Chapter 30: Principles of Sensorimotor Control

Introduction

THE PRECEDING CHAPTERS IN THIS BOOK consider how the brain constructs internal representations of the world around us. These representations are behaviorally meaningful when used to guide movement. Thus, an important function of the sensory representations is to shape the actions of the motor systems. This chapter describes the principles that govern the neural control of movement using concepts derived from behavioral studies and computational models of the brain and musculoskeletal system.

We start by considering the challenges motor systems face in generating skillful actions. We then examine some of the neural mechanisms that have evolved to meet these challenges and produce smooth, accurate, and efficient movements. Finally, we see how motor learning improves our performance and allows us to adapt to new mechanical conditions, such as when using a tool, or to learn novel correspondences between sensory and motor events, such as when using a computer mouse to control a cursor. This chapter focuses on voluntary movement; reflexes and rhythmic movements are discussed in further detail in Chapters 32 and 33.

Voluntary movements are generated by neural circuits that span different levels of the sensory and motor hierarchies, including regions of the cerebral cortex, subcortical areas such as the basal ganglia and cerebellum, and the brain stem and spinal networks. These different structures have unique patterns of neural activity. Moreover, focal damage to different structures can cause distinct motor deficits. Although it is tempting to suggest that these individual structures have distinct functions, these brain and spinal areas normally work together as a network, such that damage to one component likely affects the function of all others. Many of the principles discussed in this chapter cannot be easily attributed to a single brain or spinal area. Instead, distributed neural processing is likely to underlie the computational mechanisms that subserve sensorimotor control.

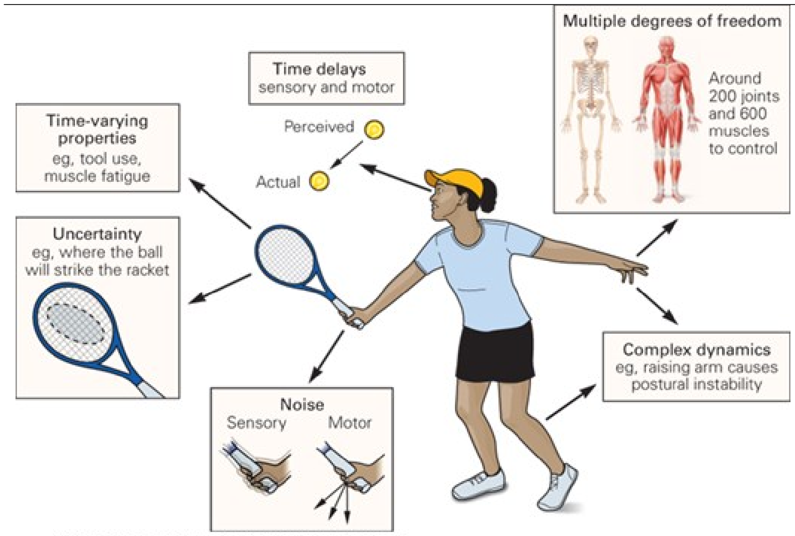
The Control of Movement Poses Challenges for the Nervous System

Motor systems produce neural commands that act on the muscles, causing them to contract and generate movement. The ease with which we move, from tying our shoelaces to returning a tennis serve, masks the complexity of the control processes involved. Many factors inherent in sensorimotor control are responsible for this complexity, which becomes clearly evident when we try to build machines to perform human-like movement (Chapter 39). Although computers can now beat the world's best players at chess and Go, no robot can manipulate a chess piece with the dexterity of a 6-year-old child.

The act of returning a tennis serve illustrates why the control of movement is challenging for the brain (Figure 30–1). First, motor systems have to contend with different forms of uncertainty, such as our incomplete knowledge with regard to the state of the world and the rewards we might gain. On the sensory side, although the player may see the serve, she cannot be certain where her opponent will aim or where the ball might strike the racket. On the motor side, there is uncertainty as to the likely success of different possible returns. Skilled performance requires reducing uncertainty by anticipating events we may encounter (the trajectory of an opponent's tennis serve) and by motor planning (adopting an appropriate stance to return the expected serve).

Figure 30–1

The challenges of sensorimotor control.



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Second, even if the player can reliably estimate the ball's trajectory, she must determine from sensory signals which of the 600 muscles she will use in order to move her body and racket to intercept the ball. Controlling such a system can be challenging as it is hard to explore all possible actions effectively in a system with many degrees of freedom (eg, a large number of individual muscles), making learning difficult. We will see how the motor system reduces the degrees of freedom of the musculoskeletal system by controlling groups of muscles, termed synergies, to simplify control.

Third, unwanted disturbances, termed noise, corrupt many signals and are present at all stages of sensorimotor control, from sensory processing, through planning, to the outputs of the motor system. For example, in a tennis serve, such noise will cause the ball to land in different places even when the server is trying to hit the same location on the court. Both sensory feedback, reflecting the ball's location, and motor outputs are contaminated with noise. The variability inherent in such noise limits our ability to perceive accurately and act precisely. The amount of noise in our motor commands tends to increase with stronger commands (ie, more force). This limits our ability to move rapidly and accurately at the same time and thus leads to a trade-off between speed and accuracy. We will see how efficient planning of movement can minimize the deleterious effects of noise on task success.

Fourth, time delays are present at all stages of the sensorimotor system, including the delays arising from receptor dynamics, conduction delays along nerve fibers and synapses, and delays in the contraction of muscles in response to motor commands. Together, these delays, which can be on the order of 100 ms, depend on the particular sensory modality (eg, longer for vision than proprioception) and complexity of processing (eg, longer for face recognition than motion perception). Therefore, we effectively live in the past, with the control system only having access to out-of-date information about the world and our own body. Such delays can result in instability when trying to make fast movements, as we try to correct for errors we perceive but that no longer exist. We will see how the brain makes predictions of the future states of the body and environment to reduce the negative consequences of such delays.

Fifth, the body and environment change both on a short and a long timescale. For example, within the relatively short period of a game, a player must correct for weakening muscles as she fatigues and changes in the court surface when it rains. On a longer timescale, the properties of our motor system change dramatically during growth as our limbs lengthen and increase in weight. As we will see, the ever-changing properties of the motor system place a premium on our ability to use motor learning to adapt control appropriately.

Finally, the relation between motor command and the ensuing action is highly complex. The motion of each body segment produces torques, and potentially motions, at all other body segments through mechanical interactions. For example, when a player raises the racket to hit the ball, she must anticipate destabilizing forces and counteract them to maintain balance. Indeed, when we raise our arms forward while standing, the first muscle to activate is an ankle flexor ensuring you remain upright. We will see how the sensorimotor system controls movement of different segments to maintain fine coordination of actions.

Actions Can Be Controlled Voluntarily, Rhythmically, or Reflexively

Although movements are often classified according to function—as eye movement, prehension (reach and grasp), posture, locomotion, breathing, and speech—many of these functions are subserved by overlapping groups of muscles. Moreover, the same groups of muscles can be controlled voluntarily, rhythmically, or reflexively. For example, the muscles that control respiration can be used to take a deep breath voluntarily before diving under water, to breathe automatically and rhythmically in a regular cycle of inspiration and expiration, or to act reflexively in response to a noxious stimulus in the throat, producing a cough.

Voluntary movements are those that are under conscious control. Rhythmic movements can also be controlled voluntarily but differ from voluntary movements in that their timing and spatial organization are to a larger extent controlled autonomously by spinal or brain stem circuitry. Reflexes are stereotyped responses to specific stimuli that are generated by neural circuits in the spinal cord or brain stem (although some reflexes involve pathways through cortex). These responses occur on a shorter timescale than voluntary responses.

Although we may consciously intend to perform a task or plan a certain sequence of actions, and at times are aware of deciding to move at a particular moment, movements generally seem to occur automatically. Conscious processes are not necessary for moment-to-moment control of movement. We carry out the most complicated movements without a thought to the actual joint motions or muscle contractions required. The tennis player does not consciously decide which muscles to use to return a serve with a backhand or which body parts must be moved to intercept the ball. In fact, thinking about each body movement before it takes place can disrupt the player's performance.

Motor Commands Arise Through a Hierarchy of Sensorimotor Processes

Although the final output to the musculoskeletal system is via motor neurons in the spinal cord, the motor control of muscles for a specific action occurs through a hierarchy of control centers. This arrangement can simplify control: Higher levels can plan more global goals, whereas lower levels are concerned with how these goals are implemented.

At the lowest level, muscles themselves have properties that can contribute to control even without any change in the motor command. Unlike the electric motors of a robot, muscles have substantial passive properties that depend on both the motor command acting on the muscle as well as the muscle's length and rate of change of length (Chapter 31). As a simple approximation, a muscle can be seen as acting like a spring (increasing tension as it is stretched and reducing tension as it is shortened) and damper (increasing tension as the rate of stretch increases). For small perturbations, these properties tend to act to stabilize the length of a muscle and hence stabilize the joint on which the muscle acts. For example, if an external perturbation extends a joint, the flexor muscles will be stretched, increasing their tension, while the extensor muscles will be shortened, reducing their tension, and the imbalance in tension will tend to bring the joint back toward its original position. A particular advantage of such control is that, unlike higher levels in the motor hierarchy, such changes in force act with minimal delay as they are simply an effect of passive physical properties of the muscles.

In addition to the passive properties of muscles, sensory inputs can cause motor output directly without the intervention of higher brain centers. Sensorimotor responses, such as spinal reflexes, control for local disturbance or noxious stimuli. Reflexes are stereotyped responses to specific stimuli that are generated by simple neural circuits in the spinal cord or brain stem. For example, a spinal flexor withdrawal reflex can remove your hand from a hot stove without any descending input from the brain. The advantage of such reflexes is that they are fast; the disadvantage is they are less flexible than voluntary control systems (Chapter 32). Again, there is a hierarchy of reflex circuits. The fastest is the monosynaptic stretch reflex, which drives contraction of a stretched muscle. In this reflex circuit, sensory neurons that are activated by stretch receptors in the muscle (the muscle spindle) directly synapse onto motor neurons that cause the same muscle to contract. The time from the stimulus to the response is around 25 ms. This reflex can be tested clinically by striking the quadriceps muscle tendon just below the patella.

While this monosynaptic stretch reflex is not adaptable on short timescales, multisynaptic reflexes, which involve higher level structures such as motor cortex, can produce responses at around 70 ms. Unlike the monosynaptic reflex, multisynaptic reflexes are adaptable to changes in behavioral goals because the circuit connecting sensory and motor neurons can be modified by task-dependent properties. The strength of a reflex tends to increase with the tension in a muscle (called gain-scaling), and therefore, reflexes can be amplified by co-contracting the set of muscles around a joint so as to respond to perturbations with a greater force. In fact, we use such co-contraction when holding the hand of a rebellious child when crossing a road. Such a strategy can amplify the reflexes, thereby reducing deviations of the arm caused by random external forces.

Finally, voluntary movements are those that are under conscious control by the brain. Voluntary movements can be generated in the absence of a stimulus or used to compensate for a perturbation. The time to generate a voluntary movement in response to a physical perturbation depends both on the nature of the perturbation (modality and size) as well as whether the response can be specified before the perturbation occurs. For example, a voluntary correction to a small physical perturbation can occur with a latency of about 110 ms.

Although we have described clear distinctions between the different levels of the motor hierarchy, from reflexes through to voluntary control, in reality, such distinctions are blurred in a continuum of responses spanning different latencies. Increasing the response time permits additional neural circuitry to be involved in the sensorimotor loop and tends to increase the sophistication and adaptability of the response, leading to a trade-off between the speed of the response and the sophistication of processing as one ascends the motor hierarchy.

Motor Signals Are Subject to Feedforward and Feedback Control

In this section, we will first illustrate some principles of control that are important for dealing with the problem of sensory delays, sensory noise, and motor noise. For simplicity, we confine our discussion to relatively simple movements, such as moving the eyes in response to head movements or moving the hand from one location to another. We consider two broad classes of control, feedforward and feedback, which differ in their reliance on sensory feedback during the movement.

Feedforward Control Is Required for Rapid Movements

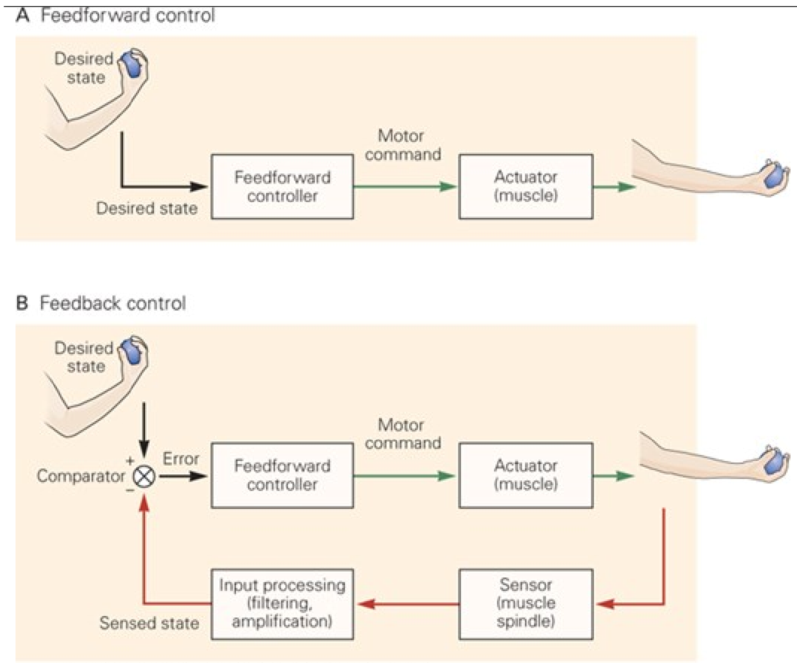
Some movements are executed without monitoring the sensory feedback that arises from the action. In such feedforward control situations, the motor command is generated without regard to the sensory consequences. Such commands are therefore also termed *open-loop*, reflecting the fact that the sensorimotor loop is not completed by sensory feedback (Figure 30–2A).

Figure 30–2

Feedforward and feedback control.

A. A feedforward control motor command is based on a desired state. Any errors that arise during the movement are not monitored. Although we illustrate the elements of feedforward control for the arm, only the initial portion of any arm movement is driven by feedforward signals and the movement typically involves feedback control.

B. With feedback control, the desired and sensed states are compared (at the comparator) to generate an error signal, which helps shape the motor command. There can be considerable delay in the feedback of sensory information to the comparator.



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Open-loop control requires some information about the body so that the appropriate command can be generated. For example, it should include information about the dynamics of the motor system. Here, “dynamics” refers to the relation between the motor command (or the torques or forces) applied and the ensuing motion of the body, for example, joint rotations. For perfect open-loop control, one needs to invert the dynamics so as to calculate the motor command that will generate the desired motion. The neural mechanism that performs this inversion is called an inverse model, a type of internal model (Box 30–1). An inverse model coupled to open-loop control can determine what motor commands are needed to produce the particular movements necessary to achieve a goal.

Box 30–1 Internal Models

The utility of numerical models in the physical sciences has a long history. Numerical models are abstract quantitative representations of complex physical systems. Some start with equations and parameters that represent initial conditions and run *forward*, either in time or space, to generate physical variables at some future state. For example, we can construct a model of the weather that predicts wind speed and temperature 2 weeks from now.

Other models start with a state, a set of physical variables with specific values, and run in the *inverse* direction to determine what parameters in the system account for that state. When we fit a straight line to a set of data points, we are constructing an inverse model that estimates slope and intercept based on the equations of the system being linear. An inverse model thus may allow us to know how to set the parameters of the system to obtain desired outcomes.

Over the past 50 years, the idea that the nervous system has similar predictive models of the physical world to guide behavior has become a major issue in neuroscience. Such a model is termed “internal” because it is instantiated in neural circuits and is therefore internal to the central nervous system. The idea originated in Kenneth Craik’s notion of *internal models* for cognitive function. In his 1943 book *The Nature of Explanation*, Craik was perhaps the first to suggest that organisms make use of internal representations of the external world:

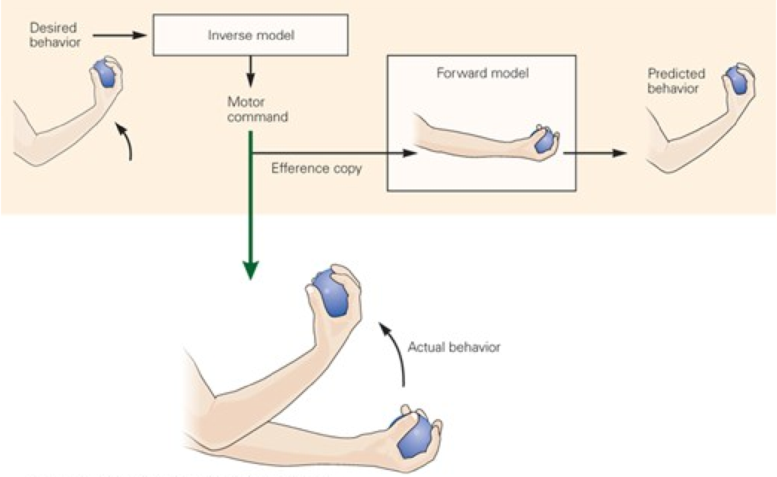
> If the organism carries a “small-scale model” of external reality and of its own possible actions within its head, it is able to try out various alternatives, conclude which is the best of them, react to future situations before they arise, use the knowledge of past events in dealing with the present and future, and in every way to react in a much fuller, safer, and more competent manner to the emergencies that face it.

In this view, an internal model allows an organism to contemplate the consequences of potential actions without actually committing itself to those actions. In the context of sensorimotor control, internal models can answer two fundamental questions. First, how can we generate motor commands that act on our muscles so as to control the behavior of our body? Second, how can we predict the consequences of our own motor commands?

The central nervous system must exercise both control and prediction to achieve skilled motor performance. Prediction and control are two sides of the same coin, and the two processes map exactly onto forward and inverse models (Figure 30–3). Prediction turns motor commands into expected sensory consequences, whereas control turns desired sensory consequences into motor commands.

Figure 30–3

Internal sensorimotor models represent relationships of the body and external world. The inverse model determines the motor commands that will produce a behavioral goal, such as raising the arm while holding a ball. A descending motor command acts on the musculoskeletal system to produce the movement. A copy of the motor command is passed to a forward model that simulates the interaction of the motor system and the world and thus can predict behaviors. If both forward and inverse models are accurate, the output of the forward model (the predicted behavior) will be the same as the input to the inverse model (the desired behavior).



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Although not monitoring the consequences of an action may seem counterproductive, there are good reasons for not doing so. The main reason, as discussed earlier, is that there are delays in both sensing and acting. That is, the conversion of a stimulus into neural signals by sensory receptors and conveyance of these signals to central neurons take time. For example, visual inputs can take around 60 ms to be processed in the retina and transmitted to the visual cortex. In addition to delays in afferent sensory systems, there are also delays in central processing, in the transmission of efferent signals to motor neurons, and in the response of muscles. In all, the combined sensorimotor loop delay is appreciable, approximately 120 to 150 ms for a motor response to a visual stimulus. This delay means that movements like saccades, which redirect gaze within 30 ms, cannot use sensory feedback to guide movement. Even for slower movements like reaching, which takes on the order of 500 ms, sensory information cannot be used to guide the initial part of a movement, so open-loop control must be used.

Open-loop control also has disadvantages. Any movement errors caused by inaccuracies in planning or execution will not be corrected, and therefore will compound themselves over time or successive movements. The more complex the system under control, the more difficult it is to arrive at an accurate inverse model through learning.

An example of a purely open-loop control system is the control of the eye in response to head rotation. The vestibulo-ocular reflex (Chapter 27) uses open-loop control to fix gaze on an object during head rotation. The vestibular labyrinth senses the head rotation and drives appropriate movements of the eyes through a three-synapse circuit. The reflex does not require (or use) vision during the movement (the eyes maintain a stable gaze when the head is rotated in the dark). Sensory information from the vestibular system does drive the eye movement, but the control is feedforward (any errors that arise are not corrected during the movement). Such precise open-loop control is possible because the dynamic properties of the eye are relatively simple, the rotation of the head can be directly sensed by the vestibular labyrinth, and the eye tends not to be substantially perturbed by external events. In contrast, it is very difficult to optimize an inverse model for a complex musculoskeletal system such as the arm, and thus, the control of arm movement requires some form of error correction.

Feedback Control Uses Sensory Signals to Correct Movements

To correct movement errors as they arise, movement must be monitored. Systems that perform error correction are known as feedback or closed-loop control because the sensorimotor loop is complete (Figure 30–2B).

The simplest form of feedback control is one in which the control system generates a fixed response when the error exceeds some threshold. Such a system is seen in most central heating systems in which a thermostat is set to a desired temperature. When the house temperature falls below the specified level, the heating is turned on until the temperature reaches that level. Although such a system is simple and can be effective, it has the drawback that the amount of heat being put into the house does not relate to the discrepancy between the actual and desired temperature (the error). A better system is one in which the control signal is proportional to the error.

Such proportional control of movement involves sensing the error between the actual and desired position of, for example, the hand. The size of the corrective motor command is in proportion to the size of the error and in a direction to reduce the error. The amount by which the corrective motor command is increased or decreased per unit of positional error is called the gain. By continuously correcting a movement, feedback control can be robust both to noise in the sensorimotor system and to environmental perturbations.

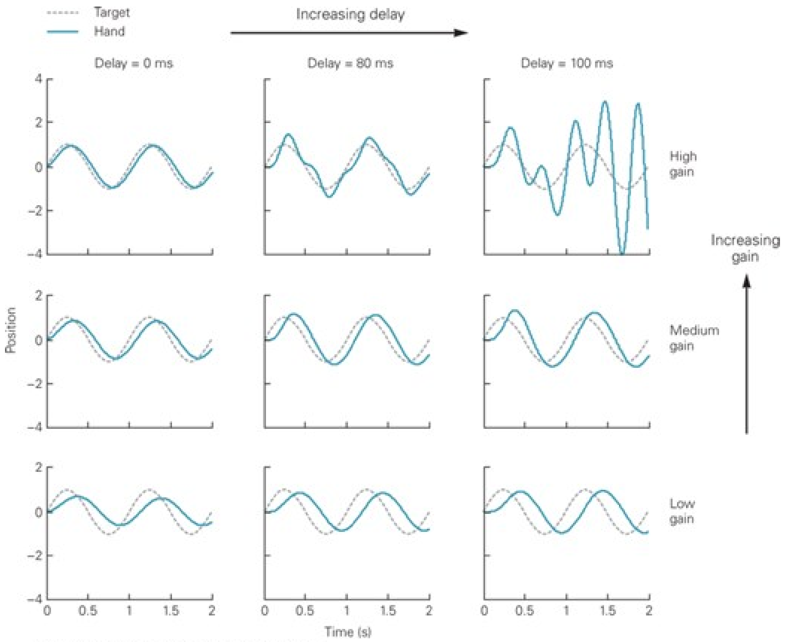
While feedback control can update commands in response to deviations that arise during the movement, it is sensitive to feedback delays. Without any delay, as the gain of the feedback controller increases, the system will track a desired position with increasing fidelity (Figure 30–4). However, as feedback delay increases, the control system may start to oscillate and eventually become unstable. This is because with a delay the system may respond to errors that no longer exist and may therefore even correct in the wrong direction.

Figure 30–4

The interplay of gain and delay in feedback control. Performance of a feedback controller trying to track a target moving sinusoidally in one dimension. The sensory feedback signal that conveys error in the position arrives after some period of time (the delay), and the motor system tries to correct for the error by increasing or decreasing the size of its command relative to the error (the gain).

The plots show the performance in which there is either instantaneous feedback (no delay) of error (**left column**) or feedback with delay of 80 or 100 ms (**middle and right columns**). When the gain is high and the delay is low, tracking is very good. However, when the delay increases, because the controller is compensating for errors that existed 80 or 100 ms earlier, the correction may be inappropriate for the current error. The gain can be lowered to maintain stability, but as the feedback controller corrects errors only slowly, tracking becomes inaccurate.

At low gain (**bottom row**), the feedback controller corrects errors only slowly and tracking is inaccurate. As the gain increases (**middle row**), the feedback controller corrects errors more rapidly and tracking performance improves. At high gain (**top row**), the system corrects rapidly but is prone to overcorrect, leading to instability when the time delay in feedback is on the order of physiological time delays (**top right**). Because the controller is compensating for errors that existed 100 ms earlier, the correction may therefore be inappropriate for the current error. This overcorrection leads to oscillations and is one mechanism proposed to account for some forms of oscillatory tremor seen in neurological disease.



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Smooth pursuit eye movement, used to track a moving object, is an example of a movement driven primarily by feedback. Smooth pursuit uses feedback to minimize the velocity error on the retina (the difference between the gaze and target velocity). We can compare the efficiency of feedforward and feedback control in minimizing error. Compare how easy it is to fixate on your outstretched stationary finger when quickly rotating your head back and forth versus trying to track your finger when it is moving it rapidly sinusoidally left and right while your head remains stationary. Although the relative motion of finger to head is the same in both conditions, the former is precise because it uses the vestibulo-ocular reflex, whereas the latter uses feedback (requiring an error in velocity to drive the eye movement) and thus is less precise, particularly as the frequency of motion increases.

In most motor systems, movement control is achieved through a combination of feedforward and feedback processes. We will see later that these two components arise naturally in a unified model of movement production.

Estimation of the Body’s Current State Relies on Sensory and Motor Signals

Accurate control of movement requires information about our body’s current state, for example, the positions and velocities of the different segments of the body. To grasp an object, we need to know not only the location, shape, and surface properties of the object but also the current configuration of our arm and fingers so as to appropriately shape and position the hand.

Estimating the state of the body is not a trivial problem. First, as we have seen, sensory signals are delayed due to sensory transduction and conduction time. Therefore, signals from our muscles, joints, and vision are all out of date by the time they reach the central nervous system. Second, the sensory signals we receive are often imprecise and corrupted by neural noise. For example, if you touch the underside of a table with the finger of one hand and try to estimate its location on the top of the table with your other hand, you can be off by a considerable distance. Third, we often do not have sensors that directly communicate relevant information. For example, although we have sensors that report muscle length and joint angle, we have no sensors within the limb that directly determine the location of the hand in space. Therefore, sophisticated computation is required to estimate current body states as accurately as possible. Several principles have emerged as to how the brain estimates state.

First, state estimation relies on internal models of sensorimotor transformations. Given the fixed lengths of our limb segments, there is a mathematical relation between the muscle lengths or joint angles of the arm and the location of the hand in space. A neural representation of this relation allows the central nervous system to estimate hand position if it knows the joint angles and segment lengths. Neural circuits that compute such sensorimotor transformations are examples of internal models (Box 30–1).

Second, state estimation can be improved by combining multiple sensory modalities. For example, information about the state of our limbs arrives from proprioceptive information from muscle spindles, the stretch of the skin, and the sight of the arm. These modalities have different amounts of variability (or noise) associated with them, and just as we average a set of experimental data to reduce measurement error, these sensory modalities can be combined to reduce the overall uncertainty in the state estimate.

The optimal way to combine these sources is for higher brain centers to take the uncertainty of each modality into account and rely on the more certain modalities. For example, the location of the hand can be sensed both by proprioception and vision. The sight of your hand in front of you tends to be more reliable than proprioception for estimating location along the azimuth (right–left) but less reliable for depth (forward–back). Therefore, visual input should be given greater weight than proprioceptive input when estimating the azimuth location of your hand, and vice versa for depth. By measuring the precision of each modality when used alone, it is possible to predict the increased precision when both are used at the same time. Experiments have shown that this process is often close to optimal. Precision can also be improved by combining prior knowledge with sensory inputs using the mathematics of Bayesian inference (Box 30–2).

Box 30–2 Bayesian Inference

Bayesian inference is a mathematical framework for making estimates about the world based on uncertain information. The fundamental idea is that probabilities (between 0 and 1) can be used to represent the degree of belief in different alternatives, such as the belief that the chance of your rolling a six with fair dice is 1 in 6.

The beauty of Bayesian inference is that by using the rules of probability we can specify how beliefs should be formed and updated based on our experience and new information from sensory input. For example, when playing tennis, we want to estimate where the ball will land. Because vision does not provide perfect information about the ball's position and velocity in flight, there is uncertainty as to the landing location. However, if we know the level of noise in our sensory system, then the current sensory input can be used to compute the *likelihood* (ie, probability) of the particular sensory input for different potential landing locations.

We can learn additional information from repeated experience of the game: The position where the ball lands is not equally probable over the court. For example, bounce locations are likely to be concentrated near the boundary lines where it is most difficult to return the ball. This distribution is termed the *prior*.

The Bayes rule defines how to combine the prior and likelihood to make an optimal estimate of the bounce location. While the Bayesian approach was originally developed in statistics, it now provides a unifying framework to understand how the brain deals with uncertainty in the perceptual, motor, and cognitive domains.

Third, the motor command can also provide valuable information. If both the current state of the body and the descending motor command are known, the next state of the body can be estimated. This estimate can be derived from an internal model that represents the causal relation between actions and their consequences. This is called a forward model because it estimates future sensory inputs based on motor outputs (Box 30–1). Thus, a forward model can be used to anticipate how the motor system's state will change as the result of a motor command. A copy of a descending motor command is passed into a forward model that acts as a neural simulator of the musculoskeletal system moving in the environment. This copy of the motor command is known as an efference copy (or corollary discharge). Forward and inverse models can be better understood if we place the two in series. If the structure and parameter values of each model are correct, the output of the forward model (the predicted behavior) will be the same as the input to the inverse model (the desired behavior) (Figure 30–3).

Using the motor command to estimate the state of the body is advantageous as, unlike sensory information that is delayed, the motor command is available before it acts on the musculoskeletal system and therefore can be used to anticipate changes in the state. However, this estimate will tend to drift over time if the forward model is not perfectly accurate, and therefore, sensory feedback is used to correct the state estimate, albeit with a delay.

It may seem surprising that the motor command is used in state estimation. In fact, the first demonstration of a forward model used a motor system that relies on only the motor command to estimate state, that is, the position of the eye within the orbit. The concept of motor prediction was first considered by Helmholtz when trying to understand how we localize visual objects. To calculate the location of an object relative to the head, the central nervous system must know both the retinal location of the object and the gaze direction of the eye. Helmholtz's ingenious suggestion was that the brain, rather than sensing the gaze direction, predicted it based on a copy of the motor command to the eye muscles.

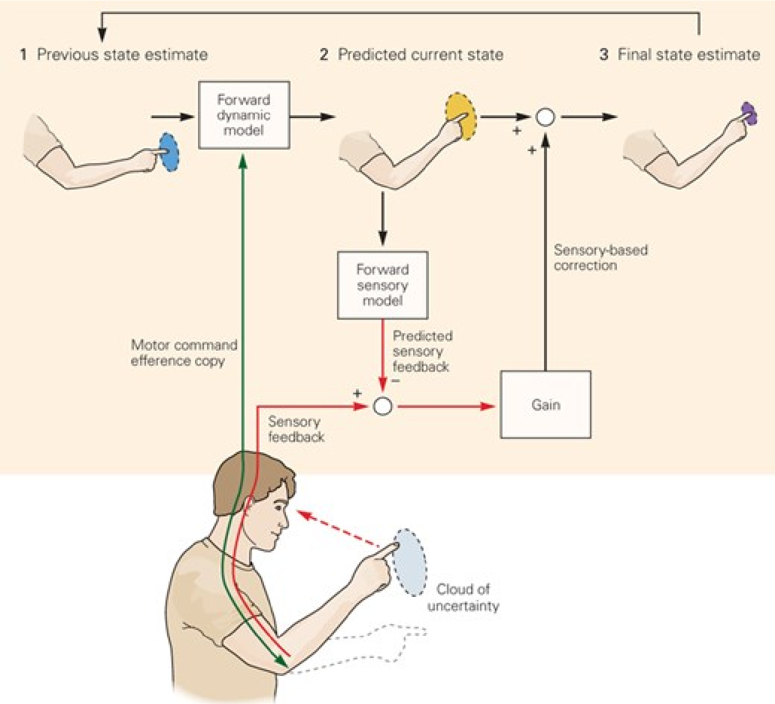
Helmholtz used a simple experiment on himself to demonstrate this. If you move your own eye without using the eye muscles (cover one eye and gently press with your finger on your open eye through the eyelid), the retinal locations of visual objects change. Because the motor command to the eye muscles is required to update the estimate of the eye's state, the predicted eye position is not updated. However, because the retinal image has changed, this leads to the false percept that the world must have moved. A more dramatic example is that if the eye muscles are temporarily paralyzed with curare, then trying to move the eyes leads to a percept that the world is moving. This is because the command leads to a state estimate that the eye has moved, but with a fixed retinal input (due to the paralysis), the only consistent interpretation is that the world has moved.

Finally, the best estimate of state is achieved by combining sensory modalities with motor commands. The drawbacks of using only sensory feedback or only motor prediction can be ameliorated by monitoring both and using a forward model to estimate the current state. A neural apparatus that does this is known as an *observer model.* The major objectives of the observer model are to compensate for sensorimotor delays and to reduce uncertainty in the estimate of current state arising from noise in both the sensory and motor signals (Figure 30–5). Such a model has been supported by empirical studies of how the nervous system estimates hand position, posture, and head orientation. We will see how such models are used to decode neural signals in brain–machine interfaces (Chapter 39).

Figure 30–5

An observer model. The model is being used to estimate the finger's location during movement of the arm. A previous estimate of the distribution of possible finger positions (**1, blue cloud**) is updated (**2, yellow cloud**) using an efference copy of the motor command and a forward model of the dynamics. The updated distribution of finger positions is larger than that of the previous estimate. The model then uses a forward sensory model to predict the sensory feedback that would occur for these new finger positions, and the error between the predicted and actual sensory feedback is used to correct the estimate of current finger position. This correction changes the sensory error into state errors and also determines the relative reliance on the efference copy and sensory feedback.

The final estimate of current finger position (**3, purple cloud**) has less uncertainty. This estimate will become the new previous estimate for subsequent movement as this sequence is repeated many times. Delays in sensory feedback that must be compensated have been omitted from the diagram for clarity.



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State estimation is not a passive process. Skilled performance requires the effective and efficient gathering and processing of sensory information relevant to an action. The quality of sensory information depends on our actions because what we see, hear, and touch is influenced by our movements. For example, the ocular motor system controls the eyes' sensory input by orienting the fovea to points of interest within the visual scene. Thus, movement can be used to efficiently gather information, a process termed *active sensing*. Active sensing involves two main processes: perception, by which we process sensory information and make inferences about the world, and action, by which we choose how to sample the world to obtain useful sensory information. Eye movements can betray the difference between skilled and amateur performers. For example, a batsman in the game of cricket will make a predictive saccade to the place where he expects a bowled ball to hit the ground, wait for it to bounce, and use a pursuit eye movement to follow the ball's trajectory after the bounce. A shorter latency for this first saccade distinguishes expert from amateur batsmen. Therefore, the motor system can also be used to improve our sensing of the world so as to gather information that, in turn, helps us achieve our motor goals.

Prediction Can Compensate for Sensorimotor Delays

As we have seen, delays in feedback can lead to problems during a movement, as the delayed information does not reflect the present state of the body and world. Two strategies, intermittency and prediction, can compensate for such delays and thus increase accuracy of information during movement. With intermittency, movement is momentarily interrupted by rest, as in eye saccades and manual tracking. Provided the interval of rest is greater than the time delay of the sensorimotor loop, intermittency fosters more accurate sensory feedback. Prediction is a better strategy and, as we have seen, can form a major component of a state estimator.

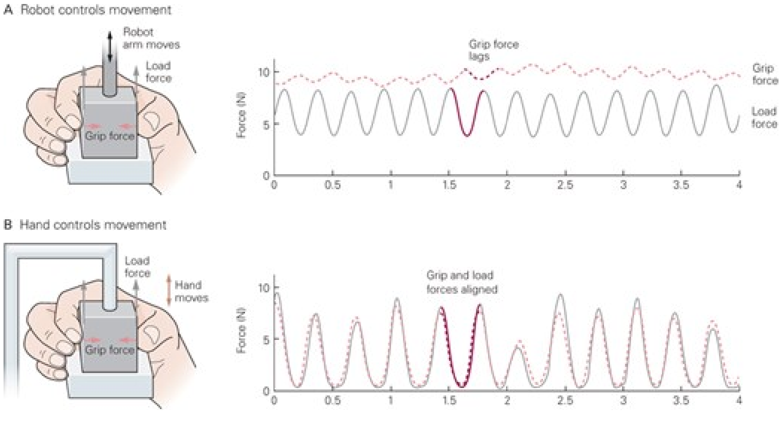
The nervous system uses different modes of control that depend on prediction and sensory feedback to different extents. These modes are nicely illustrated by differences in object manipulation under different conditions. When an object's behavior is unpredictable, sensory feedback provides the most useful signal for estimating load. For example, when flying a kite, we need to adjust our grip almost continuously in response to unpredictable wind currents. When dealing with such unpredictability, grip force needs to be high to prevent slippage because adjustments to grip tend to lag behind changes in load force (Figure 30–6A).

Figure 30–6

Anticipatory control of self-generated actions. (Adapted, with permission, from Blakemore, Goodbody, and Wolpert 1998. Copyright © 1998 Society for Neuroscience.

A. When a subject is instructed to hold an object to which a sinusoidal load force is mechanically applied, the grip force of the fingers is high to prevent slippage, and the grip force modulation lags behind the changes in load force. This is highlighted for a portion of the load force modulation (**dark red solid line**) that leads to a corresponding grip force (**dark red dashed line**), which is delayed. (Trial duration 4 s).

B. When a subject generates a similar load profile by pulling down on the fixed object, the load force can be anticipated, and thus, the grip force is lower and also tracks the load force without delay.



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However, when handling objects with stable properties, predictive control mechanisms can be effective. For example, when the load is increased by a self-generated action, such as moving the arm, the grip force increases instantaneously with load force (Figure 30–6B). Sensory detection of the load would be too slow to account for this rapid increase in grip force.

Such predictive control is essential for the rapid movements commonly observed in dexterous behavior. Indeed, this predictive ability can be demonstrated easily with the "waiter task." Hold a weighty book on the palm of your hand with an outstretched arm. If you then use your other hand to remove the book (like a waiter removing objects from a tray), the supporting hand remains stationary. This shows our ability to anticipate a change in load caused by our own action and thus generate an appropriate and exquisitely timed change in muscle activity. In contrast, if someone else removes the book from your hand, even though you are watching the removal, it is close to impossible to maintain the hand stationary. We will see how cerebellar lesions affect this ability to predict, leading to a lack of such a coordinated response (Chapter 37).

Detecting any discrepancies between predicted and actual sensory feedback is also essential in motor control. This discrepancy, termed sensory prediction error, can drive learning of internal models and also be used for control. For example, when we pick up an object, we anticipate when the object will lift off the surface. The brain is particularly sensitive to the occurrence of unexpected events or the nonoccurrence of expected events (ie, to sensory prediction errors). Thus, if an object is lighter or heavier than expected and therefore lifts off too early or cannot be lifted, reactive responses are initiated.

In addition to its use in compensating for delays, prediction is a key element in sensory processing. Sensory feedback can arise as a consequence of both external events and our own movements. In the sensory receptors, these two sources are not distinguishable, as sensory signals do not carry a label of "external stimulus" or "internal stimulus." Sensitivity to external events can be amplified by reducing the feedback from our own movement. Thus, subtracting predictions of sensory signals that arise from our own movements from the total sensory feedback enhances the signals that carry information about external events. Such a mechanism is responsible for the fact that self-tickling is a less intense experience than tickling by another. When subjects were asked to tickle themselves using a robotic interface, but a time delay was introduced between the motor command and the resulting tactile input, the ticklishness increased. With such delayed tactile input, the predictions become inaccurate and thus fails to cancel the sensory feedback, resulting in the increased tickle sensation. Such predictive modulation of sensory signals by motor actions is a fundamental property of many sensory systems.

Sensory Processing Can Differ for Action and Perception

A growing body of research supports the idea that the sensory information used to control actions is processed in neural pathways that are distinct from the afferent pathways that contribute to perception. It has been proposed that visual information flows in two streams in the brain (Chapter 25). A dorsal stream that projects to the posterior parietal cortex is particularly involved in the use of vision for action (Chapter 34), while a ventral stream that projects to the inferotemporal cortex is involved in conscious visual perception.

This distinction between the uses of vision for action and perception is based on a double dissociation seen in patient studies. For example, the patient D.F. developed visual agnosia after damage to her ventral stream. She is unable, for example, to indicate the orientation of a slot either verbally or with her hand. However, when asked to perform a simple action, such as putting a card through the slot, she has no difficulty orienting her hand appropriately to put the card through the slot (Chapter 59). Conversely, patients with damage to the dorsal stream can develop optic ataxia in which perception is intact but control is affected.

Although the distinction between perception and action arose from clinical observations, it can also be seen in normal people, as in the size–weight illusion. When lifting two objects of different size but equal weight, people report that the smaller object feels heavier. This illusion, first documented more than 100 years ago, is both powerful and robust. It does not lessen when a person is informed that the objects are of equal weight and does not weaken with repeated lifting.

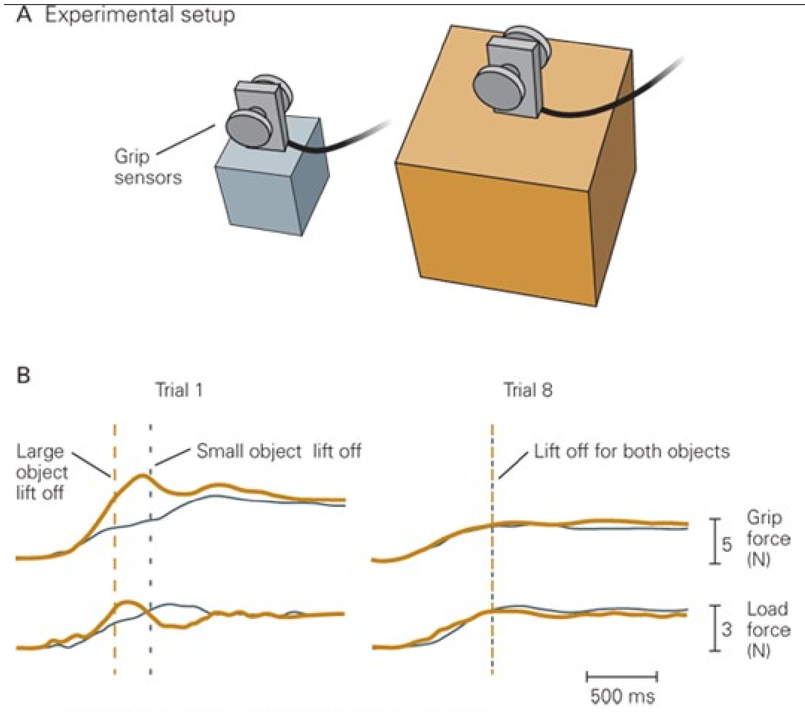
When subjects begin to lift large and small objects that weigh the same, they generate larger grip and load forces for the larger object because they assume that larger objects are heavier. After alternating between the two objects, they rapidly learn to scale their fingertip forces precisely for the true object weight (Figure 30–7). This shows that the sensorimotor system recognizes that the two weights are equal. Nevertheless, the size–weight illusion persists, suggesting not only that the illusion is a result of high-level cognitive centers in the brain but also that the sensorimotor system can operate independently of these centers.

Figure 30–7

The size–weight illusion.

A. In each trial, subjects alternately lifted a large object and a small object that weighed the same. Subjects thought the smaller object felt heavier than it actually was.

B. In the first trial, subjects generated greater grip and load forces for the bigger object (**orange traces**) as it was expected to be heavier than the small object. In the eighth trial, the grip and load forces are the same for the two objects, showing that the sensorimotor system for this action generates grip and load forces appropriate to the weights of the two objects despite the persistent conscious perception of a difference in weight. (Adapted with permission, from Flanagan and Beltzner 2000. Copyright © 2000 Springer Nature.)



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Motor Plans Translate Tasks Into Purposeful Movement

Real-world tasks are expressed as goals: I want to pick up a glass, dance, or have lunch. However, action requires a detailed specification of the temporal sequence of movements powered by the 600 or so muscles in the human body. There is clearly a gap between the statement of a goal and a motor plan that recruits specific muscles in pursuit of that goal.

Stereotypical Patterns Are Employed in Many Movements

The ability of the motor systems to achieve the same task in many different ways is called redundancy. If one way of achieving a task is not practical, there is usually an alternative. For example, the simplest of all tasks, reaching for an object, can be achieved in infinitely many ways.

The duration of the movement can be freely selected from a wide range and, given a particular choice of duration, the path and speed profile of the hand along the path (ie, trajectory) can take on many different patterns. Even selecting one trajectory still allows for infinitely many joint configurations to hold the hand on any given point of the path. Finally, holding the arm in a fixed posture can be achieved with a wide range of muscular co-contraction levels. Therefore, for any movement, a choice must be made from a large number of alternatives.

Do we all choose to move in our own way? The answer is clearly no. Repetitions of the same behavior by one individual as well as comparisons between individuals have shown that the patterns of movement are very stereotypical.

Invariance in stereotypical patterns of movement tells us something about the principles the brain uses when planning and controlling our actions. For example, when reaching, our hand tends to follow roughly a straight path and the hand speed over time is typically smooth, unimodal, and roughly symmetric (bell-shaped, Figure 30–8). The tendency to make straight-line movements characterizes a large class of movements and is surprising given that the muscles act to rotate joints.

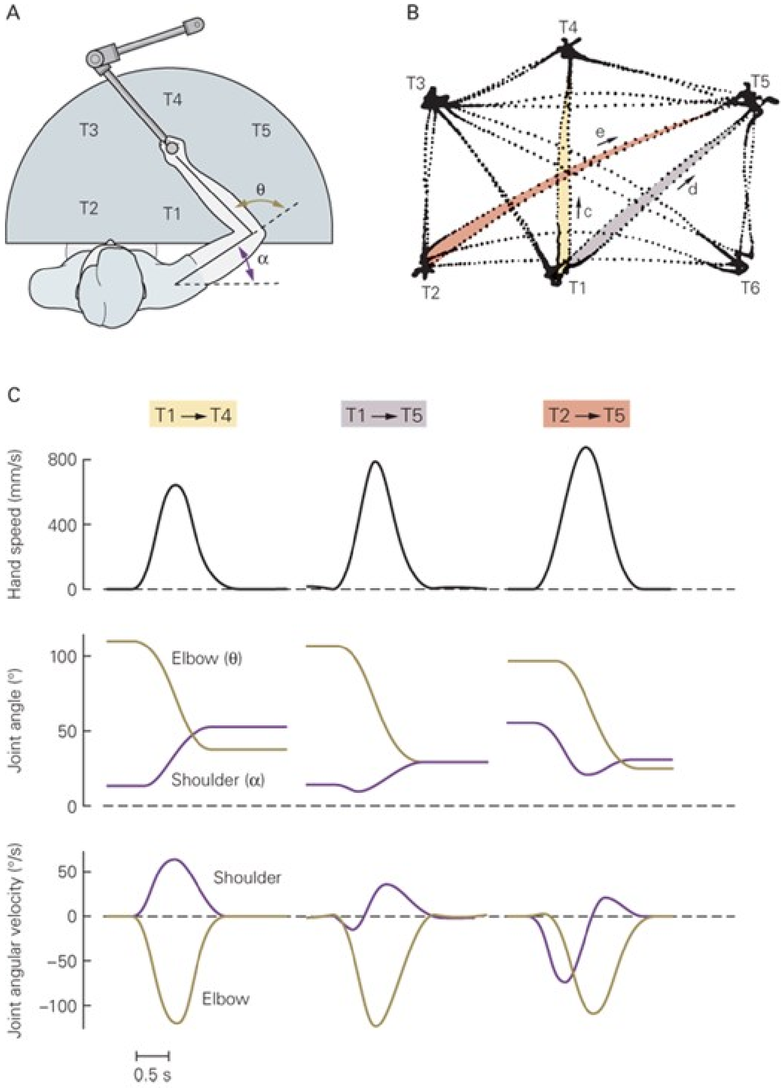
Figure 30–8

Hand path and velocity have stereotypical features. (Adapted, with permission, from Morasso 1981. Copyright © 1981 Springer Nature.)

A. The subject sits in front of a semicircular plate and grasps the handle of a two-jointed apparatus that moves in the horizontal plane and records hand position. The subject is instructed to move the hand between various targets (**T1–T6**).

B. The paths traced by one subject while moving his hand between targets.

C. Kinematic data for three hand paths (**c**, **d**, and **e**) shown in panel **B**. All paths are roughly straight, and all hand speed profiles have the same shape and scale in proportion to the distance covered. In contrast, the profiles for the angular velocity of the elbow and shoulder for the three hand paths differ. The straight hand paths and common profiles for speed suggest that planning is done with reference to the hand because these parameters can be linearly scaled. Planning with reference to joints would require computing nonlinear combinations of joint angles.



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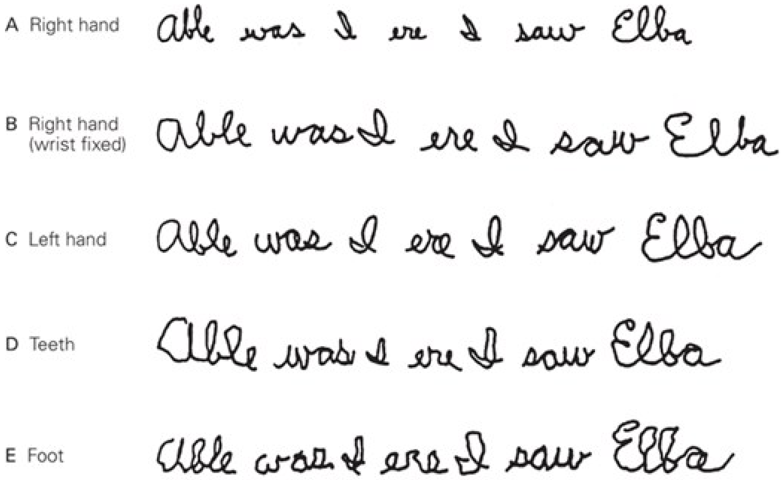
To achieve such a straight-line movement of the hand requires complex joint rotations. The motions of the joints in series (the shoulder, elbow, and wrist) are complicated and vary greatly with different initial and final positions. Because rotation at a single joint would produce an arc at the hand, both elbow and shoulder joints must be rotated concurrently to produce a straight path. In some directions, the elbow moves more than the shoulder; in others, the reverse occurs. When the hand is moved from one side of the body to the other (Figure 30–8, movement from T2 to T5), one or both joints may have to reverse direction in midcourse. The fact that hand trajectories are more invariant than joint trajectories suggests that the motor system is more concerned with controlling the hand, even at the cost of generating complex patterns of joint rotations.

Such task-centered motor plans can account for our ability to perform a specific action, such as writing, in different ways with more or less the same result. Handwriting is structurally similar regardless of the size of the letters or the limb or body segment used to produce it (Figure 30–9). This phenomenon, termed motor equivalence, suggests that purposeful movements are represented in the brain abstractly rather than as sets of specific joint motions or muscle contractions. Such abstract representations of movement, which are able to drive different effectors, provide a degree of flexibility of action not practical with preset motor programs.

Figure 30–9

Motor equivalence. The ability of different motor systems to achieve the same behavior is called motor equivalence. For example, writing can be performed using different parts of the body. The examples here were written by the same person using the right (dominant) hand (**A**), the right hand with the wrist immobilized (**B**), the left hand (**C**), the pen gripped between the teeth (**D**), and the pen attached to the foot (**E**). (Reproduced, with permission, from Raibert 1977.)



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Motor Planning Can Be Optimal at Reducing Costs

Why do humans choose one particular manner of performing a task out of the infinite number of possibilities? Extensive research has attempted to answer this question, and the fundamental idea that has emerged is that planning can be equated with choosing the best way to achieve a task. Mathematically, this is equivalent to the process of optimizing (ie, minimizing) a cost associated with the movement. The cost is a way of quantifying what is good or bad about a movement (eg, energy, accuracy, stability) with a single number.

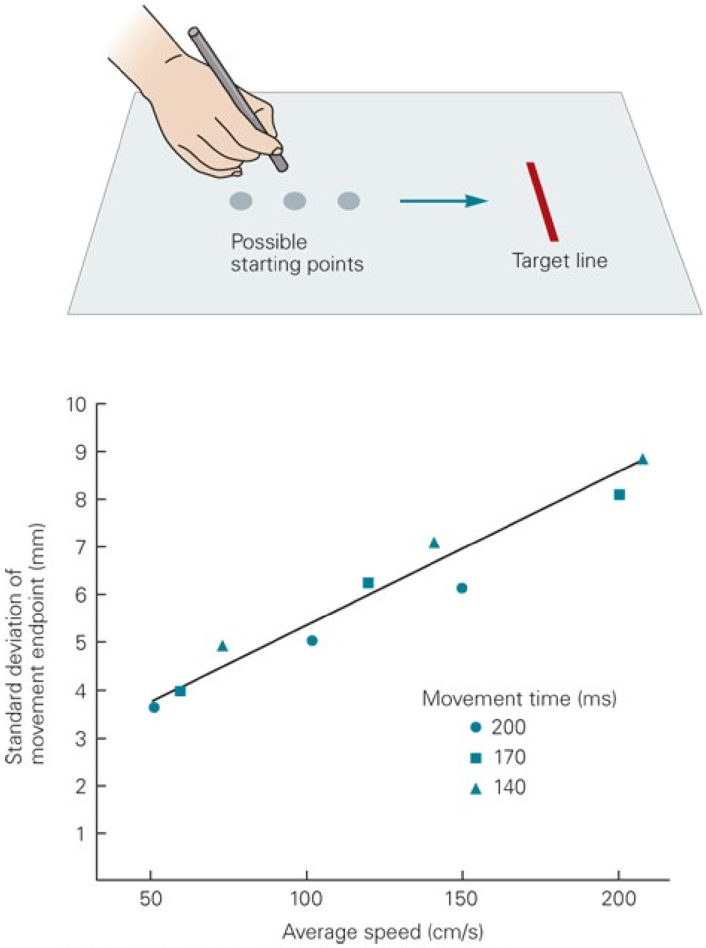
Different ways of achieving a task will lead to different costs. This allows all possible solutions to be ranked, thus identifying the one with the lowest cost. Invariances in our movements will reflect the particular cost we care about for that type of movement. Many costs have been proposed, but currently, most successful theories propose that there are two main components to movement cost: task success and effort. The effort component means that we want to achieve success but with minimal energetic cost.

To understand how task success is a component of the cost, it is useful to understand what leads to lack of success. Having inaccurate internal models or processing clearly limits our ability to complete tasks, and motor learning is designed to keep these processes accurate. However, low-level components in the motor system, such as motor noise, limit success. Movements tend to be variable, and the variability tends to increase with the speed or force of the movement. Part of this increase is caused by random variation in both the excitability of motor neurons and the recruitment of additional motor units needed to increase force. Incremental increases in force are produced by progressively smaller sets of motor neurons, each of which produces disproportionately greater increments of force (Chapter 31). Therefore, as force increases, fluctuations in the number of motor neurons lead to greater fluctuations in force.

The consequences of this can be observed experimentally by asking subjects to generate a constant force. The variability of such force production increases with the level of the force. Over a large range, this increase in variability is captured by a constant coefficient of variation (the standard deviation divided by the mean force). This dependence of variability on force also increases the variability of pointing movements as the speed of movement increases (as greater speed requires greater muscle force). The decrease in movement accuracy with increasing speed is known as the speed–accuracy trade-off (Figure 30–10). This relationship is not fixed, and part of skill learning, such as learning to play the piano, involves being able to increase speed without sacrificing accuracy.

Figure 30–10

Accuracy of movement varies in direct proportion to its speed. Subjects held a stylus and had to hit a straight line lying perpendicular to the direction in which they moved the stylus. Subjects started from one of three different initial positions and were required to complete the movement within three different times (140, 170, or 200 ms). A trial was successful if the subject completed the movement within 10% of the required time. Only successful trials were used for analysis. Subjects were informed when a trial was not successful. The variability in the motion of the subjects' arm movements is shown in the plot as the standard deviation of the movement endpoint plotted against average speed (for each of three movement starting points and three movement times, giving nine data points). The variability in movement increases in proportion to the speed and therefore to the force producing the movement. (Adapted, with permission, from Schmidt et al. 1979.)



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In general, effort and accuracy are in conflict. Accuracy requires energy because corrections require muscular activity and thus comes at some cost. The trade-off between accuracy and energy varies for different movements. When walking, we could choose to step gingerly to ensure we never trip, but this would require substantial energy use. Therefore, we are willing to save energy by allowing ourselves the risk of occasionally tripping. In contrast, while eating with a knife and fork, we prioritize accuracy over energy to ensure the fork does not end up in our cheek.

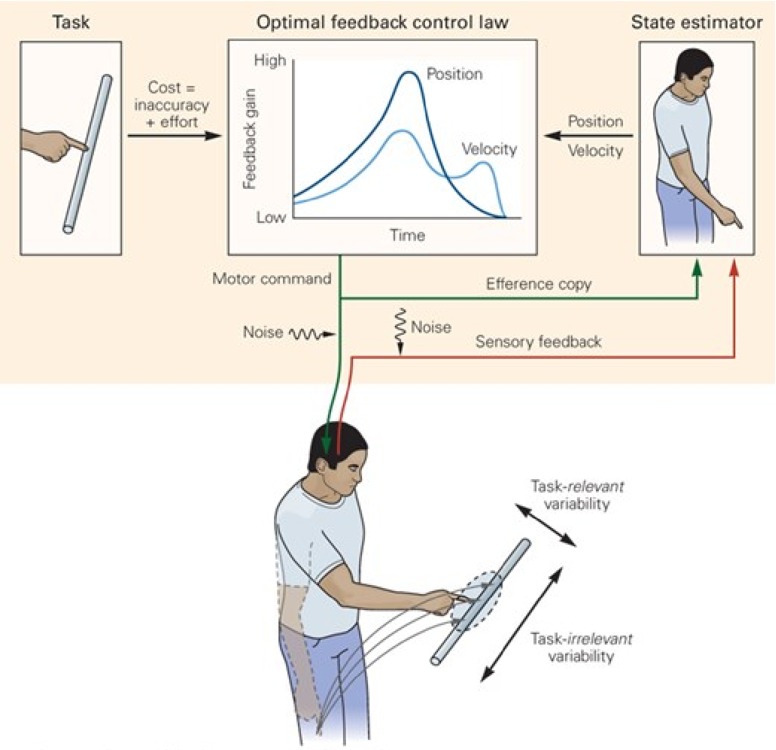
The optimal movement is thus the one that minimizes the bad consequences of noise while saving energy. One way to do this is to specify a desired movement trajectory or sequence of states that can be considered optimal. Although noise and environmental disturbances can cause the motor system to deviate from the desired behavior, the role of feedback is simply to return the movement back to the desired trajectory. However, this approach is not necessarily computationally efficient. Rather than specifying the desired state of the body, we can specify an optimal feedback controller to generate the movement.

Optimal Feedback Control Corrects for Errors in a Task-Dependent Manner

Optimal feedback control aims to minimize a cost such as a combination of energy and task inaccuracy (Chapter 34). This type of feedback control is based on the idea that people do not plan a trajectory given a particular cost. Instead, the cost is used to create a feedback controller that specifies, for example, how the feedback gain for positional errors (and other errors such as velocity and force) changes over time. Therefore, given the goal of the task, the controller specifies the motor command suitable for different possible states of the body. The trajectory is then simply a consequence of applying the feedback control law to the current estimate of the state of the body (Figure 30–11). The feedback controller is optimal in that it can minimize the cost even in the presence of potential disturbances.

Figure 30–11

Optimal feedback control. In order to generate a movement for a given task, such as touching a horizontal bar, the sensorimotor system specifies a cost that is a combination of accuracy (eg, distance of the finger to the bar) and effort. To generate a movement that minimizes this cost, the sensorimotor system sets up an optimal feedback control rule that specifies the time-varying gains. These gains specify how the motor command should depend on states such as positional error and hand velocity. The form of this feedback control law assures that the movement is the best it can be in the presence of internal noise and external perturbations. The optimal behavior tends to let variability (**blue ellipsoid**, showing the possible final locations of the hand) accumulate in dimensions that do not affect task success (task-irrelevant variability), such as along the axis of the bar, while controlling variability that would lead to the hand missing the bar (task-relevant variability). Three paths for reaching from the same starting point are shown; corrections are made only in the task-relevant dimension.



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Optimal feedback control, therefore, does not make a hard distinction between feedforward and feedback control. Rather, during a task, the balance between feedforward and feedback control varies along a continuum that depends on the extent to which the estimate of current body state is influenced by predictions (feedforward) or by sensory input (feedback).

An important feature of optimal feedback control is that it will correct only for deviations that are task relevant and allow variation in task-irrelevant deviations. For example, when reaching to open an exit door that has a long horizontal handle, it is of little importance where along the handle one makes contact, so deviations in the horizontal direction can be ignored. Such considerations lead naturally to the minimal intervention principle that one should only intervene in an ongoing task if deviations will affect task success.

Intervening will generally add noise into the system (and require an increased effort), so intervening unnecessarily will lead to a decrement in performance. The aim of optimal feedback control is not to eliminate all variability, but to allow it to accumulate in dimensions that do not interfere with the task while minimizing it in the dimensions relevant for the task completion. The minimal intervention principle is supported by studies that show that feedback does not always return the system to the unperturbed trajectory but often acts in a manner to reduce the effect of the disturbance on the achievement of the task goal and to ensure that corrections are task-dependent.

Optimal feedback control emphasizes the setting of feedback gains, which can be partially instantiated by reflexes that generate rapid motor responses. Optimal feedback control proposes that these rapid responses should be highly tuned to the task at hand. Although the short-latency (monosynaptic) stretch reflex responds only to muscle stretch, the long-latency response has long been known to respond to task-dependent factors (Chapter 32). Optimal feedback control is important because it combines trajectory generation, noise, and motor cost and provides a clear comparison for the results of experimental work.

Multiple Processes Contribute to Motor Learning

Animals have a remarkable capacity for learning new motor skills simply through everyday interaction with their environment. Although evolution can hard wire some innate behaviors, such as the ability of a foal to stand or a spider to spin a web, motor learning is required to adapt to new and varying environments.

New motor skills cannot be acquired by fixed neural systems. Sensorimotor systems must constantly adapt over a lifetime as body size and proportions change, thereby maintaining an appropriate relationship between motor commands and body mechanics. In addition, learning is the only way to acquire motor skills that are defined by social convention, such as writing or dancing.

Most forms of motor learning involve *procedural* or *implicit* learning, so-called because subjects are generally unable to express what it is they have learned. Implicit learning often takes place without consciously thinking about it and can be retained for extended periods of time without practice (Chapter 52). Typical examples of procedural learning are learning to ride a bicycle or play the piano. In contrast, *declarative* or *explicit* learning refers to knowledge that can be expressed in statements about the world and is available to introspection (Chapter 52). Memorizing the names of the cranial nerves or the directions to the local hospital are examples of explicit learning. Declarative memory tends to be easily forgotten, although repeated exposure can lead to long-lasting retention. We use explicit learning strategies when initially learning some motor tasks, such as driving a car, but the skill becomes automatic with time and practice.

Motor learning can occur more or less immediately or over time. We learn to pick up an object of unknown weight almost immediately, and we learn to ride a bicycle after a few weeks of practice, but mastering the piano requires years. These different timescales may reflect the intrinsic difficulty of the task as well as evolutionary constraints that have to be unlearned to perform the task. For example, piano playing requires learning precise control of individual fingers, whereas in normal movements, such as reaching and grasping, individuated finger movements are rare. Sensorimotor learning can be divided into two broad, but overlapping, classes: adaptations to alterations in the properties of sensorimotor systems and learning new skills. We focus on each in turn.

Error-Based Learning Involves Adapting Internal Sensorimotor Models

Error-based learning is the driving force behind many well-studied sensorimotor adaptation paradigms. For example, the relation between the visual and proprioceptive location of a limb can be altered by wearing prismatic glasses (or even spectacles). This shifts the visual input so that a person's reach for an object is misdirected. Over repeated attempts, the reach trajectories are adjusted to account for the discrepancy between vision and proprioception, a process termed visuomotor learning. Similarly, to control a computer mouse, we must learn the kinematic relation between the movement of the mouse and the cursor on the screen. In addition, the properties of the limbs change with both growth and tool use. The brain must adapt to such changes by reorganizing or adjusting motor commands.

In error-based learning, the sensorimotor system senses the outcome of each movement and compares this to both the desired outcome and the predicted outcome. For example, when shooting a basketball the desired outcome is for the ball to go through the hoop. However, once you let go of the ball you may predict that the ball will miss to the right of the hoop. The difference between the prediction and actual outcome, termed the sensory prediction error, can be used to update the internal model of how the ball responds to your actions. The difference between the actual and desired outcome, termed the target error, can be used to adjust your plan (i.e. aim direction) to reduce the error. Both sensory prediction errors and target errors are important for driving learning.

Additional transformations may have to be applied to the error signal before it can be used to train an internal model. For example, when we throw a dart, errors are received in visual coordinates. This sensory error must be converted into motor command errors suitable for updating a control process such as an inverse model. Error-based learning tends to lead to trial-by-trial reduction in error as the motor system learns the novel sensorimotor properties.

An example of such error-based learning in reaching occurs when the dynamics of the arm are unexpectedly changed. As we saw earlier, we normally move the hand with a straight-line path to reach an object. Unexpected dynamic interactions can produce curved paths, but subjects learn to anticipate and compensate for these effects. This learning is conveniently studied by having subjects make reaching movements while holding the end of a robotic apparatus that can introduce novel forces on the arm (Figure 30–12A–C). Applying a force that is proportional to the speed of the hand but that acts at right angles to the direction of movement will produce a curved movement before finally reaching the target. Over time, the subject adapts to this perturbation and is able to maintain a straight-line movement (Figure 30–12D).

Figure 30–12

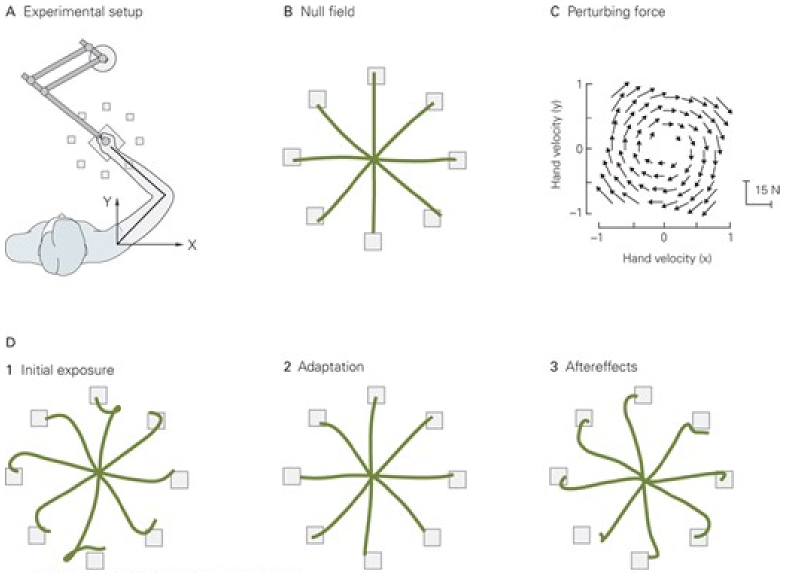
Learning improves the accuracy of reaching in a novel dynamic environment. (Adapted, with permission, from Brashers-Krug, Shadmehr, and Bizzi 1996. Copyright © 1996 Springer Nature.)

A. A subject holds a robotic apparatus that measures the position and velocity of the hand and applies forces to the hand.

B. When the motors are off (null field), the subject makes approximately straight movements from the center of the workspace to targets arrayed in a circle.

C. A clockwise force is then applied to the hand, shown as a function of hand velocity. This field produces a force proportional to the speed of the hand that always acts at right angles to the current direction of motion.

D. Initially, the hand paths are severely perturbed in response to the perturbing force (**1**). After some time, the subject adapts and can again follow a straight path during the entire movement (**2**). When the motors are then turned off, movement is again perturbed, but in a direction opposite to the earlier perturbation (**3**).



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Subjects might adapt to such a situation in either of two ways. Subjects could co-contract the muscles in their arm, thereby stiffening the arm and reducing the impact of the perturbation, or they could learn an internal model that compensates for the anticipated force. By examining the aftereffects (movements after the robot is turned off), we can distinguish between these two forms of learning. If the arm simply stiffens, it should continue to move in a straight path. If a new internal model is learned, the new model should compensate for a force that no longer exists, thereby producing a path in the direction opposite from the earlier perturbation. Early in learning, co-contraction is used to reduce the errors before an internal model can be learned, but the co-contraction then decreases as the internal model is able to compensate for the perturbation. Therefore, when the force is turned off after learning, subjects normally show a large aftereffect in the opposite direction, demonstrating that they have compensated for the perturbation (Figure 30–12D).

Such error-based processes appear to underlie adaptation across a number of different movement types and effectors, from the eye to whole-body movements. For example, our normal symmetric pattern of gait seems to rely on error-based learning. When the gait pattern of subjects is perturbed by walking on a split-belt treadmill in which one belt moves faster than the other, they initially limp. However, step by step the gait pattern naturally regains its symmetry (Figure 30–13), thus showing that error-based learning can drive complex whole-body coordinated movements. There is extensive evidence that fast trial-by-trial error-based learning relies on the cerebellum (Chapter 37).

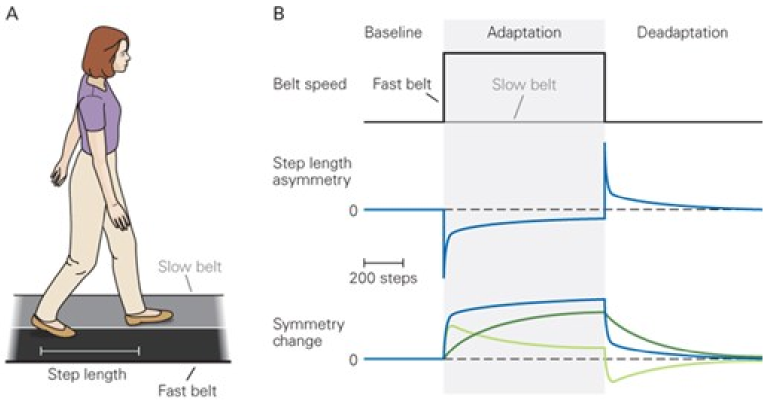
Figure 30–13

Learning new coordination patterns in walking.

A. A subject walks on a split-belt treadmill. When the two belts move at the same speed, subjects have a symmetric gait pattern with equal step lengths.

B. In an adaptation study, the speeds of the belts are initially the same, then become split so that the right belt moves faster than the left, and then finally return to the same speed (**top**). Step length symmetry is initially lost when the belts move at different speeds, causing the subject to limp. Over time, the symmetry is restored and the limping is abolished. When the belts are once again moving at the same speed, an aftereffect is seen (**middle**).

Maurice Smith and colleagues have shown that this type of adaptation is composed of multiple underlying processes that adapt on different timescales (**bottom**). The change in the step length symmetry is composed of two processes: a fast process (**light green line**) that adapts quickly but also rapidly forgets what has been learned, and a slow process (**dark green line**) that learns more slowly but has better retention. These processes both adapt to learn from the error, and the sum of these processes is the final adaptation (**blue line**). This dual-rate learning system gives rise to the typical double exponential learning curves seen in many forms of adaptation in which adaptation is initially fast but tends to slow down as learning proceeds. (Adapted, with permission, from Roemmich, Long, and Bastian 2016.)



Motor adaptation may not be a single unitary process. Recent evidence suggests that adaptation is driven by interacting processes whose outputs are combined. These interacting processes could have different temporal properties: one process quickly adapting to perturbations but also rapidly forgetting what was learned and the other learning more slowly but retaining learning for a longer period (Figure 30–13B). The advantage of such a mechanism is that the learning processes can be matched to the temporal properties of the perturbations, which can range from short-lived (fatigue) to long-lasting (growth).

Although motor learning often takes much practice, once a task is no longer performed, deadaptation is typically faster. However, the sensory inputs associated with the particular action can be enough to switch behavior. When subjects wear prismatic glasses that shift visual space, for example, they initially miss when reaching to targets but soon learn to reach correctly. After repeated trials, the mere feel of the glasses, without the prisms in place, is sufficient to evoke the adaptive behavior appropriate for the prisms.

In general, we can quantify performance with two measurements, accuracy and precision. Accuracy is a measure of systematic errors or biases, for example, on average how far a series of thrown darts are away from the target. In contrast, precision is a measure of random errors, or statistical variability, in our actions. Both accuracy and precision contribute to performance. In general, accuracy can be improved by adapting or calibrating motor commands so as to reduce systematic errors. Although there is always some variability in movement arising from irreducible sensory and motor noise, the variability, as we have seen, can be reduced through planning so as to have minimal impact on task success. Most motor learning tends to become automatic (ie, implicit) with time, but early learning of some tasks can be aided by explicit learning (ie, strategy), such as a verbal instruction on how best to approach the task.

Not all sensory modalities are equally important in learning all motor tasks. In learning dynamic tasks, proprioception and tactile input are more important than vision. We normally learn dynamic tasks equally well with or without vision. However, individuals who have lost proprioception and tactile input have particular difficulty controlling the dynamic properties of their limbs or learning new dynamic tasks without vision (Box 30–3).

Box 30–3 Proprioception and Tactile Sense Are Critical for Sensorimotor Control

While visual impairment certainly has limiting effects on sensorimotor control, blind people are able to walk normally and reach and grasp known objects with ease. This is in stark contrast to the rare loss of proprioceptive and tactile sense.

Some sensory neuropathies selectively damage the large-diameter sensory fibers in peripheral nerves and dorsal roots that carry most proprioceptive information. Impairments in motor control resulting from loss of proprioception have fascinated neurologists and physiologists for well over a century. Studies of patients with sensory neuropathies provide invaluable insight into the interactions between sensation and movement planning.

As expected, such patients lose joint position sense, vibration sense, and fine tactile discrimination (as well as tendon reflexes), but both pain and temperature senses are fully preserved. Patients with peripheral neuropathies are unable to maintain a steady posture, for example, while holding a cup or standing, with the eyes closed. Movements also become clumsy, uncoordinated, and inaccurate.

Some recovery of function may occur over many months as the patient learns to use vision as a substitute for proprioception, but this compensation still leaves patients completely incapacitated in the dark. Some of this difficulty reflects an inability to detect errors that develop during unseen movements, as occurs if the weight of an object differs from expectation.

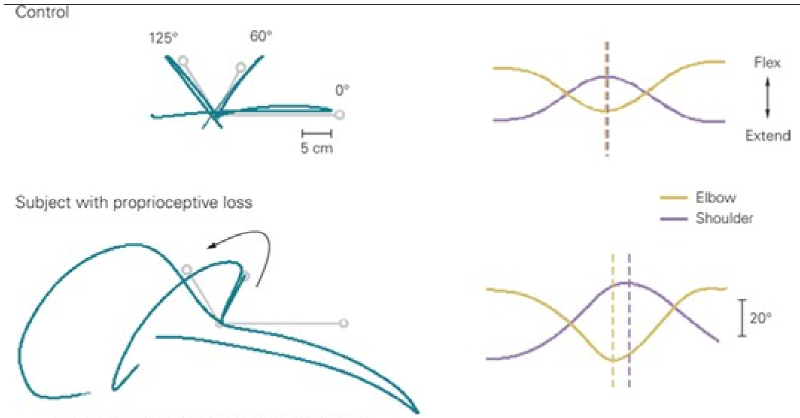
Peripheral neuropathies are particularly incapacitating when patients try to make movements with rapid direction reversals. Analyses of the joint torques during these movements show that subjects with intact proprioception anticipate intersegmental torques, whereas those without proprioception fail to do so (Figure 30–14).

However, the same patients easily adapt to drastic kinematic changes, such as tracing a drawing while viewing their hand in a mirror. In fact, they perform better than normal subjects, perhaps because they have learned to guide their movements visually and, because they lack proprioception, do not experience any conflict between vision and proprioception.

Even in normal subjects, the relative importance of tactile input in manipulation tasks can be easily demonstrated. It is relatively easy to light a match with one's eyes closed. However, if the tips of the digits are made numb with local anesthetic, then even under full vision the task is remarkably hard because the match tends to slip from the fingers.

Figure 30–14

Patients lacking proprioception cannot make an accurate movement that requires a rapid reversal in path. (*Left*) The subject tries to trace a template (**gray line**) while her hand is hidden from view. The joint angles for the elbow and shoulder of a normal subject show good alignment (*Right top*), leading to an accurate reversal (*Left top*). In contrast, the timing of the joint reversal is poor in subjects who lack proprioceptive input (*Right bottom*), leading to large errors in the path (*Left bottom*). These patients cannot anticipate and correct for the intersegmental dynamics that occur around the path reversal. (Adapted, with permission, from Sainburg et al. 1995.)



Source: Eric R. Kandel, John D. Koester, Sarah H. Mack, Steven A. Siegelbaum: Principles of Neural Science, 6e Copyright © McGraw-Hill Education. All rights reserved.

Skill Learning Relies on Multiple Processes for Success

In contrast to error-based learning in which the sensorimotor system adapts to a perturbation to return to pre-perturbation performance, learning skills such as tying one's shoelaces, juggling, typing, or playing the piano instead involves improving performance in the absence of a perturbation. Such learning tends to improve the speed–accuracy trade-off. Initially, we may be able to hit the correct keys on a keyboard when paced 1 second apart, but with practice, the same accuracy can be achieved at an increasingly quickening pace.

For some skills, there can be a complex relation between the actions performed and success or failure at the task. For example, when children first sit on a swing, they have to learn the complex sequence of leg and body movements required to make the swing go higher. In contrast to error-based learning, there is no readily available error signal that can be used to adjust the current action because the swing's height is not directly determined by the current action but by a long history of body and leg motion. Learning in such complex scenarios can be achieved using reinforcement learning in which the sensorimotor system adjusts its commands in an effort to maximize reward, that is, task success. In the most general form, the performance measure that the reinforcement learning tries to maximize is the sum of all future rewards. However, as we tend to favor an immediate versus time-delayed reward, the sum is typically weighted to reflect this by progressively discounting future rewards.

Reinforcement learning is more general than error-based learning in that the training signal is success or failure, rather than an error at each point in time. Another distinguishing property of reinforcement learning is that the success or failure that the learning system receives can depend in nontrivial ways on the history of the actions taken. For tasks that require a complex sequence of actions to take place to achieve a goal, such as tying one's shoelaces, and the outcome or reward is removed in time from the action, error-based learning cannot easily be applied. A key problem that reinforcement solves is that of credit assignment: Which action within a sequence should we credit or blame when we eventually succeed or fail? This is just the sort of problem reinforcement learning algorithms are good at solving.

There are two main classes of reinforcement learning, those that depend on an internal model and those that do not. Model-based reinforcement builds a model of the task (eg, the structure of a maze). With such a model, the learner can efficiently plan in a goal-directed manner. In contrast, with model-free reinforcement learning, the learner simply associates movements with success or failure; those that lead to success are more likely to be performed again. Such learning can lead to motor habits. While model-free learning avoids the computational burden of building a model, it is also less able to generalize to novel situations. These two types of reinforcement learning can even act together, and different tasks can rely on them to different extents. Dopaminergic systems in the basal ganglia have been tied to signals that one would expect in reinforcement learning, such as expected reward. Moreover, dysfunction in these systems is related to movement disorders, addiction, and other problems that could be related to reinforcement signals (Chapter 38).

Finally, the development of efficient strategies plays a key part in motor skill acquisition. Skill learning for real-world tasks typically involves a sequence of decision-making processes at different spatiotemporal scales. The skill of a tennis player, for example, is not only determined by the precision with which she can strike the ball but also by the speed with which she can make the correct decision on where to aim it and how well she uses her senses to extract task-relevant information.

Sensorimotor Representations Constrain Learning

The information obtained during a single movement is often too sparse or noisy to unambiguously determine the source of error. For example, if a tennis player hits a shot into the net on the serve, the problem could be that the ball was not thrown high enough, the ball was hit too early, the racquet strings are loose, there was a gust of wind, or the player is fatigued. If the racquet dynamics have changed, the player would do well to adapt to these for the next shot. If a temporary gust of wind was the problem, then no adjustment is needed. To resolve this issue, the sensorimotor learning system constrains the way in which the system is updated in response to errors. These constraints reflect the internal assumptions about the task structure and the source of errors and determine how the system represents the task. Indeed, on a slower timescale, learning itself can alter the representation.

While the final output of the motor system is the contraction of its 600 or so muscles, it is not the case that the brain controls each independently. In current models of sensorimotor control, motor commands are generated by multiple modules that can be selectively engaged depending on the requirements of the task. Examples of modular architectures include multiple internal models, motor primitives, and motor synergies (Chapter 36).

Motor primitives can be thought of as neural control modules that can be flexibly combined to generate a large repertory of behaviors. A primitive might represent the temporal profile of a particular muscle activity or a set of muscles that are activated together, termed a synergy. The overall motor output will be the sum of all primitives, weighted by the level of the activation of each module. The makeup of the population of such primitives then determines which structural constraints are imposed on learning. For example, a behavior for which the motor system has many primitives will be easy to learn, whereas a behavior that cannot be approximated by any existing primitives would be impossible to learn.

Highlights

1. The primary purpose of the elaborate information processing and storage that occurs in the brain is to enable us to interact with our environment through our motor system.
2. Our infinitely varied and purposeful motor behaviors are governed by the integrated actions of the motor systems, including the motor cortex, spinal cord, cerebellum, and basal ganglia.
3. To control action, the central nervous system uses a hierarchy of sensorimotor transformations that convert incoming sensory information into motor outputs.
4. There is a trade-off in the speed versus sophistication of the different levels of sensorimotor response from rapid reflexes to slower voluntary control.
5. The motor systems generate commands using feedforward circuits or error-correcting feedback circuits; most movement involves both types of control.
6. The brain uses internal models of the sensorimotor system to facilitate control.
7. The state of the body is estimated using both sensory and motor signals together with a forward predictive mode to reduce the adverse effects of delays in feedback.
8. Variability in the sensory inputs and motor outputs together with inaccuracies in sensorimotor transformations underlie the errors and variability in movement, leading to the trade-off between speed and accuracy.
9. Motor planning can use the redundancy of the motor system to move in such a way as to reduce the negative consequences of motor noise while reducing effort.
10. Motor control circuits are not static but undergo continual modification and recalibration throughout life.
11. Motor learning improves motor control in novel situations, and different forms of sensory information are vital for learning. Error-based learning is particularly important for adapting to simple sensorimotor perturbations. Reinforcement learning is particularly important for more complex skill learning and can rely on a model (model-based) or on simply reinforcing motor actions directly (model-free).
12. The motor representations used by the brain constrain the way the sensorimotor system updates during learning.
13. Studies of sensorimotor control have focused on developing a detailed understanding of relatively simple tasks, such as reaching and walking.

Although these tasks are amenable to analysis and modeling, they do not capture the full complexity of real-world motor control. The challenge will be to determine if these principles can be generalized to tasks such as tying shoelaces and learning to skateboard.

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