Control strategies in physiological systems

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ABSTRACT
In this paper, written for a general audience, I review and contrast various strategies that the body uses to control homeostasis and movement. Messages, signals, communication channels, and control systems are dealt with from both a cellular and an integrative perspective. The major global control strategies are feedback, feedforward, and adaptive control, and examples of each are presented to highlight advantageous and disadvantageous features. Many physiological systems use these three strategies in combination. — Houk, J. C. Control strategies in physiological systems. FASEB J. 2: 97–107; 1988.

Key Words: communication channels • control systems • feedforward • feedback • motor neurons

A SYMPOSIUM ON CONTROL STRATEGIES in physiological systems was held at the APS Centennial meeting in Washington, DC, in the spring of 1987.1 The symposium was organized because I thought it might be productive to compare and contrast various strategies used by the body to control different types of physiological systems. This brief article highlights a few of the themes that came from the symposium.

The basic idea that the body has a multitude of automatic control systems was clearly enunciated in the 17th century writing of René Descartes (1), although the fluid mechanical mechanism he proposed for the transmission of nerve signals was quite erroneous. Bernard’s (2) discovery that many internal variables are automatically regulated, Cannon’s (3) analyses of mechanisms that underlie homeostasis, and Sherrington’s (4) studies of spinal reflexes set the stage for the symbiotic relationship between physiology and engineering control theory that was to follow. Wiener’s (5) influential book on cybernetics promoted human/machine analogies and particularly emphasized the negative feedback concept derived from engineering control theory as a mechanism in physiological systems.

In recent years, there has been considerable progress on two fronts relevant to the control of physiological systems. First, there has been an enormous expansion in our knowledge of the cellular mechanisms used to transmit signals and to process information. Many investigators have wondered why more of this knowledge is not incorporated into current accounts of physiological control systems. Thus, I attempt to relate cellular and integrative views of communication and control. Second, our knowledge of the integrative level has improved greatly, to the point where we may speak with some confidence about the strategies that are, via evolutionary pressures, designed into physiological control systems. There has been a growing awareness that feedback is not the only strategy used by the body to control physiological systems, and one of the main topics of this article is a comparative analysis of the advantages and disadvantages of feedback, feedforward, and adaptive control strategies.

OVERVIEW OF COMMUNICATION AND CONTROL
Messages, signals, and communication channels

Because of the physical separation of the tissues and organs, mechanisms for communication over distances are required to control body functions. The communication channels of the body are nerve fibers along which action potentials propagate, the circulation that carries endocrine signals, and the extracellular space through which hormones and neurotransmitters diffuse.

From the cellular standpoint, neural and endocrine mechanisms for communication have many similarities. One can make a strong case for a single cell type, the neuroendocrine cell, that secretes chemical signals and is widely distributed in the body (6). A neuroendocrine cell that secretes a given chemical substance will develop glandular features at some locations and neuronal features at others. In the former case the secreted substance is called a hormone, and in the latter case the same substance is called a neurotransmitter. We now know that there are a tremendous variety of secreted substances, many of which are used as chemical signals in both the nervous and endocrine systems.

Alternatively, it is instructive to examine neural and endocrine systems from the perspective of communication.

1 The participants at this symposium were Arthur C. Guyton from the University of Mississippi, Fred C. Grodins from the University of Southern California, William F. Ganong from the University of California at San Francisco, and James C. Houk from Northwestern University.
tion theory (7). This theory deals with the problem of sending messages from an information source, via a communication channel, to a receiver at some destination (Fig. 1). The information source, which might be a nucleus in the brain or a cluster of endocrine cells, must first compute or otherwise select the message to be sent. The message is then converted into a signal that is suitable for transmission along an available communication channel via a process called encoding. I am using the term message in its semantic sense and the term signal to refer to the physicochemical events that encode the message.

From this integrative standpoint, neural and endocrine channels for communication have clear similarities but also important differences. Both types of channel transmit messages from source to destination, although the biophysical signals used to transmit messages take various forms. If the channel is the circulation (Fig. 2A), the message is encoded by the release of a hormone, and the concentration of circulating hormone constitutes the signal. In contrast, if the channel is a nerve fiber (Fig. 2B), the message is encoded by the production of action potentials, and the pattern of discharge propagated along an axon constitutes the signal.

The circulation provides a single, common channel for broadcasting a set of public messages, encoded as hormone signals. In contrast, nerve fibers provide multiple channels for directing an enormous variety of private messages between specific locales. The former situation is analogous to public radio, whereas the latter is more like our telephone system. Intermediate cases also exist. Endocrine communication becomes more private when specialized vasculature is involved. For example, the portal hypophyseal vessels provide a semiprivate communication channel that carries tropic hormones between the hypothalamus and the anterior pituitary gland. Similarly, neural communication becomes more public when nerve terminals are dispersed rather than forming discrete synapses. For paracrine systems, the extracellular space in a given tissue provides a semiprivate communication channel through which local hormones diffuse to act on clusters of nearby cells.

At the receiving end of the body’s communication channels, the chemical and electrical signals used to transmit messages must be decoded, and the decoded messages must be interpreted and acted on. When an endocrine signal is delivered to a target cell, specific receptor molecules on the surface or within the cell recognize and decode the signal (8). The received message, having reached its destination, is then translated into specific actions by complex sequences of intracellular biochemical reactions. Although these intracellular events can be viewed as additional intracellular communication processes, for the present discussion I will consider them as a single, lumped process that leads to a characteristic response of the target tissue.

When messages encoded as nerve signals reach their destination, they initially undergo recoding to convert them into chemical signals, via release of neurotransmitter, before being decoded by the postsynaptic cell. In essence, the message is sent through a second, short communication channel (the synaptic cleft) to reach its next destination. From the perspective of communication between remote sites, nerve fibers constitute the primary communication channels, although a cell biologist might be more inclined to consider the synaptic cleft as the primary channel, to emphasize the distinction between intercellular and intracellular processes. What should be clear is that the two channels sequentially transmit the same message, first encoded as a pattern of neural discharge for transmission along the axon and then encoded as transmitter concentration for diffusion across the synaptic cleft.

Control systems

A control system can be viewed as a set of communication channels interconnecting subsystems that process information. Block diagrams nicely capture this situation, as illustrated in Fig. 3. Boxes are used to represent the information-processing subsystems, and arrows are used to represent the communication channels that transmit messages between subsystems. A subsystem receives incoming messages and performs computations based on them to generate an outgoing message.

As physiologists, we learn about how control systems operate in three ways. One approach is to study the physicochemical events that process information within subsystems. Owing to major advancements in molecular and cellular biology in recent years, we now know much about receptor molecules, membrane channels, and intracellular messengers. However, this knowledge must be integrated into a more global picture to assess

![Diagram](image)

**Figure 1.** The communication process. A message from an information source is encoded into a signal that is sent along a communication channel. At the destination, the signal is decoded into a received message.
A. Endocrine Communication

![Diagram of Hormone Levels and Circulation]

**Figure 2.** Comparison of endocrine and neural channels for communication. In the case of the endocrine system (A), the circulation serves as a single common channel for transmitting a set of endocrine signals. This composite signal, composed of the elements (H₁, H₂, . . . , Hₙ), functions as a public message that is broadcast to cells throughout the body, two of which are shown. Different cells will decode this message in different ways depending on the particular set of receptors they have and the manner in which these receptors are coupled to intracellular events. Thus the message will produce different actions on different target tissues. This is an efficient method for the global distribution of general information, allowing it to be used in a manner that depends on the site of action. In contrast, the nervous system (B) uses numerous private communication channels, the nerve fibers, to transmit specific information from one site to another. The diagram shows a given neuron receiving a set of private messages through the channels provided by its afferent fibers. The synapses at the afferent nerve terminals decode these messages, translating them into postsynaptic events, whereupon they are combined to compute an output message. The latter is encoded into a sequential pattern of action potentials and then distributed by transmission along the efferent fiber to new sites of action.

B. Neural Communication

![Diagram of Neural Communication]

the specific computations that are performed within subsystems to generate outgoing messages.

A second approach is to sample the coded messages sent between the information-processing subsystems. Here we use radioimmunooassays and extracellular microelectrodes to sample many of the chemical and electrical signals sent between subsystems. Although these data are extremely helpful, one is still left with the problem of deciphering the meaning of the signals, i.e., the actual messages that are being sent in coded format from one locale to another.

A third approach is to study the global structure of the system, i.e., the map of interconnections between subsystems. Surprisingly powerful statements about the properties of control systems can be made without recourse to the specific physical and chemical quantities that characterize mechanisms within subsystems and signals sent between them. These emergent properties depend simply on the patterns of interconnection.

Strategies for automatic control

Three basic strategies for organizing information flow in automatic control processes are negative feedback, feedforward, and adaptive control (9). Figure 3 contrasts the structural features of the three control strategies and also illustrates how they can be used in combination.

In all cases, the ultimate target of control is a controlled system. A system is said to be controlled when its forcing function inputs (Fig. 3) are manipulated to
cause a particular output, designated the controlled variable, to vary in some prescribed manner or to remain constant at a prescribed value. The other set of inputs to the controlled system are called disturbances inasmuch as they cause undesired changes in controlled variables.

A feedback controller generates forcing functions by comparing desired performance as dictated by command signals with actual performance as monitored by a feedback loop. The method of comparison is not critical; the essential requirement is that there be a closed loop of continuous control that uses changes in controlled variables to generate forcing functions that in turn oppose those changes (Fig. 3).

A feedforward controller, by exclusion, generates commands without using continuous negative feedback, i.e., its moment-to-moment operations are open loop. Output from a feedforward controller can be sent either to a feedback controller as a command (as shown in Fig. 3) or directly to the controlled system as a forcing function. Its inputs specify the goals or targets of the overall control process. Sensors that monitor disturbances also provide useful inputs when feedforward is used for regulation.

An adaptive controller modifies the elements of a control system rather than causing immediate changes in output. The purpose of such modifications is to improve the properties of feedforward or feedback controllers, or to promote beneficial alterations in the controlled system. Although an adaptive controller uses feedback information, it does so in a slow or intermittent manner. Usually one defines an adaptive modification as a change in the moment-to-moment properties of a system that occurs over a time span of several to many responses.

REGULATORY FUNCTION

A control system that is designed primarily to compensate for disturbances is usually called a regulator. The maintenance of homeostasis is primarily a regulatory function, whereas the production of movement involves generalized aspects of control in addition to regulation. In this section I contrast feedback and feedforward as regulatory strategies for homeostasis (9).

Simplicity and generality of feedback

The main advantages of feedback concern its computational simplicity and its ability to compensate for all categories of disturbance regardless of their source. Figure 4 will serve to illustrate computational simplicity. In this diagram a single neuron functions as a complete feedback controller. Excitatory input to the neuron is assumed to deliver command signals that are compared, via the mechanisms of synaptic excitation and inhibition, with a feedback signal sent from a sensory receptor that monitors the controlled variable. The output of the neuron thus represents the error, namely, the difference between the commanded performance and the actual performance as registered by feedback. This error is then amplified (divergence in the axonal terminations performs amplification) and sent as a forcing function to the controlled system where its acts to counteract disturbances.

Single endocrine cells can also function as a complete feedback controller. For example, the β cells of the pancreas receive commands from sympathetic and parasympathetic nerve fibers and feedback about plasma glucose concentration from glucose receptors in the cell membrane. Because the rate of insulin secretion is inhibited by sympathetic activity and excited by glucose, secretion rate functions like an inverted error signal. Insulin is then distributed by the circulation (serving the amplification function) to target cells. The insulin concentration at these sites serves as a forcing function in the control of glucose concentration.

In spite of its computational simplicity, feedback is remarkably general in its regulatory capability in that it compensates for all categories of disturbance. This
Attractive feature occurs because feedback sensors (e.g., glucose receptors) are situated to signal any alteration in the regulated variable (glucose concentration), regardless of the particular disturbance that causes it (eating, exercise, or shivering). Error detection, amplification, and the generation of an appropriate forcing function to counteract the disturbance follow automatically.

Trade-off between error, speed, and stability

The disadvantages of feedback are 1) compensation is generally incomplete, 2) responses may be slow, and 3) too much feedback causes instability. The extent to which negative feedback reduces steady-state errors caused by disturbances is uniquely determined by a single parameter called the loop gain of the system. As the name implies, loop gain $G_l$ is the net amplification in the total pathway around a feedback loop; it is a dimensionless number. The amount of error attenuation $A_e$ is then given by the simple equation

$$A_e = \frac{1}{1 + G_l}$$

If the loop gain is 10, as it is for the respiratory regulation of $P_{CO_2}$ (10), error attenuation will be $1/11$, and all errors produced by disturbances will be reduced to 9% of what they would be in the absence of feedback. It is clear that higher values of loop gain will result in greater error reduction, but there is a trade-off because too high a gain causes instability in the form of feedback oscillations. Physiological control systems generally have modest gains and are quite stable, although they may become unstable when disease processes alter the properties of the system. For example, Cheyne-Stokes breathing is a cyclic variation in ventilation that may result when disease processes lengthen the delay between changes in blood gas concentration and the corresponding compensatory responses. It would appear that evolutionary pressures have pushed the values of loop gain in physiological systems about as high as they can go without excessive danger of instability.

Another factor that enters into the trade-off between steady-state error and stability is the speed of response. Loop gain can be raised to substantially higher values and yet not provoke instability if one is willing to limit response speed. This three-way trade-off is well illustrated by blood pressure regulation where seven separate feedback loops that contribute to the regulation of arterial pressure have been identified (11). The fastest of these, the baroreceptor reflex, operates over a time course of seconds but has appreciable error owing to a low loop gain, somewhere between 1.6 and 7, depending on the method used to measure it. In contrast, one of the slowest mechanisms, a loop that involves the kidney, operates over a sluggish time course of days, although it has very high gain with essentially no steady-state error.

Feedforward regulation

Feedforward is a useful regulatory strategy that can be used effectively in combination with feedback. It is capable of overcoming each of the three disadvantages of feedback listed above. Specifically, feedforward can 1) improve the speed of response, 2) cancel steady-state errors, and yet 3) not provoke instability. Disturbances generally occur in advance of the effects they provoke. Thus, if a sensor is situated to detect the disturbance, this information can be sent immediately to a feedforward controller as shown by the feedforward path in Fig. 3. The controller can then generate a corrective command that anticipates changes in the controlled variable. If an appropriate command is chosen, it can actually prevent the controlled variable from ever changing.

A simple example occurs in temperature regulation. Thermoreceptors within the body function as conventional feedback sensors, because they respond to core temperature, which is the controlled variable.
trast, thermoreceptors in skin function as feedforward sensors, because they are sensitive to changes in environmental temperature, which constitute disturbances to thermoregulation. Thus, decreases in environmental temperature are rapidly sensed by skin thermoreceptors, and compensatory thermoregulatory responses are initiated before there is any appreciable fall in body temperature.

A more complex feedforward mechanism appears to be responsible for the cardiovascular and respiratory responses to exercise. The pronounced metabolic vasodilation of muscle arterioles during exercise is a disturbance to blood pressure regulation that would be expected to reduce arterial pressure by 10–20 mm Hg, based on the assumption that the only compensatory mechanism is negative feedback and that the loop gain is approximately four (9). Instead, one observes no reduction in arterial pressure, or even a slight rise. Furthermore, one often sees an anticipatory increase in blood flow and pressure just before or at the onset of exercise. Both the cancellation of steady-state error and the anticipatory response are explained by postulating a feedforward command that increases the set point of the baroreceptor reflex. The situation is similar for the respiratory system, where minute ventilation increases abruptly at the onset of exercise before any changes in blood gas concentration, and normal gas concentrations are well maintained during the ensuing exercise when muscles greatly increase the production of carbon dioxide and the utilization of oxygen.

Mechanisms mediating feedforward regulation

The mechanisms responsible for generating and sending feedforward commands to the cardiovascular and respiratory systems during exercise are only partially understood (12). Although much experimental effort has been devoted to finding peripheral receptors, such as venous CO₂ sensors, that might mediate the respiratory response to exercise, these attempts have been largely unsuccessful. It thus seems likely that these feedforward commands originate within the central nervous system. For example, Fig. 5 shows how signals that the motor system uses to initiate locomotion and other forms of muscular exercise could also be used to initiate feedforward actions on the cardiovascular and respiratory systems, thus producing a coordinated exercise response. This diagram also illustrates how coordination between feedback and feedforward mechanisms can be achieved.

The disadvantages of feedforward are that 1) the computations required may be complex and 2) errors in response are not corrected. For example, a key problem faced by feedforward controllers of circulation and respiration is matching the magnitude of feedforward commands to the degree of exercise. This is likely to be a complex problem, because energy expenditure depends on the type of exercise and on the precise mechanical interaction with the environment, and cannot just be proportional to the magnitude of a motor signal. If the controller makes an erroneous calculation, it will result in a persistent error. For example, if the controller calculated too large a feedforward command, blood pressure would be excessively elevated and/or arterial CO₂ would be depressed throughout the entire period of exercise.

Because the observed responses are in fact remarkably well matched to the degree and type of exercise, one concludes that there must be special adaptive mechanisms that periodically adjust the feedforward con-

![Diagram](image.png)

**Figure 5.** Coordination of feedforward and feedback control of the circulation. In analogy with the general scheme in Fig. 3, the feedback controller for the circulation sends its forcing functions to a controlled system, the heart and vasculature, to regulate the controlled variable, blood pressure. Coordination with feedforward control is achieved by sending the feedforward command to the feedback controller where it serves as a set point for blood pressure regulation. The feedforward controller requires adaptive adjustment to match the set point to the degree and type of exercise. The diagram also shows how circulatory control may be integrated into a generalized exercise response.
controllers. I will come back to this important concept of adaptive control after I have reviewed how feedback and feedforward are used to control movement.

**CONTROL OF MOVEMENT**

The emphasis in the previous sections has been on regulation, where the apparent goal is to maintain controlled variables constant. It is clear that feedback and feedforward are both quite effective as regulatory strategies, and that homeostatic systems often use the two in combination. Now I wish to turn to the control problem, where the goal is to cause the controlled variable to vary in some prescribed manner rather than remain constant (9). Here I will draw on examples of limb (13, 14) and eye (15) movement control. Although feedback can help to improve performance in some motor tasks, feedforward strategies often are more effective.

Control strategies for goal-directed movements

Movements are made in response to visual, auditory, or somesthetic stimuli, or they can be made to remembered or imagined positions in space. In the case of visuomotor coordination, there are reasonably clear goals, namely, to project the arm toward visual targets, to grasp or manipulate them, or simply to aim the eyes at them.

Figure 6 diagrams three sequential stages of visuomotor coordination. First, a visuomotor controller recognizes potential targets and generates motor commands suitable for the acquisition or manipulation of visual objects. In the second stage, these central motor commands are translated into suitable patterns of motor discharge by a motoneuronal network. In the third stage, muscles activated by motor discharge interact with the mechanical load to determine the actual trajectory of limb or eye position, the controlled variable of the overall system. As will become apparent in the subsequent discussion, the three stages in Fig. 6 are roughly analogous to the feedforward, feedback, and controlled system stages shown in Figs. 3 and 5.

For limb muscle control, motoneuronal networks in the spinal cord serve as feedback controllers. Motor neurons together with interneurons in reflex pathways function as summing junctions analogous to the simpler single-neuron controller in Fig. 4. This network of summing junctions combines proprioceptive feedback from muscle stretch receptors with descending motor commands to produce a forcing function in the form of motor discharge. For eye muscle control, the proprioceptive feedback loop is absent, and the motoneuronal networks operate as feedforward elements.

Why is proprioceptive feedback to motor neurons used to control movements of the limb but not of the eye? One idea holds that feedback is present to provide load compensation. The limbs are used to hold tools and manipulate objects and, correspondingly, must operate against highly variable loading conditions. In contrast, the eyes have a relatively fixed load consisting of the eyeball and orbit. Although high-gain length and velocity feedback could be used to remove a dependence of limb movements on loading conditions, the evidence indicates that gain is relatively low, compensation is poor, and the observed pattern of feedback actions is actually inconsistent with load compensation.

According to another theory, proprioceptive feedback serves to regulate stiffness. Stiffness is the ratio of length change to force change, in analogy with a spring. Having muscles behave like springs is advantageous in absorbing the impacts of mechanical interactions between the body and the world (like shock absorbers in automobiles). The mechanical stiffness of limb muscles is highly variable, and proprioceptive feedback compensates well for these variations, thus creating a reliable spring. Proprioceptive feedback also compensates for the slow response time of skeletal muscle, thus improving the dynamics of movement trajectories. Eye muscles are faster and less variable than limb muscles, and they do not have mechanical interactions with the world, which may explain the absence of peripheral feedback in this system.

The visuomotor controller in Fig. 6 has the job of computing appropriate motor commands. The retina supplies visual input about potential targets for a movement and visual feedback about current position. The

![Figure 6](image)

*Figure 6. Coordination of movement. A visuomotor controller uses visual information about potential targets, intermittent visual and proprioceptive feedback, and internal feedback to generate feedforward motor commands. A motoneuronal network functions as a feedback controller to produce motor discharge, which serves as a forcing function. The muscles and their mechanical load constitute the controlled system.*
utility of visual feedback is marginal, however, owing to the time delay associated with visual processing. Time delays always increase the tendency for feedback loops to oscillate, and the magnitude of visual delay effectively nullifies the utility of continuous negative feedback in visuomotor tracking. In addition, muscle proprioceptors provide information about current limb position to the visuomotor controller. Although the time delays in this loop are shorter than the visual delays, they are nevertheless too long to be used for continuous feedback control.

One strategy the brain uses to circumvent these problems is to issue motor commands independently of feedback information except at discrete intervals. Although this constitutes feedback in the general sense of the word, one can also view this use of intermittent feedback as a form of feedforward control. In essence, the visuomotor controller uses visual and proprioceptive information to formulate a motor command. However, after the command is issued, this controller operates in a feedforward fashion until a movement segment is completed, or at least until it is well under way. It then uses a short-term store of visual and proprioceptive information to update its feedforward command.

As an additional strategy, the brain uses internal negative feedback loops as a substitute for normal feedback. These loops are stable because they have short time delays. The internal feedback shown in Fig. 6 sends the visuomotor controller an effereence copy of the motor command, as a substitute for actual position information. This signal is used to predict the position that is likely to result some time in the future. When internal feedback loops are used as a substitute for external loops, the overall system can no longer compensate for disturbances, which eliminates one of the key advantages of normal feedback, as discussed before. Here it is important to note that the controller, as an entity, operates in a feedforward mode, even though it contains an internal feedback loop.

Mechanisms for producing feedforward commands

Feedforward commands are time-varying signals that could be produced simply by amplifying and filtering time-varying sensory input. This simple strategy is used in the vestibuloocular reflex. At the other extreme, feedforward commands could be generated de novo by central pattern generators that receive no sensory inputs other than brief triggering events. This approximates the situation for some invertebrate pattern generators. At present, we know relatively little about the mechanisms for the production of feedforward commands in vertebrate motor systems. However, one anticipates that the mechanisms will occupy a continuum between the two extremes just described.

As an example of a feedforward controller that is relatively well understood, I will describe the feedforward mechanism used to command saccadic eye movements (15). Once a target is selected by the visual system, a network of brain-stem neurons generates what is referred to as a pulse-step command. A large pulse component moves the eyes rapidly to a new position and a smaller step component holds the eyes at the new position.

The controller that generates pulse-step commands is considerably more complex than the feedback controllers discussed earlier. Current models include several elements as shown in Fig. 7—a pulse generator, an integrator that converts the pulse to a step, a vari-

Figure 7. Model of the feedforward controller for saccadic eye movements. A triggered pulse generator uses information about target position and internal feedback to produce pulses. The integrator converts the pulses into the step part of the command. A summing junction combines step and pulse components, after the amplitude of the latter has been adjusted, to produce the composite pulse-step motor command that drives eye movements. An adaptive controller is needed to adjust pulse-to-step ratios and to match overall command amplitudes to target positions.
able gain element that permits adjustment of pulse amplitude, and a summing junction that produces the composite pulse-step command. The simplest element is the summing junction, which from a mechanistic viewpoint represents the same order of complexity as the complete feedback controllers discussed earlier. The cellular mechanisms that underlie the pulse generator, integrator, and variable gain elements have not yet been identified, but one expects them to include special membrane channels and other mechanisms more complex than the simple excitatory and inhibitory synaptic processes that form feedback controllers. This feedforward controller is thus considerably more complex than a typical feedback controller.

ADAPTIVE STRATEGIES

Whereas feedback and feedforward are strategies for immediate resolution of control problems, adaptation is a form of long-range planning. On the input side, an adaptive controller gathers information about performance and evaluates it over some period of time before coming to a decision. On the output side, adaptive actions alter the way the system will respond to future inputs, rather than producing immediate responses. Because of these information storage features, an adaptive system is capable of progressive improvement in performance, and it can adjust to entirely new situations. Its main disadvantages are that it is slow and it may be complex computationally.

Although the adaptive control of feedback controllers and of controlled systems can be useful, adaptive control is particularly effective (and necessary) as an adjunct to feedforward control. Thus, in this section I will emphasize adaptive actions on feedforward controllers and will provide a few examples of mechanisms that could be used to implement adaptive control.

Adaptive adjustment of feedforward controllers

As mentioned earlier, feedforward controllers generally make persistent errors unless they are adjusted by an adaptive controller. In the case of saccadic eye movement control, two types of error are prevented by adaptive mechanisms. One mechanism adjusts the pulse-step ratio. The selection of an appropriate ratio for this composite command is critical because a mismatch will cause too large or too small an initial movement with a slow postsaccadic drift to the final position. This drift must be eliminated to prevent blurred vision. A second mechanism adjusts the overall magnitude of the eye movement command, thus preventing dysmetric (wrong-sized) eye movements. Figure 7 indicates likely sites of action of these adaptive adjustments to the saccadic command generator.

Adaptive mechanisms are even more important in the control of limb movements. In addition to the basic problem of adjusting the speed, damping, and magnitude of simple movements, one needs to adjust to mechanical loads that vary over a wide range, and one must control the angular positions and torques about a large number of joints simultaneously. It is likely that both of these tasks are handled in an adaptive, feedforward manner.

Although the requirement for adaptation adds complexity to the strategy of feedforward control, it also adds valuable versatility. Once a feedforward mechanism for the generation of motor commands has been implemented, a variety of simple cues can be used to trigger the movements. For example, crude somatosensory cues at the onset of a mechanical disturbance are used to initiate movements that compensate for disturbances before the latter have completed their disturbing actions. Similarly, the snap of a twig or touch of a limb are simple sensory events; yet they can be used to trigger orienting responses that allow the animal to locate the source of the stimulus and react to it. Via the mechanism of associative conditioning, a great variety of sensory events can be used to trigger an equal variety of movements selected from the animal's repertoire. Such flexibility in sensorimotor relations is a hallmark of our remarkable motor skills.

Adaptive controllers

In the previous section I discussed several examples of how the adaptive adjustment of feedforward and feedback controllers can improve performance. However, I have not yet dealt with the issue of how an adaptive controller actually functions, i.e., how does it know when to make an adjustment and how much to adjust (9).

In engineering systems, performance is typically evaluated by some error function derived from the difference between desired and actual performance (16). For the model reference type system shown in Fig. 8, a desired output is computed by sending the system input through a reference model that has been chosen to represent the ideal properties of the controlled system. This desired output is compared with actual output to compute instantaneous error. The latter is then compiled over some time period to compute an integrated error function. If the integrated error exceeds a criterion level, the evaluator in Fig. 8 might decide to make an adjustment. Adjustments can also be made continually, with the magnitude of the adjustment proportional to integrated error.

The structure and innervation of muscle spindle receptors suggest a model reference computation (13). Motor commands are sent to intrasural muscle fibers within the muscle spindle at the same time they are sent to the main muscle, and the sensory endings in spindles detect the difference between the amount of intrafusal and main muscle shortening. Thus, spindle output is analogous to the instantaneous error signal in a model reference system.

Because muscle spindles project to motor neurons and modify the forcing function sent to the main muscle, does this system constitute a simple form of adaptive control? The answer is no for two reasons. First, the system lacks a process that compiles error over time.
before making a judgment about the necessity for an adaptive adjustment. Second, feedback from spindle receptors has an immediate effect on motoneuronal output whereas adaptive adjustments typically produce no immediate output, but rather change the way the control system responds to its next trial. This example clarifies a point I made earlier, namely, that adaptive controllers certainly use feedback; however, they do so in a slow or intermittent manner. The immediate use of the spindle's reference error instead represents a variation on negative feedback called conditional feedback.

Currently, we are at a primitive stage in understanding the adaptive mechanisms used by the brain. Signals such as the reference error from spindles are sent to the brain and may be used there to compute adaptive adjustments; however, a simpler mechanism from a computational standpoint is hypermetrophy, and its inverse, atrophy. This type of adjustment applies both at the organ level and at the level of central synapses where we usually refer to it as sensitization, up-regulation, or long-term potentiation. The phenomena of associative and operant conditioning are somewhat more elaborate processes, although the cellular mechanisms may not be that different. The recent evidence for a cerebellar involvement in these types of learning (17) is particularly interesting in view of the known cerebellar involvement in the adaptive control of eye movements (18) and evidence that the cerebellum may be a source of adjustable motor programs (19). Although we still lack good examples illustrating how plasticity at the cellular level is coupled to signal processing on the more global level required to understand the adaptive control of movement and homeostasis, the rapidity of recent progress suggests that exciting new developments will soon be forthcoming.

REFERENCES


