THE APPARENT EASE OF SKILLED MOTOR BEHAVIOR MASKS THE COMPLEX NEURAL PROCESSES INVOLVED IN THE CONTROL OF MOVEMENT. TO HANDLE THE COMPLEXITY OF MOST MOTOR TASKS, OPTIMAL FEEDBACK CONTROL SUGGESTS THAT THE BRAIN CONTINUOUSLY PROCESSES SENSORY FEEDBACK AND SELECTIVELY COMPENSATES FOR NOISE DISTURBANCES AS WELL AS EXTERNAL PERTURBATIONS. MOTIVATED BY THIS POWERFUL PREDICTION, RECENT STUDIES HAVE USED PERTURBATION PARADIGMS TO INVESTIGATE THE NEURAL CONTROL OF MOVEMENT. AFTER INTRODUCING THE BASIC MATHEMATICAL CONCEPTS OF OPTIMAL FEEDBACK CONTROL, WE REVIEW EVIDENCE THAT THE BRAIN GENERATES FLEXIBLE FEEDBACK STRATEGIES FOLLOWING PERTURBATIONS PERCEIVED FROM VISUAL FEEDBACK (E.G., A SUDDEN CHANGE IN THE TARGET LOCATION), AS WELL AS MECHANICAL PERTURBATIONS APPLIED TO THE LIMB. IMPORTANTLY, WE HIGHLIGHT EVIDENCE THAT THE MOTOR SYSTEM CAN GENERATE GOAL-DIRECTED RESPONSES IN AS LITTLE AS 50–60 MS FOLLOWING A MECHANICAL PERTURBATION. A TRANSCORTICAL FEEDBACK PATHWAY THROUGH PRIMARY MOTOR CORTEX APPEARS TO PLAY AN IMPORTANT ROLE IN THESE RAPID CORRECTIVE RESPONSES.

ELITE ATHLETES PUSH THE LIMITS OF THE SENSORMOTOR SYSTEM, INTEGRATING SENSORY INFORMATION TO GENERATE RAPID YET REMARKABLY PRECISE MOVEMENTS. A GOOD EXAMPLE IS A HOCKEY PLAYER BREAKING AWAY FROM HIS DEFENDERS. IN A SPLIT SECOND, THE PLAYER HAS TO READ THE GOALTENDER’S MOVEMENT AND DECIDE WHETHER TO SHOOT THE PUCK OR FAKE THE GOALTENDER AND WAIT FOR AN OPENING. EVEN THE SIMPLEST MOVEMENTS THAT WE PERFORM IN DAILY LIFE, SUCH AS REACHING FOR A CUP OF COFFEE, ALSO INVOLVE COMPLEX SENSORMOTOR COORDINATION. THE ABILITY TO USE SENSORY INFORMATION TO FLEXIBLY GUIDE, CORRECT, OR MODIFY OUR ACTIONS IS THE HALLMARK OF SKILLED BIOLOGICAL CONTROL.

RECENTLY, OPTIMAL FEEDBACK CONTROL (OFC) HAS BEEN USED AS A MODEL OF HOW THE BRAIN PROCESSES SENSORY INFORMATION TO CONTROL MOVEMENT. A POWERFUL FEATURE OF THIS MODEL IS THAT IT DESCRIBES HOW THE MOTOR SYSTEM SHOULD HANDLE PERFORMANCE ERRORS CAUSED BY NEURAL VARIABILITY OR ENVIRONMENTAL DISTURBANCES. THIS FEATURE HAS RENEWED INTEREST IN FEEDBACK RESPONSE STRATEGIES, IN PARTICULAR BECAUSE THEY MAY PROVIDE A WINDOW INTO THE VOLUNTARY CONTROL OF MOVEMENT. IN THIS CHAPTER, WE INTRODUCE THE BASIC NOTIONS UNDERLYING OPTIMAL CONTROL THEORY AND DISCUSS HOW THIS APPROACH MAY HELP US IDENTIFY PROBLEMS THAT THE BRAIN MUST SOLVE TO PERFORM EVEN THE SIMPLEST MOVEMENTS. THEN, WE REVIEW RECENT FINDINGS THAT EMPHASIZE THE SIMILARITY BETWEEN BIOLOGICAL CONTROL AND THE SOPHISTICATION OF OPTIMAL CONTROL MODELS. IN PARTICULAR, WE FOCUS ON PERTURBATION PARADIGMS SHOWING THAT MANY ASPECTS OF OPTIMAL CONTROL MODELS ARE OBSERVED IN CORRECTIVE RESPONSES GENERATED BY HUMANS: (1) CONTINUOUS PROCESSING OF SENSORY FEEDBACK UNDERLIES THE CONTROL OF MOVEMENT, AND (2) FEEDBACK CONTROL IS TAILORED TO THE CONSTRAINTS IMPOSED BY THE TASK AT HAND. WE FINISH OUR CHAPTER BY BRIEFLY DISCUSSING HOW SOPHISTICATED MOTOR BEHAVIOR MAY BE LINKED TO PROCESSING IN DISTRIBUTED BRAIN CIRCUITS, HIGHLIGHTING RECENT EVIDENCE THAT NEURAL PROCESSING IN PRIMARY MOTOR CORTEX (M1) MAY POSSESS SOME OF THE ATTRIBUTES REQUIRED FOR FLEXIBLE FEEDBACK CONTROL.

**Optimal control: Definitions and applications in neuroscience**

Flash and Hogan (1985) introduced optimal control principles to movement neuroscience almost 30 years ago. Intuitively, this approach is based on the assumption that the brain selects motor commands that maximize or minimize a performance criterion. In the context of reaching movements, Flash and Hogan suggested that the brain selects motor plans that minimize the derivative of the hand’s acceleration (or the jerk). This hypothesis was justified by the fact that point-to-point movements tend to be smooth with a bell-shaped velocity profile, which is reproduced nicely by minimizing the derivative of the hand’s acceleration during reaching movements. Following Flash and Hogan’s work, a wealth of studies have proposed biological cost functions that incorporate kinetic parameters (e.g.,
minimum torque change; Nakano et al., 1999; Uno, Kawato, & Suzuki, 1989) and energy consumption (Biess, Liebermann, & Flash, 2007; Berret, Chiovettò, Nori, & Pozzo, 2011) to identify movement variables that the motor system may control and optimize.

This approach is grounded in the theory of optimal control, a formalism that applies optimization principles to describe what the motor system should do according to how our limbs move, as well as the performance criteria (e.g., energy consumption) and constraints (e.g., time constraint) associated with movement. The following section outlines the basic notions of control theory and defines (optimal) control problems that are often encountered in movement neuroscience.

**Dynamical Systems and Control Problems** At the basis of control engineering is the notion of a dynamical system: a set of variables evolving as a function of time. For instance, the angular motion of a body segment can be seen as a dynamical system described by state variables, such as the joint angle and velocity. In general, the evolving state of a dynamical system can be described by a differential equation of the form:

\[
\dot{x} = f(x, u),
\]

where \( x \) is the vector of state variables and the dot expresses its time derivative. This derivative is a function of the state vector itself and an additional variable, \( u \), called the control vector. It is assumed that the controller influences the state of the system by changing the value of the control vector. For example, varying muscle activity changes the torque acting on a joint and alters segmental motion through the dynamical properties captured in the function \( f \).

With these definitions, we can define a control problem as follows: find a time-varying control vector that steers the state variables to a desired location. Assuming that the initial state \( x_0 \) is known, the problem is to find a control function \( u(t) \), \( b_0 \leq t \leq b_f \), such that the solution of Eq. 1:

\[
\begin{align*}
\dot{x}(t) &= x_0 + \int_{b_0}^{t} f(x(s), u(s)) ds,
\end{align*}
\]

meets the constraints of the control problem. A reaching movement, for example, may be described as a control problem where the brain must steer the hand to the spatial location of a goal target. Expressing a simple task such as reaching as a control problem is a powerful approach to identify the challenges that motor control presents for the brain. As we will see, even the simplest movements impose complex sensorimotor transformations.

**Deterministic Optimal Control** In general, the solution of a particular control problem is not unique. This also applies to biological motor control, where reaching movements may follow distinct paths to the same target or even have different velocities along the same movement path. Given that each of these movements satisfy the goal of reaching the target (i.e., motor equivalence), extensive research has been conducted to identify how the brain selects one control solution among infinitely many alternatives. One way to reduce the set of possible movement solutions is to constrain the problem using a cost function. For instance, we may be interested in applying a sequence of joint torques that allows us to reach a target while minimizing the intensity of muscle activity to avoid fatigue. In this example, the cost is directly related to the motor command, and the problem is to find the reaching path that minimizes muscle energy expenditure. This approach uses optimization principles to determine the best way to reach the target among all possible movement solutions.

A typical cost function contains a final cost, \( g(x) \), and a running cost, \( L(x,u) \), that accumulates along the trajectory followed by the state variables:

\[
\begin{align*}
J(x,u) &= g(x(t_f)) + \int_{b_0}^{t_f} L(x(t), u(t)) dt.
\end{align*}
\]

With these definitions, an optimal control problem can be defined as follows: find a control function that minimizes \( J(x,u) \) (Eq. 3), subject to the initial condition \( x(t_0) = x_0 \) and to the system dynamics (Eq. 1). It can be shown that, under the optimal solution, \( J(x,u) \) satisfies the Hamilton-Jacobi-Bellman equation (\( U \) represents the set of admissible control actions):

\[
-\frac{\partial f(x,u)}{\partial t} = \min_{u \in U} \left\{ L(x(u)) + \frac{\partial f(x,u)}{\partial x} f(x,u) \right\}.
\]

The function \( f(x,u) \) is the cost to accumulate from the present time until the end of the problem horizon, \( t_f \). This quantity is called the cost-to-go and plays a central role in the derivation of numerical solutions (Todorov, 2006). An intuitive interpretation of Eq. 4 is that the control vector can vary the orientation of the instantaneous direction of the state trajectory \( \langle f(x,u) \rangle \), which should ideally follow the direction that is opposite to the gradient of the cost-to-go \( (\partial f/\partial x) \). However, the optimization also takes into account the instantaneous cost \( (L(x,u)) \), and as a result, Eq. 4 achieves the best compromise between the gradient of the cost-to-go and the instantaneous cost \( (L(x,u)) \). This compromise determines the instantaneous variation of the cost-to-go \( (\partial f/\partial t) \).
The many studies that have used this approach have agreed on the general conclusion that healthy motor systems favor smooth and efficient movements. The shortcoming of this approach, however, is that because the laws of physics relate all movement parameters, virtually every meaningful cost function in the form of Eq. 3 partially captures the smoothness and efficiency of biological motor control. Also, this approach does not systematically account for the continuous update of motor commands that is necessary to correct for motor errors.

**Stochastic Optimal Control.** In general, factors that can induce motor errors and trial-to-trial variability fall into two broad categories. First, the variable activation of neural circuits induces variable motor behavior. Neural noise can be found in sensory systems, movement preparatory activity, and the activation of muscles in the motor periphery (Churchland, Afshar, & Shenoy, 2006; Faisal, Selen, & Wolpert, 2008; Osborne, Lisberger, & Bialek, 2005; Scott & Loeb, 1994; van Beers, Haggard, & Wolpert, 2004). Additionally, motor errors can be produced by external disturbances resulting from our interaction with the environment. Both neural variability and external disturbances require that the brain continuously update motor commands based on the available sensory data to produce successful behavior.

Harris and Wolpert (1998) considered the influence of neural variability on movement planning and suggested that motor commands are selected to minimize the variance of movement end points, assuming the intensity of motor noise scales with the size of the motor command. While this model explicitly considers the effect of motor noise, it does not address the online adjustment of motor commands required when disturbances alter performance. The control of stochastic processes was introduced to address this limitation. In this framework, feedback is essential to update motor commands and compensate for neural variability. Online monitoring and control are often described in terms of a state estimator combined with a controller (figure 39.1). The state estimator typically combines sensory and motor signals to compute the present state of the body (figure 39.1; optimal state estimator), and the controller uses the estimated state of the body to select control actions that best reflect the goal and constraints of the task (figure 39.1; optimal feedback control policy). This section presents the basic formalism of the problems of estimation and control of stochastic processes.

Because random (Brownian) motion does not have finite instantaneous variations, the control problem is formulated in discrete rather than continuous time (Arnold, 1974). To begin, the analog of Eq. 1 becomes:

\[ dX = F(X, u)dt + G(X, u)dW. \] (5)

In Eq. 5, the capital X signifies that the state vector is now a stochastic variable. Eq. 5 expresses that small changes in the state \((dX)\) follow a deterministic law described by the function \(F\) that captures the system dynamics as in Eq. 1, and a stochastic term that captures random disturbances in the process \((dW)\). We now convert this equation to discrete time by considering changes in the process over a time step of \(\delta t\). From the definition of Brownian motion (Arnold, 1974), the accumulation of random noise over \(\delta t\) follows a Gaussian distribution with zero mean and variance equal to \(\delta t\). We use \(\xi(t)\) to designate these Gaussian disturbances at each time step. The formulation in discrete time becomes

![Figure 39.1](image)

**Figure 39.1** Illustration of basic processes expected under the OFC framework. The selection of the behavioral task determines the feedback control policy (task selection). The purpose of the feedback control policy is to continuously process and convert sensory data into motor commands that best satisfy the task demand (optimal feedback control policy). Once the sensory feedback is processed, motor commands are sent to the peripheral motor system (biomechanical plant or musculoskeletal system). An efference copy of the descending motor command is used internally to predict the consequences of motor actions. These internal predictions are combined with feedback from sensory receptors to compute the posterior estimate of the state of the body (optimal state estimator). This state estimate is used to adjust the motor commands during the ongoing motor action.
The optimal control problem consists in finding a sequence of control variables that minimize the total expected cost, that is:

\[
J = E \left[ \sum_{t=1}^{N} L(X_t, u_t) \right].
\]

For this class of control problems, the optimal control policy turns out to be a linear function of the estimated state, denoted \( \hat{x}_t \):

\[
u_t = C_t \hat{x}_t.
\]

The sequence of optimal feedback gains, \( C_t \), is determined by the cost matrices \( Q \) and \( R_t \) in Eq. 10 and by the system dynamics \( A \) and \( B \) in Eq. 8. The result is a time-varying feedback gain that tells us how the motor system should transform the estimated state of the system into motor commands.

The optimal estimate of the state is calculated in two steps (Kalman filter). First, the prediction of the next system state is obtained by simulating the dynamics over one time step given the current motor command, \( u_t \), and taking the expected value of the outcome:

\[
\hat{x}^f_t = A \hat{x}_{t-1} + Bu_{t-1}.
\]
This prediction (or prior belief) is then corrected with the difference between actual and expected feedback, weighted by the Kalman gain:

$$\hat{z}_t = \hat{z}_t^p + K_t(Y_t - H\hat{z}_t^p).$$  \hspace{1cm} (14)

The Kalman gains are determined by the system dynamics (Eq. 8), feedback (Eq. 9), and the covariance matrices of the motor and feedback noise. The Kalman gain ($K$) specifies how much the prior estimate (Eq. 13) should be changed according to the available sensory data. Recent studies have extended the LQG framework to take properties of biological motor control into account, such as the scaling of noise variability with the intensity of the neural signal (Crevecoeur, Sepulchre, Thonnard, & Lefèvre, 2011; Qian, Jiang, Jiang, & Mazzoni, 2013; Todorov, 2005), as well as the nonlinearity of the musculoskeletal system (Li & Todorov, 2007).

A complete derivation of the optimal feedback gains and Kalman gains is beyond the scope of the present review, but can be found elsewhere (Åström, 1970; Brown, 1983; Bryson & Ho, 1975).

Figure 39.1 recapitulates the different components of the full control algorithm (estimation and control) and illustrates how they may describe some aspects of motor control. In the framework of optimal control, task selection specifies the movement goal and constraints and can be seen as the definition of the cost function (Eqs. 3 or 10). Indeed, the cost function determines which state variables will be constrained, and how much motor commands will be penalized to attain that goal. Once the cost function is defined, an optimal control policy can be derived as the solution of a well-defined problem. In this respect, the approach based on optimal control makes a theoretical link between motor behavior and the control of a biomechanical plant, which are two fundamental aspects of movement neuroscience (Scott, 2004).

Optimal control provides a normative tool to describe how the biomechanical plant should be controlled according to a given behavioral objective. The online control of movement is then realized by applying the feedback control policy (figure 39.1 and Eq. 12) to the estimated state of the body (figure 39.1 and Eqs. 13 and 14).

**Optimal Control and Internal Models**

The notion of an internal model is an important conceptual framework in motor neuroscience that is often defined as a group of neurons or circuits that mimic the input-output relationship of the peripheral motor system and environment. A traditional view was that inverse models transform a desired movement into a sequence of motor commands, and forward models predict the consequences of these motor commands (for a review, see Kawato, 1999). Pairing inverse and forward models according to the intended movement was proposed as a model for sensorimotor coordination (Wolpert & Kawato, 1998).

Optimal feedback control generalizes the neural computations identified within the framework of internal models and bridges the gap between movement planning and execution by providing a goal-related feedback control policy (Eq. 12 for linear systems). In the optimal control framework, the controller must transform the movement goal expressed by the cost function (Eqs. 3 or 11) into a control policy. This operation is similar to the one performed by inverse models, in the sense that they both use knowledge of the body dynamics to map intended movements into motor commands. The notion of a forward model is also present in the optimal control framework. A common perspective is that forward models predict the consequences of motor actions, thereby allowing the brain to compensate for their effect ahead of sensory information. The computation of a prior belief about the state of the body can be seen as a forward prediction of the future state of the body (Eq. 13), based on the current motor commands and internal knowledge of the system dynamics (represented by the matrices A and B; figure 39.1, musculoskeletal system). Motor prediction from forward models is therefore a critical component of optimal feedback control models.

Aside from the problems related to the derivation of the control policy, an important challenge for the motor system is the computation of the state estimate. Indeed, we have only partially addressed the problem of state estimation with the Kalman filter, dealing with the variability of prediction and sensory signals. Additionally, the brain must cope with time delays resulting from the transmission of neural signals along the nerves. Given the presence of sensory delays, the hypothesis that the brain uses state estimation requires converting delayed sensory feedback into present estimates of the state of the body, which involve prediction based on sensory signals that is independent from the motor prediction (Ariff, Donchin, Nanayakkara, & Shadmehr, 2002; Mehta & Schaal, 2002). Compatible with this prediction, we recently showed that rapid sensory predictions are performed following a perturbation (Crevecoeur & Scott, 2013).
internal representation of the body and environmental dynamics is available, while uncertainty is handled by considering the presence of random noise in the system. However, uncertainty in the internal model of dynamics can also alter the control of a movement. For instance, the inertia of the limb differs slightly according to the weight of a watch, clothing, or hand-held objects. In addition, muscle dynamics may vary depending on the level of background activity, biochemical factors, or fatigue (Zahalak, 1981). This class of model disturbances does not fall under those disturbances modeled by random noise, as they potentially introduce systematic biases during movement.

In general, researchers have approached this problem with learning or adaptation studies (Shadmehr, Smith, & Krakauer, 2010; Wolpert, Diedrichsen, & Flanagan, 2011). In this framework, changes in motor commands reflect adaptive adjustments of how the brain represents environmental dynamics. While tremendous progress has been made with this approach, a clear shortcoming is that the body and environment can change more rapidly than the adaptation processes typically investigated in motor learning studies (e.g., learning curves varying over tens to hundreds of trials). For instance, muscle dynamics rapidly change during effort without giving us the chance to practice tens of trials to adapt to those changes.

Engineers have developed an approach based on the concept of robustness to deal with these internal model uncertainties. The idea is to make the control design as insensitive to model errors as possible (Bhattacharyya, Chapellat, & Keel, 1995; Doyle, Francis, & Tannenbaum, 1992). This approach typically focuses on properties of the controller rather than on the actual system trajectories emphasized in the classical optimal control approach. An important theoretical result is that the controllers that are the most robust against model errors do not always correspond to the controllers that are the most efficient (Boulet & Duan, 2007; Michiels & Niculescu, 2007). In other words, improving the robustness of control may degrade performance, whereas optimizing a performance criterion can make the control design more fragile to model errors. Compatible with these principles, previous studies have suggested that motor performance is altered to maintain performance or preserve movement smoothness in conditions of higher uncertainty (Grevecouer, McIntyre, Thonnard, & Lefèvre, 2010; Ronsse, Thonnard, Lefèvre, & Sepulchre, 2008). However, to our knowledge, the trade-off between the efficiency and robustness of biological motor control and its influence on motor planning and execution has not been thoroughly investigated. Given that internal models of body and environmental dynamics can never be known exactly, robustness may be an important consideration in motor neuroscience.

**Application to biological control: Flexible sensorimotor control strategies**

The motor system has a remarkable ability to perform successfully while never reproducing exactly the same movement. This consistent success in the presence of variability suggests the central nervous system is well aware of the constraints of the task at hand and is less concerned about errors that do not affect performance. This tendency is often referred to as the *minimum intervention principle* (Todorov & Jordan, 2002) and is captured by the ability to ignore limb deviations that do not interfere with task completion. The same idea is reflected in the notion of *structured variability* or an uncontrolled manifold, where limb and whole-body motion are more variable along dimensions that are irrelevant for the task (Balasubramaniam, Riley, & Turvey, 2000; Scholz & Schoner, 1999; Valero-Cuevas, Venkadesan, & Todorov, 2009; Cluff et al., 2011).

Optimal feedback control provides a framework for us to understand task-related error corrections. Because motor commands have a cost, there is no need to control movement errors that do not interfere with the intended goal. This trade-off between behavioral performance and motor costs, expressed in a straightforward way by the quadratic cost function in Eq. 10, is only possible if the brain continuously processes sensory data to select control actions that are appropriate for the goal and constraints of the task. In agreement with this principle, we review several studies emphasizing that this type of flexible, task-dependent feedback control underlies both voluntary motor behavior and responses to external perturbations.

**Visuomotor Feedback Responses** Liu and Todorov (2007) provided compelling evidence for flexible biological control strategies by demonstrating that feedback responses depend on the hand’s position when a goal target changes location during reaching. In this experiment, visual target perturbations were introduced at the start (early) or near the end of a reaching movement (late; figure 39.1A) in a task where subjects were instructed to stop at a peripheral target. When the target location was perturbed early in the movement, the participants corrected their hand path smoothly (figure 39.1B). In contrast, hand path corrections were incomplete when the same perturbation was introduced late in the movement (figure 39.1B). Liu and Todorov suggested that the dependency of the correction upon...
the timing of the target jump was caused by the inherent trade-off between end point accuracy and motor costs. In order to stop near the target, the controller became more sensitive to movement velocity than end point accuracy, leading to consistent under-compensation for target errors introduced at the end of the reaching movement. This systematic under-compensation was reduced when the task instructions were to hit rather than stop at the target (figure 39.1B). Hitting the target removes the constraint on final hand velocity and allows participants to fully correct for positional errors introduced near the target.

Several other attributes of visuomotor control have been addressed in the context of target or cursor (i.e., hand feedback) jumps. In agreement with the principles of stochastic optimal control, several studies have shown that visual perturbation responses are modulated by the reliability of the cursor or target location (Izawa & Shadmehr, 2008; Körding & Wolpert, 2004), by the shape of the goal target (Knill, Bondada, & Chhabra, 2011), and by the relevance of the visual cursor jump relative to the reaching target (Franklin & Wolpert, 2008). As we mentioned earlier, the aim of OFC models is not to eliminate all variability, but rather, allow it to accumulate in dimensions that do not interfere with performance (Todorov, 2004) while minimizing it in dimensions that are relevant for task completion. Knill and colleagues (2011) outlined the same type of selective motor corrections during visuomotor control. Indeed, Knill and colleagues showed that motor corrections following lateral cursor jumps were nearly twice as large for rectangular targets oriented parallel to the movement path compared to when the target was perpendicular to the reach.

Another clear example of flexible visuomotor control is when subjects reach in the presence of visual perturbations that may or may not affect reaching performance (Franklin & Wolpert, 2008). Franklin and Wolpert characterized these selective corrections by unexpectedly shifting hand feedback during point-to-point reaching movements. The hand cursor disturbance either persisted until the end of movement (relevant), or returned to the veridical hand location before the end of the movement (irrelevant, figure 39.2D). By shifting the visual cursor location, it was shown that the motor system selectively corrects hand feedback perturbations that affect the outcome of the task (figure 39.2E), while ignoring perturbations that do not affect performance (figure 39.2F).

In summary, visuomotor perturbation studies have shown that the brain produces distinct feedback responses when the same perturbation is encountered in different behavioral contexts. Consistent with optimal control models, these results reveal that the motor system selectively corrects for visual perturbations that jeopardize task performance while taking into consideration the constraints of the task. The latency of visuomotor corrections was consistently observed in 150–230 ms (Franklin & Wolpert, 2008; Knill et al., 2011), which, after removing delays associated with signal transmission, suggests the brain can rapidly implement flexible feedback responses after a perturbation. In the following section, we present results from mechanical perturbation studies suggesting that flexible feedback responses can be implemented in as little as ~50 ms when they are mediated by rapid changes in limb afferent feedback.

**Mechanical Perturbations** Investigating how quickly the motor system implements flexible control strategies can provide important insight into the neural pathways involved in feedback control. Mechanical perturbations offer a powerful means to address this problem, because muscle afferent feedback evokes motor responses on a time scale of tens of milliseconds. In fact, when the limb is displaced by a mechanical perturbation, the motor system produces a stereotyped sequence of muscle activity, beginning with the short-latency stretch reflex (response epoch called R1: 20–50 ms post-perturbation) and ending with a voluntary response (>100 ms). The short-latency stretch reflex is the earliest of these responses, and due to its timing, it can be attributed to spinal processing. These spinal stretch responses are sensitive to joint motion, but show little of the functional complexity expressed during voluntary behavior (Pruszynski, Kurtzer, & Scott, 2008).

Between the short-latency and voluntary responses is the long-latency stretch response (R2/R3: 50–105 ms post-perturbation), which includes responses generated from multiple neural substrates (Pruszynski, Kurtzer, & Scott, 2011), including spinal (Ghez & Shioda, 1978; Matthews, 1984; Schuurmans et al., 2009) and supraspinal pathways (Evarts, 1973; Phillips, 1969). A robust observation in motor physiology studies is that feedback corrections in the long-latency time window exhibit remarkable flexibility and can be modified by the subject’s voluntary intent (Crago, Houk, & Hasan, 1976; Hammond, 1956; Rothwell, Traub, & Marsden, 1980) or the demands of an ongoing motor action (see Hasan, 2005; Matthews, 1991; Pruszynski & Scott, 2012, for a comprehensive review).

As we mentioned earlier, OFC models suggest the ability to alter feedback responses to a mechanical perturbation is a direct consequence of task-dependent sensorimotor processing (Scott, 2004). Nashed and
Figure 39.2 Visuomotor responses account for the goal of the ongoing task. (A) Subjects were instructed to reach and stop at a target ("stop" condition) that either stayed in the central location or jumped in the lateral direction after the start of the movement. Data are the population average trajectories when participants were instructed to stop at the target. Color code: black, baseline; red, early perturbation; blue, late perturbation. (B) Hand path deviation in the direction of the displaced target. Note that subjects were unable to compensate when the target jumped late in the movement, demonstrating that feedback responses depend on the task constraints. Color scheme is the same as in A. Dashed lines, “hit” condition; solid lines, “stop” condition. (C) Results from target intercept experiment. In this experiment, the target jumped laterally and then moved downward at a fixed rate. The subjects were instructed to "stop" or "hit" the target before it stopped moving. (Adapted from Liu & Todorov, 2007.) (D) Visuomotor responses only correct for errors that are relevant to the ongoing task. In the normal condition, the hand feedback cursor reproduced the hand trajectory. In the task-relevant feedback condition (orange traces), the visual cursor moved away from the hand trajectory and remained as this point for the rest of the movement. In contrast, in the task-irrelevant feedback condition (blue traces), the hand feedback cursor moved away from the hand trajectory but returned to the true hand position by the end of the movement. (E) Time course of adaptation to task-relevant feedback perturbations. Data are the mean (solid line) and standard deviation (shaded region) force difference across subjects between right and left visual perturbations (180–250 ms after cursor jump). Note that subjects produced larger corrections when the cursor displacements were relevant to the ongoing task. (F) Time course of adaptation to task-irrelevant feedback perturbations. Note that subjects did not adapt when the perturbations were irrelevant to the ongoing task. (Adapted from Franklin & Wolpert, 2008.) (See color plate 35.)
colleagues (2012) recently investigated whether long-lateness responses selectively correct for task-relevant errors when subjects made reaching movements to a circular target or rectangular bar oriented perpendicular to the reach (figure 39.3A). On certain trials, a mechanical perturbation was applied to displace the hand in the lateral direction. When the perturbation pushed the hand away from the circular target, the participants performed rapid corrective responses to direct their hand back to the target. In contrast, when the same perturbation was applied while subjects reached to the rectangular bar, the participants redirected their hand to new locations on the bar. Similar context-dependent responses were evoked when obstacles in the environment required that the participants navigate to the target through a narrow channel (figure 39.3B). These behavioral results were reproduced by an optimal feedback control model with differing sensitivity to lateral hand errors. Further, the model predicted that the shape of the goal target should influence the feedback response as early as sensory feedback about the perturbation became available. In agreement with these model predictions, differences in muscle responses between tasks were observed in as...
little as 70 ms following the perturbation, establishing that rapid motor corrections (i.e., long-latency responses) integrate muscle stretch information with knowledge about the behavioral goal and spatial features of the environment (Nashed et al., 2012).

**Flexible Bimanual Feedback Control** In the context of sudden mechanical perturbations, Marsden and colleagues (Marsden, Merton, & Morton, 1981) first outlined the task-dependency of interlimb responses, noting that long-latency muscle stretch responses in the right arm after left arm perturbations reflected the task the right arm was performing. If the right arm held a table for support, the extensors were activated to stabilize the participant following the left arm perturbation. Remarkably, subjects even reversed their corrective responses and activated the flexor muscles of the right arm if they had to stabilize a cup of tea. Perhaps the most powerful example of how the task modulates interlimb feedback responses is that muscle responses were absent if the subject grasped a loose handle and benefitted little from right arm responses. The coordinated responses observed in the muscles of the unperturbed arm clearly emphasize that online feedback control is not hard-wired but can be engaged at will, depending on the context and on the intended behavior.

Bimanual control therefore provides a remarkable tool to address how sophisticated feedback control can be distributed across different body parts. Motivated by the capacity of OFC models to exploit many different ways to attain the same movement goal (i.e., task redundancy), recent studies have examined feedback corrections in bimanual tasks by comparing motor responses when the two arms act independently or are coupled by the task demand. A compelling example of this flexibility is when one hand is gradually perturbed in a task that requires bimanual reaching movements (Diedrichsen, 2007). If each hand controls its own cursor while reaching to separate targets (two-cursor task), only the perturbed hand shows a corrective response. However, when the two arms control a single cursor (one-cursor task), displayed as the spatial average position of the two distinct cursors, perturbations applied to one hand elicit bilateral responses to correct the cursor’s trajectory (Diedrichsen, 2007). These flexible responses were reproduced by expressing the task constraints (Q in Eq. 7) for each hand independently, or as the average of the two hands. The flexibility of bilateral corrections is not restricted to changes in the size of the response, as even the direction of these coordinated responses can be reversed if required by the task (Diedrichsen & Gush, 2009).

Studies have since confirmed that sensory information from one limb in both reaching (Mutha & Sanburg, 2009) and posture (Dimitriou, Franklin, & Wolpert, 2012; Omrani, Diedrichsen, & Scott, 2013) rapidly modifies corrective responses in the other limb during the long-latency time window. When the two hands control independent cursors and are perturbed in opposite directions, robust long-latency responses are observed in both arms to counter the perturbation (Omrani et al., 2013). In contrast, long-latency stretch responses are substantially smaller when the two hands are perturbed in opposite directions while controlling a single cursor displayed at the spatial average position of the two hands. In this context, corrective responses are unnecessary because the position of the single feedback cursor is not disturbed by the perturbation. When the direction of the left arm perturbation was not predictable, stretch responses in the right arm depended on proprioceptive input from the left arm in the one-cursor condition, and were larger if both arms were perturbed in the same direction (figure 39.3C, D, and E). These differential feedback responses were not observed when each hand controlled its own independent cursor. Why should the brain distribute corrective responses when several effectors are involved in the task? Optimal feedback control predicts this behavioral pattern, since dividing the response across effectors reduces the effort and variability of motor corrections (Diedrichsen & Dowling, 2009).

**Internal Models of Multijoint Dynamics** We have so far focused on evidence that the motor system continuously processes sensory data to generate task-dependent feedback responses. It is important to recognize, however, that task-dependent feedback responses can only be achieved if the motor system has knowledge of how the body should move in response to external forces that arise from our environmental interactions or forces generated by muscles. An important feature of body dynamics is the presence of interaction torques between joints that require coordinated multijoint responses to control the motion at each joint. Extensive evidence has shown that the voluntary motor system compensates for these interaction torques to produce straight reaching movements (Gribble & Ostry, 1999; Hollerbach & Flash, 1982), but an interesting question is whether corrective responses also reflect knowledge of limb mechanics.

Previous work emphasized that mechanical perturbations evoked rapid responses in muscles that are not directly stretched by the perturbation, suggesting that coordinated motor responses occur in the long-latency time window (Gielen, Ramackers, & van Zuylen, 1988;
Figure 39.4 Long-latency responses express knowledge of multijoint limb mechanics. (A) Subjects were instructed to maintain their hand at a central target, and step-torque perturbations were applied to the shoulder and elbow joints (flexor torques at both joints, dark gray shading and denoted by (F), extensor torques at both joints, light gray shading and denoted by (E)). Stretch responses were recorded from the posterior deltoid muscle (PD) (B) Limb configuration and applied multijoint torques were selected to cause substantial elbow motion (dashed lines) but minimal shoulder motion (solid lines). (C) Posterior deltoid (shoulder extensor) muscle activity aligned on perturbation onset. Note that although there was no change in the length of the posterior deltoid muscle, there is still a robust long-latency response (excitatory and inhibitory). Data are the population-level muscle response, and shaded region corresponds to SEM. Same color scheme as in A and B. (Adapted from Kurtzer et al., 2008.) (D) Population-level response of shoulder-like M1 neurons. Shoulder-like neurons respond to the underlying shoulder torque even though local information from the shoulder is ambiguous about the underlying torque. Note that the response to the underlying torque begins about 50 ms after the onset of the shoulder and elbow perturbations. (Adapted from Pruszynski et al., 2012.)

Soechting & Lacquaniti, 1988). The question of whether these responses relate to limb dynamics was recently addressed by applying different combinations of perturbations to the shoulder and elbow. In one experiment, multijoint loads applied to the shoulder and elbow did not produce motion at the shoulder but led to either flexion or extension motion at the elbow (Kurtzer, Pruszynski, & Scott, 2008, 2009; figure 39.4A, B, and C). The authors found that there was no short-latency muscle stretch response in the posterior deltoid, a shoulder extensor, highlighting that this spinal reflex is not elicited without overt motion at the joint (figure 39.4B, C). In contrast, the long-latency response (50–105 ms post-perturbation) integrated motion information from both joints and generated a large response in the posterior deltoid to counter the shoulder flexor torque, even though there was no motion at the joint (figure 39.4C). These results clearly showed that rapid motor corrections map the sensed motion of the shoulder and elbow joints onto a response that is appropriate for the actual underlying torque rather than the observed motion pattern.

It is important to emphasize that OFC as a theory of motor behavior can only tell us what the optimal motor solution should look like. The studies presented above highlight feedback responses that possess an impressive degree of flexibility and can be modified to suit the needs of many behavioral tasks. It has been demonstrated that long-latency stretch responses are modified in different dynamic environments (Ahmadi-Pajouh, Towhidkhah, & Shadmehr, 2012; Kimura & Gomi, 2009; Krutky, Ravichandran, Trumbower, & Perreault, 2010), and a direct prediction is that corrective responses should be modulated by the novel dynamical context. Changes in corrective responses to a gradual perturbation have been observed over longer time scales (Wagner & Smith, 2008). A recent study shows that long-latency responses also express knowledge of
internal models acquired during motor learning (Cluff & Scott, 2013). This result emphasizes that adaptive changes to novel dynamics alter voluntary behavior and rapid feedback responses.

In summary, the studies outlined above emphasized the following principles: (1) upper-limb postural control and reaching involve continuous sensory processing; (2) feedback control processes selectively compensate for errors that interfere with the ongoing task, producing motor strategies appropriate for the movement goal; (3) these principles describe voluntary motor behavior as well as responses to visual and mechanical perturbations; and (4) sophisticated feedback responses emerge ~50–60 ms following a mechanical perturbation, coinciding with the long-latency stretch response.

**M1 as part of a flexible feedback controller**

A robust observation across the studies outlined above is that short-latency responses (~20–50 ms) are predominantly sensitive to muscle stretch (Pruszynski & Scott, 2012), whereas task-dependent responses consistently emerge in the long-latency time window (~50–100 ms). Long-latency responses coincide with the contribution of long-loop mechanisms, including a transcortical pathway through M1 (Cheney & Fetz, 1984; Desmedt, 1978; Matthews, 1991). Indeed, single-unit recordings in monkeys indicate that M1 receives somatosensory feedback (Evarts & Fromm, 1977; Scott & Kalaska, 1997) or mechanical perturbations (Herter, Korbel, & Scott, 2009; Picard & Smith, 1992). Moreover, human studies using transcranial magnetic stimulation emphasize a causal link between M1 processing and long-latency stretch responses, since motor cortex stimulation disrupts the task-dependent features of long-latency responses (Capaday, Forget, Fraser, & Lamarre, 1991; Day, Riescher, Struppler, Rothwell, & Marsden, 1991; Kimura, Haggard, & Gomi, 2006, but see also Shemmell, An, & Perreault, 2009). Given the involvement of M1 in the generation of voluntary behavior (Porter & Lemon, 1993) and rapid feedback pathways, this brain region is a clear candidate to implement flexible feedback control strategies (Scott, 2004).

A number of neurophysiological studies in nonhuman primates have highlighted that a transcortical feedback through M1 provides important task-dependent processing following mechanical perturbations. In a seminal study, Evarts and Tanji (1976) found that within 40 ms of an upper limb perturbation, the response of pyramidal tract neurons differ depending on whether the monkey was instructed to push or pull a handle. The authors suggested that these task-dependent neural responses contribute to volitional control of the limb during the long-latency time window. This idea was recently tested in a study examining whether the transcortical feedback pathway through M1 exhibits knowledge of the limb’s biomechanical properties (Pruszynski et al., 2011) using the paradigm developed by Kurtzer et al. (2008). The authors applied different combinations of shoulder and elbow torques evoking flexor or extensor motion at the elbow and no motion at the shoulder. As a result of these multijoint perturbation loads, shoulder motion (none, in this case) is ambiguous about the applied perturbation, and the motor system can only appropriately counter the underlying torque by taking elbow motion into consideration. The responses of shoulder-related neurons in M1 were found to appropriately respond to the applied load at ~50 ms, about 15 ms before long-latency responses were recorded in shoulder muscles (figure 39.4D).

How this transcortical feedback pathway resolves this multijoint integration problem is unclear. One clue is that the earliest activity in MI, from 20 to 50 ms after a perturbation, does not reflect specific features of the perturbation (figure 39.4D). That is, regardless of perturbation direction, all neurons sensitive to shoulder or elbow motion display similar responses until 50 ms after the perturbation is applied. This may suggest that M1 requires ~30 ms to identify the appropriate response, or that knowledge of limb mechanics is computed elsewhere in sensorimotor circuits. Several brain regions that receive sensory feedback from the limb project to M1, including primary somatosensory cortex, parietal area 5, and cerebellum (Fromm & Evarts, 1982; Martin, Cooper, Hacking, & Ghez, 2000; Mason, Miller, Baker, & Houk, 1998). There was considerable interest in examining how brain regions including M1 responded to sensory feedback in the 1970s (for a review, see Desmedt, 1978), but since then the role of sensory feedback in M1 processing has received little attention from the scientific community. Given the tight link between voluntary control and sensory feedback processing, the use of OFC as a framework to understand voluntary motor control has led to a renewed interest in how different cortical and subcortical circuits participate in feedback processing for motor control (Scott, 2012).

**Conclusion**

We have argued that OFC is a powerful tool for understanding biological motor control and that it has shed light on many of the complexities the brain must consider to move successfully in the presence of neural variability or environmental disturbances. Perhaps the most important contribution of OFC in movement
neuroscience has been to unify motor planning and feedback responses to perturbations in a common framework. These two aspects of motor control have been almost relegated to distinct fields of investigation (Scott, 2008). The major conceptual advance of OFC is the idea that movement planning and execution are two sides of the same story: a goal-directed feedback control policy. We expect that future research will address how the computations underlying flexible feedback control are distributed across different brain regions.

REFERENCES


