

(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).

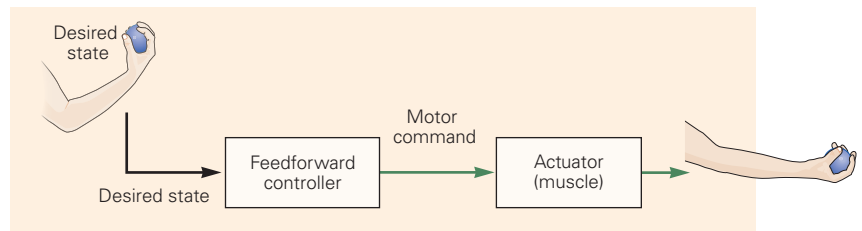
Open-loop control requires some information about the body so that the appropriate command can be generated. For example, it should include information about the dynamics of the motor system. Here, “dynamics” refers to the relation between the motor command (or the torques or forces) applied and the ensuing motion of the body, for example, joint rotations. For perfect open-loop control, one needs to

Figure 30–2 Feedforward and feedback control.

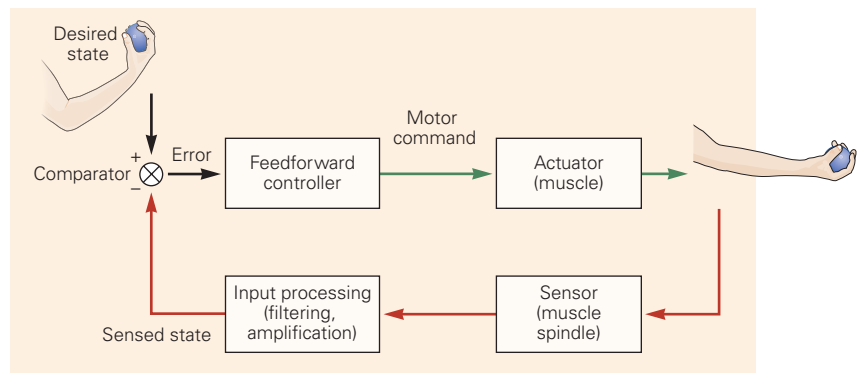
A. A feedforward control motor command is based on a desired state. Any errors that arise during the movement are not monitored. Although we illustrate the elements of feedforward control for the arm, only the initial portion of any arm movement is driven by feedforward signals and the movement typically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

A Feedforward control



B Feedback control



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.

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.

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.

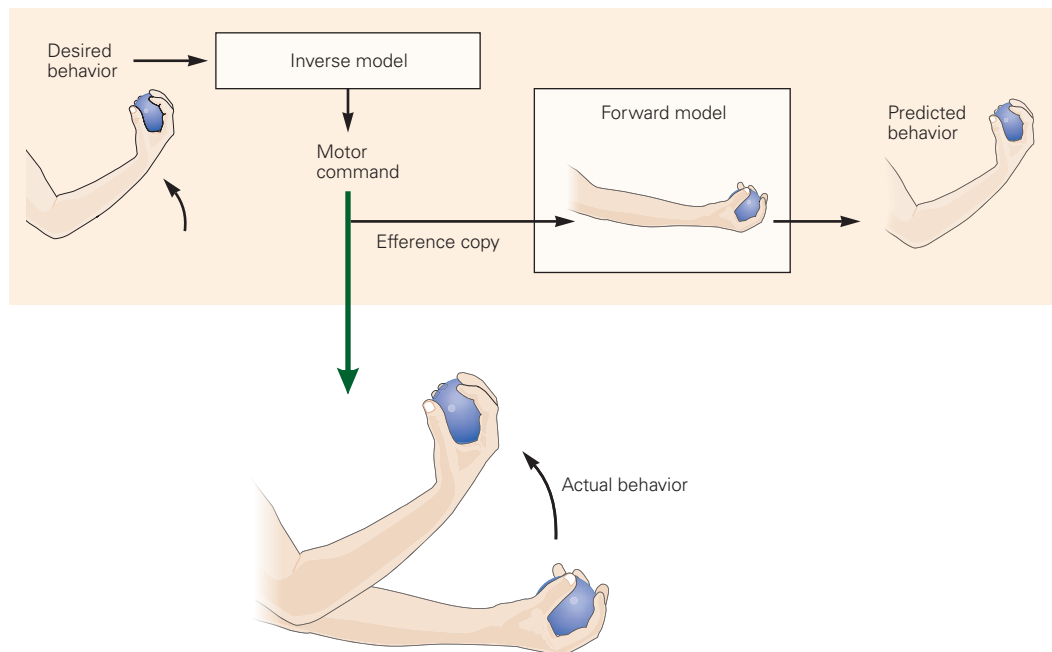


Figure 30–3 Internal sensorimotor models represent relationships of the body and external world. The inverse model determines the motor commands that will produce a behavioral goal, such as raising the arm while holding a ball. A descending motor command acts on the musculoskeletal system to produce 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).

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.

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

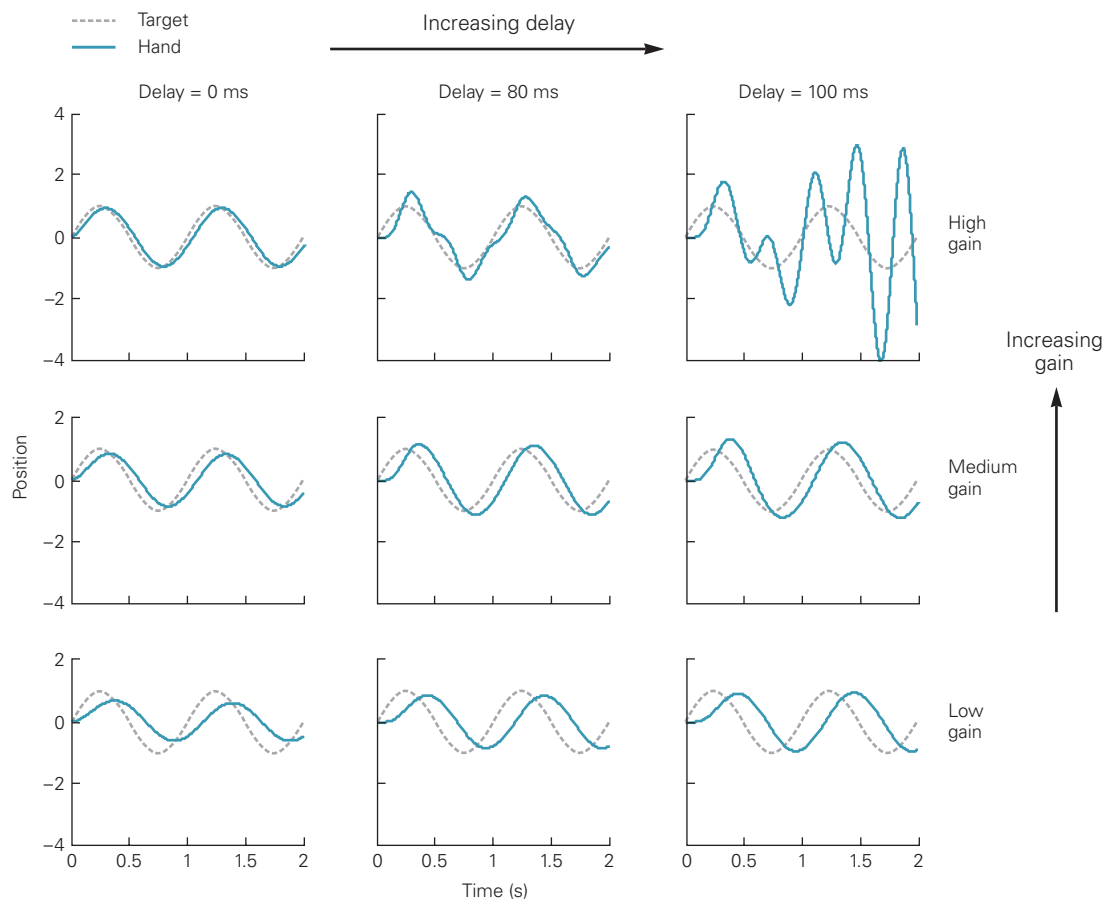


Figure 30-4 The interplay of gain and delay in feedback control. Performance of a feedback controller trying to track a target moving sinusoidally in one dimension. The sensory feedback signal that conveys error in the position arrives after some period of time (the delay), and the motor system tries 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.

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

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.

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).

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).

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

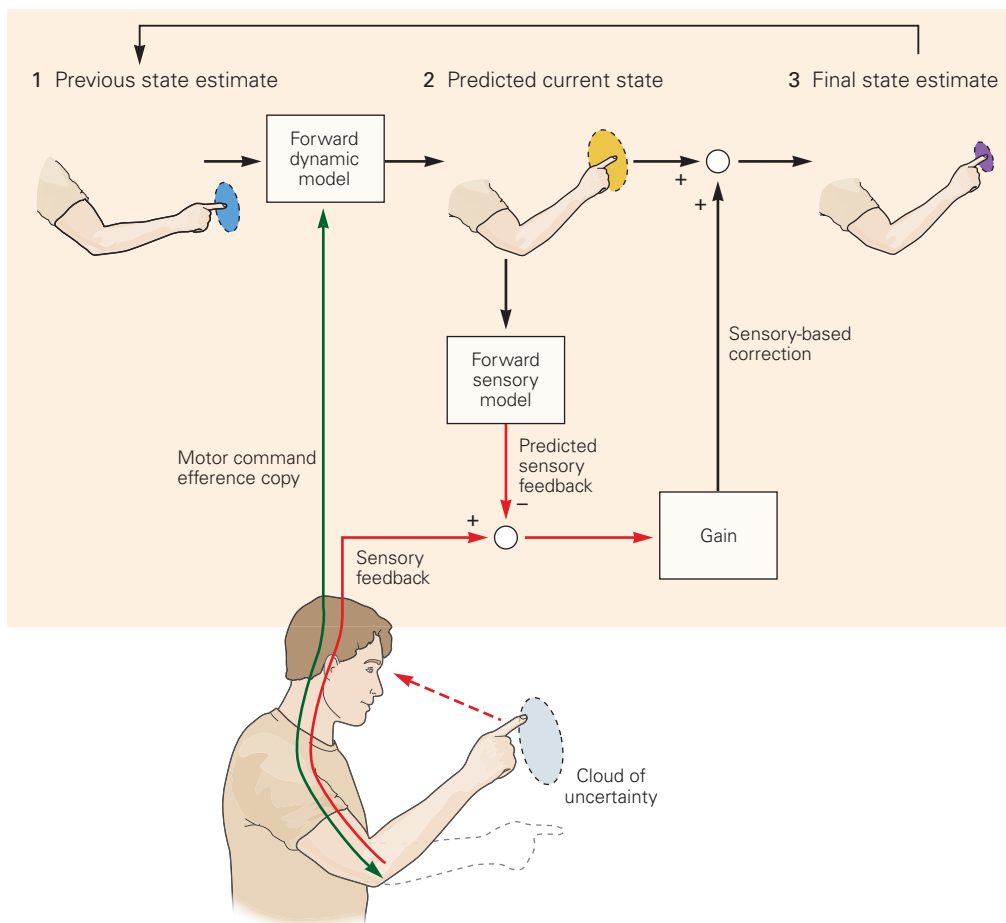


Figure 30–5 An observer model. The model is being used to estimate the finger's location during movement of the arm. A previous estimate of the distribution of possible finger positions (1, blue cloud) is updated (2, yellow cloud) using an efference copy of the motor command and a forward model of the 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.

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).

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

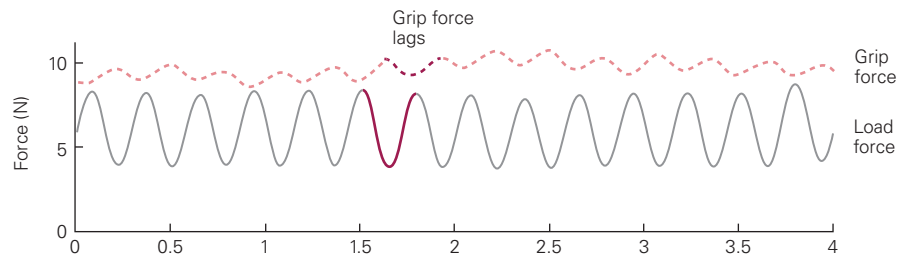
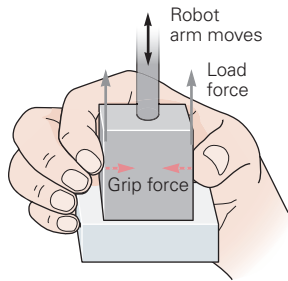
instantaneously with load force (Figure 30–6B). Sensory detection of the load would be too slow to account for this rapid increase in grip force.

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

A Robot controls movement



B Hand controls movement

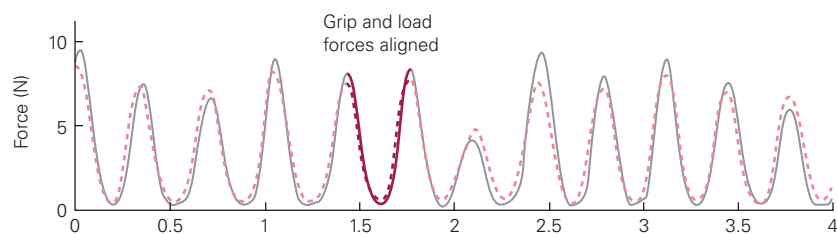
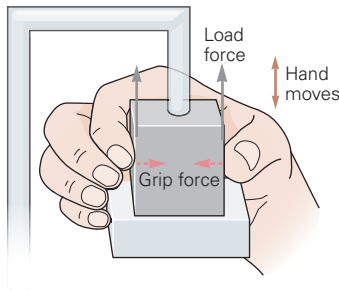


Figure 30-6 Anticipatory control of self-generated actions. (Adapted, with permission, from Blakemore, Goodbody, and Wolpert 1998. Copyright © 1998 Society for Neuroscience.)

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 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.

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