needed. For example, nonlinearities may not even be a problem for the motor system since nonlinear systems can be controllable, similar to linear systems, without the need to linearize them. While it is computationally harder for us to characterize these systems and understand how they are controlled, it does not necessarily mean that the motor system cannot handle this. Moreover, other features may also benefit movement performance. In the sensory system, noise can increase the probability to detect subthreshold sensory signals through stochastic resonance (242). Across the three stages, some of the learning and control architectures are actually based on the idea that the system is not deterministic. For example, movement variability is usually considered to be a negative consequence; after all, when we try to perform the same action, we would like the actual movement to be the same. Indeed, the ability to estimate and then hit an object a fixed distance with little variance is rewarded with large sums of money to professional golfers. However, it is important to note that variability in performance can also be a beneficial feature of performance. For example, it has been suggested that motor variability can assist with learning. That is, when learning a new skill, especially a complex skill, we often initially find a solution that may not be optimal—a local minima within the infinite possible solutions. In this case, small variations in the attempted motions do not necessarily improve performance in a way in which we can improve our performance.

Large variability, especially early in learning, can move our solution closer to the optimal solution even if it initially impacts negatively upon our performance. Indeed it has been shown that subjects with larger motor variability show the fastest learning when introduced to novel skills (3, 407). While the generalizability of these results is still in debate (36, 148, 339), it suggests that variability in the motor output actively promotes exploration of the environment. This is certainly the case for reinforcement learning algorithms in which random exploitation forms an essential aspect to their learning operation (356). In contrast, insufficient variability can prevent people from finding a new minimum, even with a well-practiced skill such as walking (405). This suggests that, absent sufficient variability, past experience can be as influential on movement as any proposed cost function or observed movement invariant. In this framework, variability is an important characteristic of motor control, particularly increasing performance early in learning and allowing reward to drive learning, rather than only the reduction in motor error.

Another example can be seen in the issue of redundancy in muscle activation. The infinite number of muscle activation patterns that can be used for a simple movement can be thought as a computational burden on the motor system that needs to choose only one plan out of many. However, if we suffer from an injury or muscle fatigue, the existence of multiple activation patterns is beneficial since we can switch to a different pattern without failing the task (212). Similarly, the existence of multiple solutions to a problem means that we can change our solution to optimize our performance to the addition of a new cost or new task constraint.

Other factors, such as delays, may also be beneficial for the sensorimotor system for sensation or control of motor activities. For instance, delays can be used for sound source localization via interaural time difference (183), although this system may work differently in mammals (241). These examples emphasize the need to further explore other ways in which the sensorimotor system might utilize the different factors or problems that affect motor performance.

One way in which the sensorimotor system should be explored is by expanding our observation to real world and more complex tasks (398). By observing human behavior in natural environments and in real-world activities, we can remove the constraints of any laboratory-based studies and support results or expand them by revealing other movement strategies in natural scenarios. For example, analysis of natural behavior supported characteristics of bimanual activities (168), digit independence (179), reach-to-grasp movements (179), eye movements (216), and motor learning (145, 313). In addition to confirming observations of laboratory-based behaviors, studies of natural movements provide new insights into motor behavior such as in the case of vergence movements of the eyes (353) or the coordinate frame used in bimanual movements (168). Compared with laboratory settings, real-world movements usually involve the whole body, increasing the complexity of the motor plan and control and requiring a certain control over the stability of the body. Moreover, such real-world activities contain the full breadth of the motor problems that need to be solved. Such complexity sets a promising and challenging way to examine both validity of previous results and new research directions for motor performance.

Conclusion

When we attempt to perform a task, the three stages of the sensorimotor control system (sensing, planning, and acting) either accomplish the task or adjust in the case of poor performance or even a failure. Within these stages, we identified major mechanisms that may assist the sensorimotor system to overcome the computational, physiological, and environmental problems that deteriorate motor performance. Different prowess or expertise in any of these mechanisms might explain why certain individuals perform more skillfully than others, for example, elite basketball players compared to professional-level players, or why humans in general are still much better than robots at many motor tasks. However, determining which of these and how they might affect performance is extremely difficult, partially because each stage is far more complex than our current understanding and models. For example, here we focused on control systems with continuous feedback while there is evidence for intermittent control in some tasks (127). The system might have both continuous and intermittent control architectures, switching between them according to the task or conditions. Such switching could also occur among movement goals, cost functions, or sensory attention, making the characterization of the sensorimotor system much more complicated.

To understand the structure and operating mechanisms of the sensorimotor control system, we can observe the evolution of optimal principles or invariant movement characteristics. This can be seen, for example, in neurological conditions such as after a stroke, where individuals perform movements that may differ from movements of unaffected individuals. In such cases, movement characteristics may evolve over time and can suggest either a process of finding the optimal movement solution or shifting between optimal solutions. That is, it is unclear whether the affected motor behavior is optimal under the imposed constraints that then change with the progress of the condition, or whether patients are not optimal and need to relearn the optimal solution over time. While here we did not focus on how we can change the computational mechanisms underlying motor performance, sophisticated rehabilitation techniques could target any of the three stages in the sensorimotor loop and cause a shift toward the preferred solution.

In our view, the performance of human motor behavior relies on all three major stages. This means that considering any one of these systems on its own in the production of motor behavior is simplistic. We also argue that examining motor behavior and motor performance is critical to understand the computations that occur within the nervous system. If we do not understand the full range of problems that are being solved by the nervous system, we are unlikely to understand the function or solution the neural circuits provide. This is a critical direction for research in neuroscience, understanding that we cannot simply separate the neural circuits from the sensors, actuators, and, most importantly, the motor behavior that connects them all.

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