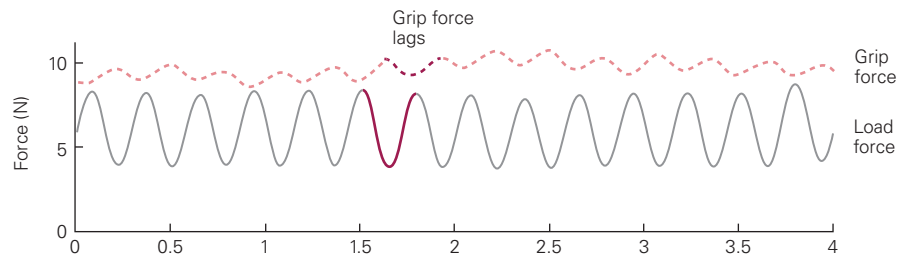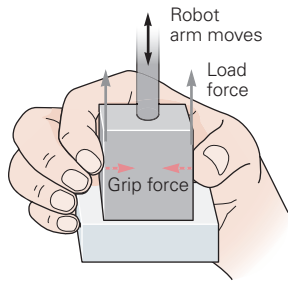A Robot controls movement

B Hand controls movement
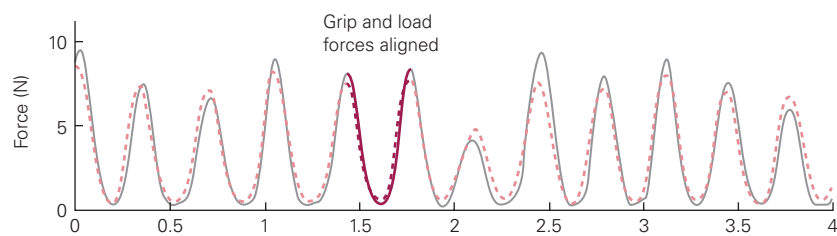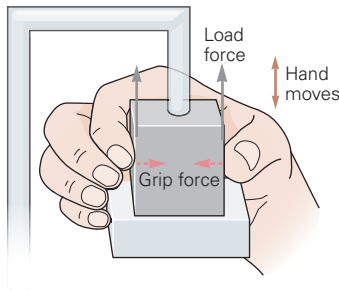

Figure 30–6 Anticipatory control of self-generated actions. (Adapted, with permission, from Blakemore, Goodbody, and Wolpert 1998. Copyright © 1998 Society for Neuroscience.

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 high-lighted 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.

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.
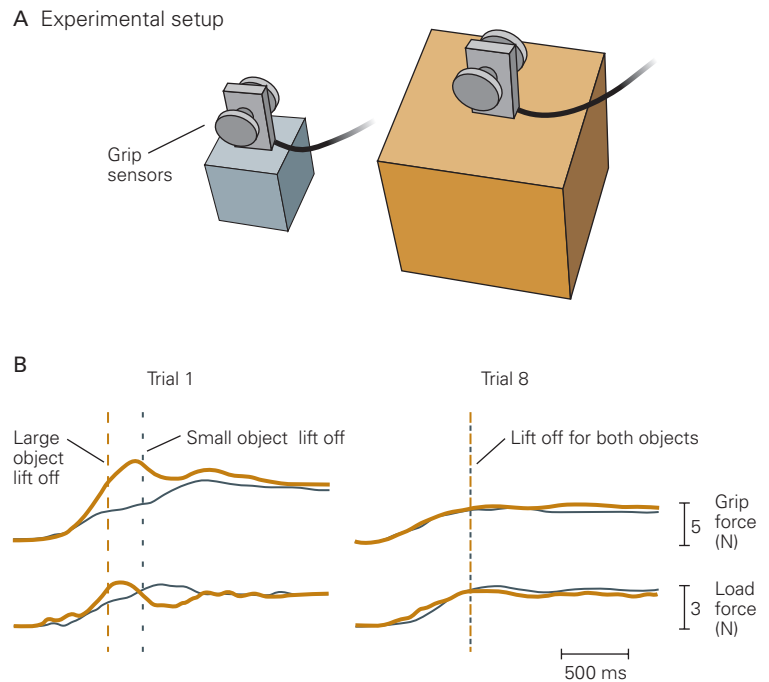
Although the distinction between perception and action arose from clinical observations, it can also be seen in normal people, as in the size–weight illusion. When lifting two objects of different size but equal weight, people report that the smaller object feels heavier. This illusion, first documented 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

A Experimental setup

Grip sensors

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.)

B

Trial 1

Large object lift off — Small object lift off

Trial 8

Lift off for both objects

Grip force (N) 5

Load force (N) 3

500 ms

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

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.

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.

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

A

B

A. The subject sits in front of a semicir-
cular plate and grasps the handle of a
two-jointed apparatus that moves in the
horizontal plane and records hand posi-
tion. 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 refer-
ence to the hand because these param-
eters can be linearly scaled. Planning
with reference to joints would require
computing nonlinear combinations of
joint angles.

C
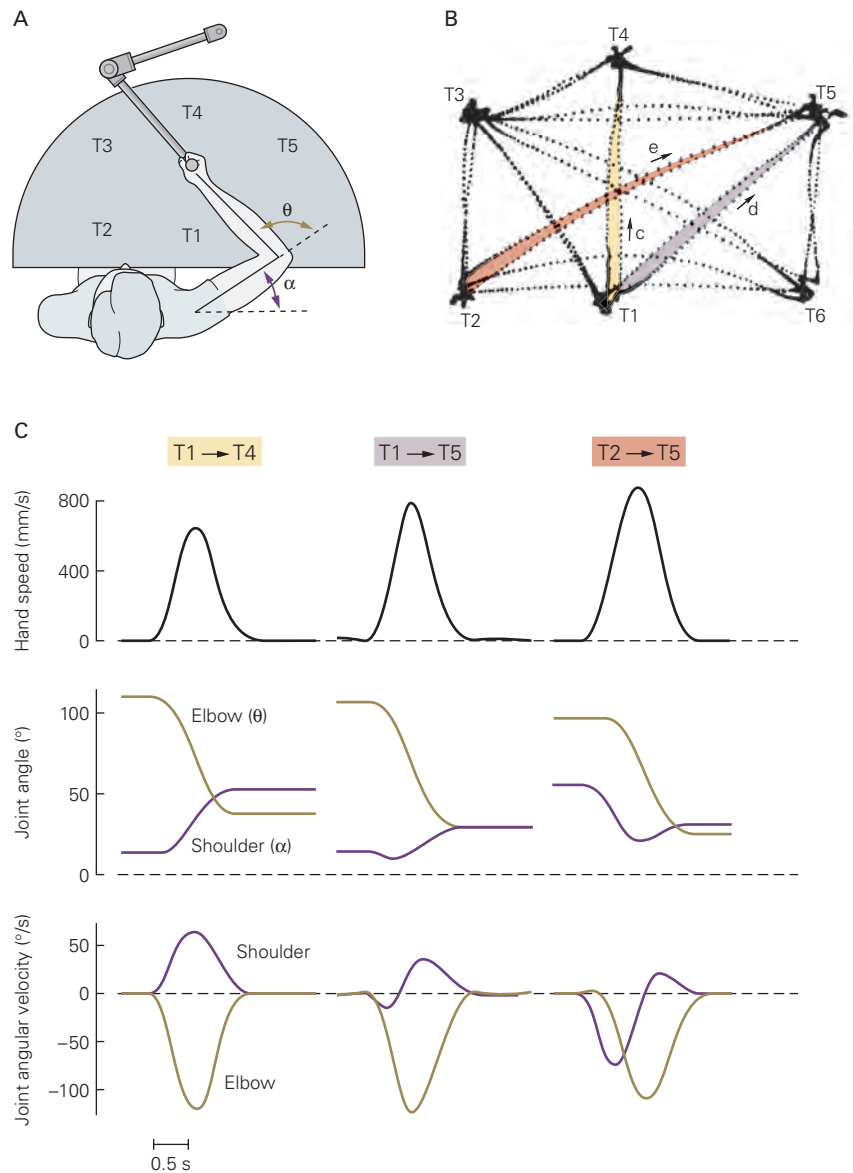
produce an arc at the hand, both elbow and shoulder
joints must be rotated concurrently to produce a straight
path. In some directions, the elbow moves more than the
shoulder; in others, the reverse occurs. When the hand
is moved from one side of the body to the other (Figure
30–8, movement from T2 to T5), one or both joints may
have to reverse direction in midcourse. The fact that
hand trajectories are more invariant than joint trajecto-
ries 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 writ-
ing, 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 pro-
duce 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.

Motor Planning Can Be Optimal at Reducing Costs

Why do humans choose one particular manner of per-
forming a task out of the infinite number of possibilities?

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.)

A Right hand

B Right hand (wrist fixed)

C Left hand

D Teeth

E Foot
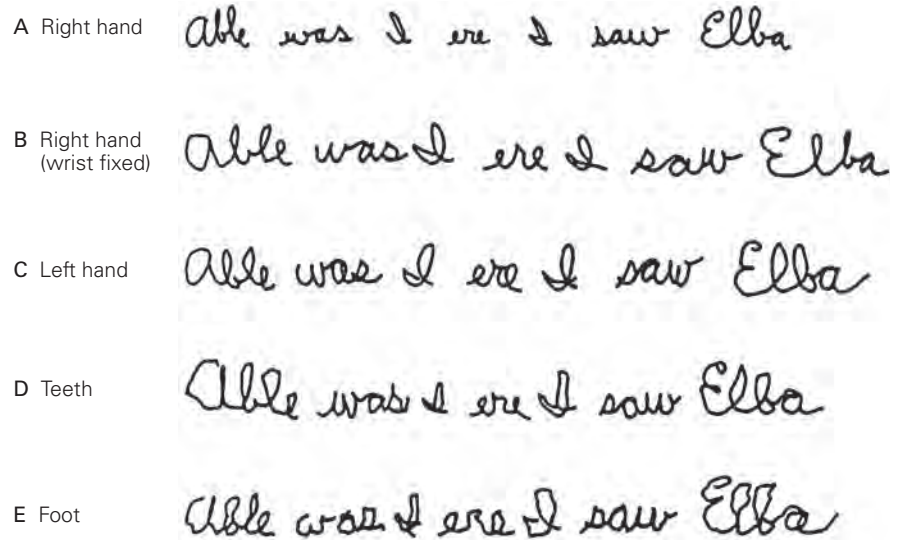
Extensive research has attempted to answer this question, and the fundamental idea that has emerged is that planning can be equated with choosing the best way to achieve a task. Mathematically, this is equivalent to the process of optimizing (ie, minimizing) a cost associated with the movement. The cost 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.

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
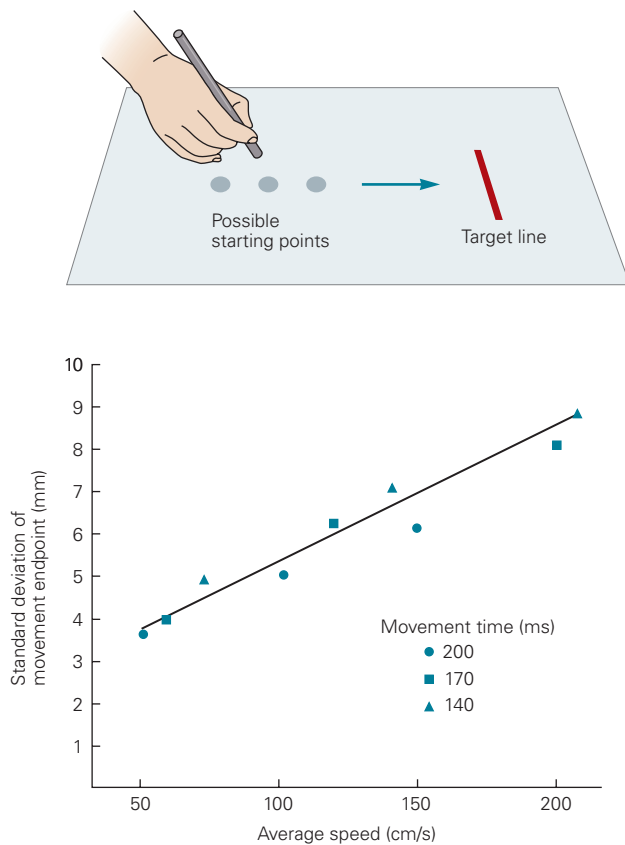
Figure 30–10 Accuracy of movement varies in direct proportion to its speed. Subjects held a stylus and had to hit a straight line lying perpendicular to the direction in which they moved the stylus. Subjects started from one of three different initial positions and were required to complete the movement 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.)

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.

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.
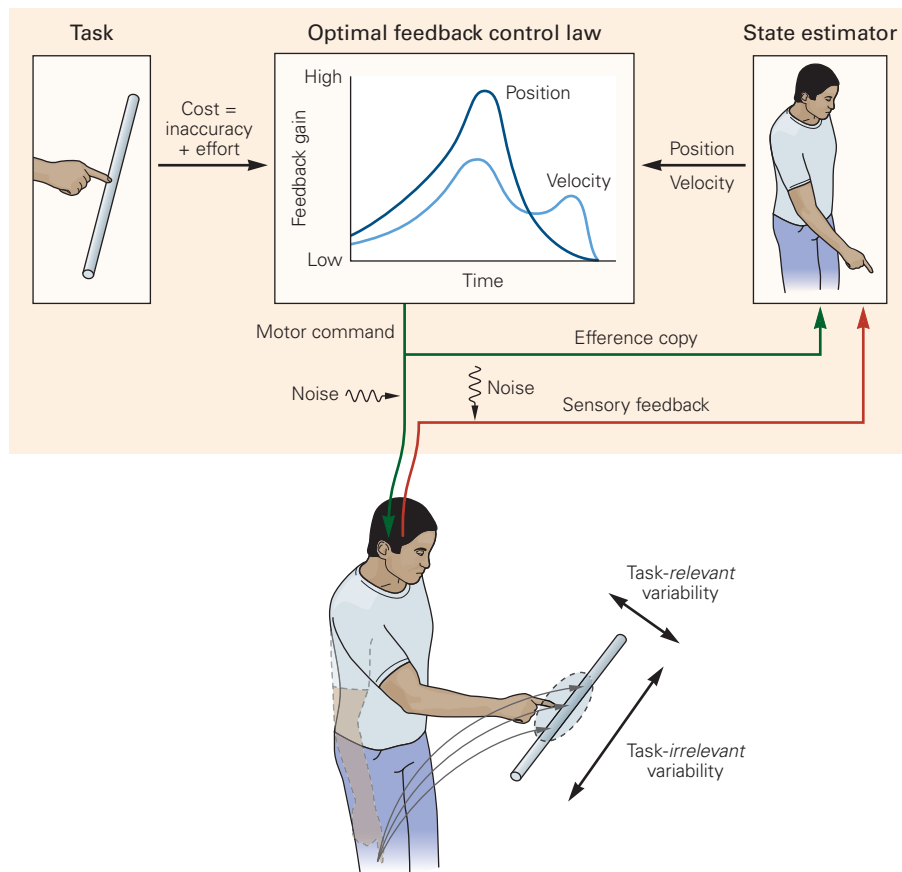
Figure 30–11 Optimal feedback control. In order to generate a movement for a given task, such as touching a horizontal bar, the sensorimotor system specifies a cost that is a combination of accuracy (eg, distance of the finger to the bar) and effort. To generate a movement that minimizes this cost, the 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.

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).

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
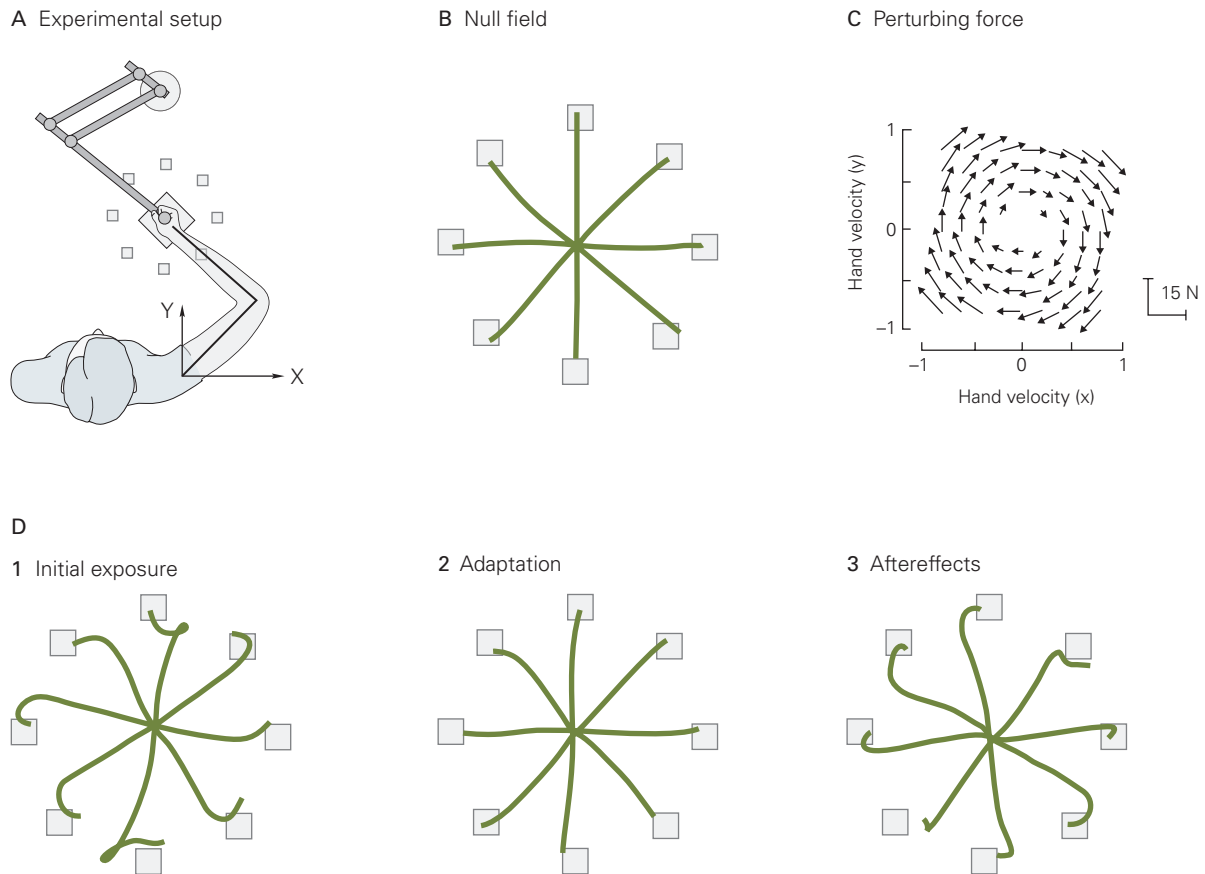
A Experimental setup

B Null field

C Perturbing force

D

1 Initial exposure

2 Adaptation

3 Aftereffects

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).

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).

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
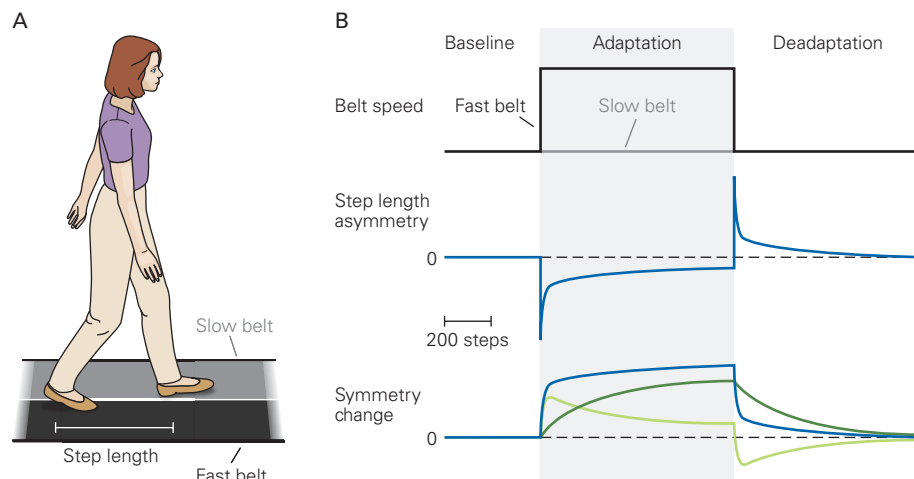
Figure 30–13 Learning new coordination patterns in walking.

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.)

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).

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.