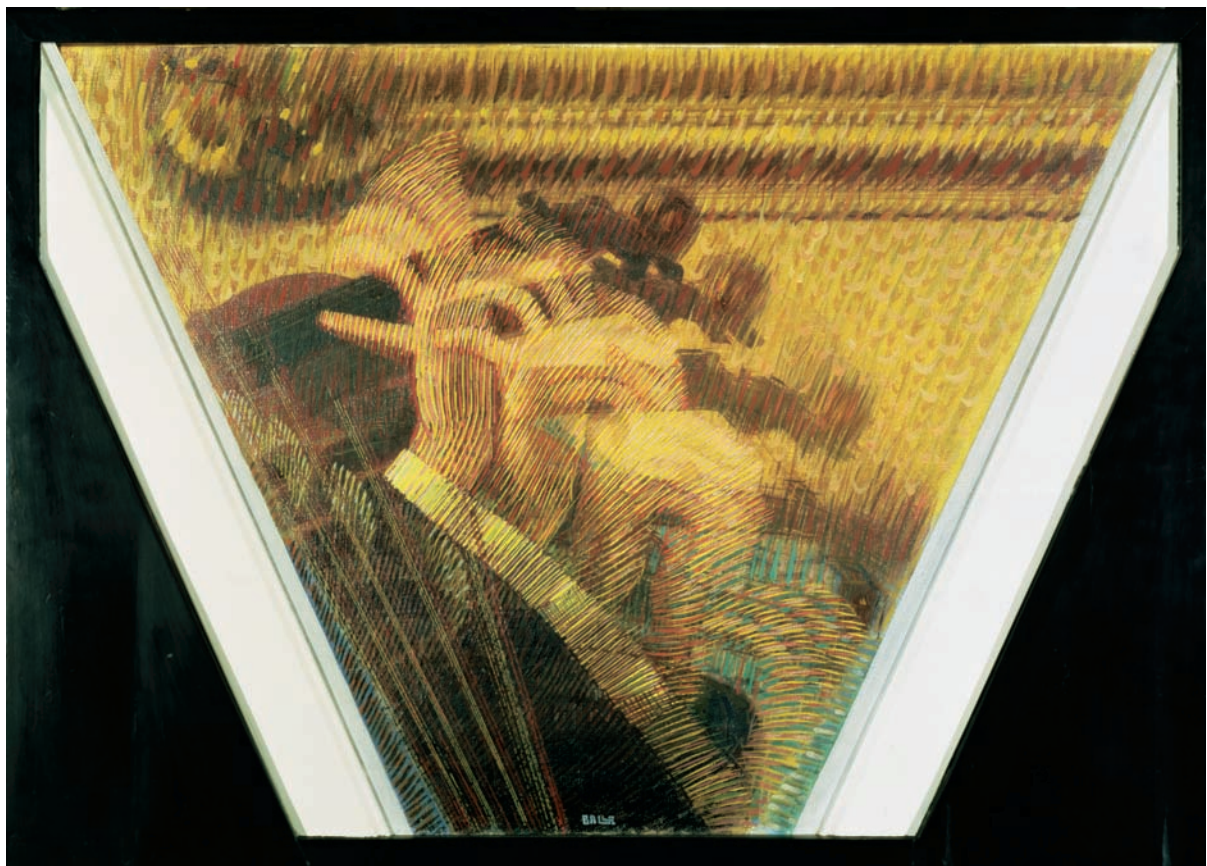


Part VI



Preceding Page

The characteristic movement of a musician's hand is captured in a painting by Giacomo Balla from 1912, "The Hand of the Violinist." Balla studied violin as a boy and, like his contemporaries in the Futurist movement, was interested in depicting motion and speed. The rhythmic brushstrokes evoke the energy of the performer and the vibrations of the music. (Reproduced, with permission, from the Copyright 2011 Artists Rights Society (ARS), New York/SIAE, Rome; and the Bridgeman Art Library International, NY.)

VI

Movement

THE CAPACITY FOR MOVEMENT, as many dictionaries remind us, is a defining feature of animal life. As Sherrington, who pioneered the study of the motor system pointed out, “to move things is all that mankind can do, for such the sole executant is muscle, whether in whispering a syllable or in felling a forest.”*

The immense repertoire of motions that humans are capable of stems from the activity of some 640 skeletal muscles—all under the control of the central nervous system. After processing sensory information about the body and its surroundings, the motor centers of the brain and spinal cord issue neural commands that effect coordinated, purposeful movements.

The task of the motor systems is the reverse of the task of the sensory systems. Sensory processing generates an internal representation in the brain of the outside world or of the state of the body. Motor processing begins with an internal representation: the desired purpose of movement. Critically, however, this internal representation needs to be continuously updated by internal (efference copy) and external sensory information to maintain accuracy as the movement unfolds.

Just as psychophysical analysis of sensory processing tells us about the capabilities and limitations of the sensory systems, psychophysical analyses of motor performance reveal regularities and invariances in the control rules used by the motor system.

Because many of the motor acts of daily life are unconscious, we are often unaware of their complexity. Simply standing upright, for example, requires continual adjustments of numerous postural muscles in response to the vestibular signals evoked by miniscule swaying. Walking, running, and other forms of locomotion involve the combined action of central pattern generators, gated sensory information, and descending commands, which together generate the complex patterns of alternating excitation and inhibition to the appropriate sets of muscles. Many actions, such as serving a tennis ball or executing an arpeggio on a piano, occur far too quickly to be shaped by sensory feedback. Instead, centers, such as the cerebellum, make use of predictive models that simulate the consequences of the outgoing commands and allow very short latency corrections. Motor learning provides one of the most fruitful subjects for studies of neural plasticity.

Motor systems are organized in a functional hierarchy, with each level concerned with a different decision. The highest and most abstract level,

*Sherrington CS. 1979. 1924 Linacre lecture. In: JC Eccles, WC Gibson (eds). *Sherrington: His Life and Thought*, p. 59. New York: Springer-Verlag.

likely requiring the prefrontal cortex, deals with the purpose of a movement. The next level, which is concerned with the formation of a motor plan, involves interactions between the posterior parietal and premotor areas of the cerebral cortex. The premotor cortex specifies the spatial characteristics of a movement based on sensory information from the posterior parietal cortex about the environment and about the position of the body in space. The lowest level of the hierarchy coordinates the spatiotemporal details of the muscle contractions needed to execute the planned movement. This coordination is executed by the primary motor cortex, brain stem, and spinal cord. This serial view has heuristic value, but evidence suggests that many of these processes can occur in parallel.

Some functions of the motor systems and their disturbance by disease have now been described at the level of the biochemistry of specific transmitter systems. In fact, the discovery that neurons in the basal ganglia of parkinsonian patients are deficient in dopamine was the first important clue that neurological disorders can result from altered chemical transmission. Imaging techniques can provide information as to how local transmitter abnormalities can lead to widespread changes in the networks involved in the selection and control of movements.

Understanding the functional properties of the motor system is not only fundamental in its own right, but it is of further importance in helping us to understand disorders of this system and explore the possibilities for recovery. As would be expected for such a complex apparatus, the motor system is subject to various malfunctions. Lesions at different levels in the motor hierarchy produce distinctive symptoms, including the movement-slowness characteristic of disorders of the basal ganglia, such as parkinsonism, the incoordination seen with cerebellar disease, and the spasticity and weakness typical of spinal damage. For this reason, the neurological examination of a patient inevitably includes tests of reflexes, gait, and dexterity, all of which provide information about the status of the nervous system. In addition to pharmacological therapies, the treatment of neurological disease has recently been augmented by two new approaches. First, focal stimulation of the basal ganglia has been discovered to restore motility to certain patients with Parkinson disease; such deep-brain stimulation is also being tested in the context of other neurological conditions. And second, the motor systems have become a target for the application of neural prosthetics; neural signals are decoded and used to drive mechanical devices that aid patients with paralysis caused by spinal cord injury and stroke.

Part VI

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The Organization and Planning of Movement

Motor Commands Arise Through Sensorimotor Transformations

The Central Nervous System Forms Internal Models of Sensorimotor Transformations

Movement Inaccuracies Arise from Errors and Variability in the Transformations

Different Coordinate Systems May Be Employed at Different Stages of Sensorimotor Transformations

Stereotypical Patterns Are Employed in Many Movements

Motor Signals Are Subject to Feedforward and Feedback Control

Feedforward Control Does Not Use Sensory Feedback

Feedback Control Uses Sensory Signals to Correct Movements

Prediction Compensates for Sensorimotor Delays

Sensory Processing Is Different for Action and Perception

Motor Systems Must Adapt to Development and Experience

Motor Learning Involves Adapting Internal Models for Novel Kinematic and Dynamic Conditions

Kinematic and Dynamic Motor Learning Rely on Different Sensory Modalities

An Overall View

IN THE PRECEDING PART OF THIS BOOK we considered how the brain constructs internal representations of the world around us. These internal representations have no intrinsic value and are behaviorally meaningful only when used to guide movement, whether

foraging for food or attracting a waiter's attention. Thus the ultimate function of the sensory representations is to shape the actions of the motor systems. Sensory representations are the framework in which the motor systems plan, coordinate, and execute the motor programs responsible for purposeful movement.

In this part of the book we describe the principles of motor control that allow the brain and spinal cord to maintain balance and posture; to move our body, limbs, and eyes; and to communicate through speech and gesture.

Although movements are often classified according to function—eye movements, prehension (reach and grasp), posture, locomotion, breathing, and speech—many of these functions are subserved by overlapping groups of muscles. In addition, 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 by the brain. Rhythmic movements can also be controlled voluntarily, but many such movements differ from voluntary movements in that their timing and spatial organization is to a large extent controlled autonomously by spinal or brain stem circuitry. Reflexes are stereotyped responses to specific stimuli that are generated by simple neural circuits in the spinal cord or brain stem. Although reflexes are highly adaptable to changes in behavioral goals, mainly because several different circuits

exist to connect sensory and motor neurons, they cannot be directly controlled voluntarily.

In this chapter we focus on voluntary movements, using arm and hand movements to illustrate principles of sensorimotor control. Reflexes and rhythmic movements are discussed in detail in Chapters 35 and 36.

Conscious processes are not necessary for moment-to-moment control of movement. Although we may be aware of the intent to perform a task or of planning certain sequences of actions and at times are aware of deciding to move at a particular moment, movements generally seem to occur automatically. 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.

In this chapter we review the principles that govern the neural control of movement using concepts derived from behavioral studies and from computational models that are used both to understand the brain and to control the movements of robots. First, we look at how the brain transforms sensory inputs into motor outputs through a cascade of sensorimotor transformations. Second, we examine how sensory feedback can be used to correct errors that arise during movement. Finally, we see how motor learning allows us to improve our performance; to adapt to new mechanical conditions, as when using a tool; or to adapt to novel correspondences between sensory and motor events, for example when learning to use a computer mouse to control a cursor.

Motor Commands Arise Through Sensorimotor Transformations

Motor outputs are neural commands that act on the muscles, causing them to contract and generate movement. These outputs are derived from sensory inputs in circuits that represent *sensorimotor transformations*. Sensory inputs include extrinsic information about the state of world as well as intrinsic information about our body. Extrinsic information, for example the spatial location of a target, can be provided by auditory and visual inputs. Intrinsic information includes both kinematic and kinetic information about our body.

Kinematic information includes the position, velocity, and acceleration of the hand, joint angles, and lengths of muscles without reference to the forces that cause

them. *Kinetic information* is concerned with the forces generated or experienced by our body. These different forms of intrinsic information are provided by different sensors. For example, information about muscle lengths and their rate of change is provided mainly by muscle spindles, whereas Golgi tendon organs in the muscles and mechanoreceptors in our skin provide information about the force we are exerting.

Simple reflexes, such as a tendon-jerk reflex, involve a simple sensorimotor transformation: Sensory inputs cause motor output directly without the intervention of higher brain centers. However, voluntary movement requires multistage sensorimotor transformations. The involvement of multiple processing centers actually simplifies processing: Higher levels plan more general goals, whereas lower levels concern themselves with how these goals can be implemented.

Such a hierarchy accounts for the fact that a specific motor action, such as writing, can be performed 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 33–1). 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, able to drive different effectors, provide a degree of flexibility of action not practical with preset motor programs.

How do sensorimotor transformations generate movement to a desired location? For a person to reach toward an object, sensory information about the target's location must be converted into a sequence of muscle actions leading to joint rotations that will bring the hand to the target.

First, the target is localized in space relative to some part of the body such as the head or arm (*egocentric space*). Several sources of information are combined in this process. For example, the location of the target relative to the head is computed from the location of the target on each retina together with the direction of gaze of the eyes (Figure 33–2A). A person also needs to know the initial location of his hand or the tip of the tool that he wishes to place on the target (the end-effector or *endpoint*). The initial location of the endpoint can be estimated by combining visual inputs, proprioceptive signals, and tactile sensations, each of which can provide location information. Once the current configuration of the arm and location of the target are calculated, a movement can be planned. A plan typically has to specify both a particular *path*, the successive spatial positions of the endpoint, and also the

Figure 33–1 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.)

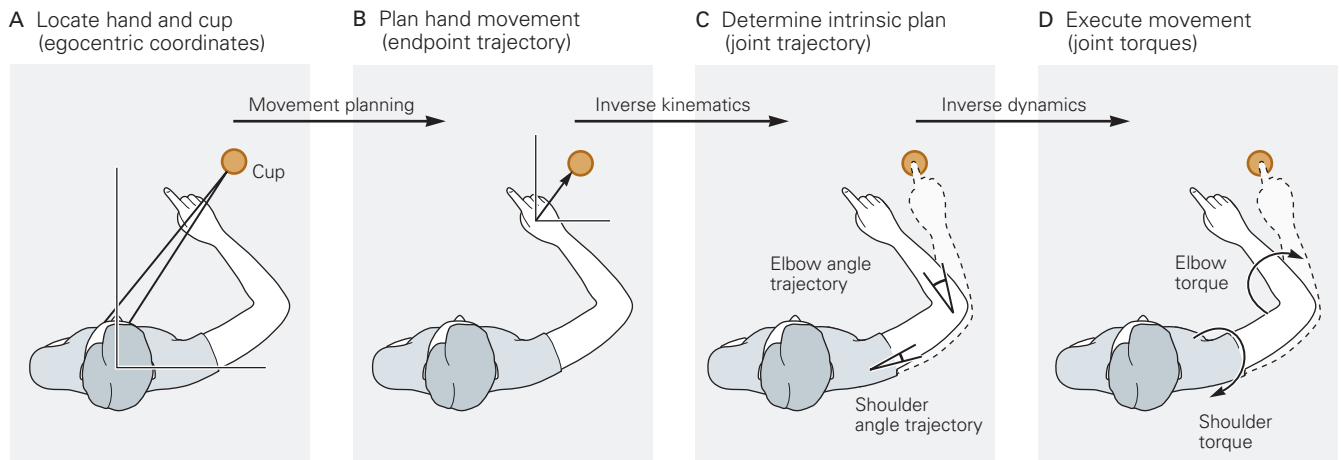
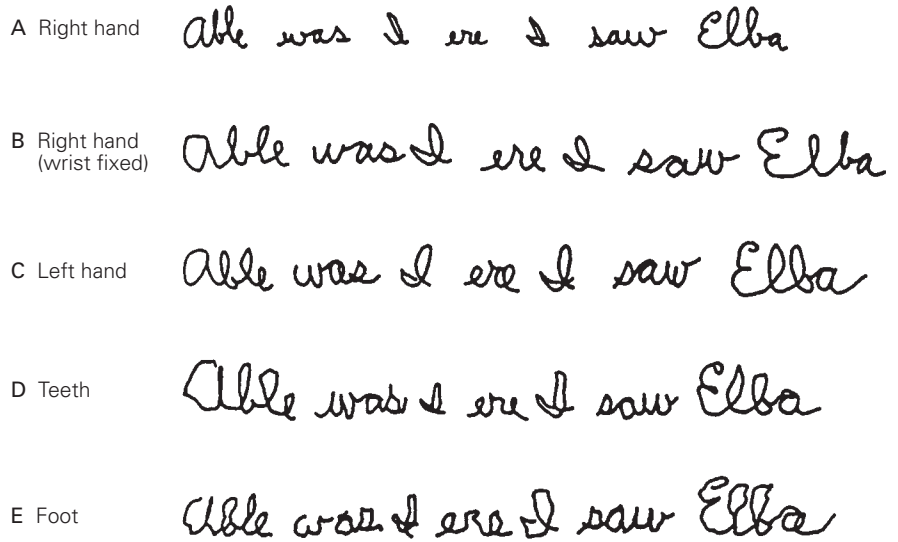


Figure 33–2 Sensorimotor transformations used to generate a particular movement. The task of generating a goal-directed movement is often broken down into a set of sequential stages, the details of which are still being elucidated. The figure shows one possible set of stages to generate a reaching movement, and the arrows indicate the processes required to move between the stages.

- A. Spatial orientation. To reach for an object, the object and hand are first located visually in a coordinate system relative to the head (egocentric coordinates).
- B. Movement planning. The direction and distance the hand must move to reach the object (the endpoint trajectory) are

- determined based on visual and proprioceptive information about the current locations of the arm and object.
- C. Inverse kinematic transformation. The joint trajectories that will achieve the hand path are determined. The transformation from a desired hand movement to the joint trajectory depends on the kinematic properties of the arm, such as the lengths of the arm's segments.
- D. Inverse dynamic transformation. The joint torques or muscle activities that are necessary to achieve the desired joint trajectories are determined. The joint torques required to achieve a desired change in joint angles depend on the dynamic properties of the arm such as the mass of the segments.

trajectory, the time course over which these positions will be covered, and thus the accelerations and speeds of the movement (Figure 33–2B).

In a hierarchical model of planning the goal can be expressed in kinematic terms, such as the desired positions and velocities of the hand, or in kinetic terms, such as the force exerted by the hand. Movement can be planned as an *endpoint trajectory*, a desired change in the configuration of the limb expressed in coordinates intrinsic to the limb. Such a coordinate system could determine the change in joint angles or be based on a desired change in proprioceptive feedback. For example, the endpoint trajectory could be defined kinematically as the distance and direction the hand has to move to reach the target, as well as the speed along the path to the target.

Transformations can be expressed as changes in kinematic variables, such as the position of the hand and the joint angles that place the hand at that position. The calculation of an endpoint from a set of joint angles is termed *forward kinematic transformation*, whereas calculation of a set of joint angles that can reach an endpoint is termed *inverse kinematic transformation* (Figure 33–2C). This transformation must take into account the geometric parameters of the arm, such as the lengths of the upper arm and forearm (recall that kinematics considers motion without reference to the forces that cause it). The motor system controls joint angle by activating muscles that produce torques (rotational forces) at the joint.

The action of motor commands on muscles that results in a set of angular positions and velocities is known as the *forward dynamic transformation*. The term “dynamic” refers to the forces required to cause motion. However, to generate a desired joint angle trajectory the system must convert kinematic parameters into motor commands. That is, the system must calculate the torques at each joint necessary to achieve the motion and relate the force required to cause this motion to the desired acceleration of the limb. This transformation is known as the *inverse dynamic transformation* (Figure 33–2D). In general, to cause any acceleration the forces applied must exceed any resistive forces arising from the viscosity or stiffness of the limb, from gravity, and from external loads. The force not required to overcome the total resistive force will cause an angular acceleration, with the acceleration being dependant on the limb’s inertia; the lower the inertia, the higher the acceleration.

Thus through a series of sensorimotor transformations, sensory input is finally converted into muscle contractions that generate movement. Although we have described one possible series of transformations

that can achieve a movement, the actual computations used by the central nervous system are still under active investigation.

The Central Nervous System Forms Internal Models of Sensorimotor Transformations

We know from cellular studies that the central nervous system contains internal representations (“neural maps”) of the various sensory receptor arrays and the musculature. Experimental and modeling studies strongly suggest that the central nervous system also maintains internal representations that relate motor commands to the sensory signals expected as a result of movement.

Given the fixed lengths of our limb segments, there is a mathematical relationship between the joint angles of the arm and the location of the hand in space. A neural representation of this relationship allows the central nervous system to estimate hand position if it knows the joint angles and segment lengths. The neural circuits that compute such sensorimotor transformations are examples of *internal models* (Box 33–1). Such neural representations may not exactly match true relationships because of structural differences (the models only approximate the true relationship between joint angles and hand position) or errors in the model’s parameters (incorrect estimates of segment lengths).

An internal model that represents the causal relationship between actions and their consequences is called a *forward model* because it estimates future sensory inputs based on motor outputs. A forward model anticipates how the motor system’s state will change as the result of a motor command. Thus, a copy of a descending motor command acting on the sensorimotor system 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) to signify that it is a copy of the efferent signal flowing from the central nervous system to the muscles. We will see later how such simulations can be learned and used in sensorimotor control.

An internal model that calculates motor outputs from sensory inputs is known as an *inverse model*. Such a model can determine what motor commands are needed to produce the particular movements necessary to achieve a desired sensory consequence.

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 33–3).

Box 33–1 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 two weeks from now. In general, the algorithms and parameters of the model should lead to one correct answer.

Other models start with a state, a set of physical variables with specific values, and operate 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 may thus inform us how to set the parameters of the system to obtain desired outcomes.

Over the last 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. 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, utilize 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 which face it."

In this view an internal model allows an organism to contemplate the consequences of current actions without actually committing itself to those actions.

Considering the human body from the viewpoint of sensorimotor control, we should ask two fundamental questions. First, how can we generate actions on the system so as to control its behavior? Second, how can we predict the consequences of our actions?

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. Prediction turns motor commands into expected sensory consequences, whereas control turns desired sensory consequences into motor commands.

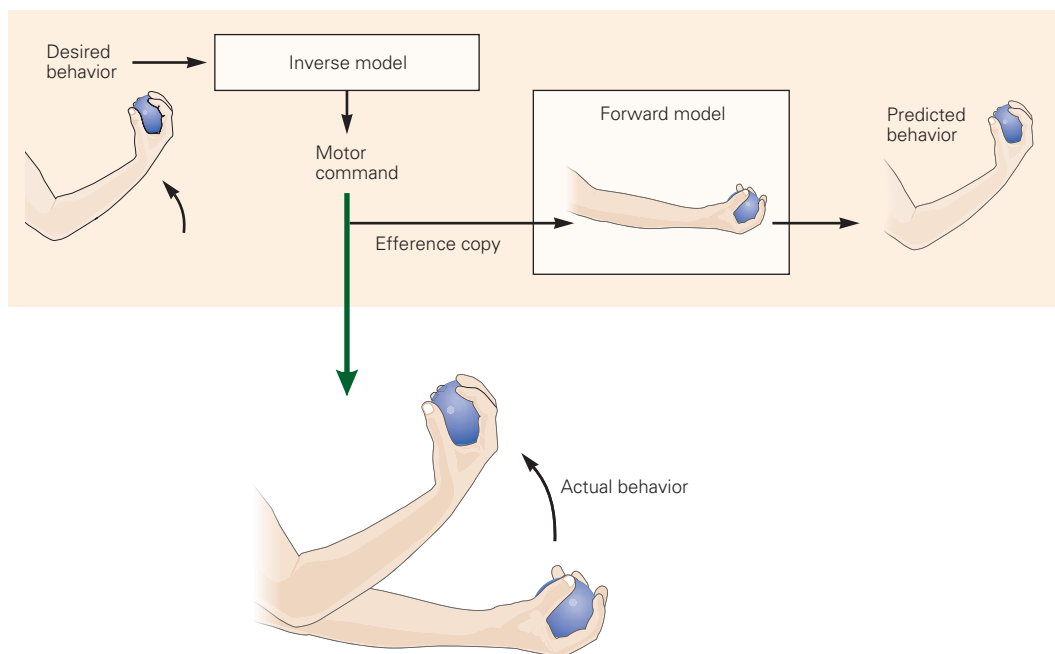


Figure 33–3 Internal models represent relationships of the body and external world. The inverse model determines the motor commands that will produce a behavioral goal, such as raising the arm while holding a ball. A descending motor command acts on the musculoskeletal system to produce the movement. A copy of the motor command is passed to

a forward model that simulates the interaction of the motor system and the world and can therefore 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).

Movement Inaccuracies Arise from Errors and Variability in the Transformations

Motor control is often imprecise. Indeed, society celebrates those who can throw a dart into a small area of a board or hit a small white ball into a hole with a club. However, even the movements of the most skilled players show some degree of variability. In the 1890s the psychologist Robert Woodworth showed that fast movements are less accurate than slow ones. People slow their movements when accuracy is demanded. Inaccuracy can arise either from variability in the sensory inputs and motor outputs or from errors in the internal representations of this information.

An important component of sensorimotor variability is the intrinsic variability of our sensors and motor neurons because of fluctuations in their membrane potential. Because of these fluctuations, known as neural noise, the level of input signals required to trigger postsynaptic action potentials also varies. On the input side, neural noise limits the *accuracy* of estimates of the location of a target or limb (how near an estimate is to the true value) as well as their *precision* (how accurate the estimate is when repeated). On the output side, neural noise limits the accuracy and precision with which we contract our muscles. Moreover, the amount of noise in motor commands tends to increase with larger motor commands, limiting our ability to move rapidly and accurately at the same time. This increase in variability is caused by random variation in both the excitability of motor neurons and the recruitment of the additional motor units needed to produce increases in force.

Incremental increases in force are produced by progressively smaller sets of motor neurons, each of which produces disproportionately greater increments of force (see Chapter 34). 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 or a force pulse of fixed amplitude. Not only are subjects unable to maintain constant force, but the variability of force also 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 corresponds to the increase in the variability of pointing movements with the average speed of movement. The decrease in accuracy of movement with increasing speed is known as the *speed-accuracy trade-off* (Figure 33–4).

Errors can also arise from inaccuracy in the internal models that compute sensorimotor transformations.

Neural representations of the musculature cannot easily capture the complex biomechanical properties of the musculoskeletal system, and this in turn significantly complicates the ability of the brain to compute accurate sensorimotor transformations. Indeed, the dependence of muscle force on the motor command is itself highly complex. A model prescribing motion in a system with just a single joint must not only estimate the muscle

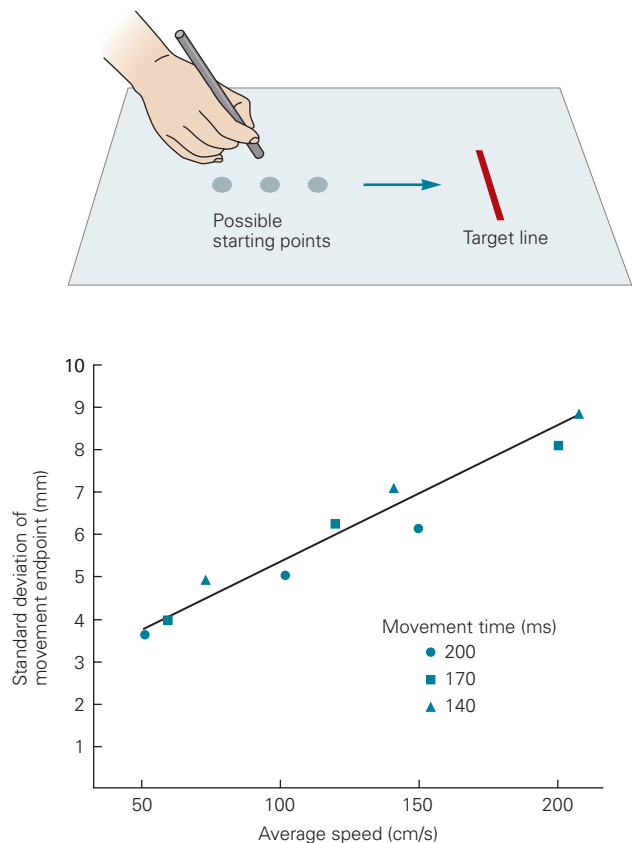


Figure 33–4 Accuracy of movement varies in direct proportion to its speed. Subjects held a stylus and were required to try and hit a target line lying perpendicular to the direction in which they moved. Each subject started from three different initial positions and was required to complete the movement within three different times (140, 170, or 200 ms). A successful trial was one in which the subject completed the movement within 10% of the required time. Only successful trials were used for analysis. Subjects were informed if their movements were more than 10% different from the required duration. The plot shows the variability in the motion of the subjects' arm movements as the standard deviation of the extent of movement versus 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. (Reproduced, with permission, from Schmidt et al. 1979.)

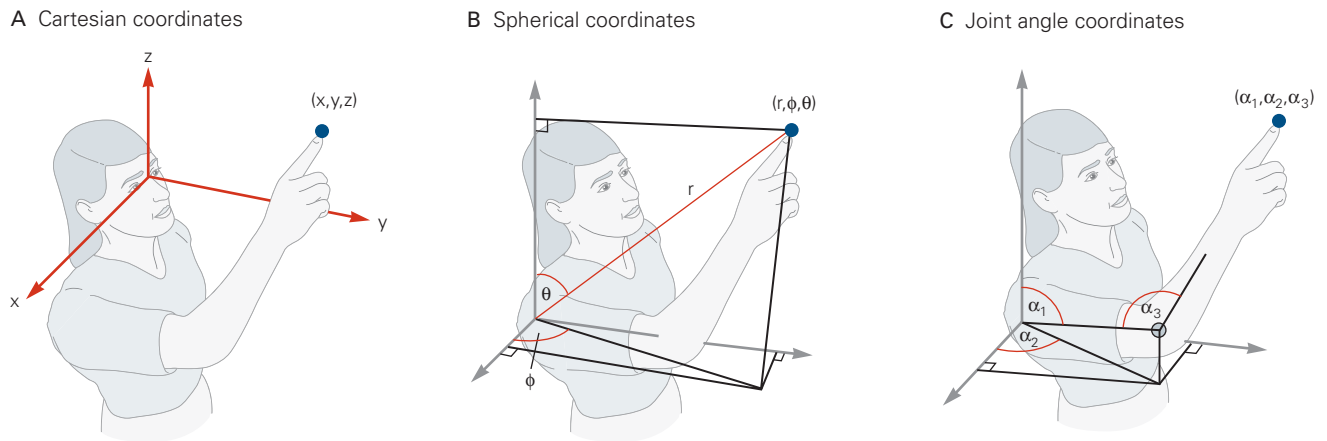


Figure 33-5 The location of the finger in space can be specified in different egocentric coordinate systems.

- A. Cartesian coordinates centered on the eyes.
 B. Spherical polar coordinates centered on the shoulder (distance r , azimuth ϕ , and elevation θ).

C. An intrinsic coordinate system based on shoulder angles (α_1 and α_2), which relate the orientation of the upper arm to the Cartesian axes, and elbow angle (α_3), which specifies the angle between the upper and lower arm.

force (or torque) but also take into account inertia (the mass resisting acceleration), viscosity (resistive forces proportional to velocity), stiffness (elastic forces proportional to displacement) produced by the muscles and tendons opposing movement, and gravity.

The dynamic relationship between segments of limbs further complicates sensorimotor transformations. The motion of each segment produces torques, and potentially motions, at all other segments through mechanical interactions. For example, flexion of the upper arm through shoulder rotation can lead to either extension or flexion of the elbow depending on the initial elbow angle. In general, because of the interactions between linked segments, the torques needed to produce a specific change in angle at a particular joint depend not only on the muscles acting directly at this joint but also on the configurations and the motions of all other joints, and especially their acceleration. The brain develops an internal model of these complex mechanical interactions through learning early in childhood. We will see later that this learning is updated throughout life and depends critically on proprioception, which provides the brain with information about changes in muscle length and joint angles.

Different Coordinate Systems May Be Employed at Different Stages of Sensorimotor Transformations

Different coordinate systems are used in sensorimotor transformations and are encoded in several

brain regions. Coordinate systems are either extrinsic or intrinsic to the body. Extrinsic coordinate systems relate objects in the outside world to other objects (allocentric coordinates) or to our body (egocentric coordinates) using exteroceptive information, usually visual or auditory (Figures 33-5A and B). Intrinsic coordinate systems, such as the set of muscle lengths or set of joint angles (Figure 33-5C), are based on information provided primarily by proprioceptive systems.

Elucidating the coordinate systems used in sensorimotor transformations is a major endeavor in neuroscience. We will see in later chapters that this issue can be fruitfully studied by examining how the firing patterns of neurons in different parts of the brain encode task features or movement parameters. Such studies aim to determine the variables (such as position or velocity) or type of coordinate system (such as allocentric or egocentric) that the neurons encode.

Behavioral studies also have used a variety of methods to examine the coordinate systems used in directing movement. One way has been to examine the details of the errors made during movement in different tasks. When subjects are asked to reach rapidly and repeatedly to a target, the error in the movements can be measured in different ways. If we average the final location of the hand across many trials, we may find a constant error or bias in the movement. We can examine the distribution of the final locations of the hand about this average position and infer from the patterns

of constant and variable error the coordinate system used in the movement (Box 33–2).

Stereotypical Patterns Are Employed in Many Movements

Given a task, motor plans are underconstrained. For example, the hand can move to a target along an infinite number of possible paths, and for each path there

is an infinite number of trajectories. Having specified the path and velocity, each point along the path could be reached by any number of combinations of arm joint angles and, owing to the overlapping actions of muscles and the ability to co-contract, each arm configuration could be achieved by many different combinations of muscles.

Although we have described different types of sensorimotor transformations, in general the inverse

Box 33–2 The Brain’s Choice of Spatial Coordinate System Depends on the Task

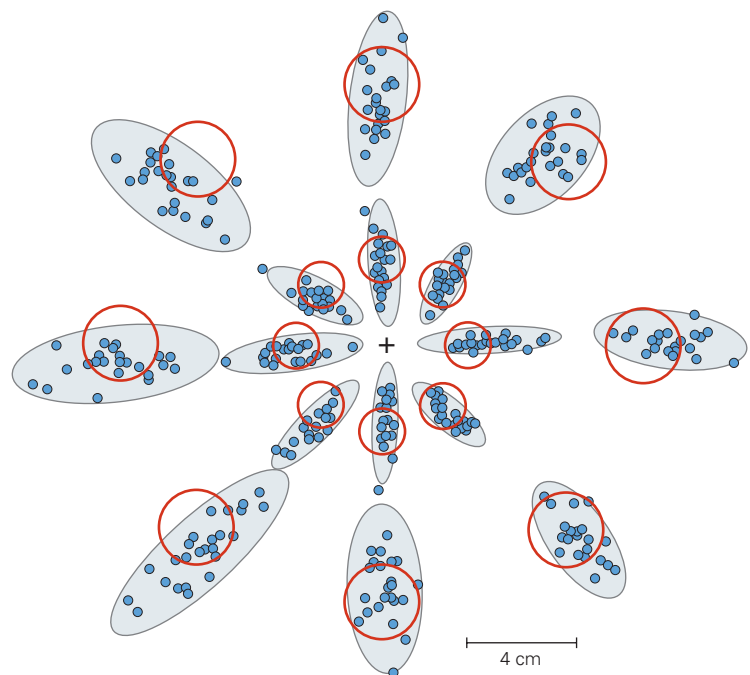
When subjects are shown a visual target and asked to reach for it repeatedly, the pattern of errors they make varies with the circumstance of the task. By examining these errors it is possible to assess which coordinate system is used to represent the target position under different conditions.

For example, when subjects are required to move their hands on a horizontal surface and can estimate the starting position of their hands before movement, the pattern of errors indicates planning in “hand-centered” coordinates. The distributions of the endpoints of the

movements demonstrate that, under the conditions of the task, errors in distance and direction are independent of each other (Figure 33–6) and thus that errors in the extent of a movement cannot be predicted from errors in direction. The independence of the two types of errors suggests that for this type of task subjects estimate distance and direction relative to a specific starting location (that is a movement vector) in Cartesian coordinates.

Conversely, when subjects make large three-dimensional movements to remembered visual targets in the dark, a different pattern of error is observed.

Figure 33–6 Errors in distance and direction of movement are independent of each other. Distribution of endpoints for reaching movements to 16 targets (eight directions and two distances) by one subject. Targets (red circles) were presented 24 times in random order, and each time the subject was asked to place a finger on the target. All movements begin from a central starting position (designated +). Endpoints for individual movements are represented by blue dots. The endpoints for the reaches to each target are fitted with an ellipse, demonstrating that errors in distance and direction are independent of each other. (Adapted, with permission, from Gordon, Ghilardi, and Ghez 1994.)



transformations cannot be uniquely specified. For example, the inverse kinematic transformation that transforms hand positions into joint angles can have many outputs based on the same input. This is because many different combinations of joint angles will put the hand in the same place. The ability of the motor systems to achieve a task in many different ways is called *redundancy*. If one way of achieving a task is not practical, there is usually an alternative.

Some of the earliest studies of movement examined how the brain determines the duration of a movement. Fitts's law describes the relationship between the amplitude, accuracy, and duration of a movement. This law relates the duration of a movement to the accuracy required of the task, as determined by the target width and amplitude of the movement, and applies to a variety of tasks such as reaching, placing pegs in holes, and picking up objects (Figure 33–8).

When the target and finger locations at the end of the reach are plotted against each other in terms of spherical coordinates centered on the shoulder, angular errors (elevation and azimuth) are small, whereas errors in the radial extent of the movement are significant (Figure 33–7). Moreover, the two types of errors are not correlated. However, if the target and finger locations are plotted in terms of spherical coordinates centered on the head, the errors are correlated.

The fact that the spherical coordinate system centered on the shoulder produces uncorrelated errors suggests that at some stage in the sensorimotor transformation the target is represented in shoulder-centered coordinates. Recent work suggests that this pattern of errors reflects planning for a final hand position rather than a particular hand trajectory.

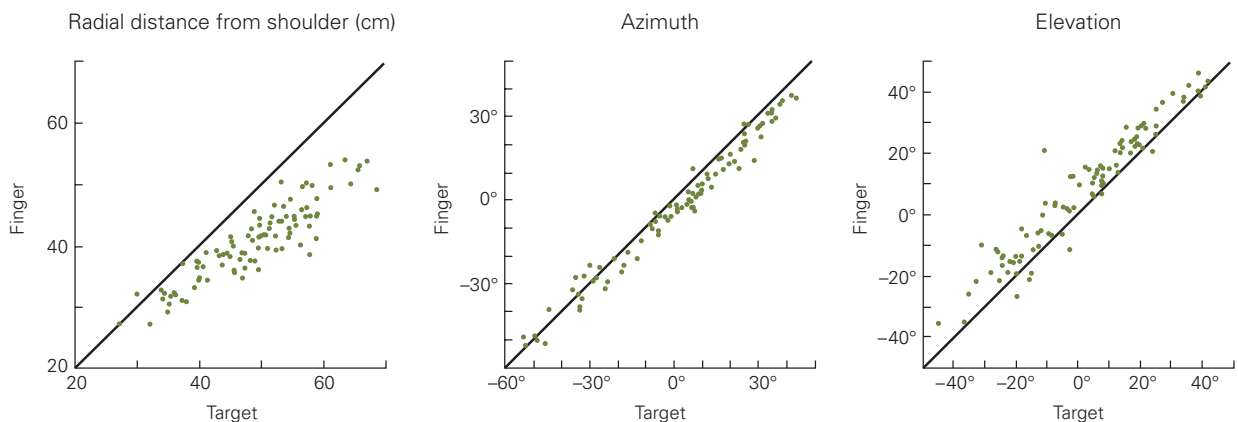


Figure 33–7 Distance errors are greater than direction errors for movements in the dark. A subject was asked to place a finger on the remembered location of a target in the dark. Final finger position and target location are plotted in spherical coordinates centered on the shoulder

(see Figure 33–5B). The straight line represents perfect performance and the dots individual reaching movements. Radial distance errors and angular errors (azimuth and elevation) are plotted separately. (Adapted, with permission, from Soechting and Flanders 1989.)

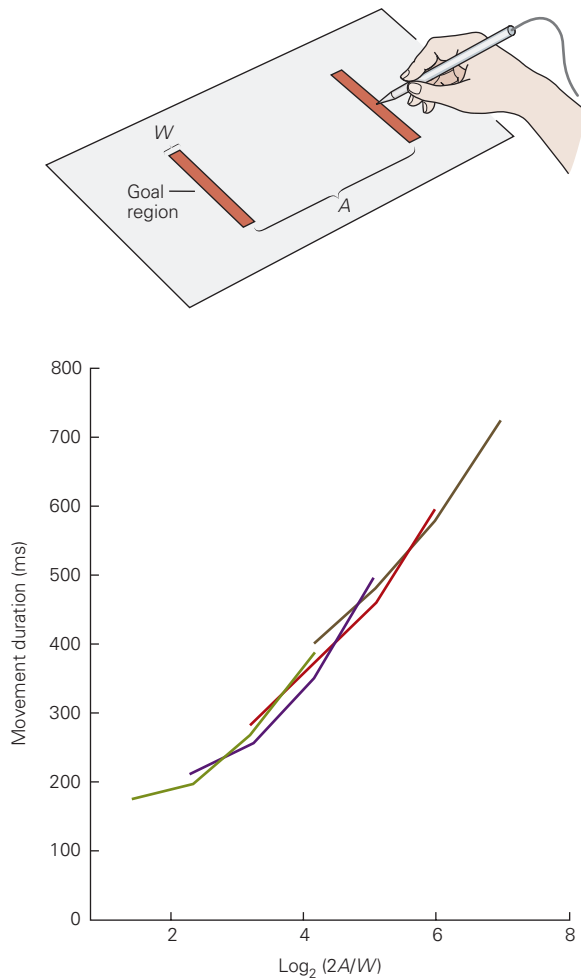


Figure 33-8 Fitts's law describes the speed-accuracy trade-off. Subjects were required to move a stylus between two targets of width W separated by distance A . The width of the targets was changed on each trial. Each line in the plot represents the results for a different target width (from narrow to wide) over four different movement amplitudes. Subjects were required to move as fast as possible while still hitting the targets. Over a large range of target widths and distance between targets, movement duration is linearly dependent on $\log_2(2A/W)$, the index of difficulty. (Adapted, with permission, from Jeannerod 1988.)

Despite variations in movement direction, speed, and location, several aspects of reaching movements are stereotypical or invariant. First, the hand tends to follow roughly a straight path (Figure 33-9A), although significant curvature is observed for certain movements, particularly vertical movements and movements near the boundaries of the reachable space. The tendency to make straight-line movements characterizes a large class of movements and is surprising given that the

muscles act to rotate joints. Second, a plot of hand speed over time is typically smooth, unimodal, and roughly symmetric (bell-shaped) (Figure 33-9B). This is not the case when movement accuracy requirements are high or corrections to the movement are made.

In contrast, the motions of the joints in series (such as 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 (see Figure 33-9A, 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 typically controls the hand by adjusting joint rotations and torques to achieve desired hand trajectories.

Invariances can also be seen in more complex movements. The nervous system puts together complex actions from elemental movements that have highly stereotyped spatial and temporal characteristics. For example, the seemingly continuous motion of drawing a figure eight actually consists of several discrete movements that are roughly constant in duration, regardless of their size. Moreover, there is a relationship between the curvature of each elemental movement and speed: Subjects tend to slow the hand as the curvature of the path increases. Empirical studies have shown that for many tasks a power law relation, the two-thirds power law, governs the relationship between hand speed and path curvature (Figure 33-10).

The simple spatiotemporal elements of a complex movement are called movement primitives or *movement schemas*. Like the simple lines, ovals, or squares in computer graphics programs, movement schemas can be scaled in size or time. The neural representations of complex actions, such as prehension, writing, typing, or drawing, are thought to be stored sets of these simple spatiotemporal elements.

Recent computational studies of a variety of tasks suggest that a repertory of movement schemas is the result of a process in which all possible ways of moving are ranked and the best is selected. This idea implies that either through evolution or motor learning our movements improve progressively until some limit is reached.

To quantify how good or bad a movement the brain assigns a cost to each possible movement, and the movement with the lowest cost is executed. The cost is specified as some function of the movement

and task, and the challenge to researchers has been to determine, from observed movement patterns and perturbation studies, the form of this function.

The cost may be kinematic; for example, lack of smoothness in a movement can be corrected by minimizing the rate of change of hand acceleration summed over a movement. Alternatively, the cost may be dynamic. For example, because the variability in the motor output is proportional to the magnitude of the motor command, repetition of the same sequence of intended motor commands many times will lead to a distribution of actual movements. Modifying the sequence of motor commands can control aspects of

this distribution, such as the spread of positions of the hand at the end of the movement. In a simple aiming movement the cost is the final error, as measured by the variability about the target. A model that minimizes this cost would accurately predict the trajectories of both eye and arm movements.

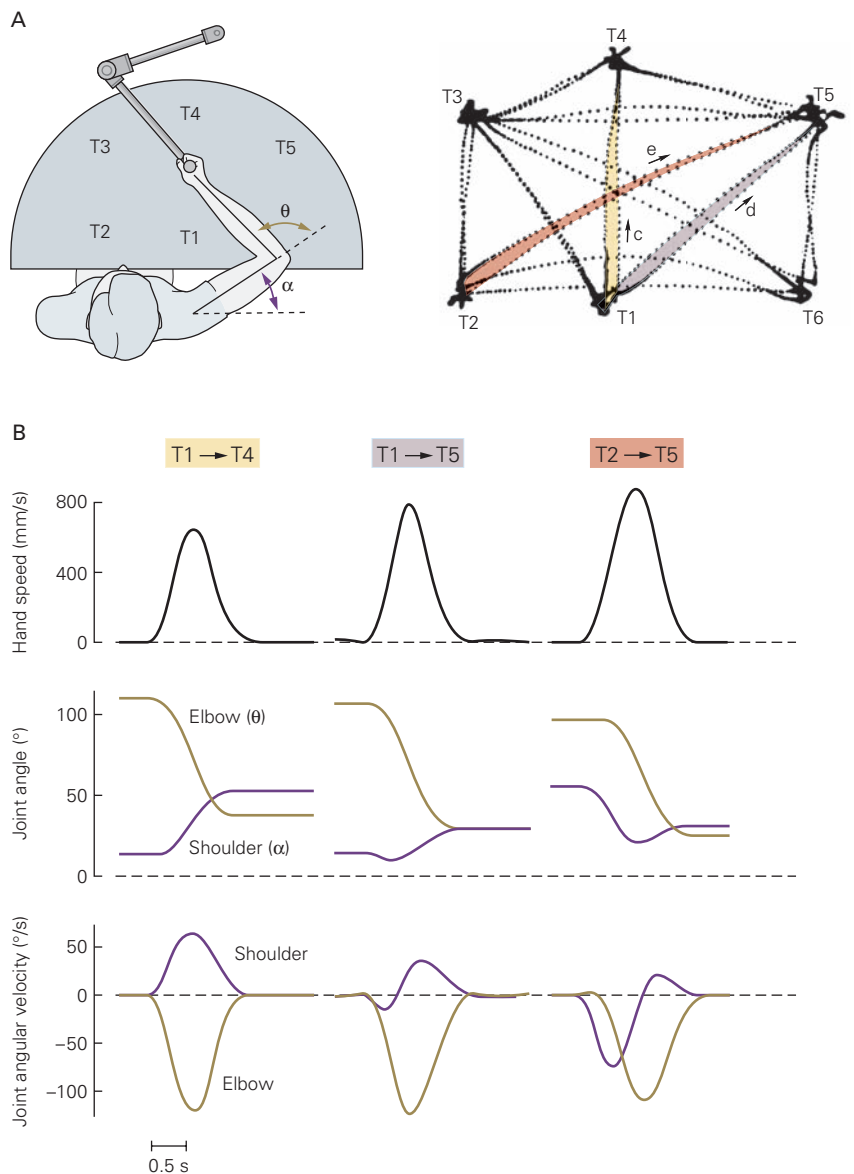
Motor Signals Are Subject to Feedforward and Feedback Control

So far we have focused on how sensory inputs are used to plan a movement and why the resulting movements

Figure 33–9 Hand path and velocity have stereotypical features. (Adapted, with permission, from Morasso 1981.)

A. The subject sits in front of a semicircular plate and grasps the handle of a two-jointed apparatus that moves in one plane and records hand position. The subject is instructed to move the hand between various targets (T1–T6). The record on the right shows the paths traced by one subject.

B. Kinematic data for three hand paths shown in part A (c, d, and e). 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.



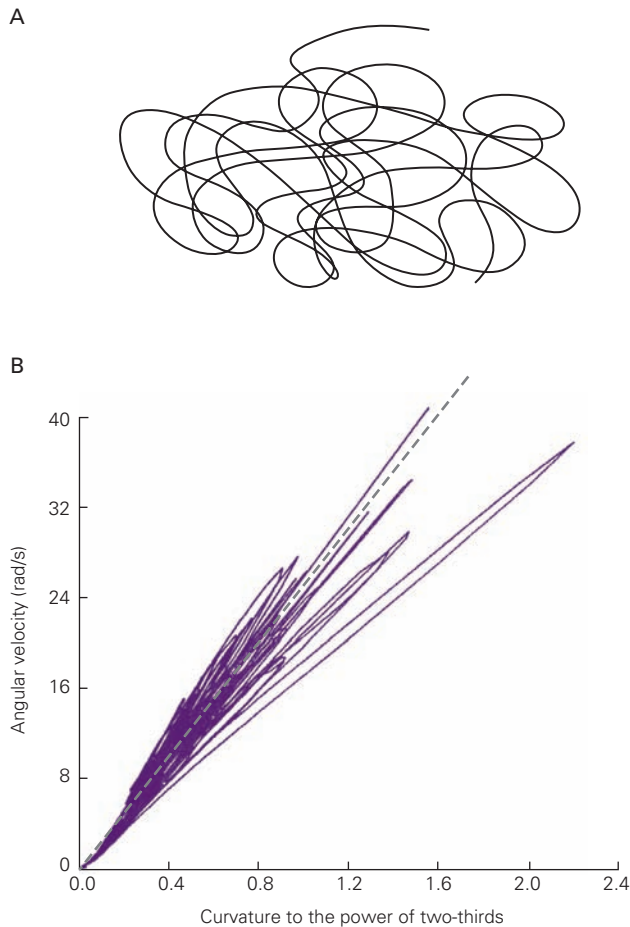


Figure 33-10 Complex movements obey the two-thirds power law. (Reproduced, with permission, from Lacquaniti, Terzuolo, and Viviani 1983.)

A. Nondirected scribbling is a complex movement.

B. Instantaneous values of the angular velocity of the hand while scribbling are plotted against the curvature of the hand's path raised to the power of two-thirds. The relation between the two variables is piecewise linear. Each segment in the bundle, corresponding to nonoverlapping segments of the trajectory, has a different slope. The slopes cluster around the average (dashed line), a typical result for this type of experiment. Therefore the relationship between the speed of hand motion and the degree of curvature of the hand path is roughly constant: Velocity varies as a continuous function of the curvature raised to the power of two-thirds. This two-thirds power law governs virtually all movements and expresses an obligatory slowing of the hand during movement segments that are more curved and a speeding up during segments that are straight. Because angular velocity is the speed of the hand multiplied by the path curvature, in the plot an increase in angular velocity represents a decrease in hand speed.

can have errors. Sensory inputs to the motor systems during a movement provide information about errors that arise from neural noise, from inaccuracies in the motor commands as a result of flaws in the internal models, or from changes in the outside world, such as the unexpected motion of a target. We now examine what part these errors play in two forms of motor control, feedforward and feedback control.

Feedforward Control Does Not Use Sensory Feedback

Movements that are not correctible during the movement are often termed *ballistic*. This term is ordinarily applied to the trajectory of unpowered projectiles (such as ballistic missiles) that, once launched, can no longer be controlled and are subject only to gravity. Because arm movements can potentially be controlled throughout their course, however, the term *feedforward control* more accurately describes the trajectory. Feedforward commands are generated without regard to the consequences. Such commands are also termed *open-loop* because the sensorimotor loop is not completed by sensory feedback (Figure 33-11A).

Open-loop control is advantageous if we consider the delays inherent in the sensorimotor system. Both conversion of stimulus energy into neural signals by stimulus receptors and conveyance of the sensory signals to central neurons take time. For example, visual feedback can take approximately 100 ms to be processed in the retina and transmitted to the visual cortex. In addition to delays in the peripheral sensory system, 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 200 ms for a response to a visual stimulus. This delay means that rapid movements, such as the saccades of the eye that last less than 100 ms, cannot use sensory feedback to guide the eye onto a target.

Even with slower movements, such as deliberate reaching, which can take approximately 500 ms, sensory information cannot be used to guide the initial part of a movement, so open-loop control must be used. This open-loop component can be clearly demonstrated. Both the initial speed and the acceleration of the hand during reaching are proportional to the distance of the target. This and the straightness of hand paths mean that the extent of a movement is planned before the movement is initiated, and the movement is generated in a feedforward manner (Figure 33-12).

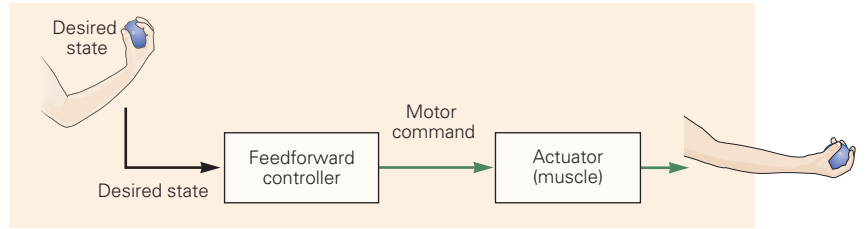
Open-loop control also has disadvantages. Any movement errors caused by inaccuracies in planning

Figure 33–11 Feedforward and feedback control.

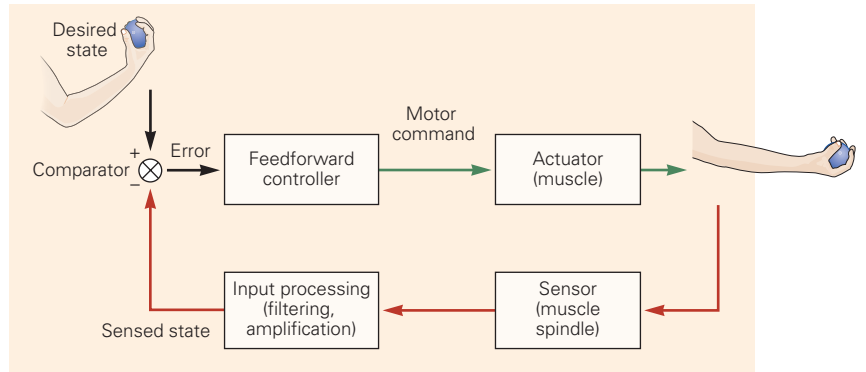
A. A feedforward controller generates a motor command based on a desired state. Any errors that arise during the movement are not monitored.

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.

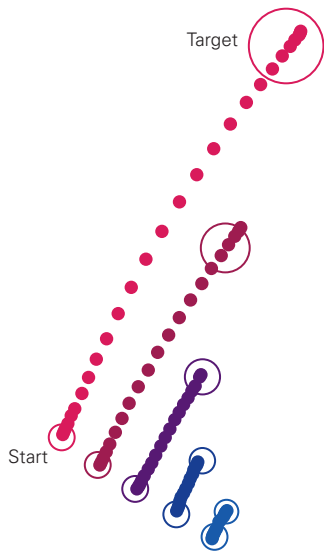
A Feedforward control



B Feedback control



A Actual hand path



B Hand path measurements

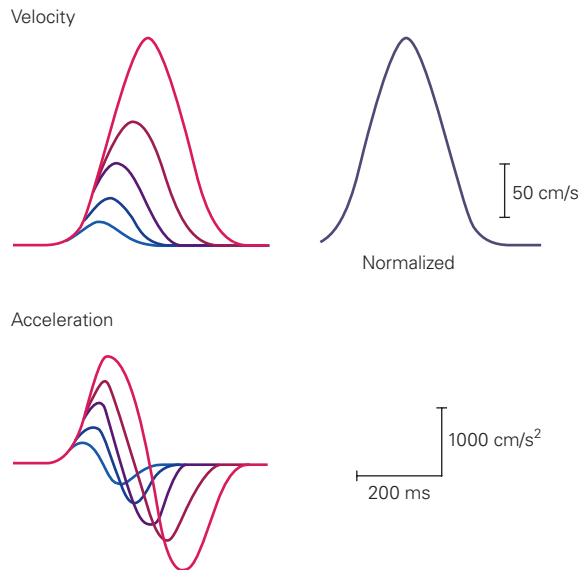


Figure 33–12 Acceleration and velocity of reaching are a function of target distance. (Modified, with permission, from Gordon et al. 1994.)

A. Hand paths measured to targets located 2.5, 5, 10, 20, and 30 cm from the starting position.

B. Average velocity and acceleration of the hand movements shown in part A. The acceleration and velocity profiles scale

linearly as a function of the distance to the target. All the velocity profiles are self-similar and when normalized in time and amplitude are nearly identical. The single peaks indicate that the extent of movement is specified prior to actual movement. If it were not, the first peak would be the same for all target distances, and secondary peaks representing feedback adjustment would be seen.

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 a perfect inverse model through learning. For example, the vestibulo-ocular reflex (see Chapter 40) uses open-loop control to maintain fixation during head rotation. This is a very efficient system as the dynamics of the eye are relatively simple, and the rotation of the head can be directly sensed by the vestibular labyrinth. The complexity of the arm, however, makes it very difficult to optimize an inverse model, and thus the control of hand movement requires some form of error correction.

Feedback Control Uses Sensory Signals to Correct Movements

To correct movement errors as they arise, the action must be monitored before it is completed. Such error-correcting systems are known as feedback or closed-loop systems because the sensorimotor loop is complete (Figure 33–11B).

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* (Figure 33–13). By continuously correcting a movement, feedback control can be robust both to noise in the sensorimotor system and to environmental perturbations.

In most motor systems movement control is achieved through both feedforward and feedback processes. Because sensory feedback is not available for the first portion of a movement, feedforward processes generate the initial motor command only. As the movement progresses, information on performance becomes available, allowing feedback control to play a role.

When lifting an object between thumb and index finger, for example, sufficient grip force (perpendicular force between the digits and the object's surface) must be generated to prevent slippage owing to load force (tangential force between the digit and object surface arising from the object's weight). We use feedforward control to set our grip force and the lifting force in accordance with the expected slipperiness and weight of the object. If cutaneous receptors indicate that slippage is occurring, our grip force is increased immediately through rapid feedback control (Figure 33–14). Because cutaneous information on slippage evokes a motor command to increase grip force only when the object is being lifted, this feedback circuit is said to be "gated" during lifting.

Feedback control cannot generate a command in anticipation of an error: It is always driven by an error. Feedforward control, conversely, is based only on a desired state and can therefore null the error.

Prediction Compensates for Sensorimotor Delays

Accurate feedback control of movement requires information on the body's current state, for example, the positions and velocities of our body segments. However, sensory feedback from the periphery is both noisy and slow. 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 can compensate for such delays and thus increase the accuracy of sensory feedback during movement: intermittency of movement and prediction of changes in body states due to 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 can form a major component of a state estimator. Although sensory signals provide necessary information about the body, the motor command also provides useful 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 is derived from a forward model that predicts how the body will change in response to the motor command. Because this estimate is predictive, it is time-advanced, thereby compensating for the feedback delays. However, this estimate will tend to drift over time if the forward model is not perfectly accurate.

The drawbacks of using only sensory feedback or only motor prediction can be ameliorated by monitoring

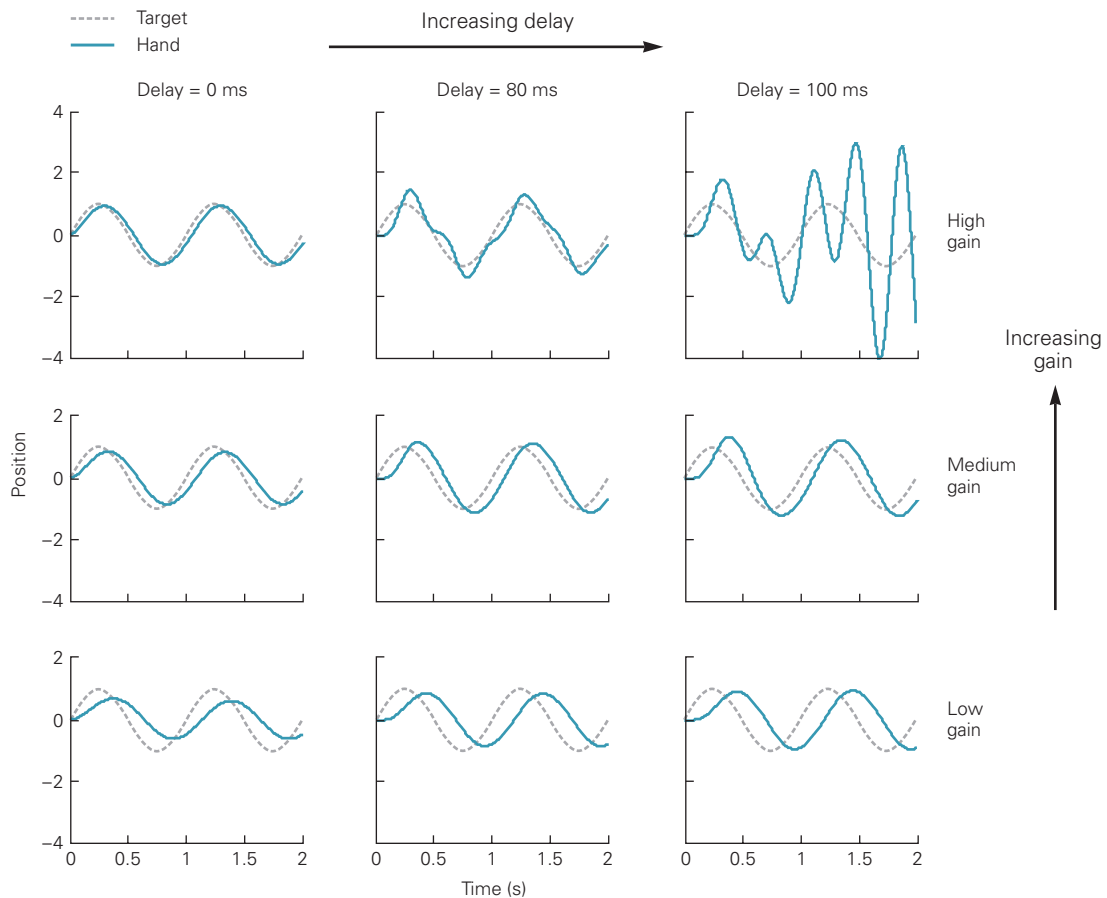


Figure 33-13 The interplay of gain and delay in feedback control. Subjects use a controller to track a target moving sinusoidally in one dimension. The sensory feedback signal that conveys error in the hand's position arrives after some period of time (the delay), and the motor system tries to correct for the error by increasing or decreasing the size of its command relative to the error (the gain).

The plots show the performance of a subject tracking a sinusoidal target in which there is either instantaneous feedback of error (**left column**) or feedback with a delay (**middle and right columns**). When the gain is high, and the delay is low, tracking is very good. However, as the delay increases, the motor system corrects for error inappropriately, and this leads to oscillations and large errors. To maintain stability, the gain can be lowered, but tracking is not perfect.

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.

both and using a forward model to estimate the current state of the body. 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 the state of the body owing to noise in both the sensory and motor signals (Figure 33-15). Such a model

has been supported by empirical studies of how the nervous system estimates hand position, posture, and head orientation.

The nervous system has several different internal models of control that use prediction and sensory feedback to different extents. The comparative advantages of these various models are nicely illustrated

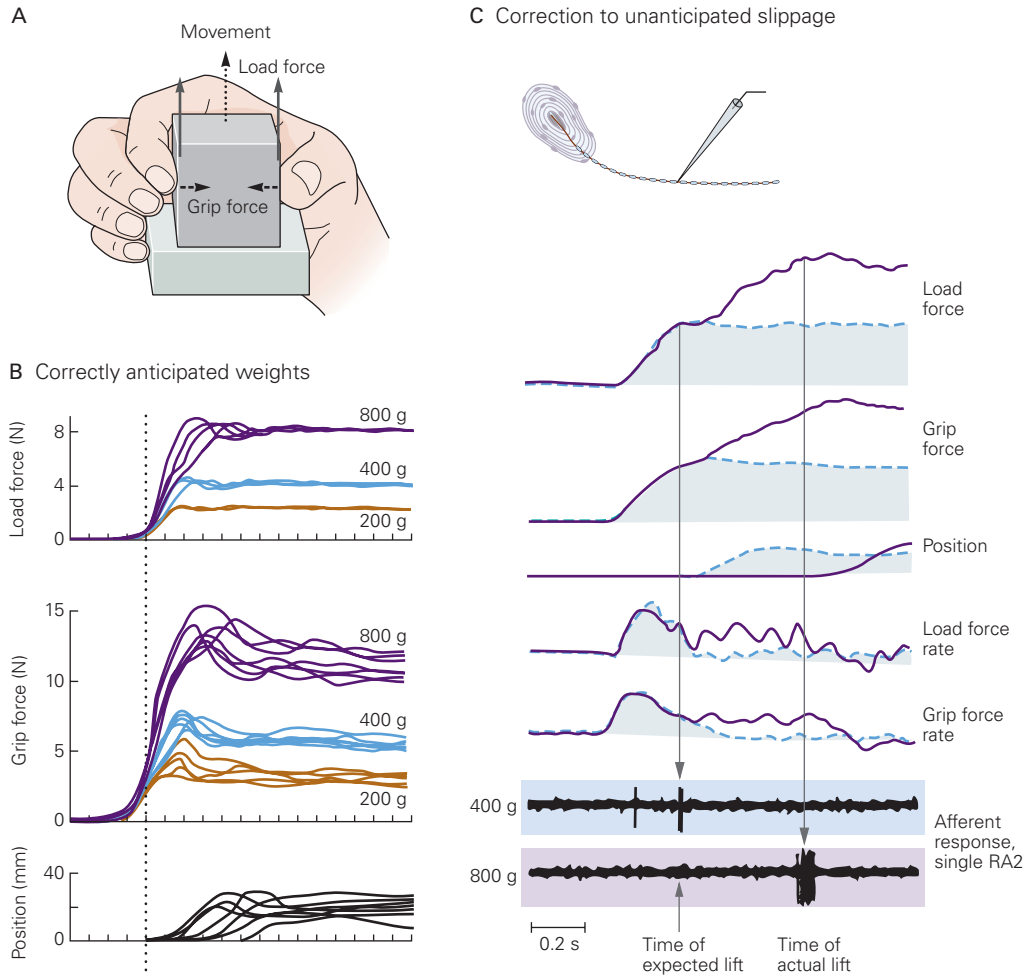


Figure 33-14 Both feedback and feedforward controls are used when lifting an object.

A. The subject lifts an object from the table. Sensory receptors measure vertical motion, grip force, and the load force applied to the object to overcome gravity and inertia. The discharge of different sensory receptors is recorded by microelectrodes inserted within identified sensory axons of the peripheral nerve, a procedure called microneurography.

B. When the subject knows the weight of the object in advance, the applied forces are adequate to lift the object. Three sets of traces (24 trials superimposed) show load force, grip force, and position as subjects lifted three objects of different weights (200, 400, and 800 g). The grip force increases in proportion to the weight of the object. This is done by scaling a

preprogrammed force profile (the profiles have the same shape but different amplitudes).

C. When the weight is larger than expected, the object slips initially, but force is increased before lifting begins. When the subject begins to lift a 400 g object, Pacinian corpuscles in the skin are activated and a burst of action potentials occurs in the afferent RA2 fibers, signaling the beginning of the hold phase during which the grip force is constant. After being presented with the 400 g object for several trials (dashed lines), the subject is given an 800 g object (solid lines). When the subject begins to lift the 800 g object, the object slips, and the RA2 fibers are not activated. The absence of RA2 signals triggers a slow increase in force that is terminated when lifting begins. (Reproduced, with permission, from Johansson et al. 1991.)

by differences in object manipulation under different conditions. When the 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 motions of the kite. When dealing with such unpredictability, grip force needs to be high to prevent slippage because it tends to lag behind load force (Figure 33–16A).

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 33–16B). 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.

The discrepancy between actual and predicted sensory feedback is also essential in motor control. For example, when we pick up an object, we anticipate when the object will lift off. The brain is particularly

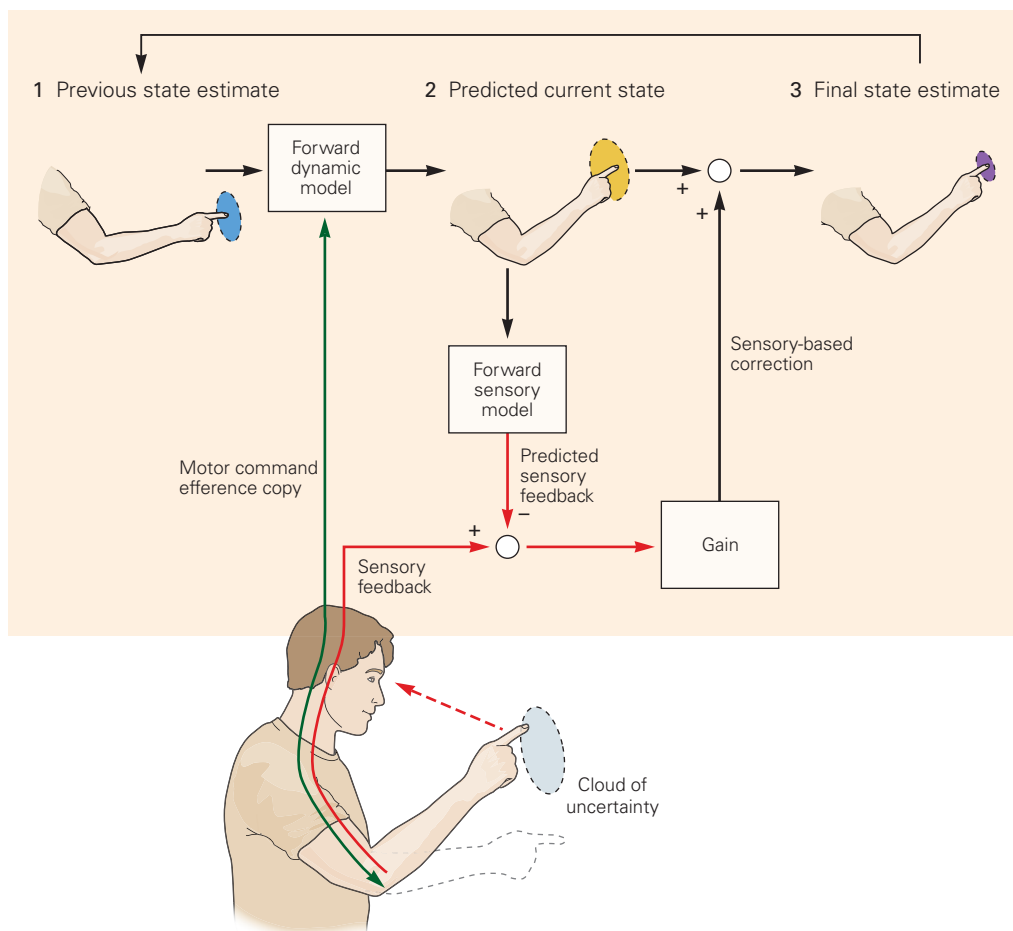
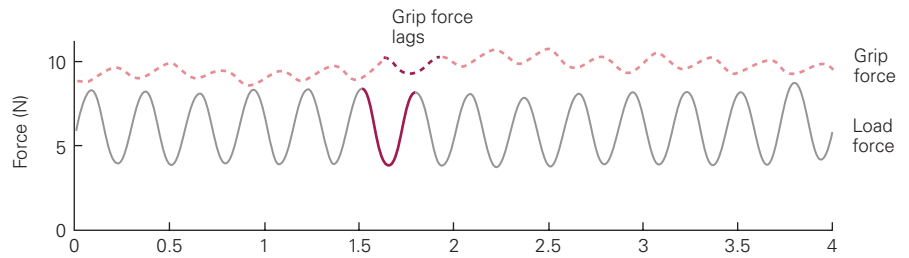
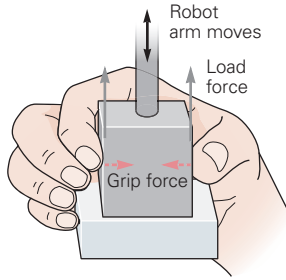


Figure 33–15 An observer model. The drawing shows how the finger's location can be estimated during movement of the arm. A previous estimate of the distribution of possible finger positions (1) is the basis for a new estimate (2). This estimation uses an efference copy of the motor command and a model of the dynamics. The new distribution of estimated finger positions (the "cloud of uncertainty") is larger than that of the previous estimate. The model then predicts 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) has less uncertainty. This estimate becomes 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.

A Robot controls movement



B Hand controls movement

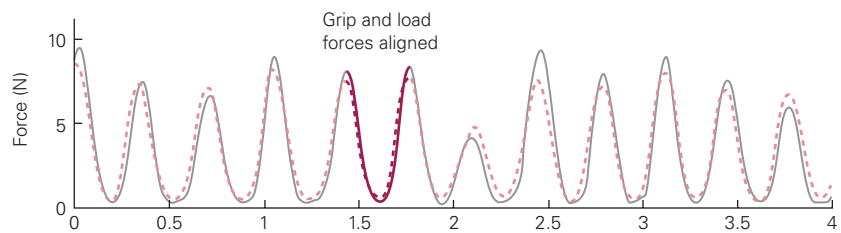
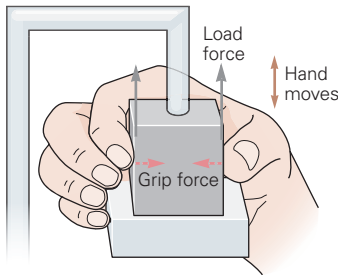


Figure 33–16 Anticipatory control of self-generated actions. (Reproduced, with permission, from Blakemore, Goodbody, and Wolpert 1998.)

A. When a subject is instructed to hold onto an object to which a robot is applying a sinusoidal load force, the grip force of the fingers is high to prevent slippage but nevertheless lags behind the increases in load force.

B. Conversely, when the subject actively pulls down the object, producing a similar load profile, the load force can be anticipated and thus the grip force is lower and tracks the load force without delay.

sensitive to the occurrence of unexpected events or the nonoccurrence of an expected event. Thus if an object is lighter or heavier than expected, and therefore is lifted too early or cannot be lifted, reactive responses are evoked. The brain seems to pay particular attention to these critical moments to determine whether the subsequent actions that are part of the task should proceed.

In addition to its use in compensating for sensory feedback delays, prediction is a key element in perceptual processing. Sensory feedback can originate from two sources: either external sources or our own movement. In the sensory receptor these two sources are not distinguished, however, and sensory signals do not carry a label “external stimulus” or “internal stimulus.”

Sensitivity to external events can be amplified by reducing the feedback from our own movement. Thus predictions of sensory signals that arise from our

own movements are subtracted from the total sensory feedback, thereby enhancing the signals that carry information about external events. Such a predictive mechanism is responsible for the fact that tickling oneself is a less intense experience than tickling by another. When participants are asked to tickle themselves with a time delay introduced between the motor command and the resulting tickle, the greater the time delay the more ticklish the sensation. As the time delay increases, the predictor becomes more inaccurate, thereby failing to cancel the sensory feedback resulting in the tickle sensation.

Sensory Processing Is Different 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. Mel Goodale and David Milner have proposed that visual information flows in two streams in the brain (see Chapter 25). A dorsal stream projects to the posterior parietal cortex and is particularly involved in the use of vision for action (see Chapter 38). Conversely, a ventral stream projects to the inferotemporal cortex and is involved in conscious visual perception (see Chapter 28).

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 explain 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. 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 33–17). 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.

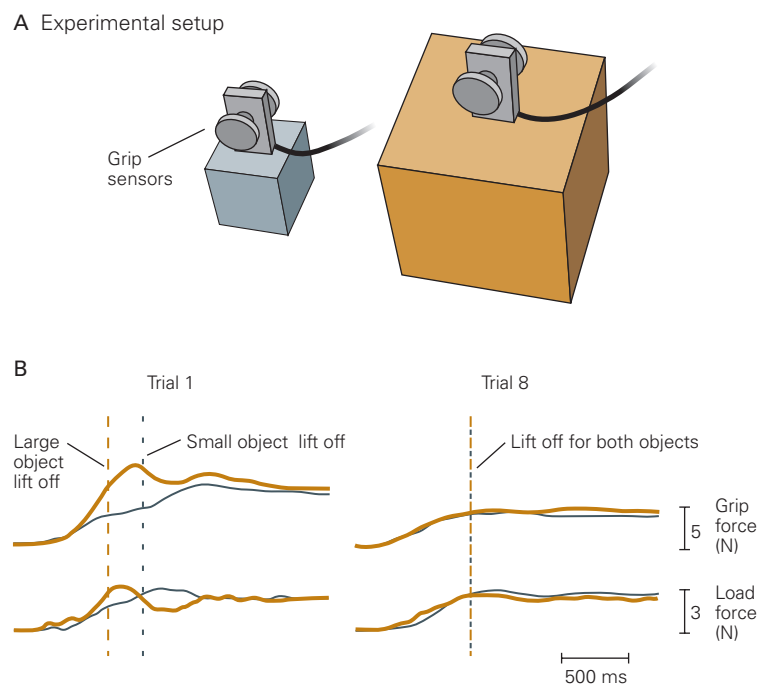
Motor Systems Must Adapt to Development and Experience

Animals have a remarkable capacity for learning new motor skills through their interaction with the environment. This learning is distinct from and independent of the development of skills through

Figure 33–17 The size-weight illusion. (Reproduced, with permission, from Flanagan and Beltzner 2000.)

A. In each trial subjects lifted first a large object and then 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 generates grip and load forces appropriate to the weights of the two objects despite the conscious perception of a difference in weight.



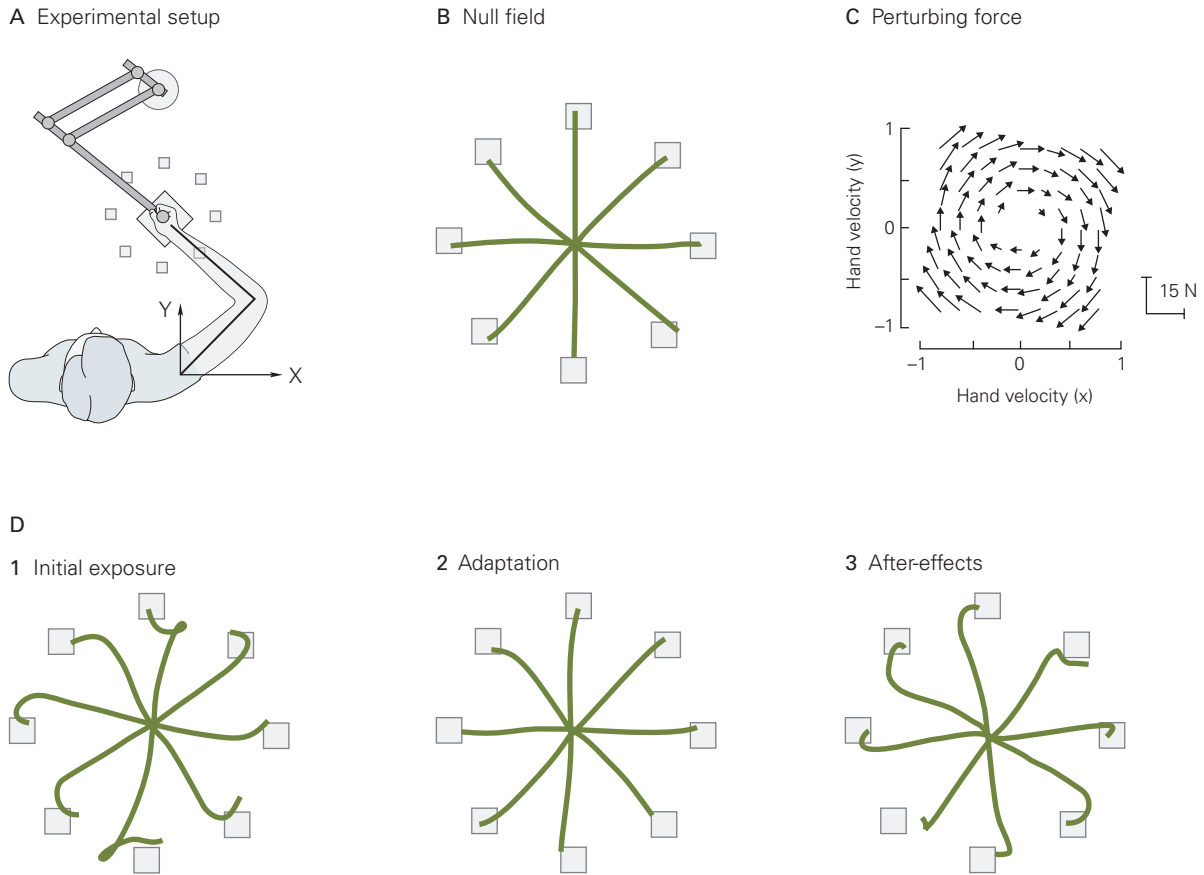


Figure 33–18 Learning improves the accuracy of reaching in a novel dynamic environment.

A. A subject holds an apparatus that measures the position and velocity of the hand and applies forces to the hand. (Reproduced, with permission, from Brashers-Krug, Shadmehr, and Bizzi 1996.)

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).

maturation. Although evolution can hard-wire some motor behaviors, such as the ability of a foal to stand, motor behavior in general must adapt to new and varying environments.

New motor skills cannot be acquired by a fixed neural control system. Sensorimotor control 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 (see Chapter 66). Typical examples of procedural learning are learning to ride a bicycle or play the piano. In contrast,

explicit or *declarative* learning involves the acquisition of knowledge that can be expressed in statements about the world and is available to introspection (see Chapter 67). Memorizing the names and routes of the cranial nerves or 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.

Motor learning can occur more or less immediately or require some time. One learns to pick up an object of unknown weight almost immediately and learns to ride a bicycle after a little 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 the fingers, whereas in normal movements, such as reaching and grasping, individuated finger movements are rare.

Motor Learning Involves Adapting Internal Models for Novel Kinematic and Dynamic Conditions

Sensorimotor transformations have kinematic and dynamic components. Kinematic transformations relate events in different spatial coordinate systems, such as joint angles of the arm and the position of the hand in space. To control a computer mouse, for example, we must learn the kinematic transformation between the handheld mouse and the image of the cursor on the screen. Dynamic transformations relate forces acting at the joints to the motion of the system. We must relate the forces we apply to the mouse to the resulting movement, a transformation that depends on the inertia of the mouse and the friction between the mouse and pad. The kinematics and dynamics of movement vary greatly as we grow and interact with new objects. The brain adapts by reorganizing or adjusting motor commands to generate new actions.

As we saw earlier, we normally move the hand in a straight line to reach an object. Unexpected dynamic interactions may produce curved paths, but subjects learn to anticipate these effects. This learning is conveniently studied by having subjects make pointing movements with an apparatus through which novel forces can be applied to the arm (Figure 33–18A). For example, applying a force that is proportional to the speed of the hand but which acts at right angles to the direction of movement forces the hand into a brief curving movement before reaching the target. Over time the subject adapts to

this perturbation and is able to maintain a straight-line movement (Figure 33–18D).

Subjects might adapt to such a situation in two possible ways. First, they could co-contract the muscles in their arm, thereby stiffening the arm and reducing the impact of the perturbation. Alternatively, they could learn an internal model that compensates for the expected forces, one that uses a new set of motor commands. By examining the subjects' movements after the force 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. In fact, when the force is turned off, subjects show a large after-effect in the opposite direction, demonstrating that they had learned to compensate for the perturbation (Figure 33–18D).

Although motor learning often takes much practice, once a task is no longer performed de-adaptation is typically quite swift. The context of the movement, that is the sensory inputs associated with a particular task, can be enough to switch behavior. When subjects wear prismatic glasses that rotate visual space, for example, they initially misreach targets but soon learn to reach correctly. After repeated trials the contextual cue of the feel of the glasses, without the prisms in place, is sufficient to switch subjects into behavior suitable with the prisms.

Kinematic and Dynamic Motor Learning Rely on Different Sensory Modalities

Not all sensory modalities are equally important in learning motor tasks. In learning dynamic tasks, proprioception is more important than vision. We normally learn dynamic tasks equally well with or without vision. Patients who have lost proprioception have particular difficulty controlling the dynamic properties of their limbs (Box 33–3) or learning new dynamic tasks without vision.

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

Box 33–3 Proprioception Is Critical for Planning Hand Trajectories and Controlling Dynamics

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 and vibration and fine tactile sensations (as well as tendon reflexes), but the sense of pain and temperature are fully preserved. These patients 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 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 or resistance differs from expectation.

However, this is not all. When the limb cannot be seen, errors in feedforward control of movements

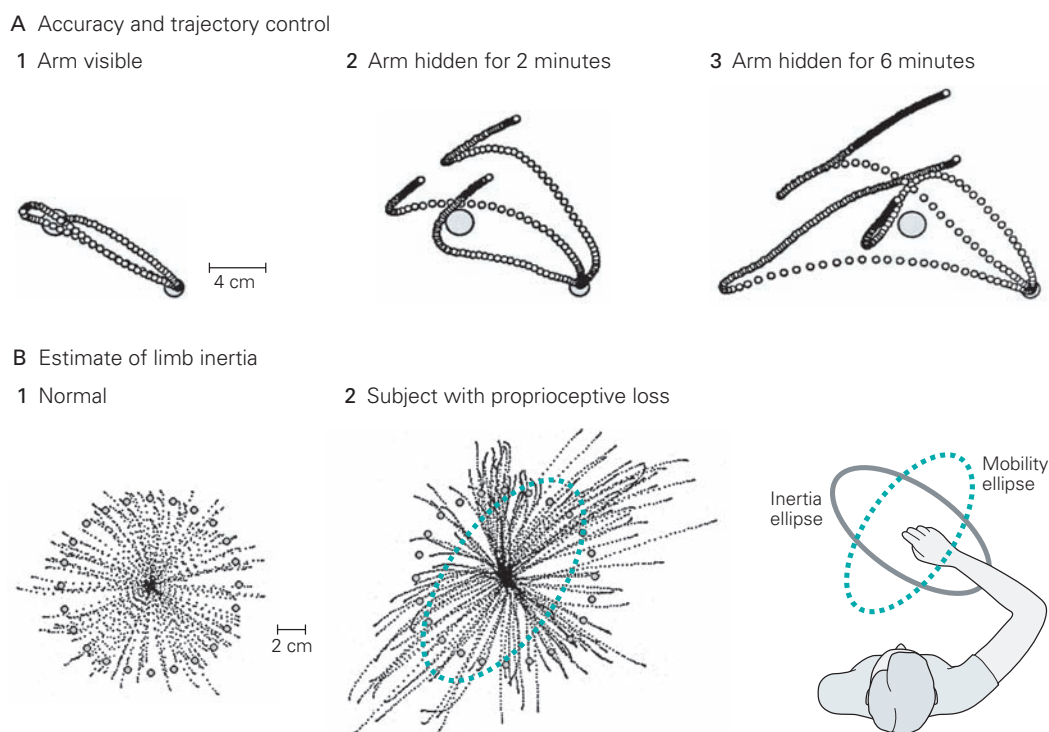


Figure 33–19 Patients lacking proprioception cannot maintain internal models of limb inertia.

A. Accuracy and trajectory control decay rapidly when patients cannot see their limbs. A patient with large-fiber sensory neuropathy, with no sense of position in the arm for several years, moved a mouse-like cursor repeatedly from a starting position to a target displayed on a computer screen in front of her. When the patient was able to see the screen cursor and her hand, movements were straight and reasonably accurate (1). Movements become increasingly curved and inaccurate after vision of her arm was removed for 2 minutes (2) and 6 minutes (3). (Reproduced, with permission, from Ghez, Gordon, and Ghilardi 1995.)

B. A patient without proprioception plans movement without taking account of variations in limb inertia. Patients and normal subjects were instructed to move a finger to 22

targets arranged concentrically. Subjects were prevented from seeing their limb. (1) Movements made by a control subject are straight and evenly distributed throughout the workspace. (2) Movements made by a patient with loss of limb proprioception vary in extent in different directions. The variation in extent is explained by the fact that directional changes in inertia vary with movement direction according to an elliptical contour (inertia ellipse). This means that a constant initial force at the hand will accelerate the limb differently in different directions (mobility ellipse); high acceleration occurs in directions that have low inertia. The mobility computed for the subject's arm plotted over the hand paths shown at left closely matches the variations in movement extent. (Reproduced, with permission, from Gordon, Ghilardi, and Ghez 1995.)

increase over a few minutes and patients become uncertain of where their hands actually move. This is seen clearly in the succession of movements in Figure 33–19A. Movements that are straight and accurate with vision become increasingly curved; instead of stopping, movements drift off to one side or another without the subject’s awareness. Thus proprioception is needed to update both inverse models used to control movement and forward models used to estimate body positions resulting from motor commands.

The defects in these models are revealed by examining the errors that occur when the hand moves to targets in different directions (Figure 33–19B). In moving to equidistant targets in many directions, a normal subject moves his hand approximately the same distance in all directions. For patients with proprioceptive loss, the distance moved varies with the direction of movement; movements along the 45-degree axis, perpendicular to the forearm, overshoot the target.

These variations match changes in the inertial resistance of the arm. When the hand moves in the direction

of the forearm (moving both arm and forearm), inertia is two to three times greater than when the hand moves perpendicular to the forearm (moving the forearm alone). Changes in inertia with movement direction fit an elliptical contour. This means that a constant force applied perpendicularly would accelerate the forearm two to three times faster than one applied in the same direction as the forearm.

In all subjects acceleration does indeed vary with movement in different directions, but normal subjects plan movements of shorter duration in directions with lower inertia. In contrast, patients without proprioception are unable to vary the duration (unless they see their limb before moving). Errors therefore reflect the rapid decay of the patient’s internal model of limb inertia.

Another form of error occurs in movements with rapid direction reversals. Analyses of the joint torques during these movements show that subjects with intact sensation anticipate intersegmental torques, whereas those without proprioception fail to do so (Figure 33–20).

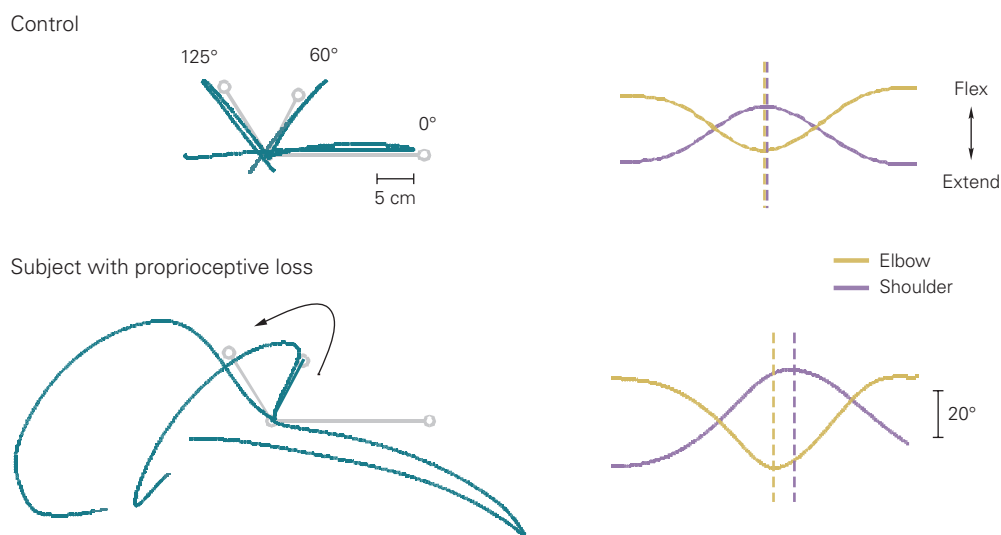


Figure 33–20 Patients lacking proprioception cannot make an accurate movement that requires a rapid reversal in path. In normal subjects the joint angles for the elbow and shoulder show good alignment, leading to an accurate reversal. In subjects who lack proprioceptive

input the timing of the joint reversal is poor, leading to large errors in the path. These patients cannot anticipate and correct for the intersegmental dynamics that occur around the path reversal. (Reproduced, with permission, from Sainburg et al. 1995.)

An Overall View

The primary purpose of the elaborate information processing and storage that occurs in the brain is to enable us to interact with our environment. Our infinitely varied and purposeful motor behaviors are governed by the integrated actions of the brain's several motor systems.

To control action the central nervous system uses a sequence of sensorimotor transformations that convert incoming sensory information into motor outputs. The brain uses internal models at each stage in the sensorimotor transformation. Variability in the inputs and outputs of these transformations and inaccuracies in their representation underlie the errors and variability in movement and lead to the ubiquitous trade-off between speed and accuracy.

The motor systems generate commands using feedforward circuits or error-correcting feedback circuits; most movement involves both types of control. The adverse effects of delays in feedback are reduced through the use of predictive processes.

Finally, motor control circuits are not static but undergo continual modification and recalibration throughout life. Motor learning improves motor control in novel situations, and different forms of sensory information are vital for learning.

The ease with which we conduct ordinary movements masks the true 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 that can perform human-like control of movement. Although computers can beat grandmasters at chess, no computer can yet control a robot to manipulate a chess piece with the dexterity of a six-year-old child.

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