Opinion

A Functional Taxonomy of Bottom-Up Sensory Feedback Processing for Motor Actions

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Humans are adept at performing an extraordinary breadth of voluntary motor actions that allow us to rapidly move around and interact with the environment. While voluntary motor actions necessarily include top-down intention to generate a motor act, a key to voluntary control is the selective use of bottom-up sensory feedback to select and guide motor actions. This review classifies the many ways in which sensory feedback is used by the motor system and highlights regularities in the timing of each class of motor responses to sensory stimuli, revealing a functional hierarchical organization of motor control. The highly automatic way in which feedback is typically used in goal-directed action blurs the distinction between reflexes and voluntary control.

Sensory Feedback for Control

It is amazing how adept we are at performing complex motor behaviors with little effort or thought. A highly skilled squash player can quickly maneuver around her opponent to strike a fast-moving ball towards the bottom corner of the front wall. The exchange of shots and ‘dance’ between players as they take turns hitting the ball can continue for some time. Simultaneously, she can also think about other things, from the enjoyable dinner with friends last night to wondering whether her kids are acting up for the babysitter. The same is true as we require minimal attention to complete the many decisions and motor actions when we drive a car along a busy street. How can such highly skilled motor behaviors be performed with so little conscious effort?

I review here the many ways that sensory information is used to guide and select motor actions (Box 1). The proposed framework uses three common building blocks to describe motor control [1,2] (Figure 1A). The first process defines the behavioral goal, or WHAT the motor system is to do. The second process defines the present state of the world, or WHERE one’s body and the behavioral goal are in the world. The third process generates the motor commands, the control policy that defines HOW to initiate the motor action as well as how to correct any errors so as to attain the goal.

I will use these three basic processes (WHAT, WHERE, and HOW) to interpret the many ways that sensory feedback is used for the selection and control of motor actions. In particular, studies on arm motor function highlight consistent regularities in the timing of motor responses generated from sensory stimuli, either mechanical disturbances to the limb, or visual feedback on hand position or the behavioral goal. Importantly, these regularities in timing reveal a functional taxonomy pertaining to what goal to attain, how to move to a goal, and the selection of future goals and movement strategies. In effect, these experimentally observed differences in the timing of corrective responses reveal a hierarchical organization within the motor system that highlights how highly skilled motor actions use bottom-up sensory feedback with minimal need

Trends

Studies on humans that use abrupt shifts in proprioceptive or visual feedback highlight the surprising speed and complexity of goal-directed motor corrections.

Regularities in the timing of goal-directed motor corrections reveal a hierarchical organization of the motor system.

A key to learning involves recalibrating and speeding up the use of sensory information for goal-directed motor actions.

The use of shifts in proprioceptive and visual feedback in behaving animals will provide a useful way to explore how distributed motor circuits support online feedback for highly skilled motor actions.

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Feedback and Theories of Motor Control

Opinions across the decades have varied dramatically on the importance of sensory feedback for motor function. The ideas of Nicholas Bernstein introduced dynamical systems to motor control highlighting the intimate interaction between the brain and the motor periphery [113]. The ideas of servomechanics have been used as a theory of the motor system [114,115], and the lambda version of the equilibrium point hypothesis also considers feedback, albeit only at the spinal level [116]. Others suggest that motor actions, particularly fast movements, are generated by motor programs—open loop commands that are prestructured motor commands that provide the details of a skilled motor action [12,117,118]. From this perspective, feedback is viewed as an add-on process that may contribute to movement control, if required [119].

Over the past decade there has been renewed interest in the role of sensory feedback in motor planning and control. Optimal feedback control (OFC) is a mathematical approach for identifying the best way to attain a behavioral goal given the physical properties of the limb (and environment), while minimizing the influence of noise and errors [1]. This framework treats the motor system as a dynamical system, but its mathematical formalisms provide testable predictions on the issues that the motor system ought to consider when moving in a complex world [2,41]. There are several variants of optimal control, such as robust and model predictive control, which also provide interesting predictions on how the motor system ought to behave under various conditions or assumptions.

for top-down attention or conscious effort. From this perspective a key to motor learning is to reduce top-down processes and exploit sensory feedback to automatically select and guide motor actions, making motor actions more fluid, accurate, and effortless.

Volition: The WHAT

The overall objective of the motor system (WHAT, as defined in Figure 1) is ultimately defined by volition. Although volition in itself can be a controversial term [3], I will simply use it to mean the self-initiated decision to generate a motor act. This voluntary decision can be as simple as deciding to reach to an object on the table (a discrete skill), maintaining the arm in a fixed posture (a continuous skill), but more commonly initiates a complex series of motor actions (a serial skill). For example, returning a shot in squash requires the player to move to a position on the court that allows her to strike the ball back to the front of the court. The swing of the racket can be further subdivided into several phases including backswing, downswing, and follow-through.

A hallmark of skilled behavior is the ability to deal with change. For example, the squash player’s opponent may inadvertently step forward, blocking the player’s initial path towards the ball and requiring her to go behind the opponent. She may then also quickly switch from forehand to drop-shot if the ball unexpectedly hits the sidewall or if she observes through peripheral vision her opponent quickly moving backwards to prepare for the forehand. While volition plays an obvious role in deciding how we move and interact in the environment, our ability to use sensory feedback to rapidly select and guide our motor actions also plays a substantial role, particularly for highly skilled motor actions (reactive control).

State and Goal Estimation: The WHERE

All sensory modalities can be used for motor function. Vision plays a dominant role for identifying where objects are located in the environment, and can also provide information about the location of our limbs. Cutaneous receptors provide tactile information about physical contact between the body and the environment, and are particularly important for manipulatory tasks. Importantly, muscle afferents play a dominant role in almost all actions because they are embedded in the muscles, our biological motors that generate force and ultimately drive movement. Thus, muscle afferents are unconditionally connected to the motor system.

Sensory feedback takes time, but not nearly as much time as top-down voluntary control. The distance from the brain has an obvious impact on transmission times: sensory transmission of feedback from primary muscle afferents to primary motor cortex is less than 20 ms for the proximal arm [4,5], and transmission back down to the motor periphery is ~10 ms [4].
As described below, goal-dependent motor responses to limb afferent feedback take at least 60 ms. While the transmission distance from the eye to the brain is short, retinal processing of visual input takes at least 30 ms [6], with goal-directed motor responses from visual feedback taking ~90 ms or more [7]. All of these delays can be devastating for control because the motor system can become unstable, particularly when attempting fast movements or corrective responses [8].
There are several ways to mitigate the influence of sensory delays for motor control. One strategy is to use internal models to convert efferent copy signals of motor commands into estimates of the state of the body, for fast feedback control [9]. However, internal feedback signals cannot counter unexpected disturbances such as someone accidentally bumping your arm. Another strategy is to estimate the present position of the body (or goal) from delayed sensory feedback using internal models [10]. External sensory and internal feedback likely both contribute to an estimate of the state of the limb.

**Control Policy: The HOW**

The control policy defines HOW to perform a motor action, given the goal of the task (WHAT) and the state of the limb and environment (WHERE). The ideas of optimal feedback control (OFC) have been influential for thinking about how the motor system generates motor commands [1,2]. OFC has been principally applied to examine online control of discrete skills with a single well-defined goal, such as reaching to a spatial target. However, the same principles can be applied to more complex behavioral tasks [2,11].

The ideas of OFC are particularly useful for recognizing that motor control is not about prespecifying a specific pattern of muscle activities to perform a motor act, as suggested by the idea of motor programs [12]. Instead, motor control is viewed as a control policy or law that defines what motor commands should be generated based on the present state of the body and the goal. In other words, it is about selecting feedback gains (potentially time-varying and non-linear) rather than explicit patterns of motor commands or muscle activities. In the absence of noise or errors, the movement will look like a pre-planned trajectory (a nominal trajectory [13]). However, internal noise (that is always present) and external disturbances influence motor execution, and thus, through feedback, lead to unique patterns of muscle activity appropriate for the present state of the system.

It is extremely difficult to disentangle a feedback system, particularly when internal feedback plays a parallel role to assist sensory feedback. The use of sensory disturbances, whether a small bump to the arm or the presentation of a new spatial goal or shift in viewed hand position, is a powerful tool to alter the state of the motor system and observe how it responds to maintain control.

The diagram in Figure 1A suggests that the control policy converts information on the present state of the body and goal directly into motor commands based on the behavioral goal. However, the actual neural implementation for control appears to be more complex. In particular, the amount of time required to generate a motor response (i.e., muscle activity) varies for different functional problems solved by the motor system (Figure 2 for examples). These response times highlight a functional taxonomy, suggesting a natural hierarchical organization to the motor system. Note in Figure 2 that response times for visual and proprioceptive feedback are relatively similar except that visual feedback is ~30 ms slower.

For highly skilled motor actions that are automatic and require minimal top-down attention, one can consider two major components, one controlling the present motor action and one selecting the next (Figure 1B). Each of these components can be further subdivided into two processes, one to define the behavioral goal (the present or next WHAT), and another to attain the goal (the present or next HOW). Novel skills also require additional non-automatic processes to map how the motor (or even perceptual and cognitive) system(s) should use sensory feedback to guide motor actions.

It is important to recognize that the fastest feedback response from the limb is not included in this control policy framework. The first feedback response following a mechanical disturbance,
Onset of mechanical load

- Load level
- Load termination

Proprioceptive feedback

- Trigged response
- Target shape
- Obstacles
- Limb biomechanics
- Environmental loads
- Timing constraints
- Constrained path

Simple RT

Alternative target

Time (ms)

Visual feedback

- Cursor jump
- Target jump
- Simple RT
- Choice RT
- Novel rule

- Mirror reverse RT

Onset or change in visual stimuli

R1: Spinal feedback (not goal-directed)
R2: Online control of the limb
R3: Online control of the goal

SRT/TR: onset of next action
CRT: selection of next motor action
Novel rule

Figure 2. Taxonomy of Bottom-Up Sensory Feedback Processing To Guide and Select Motor Actions. Timeline denotes the time from a sensory stimulus (mechanical or visual) to motor response [electromyogram (EMG) signal onset] of arm muscles related to each factor. Somatosensory and visual information are similar functional classes, although slightly delayed for the latter because of retinal processing. Each color denotes a functional class of feedback processing. Inset diagrams illustrate specific examples on the use of bottom-up sensory feedback processing. Arrows for proprioceptive feedback reflect the load (and its size) applied to the limb. Broken lines denote an unperturbed movement and a unbroken line denotes a movement when a load was applied. Filled circles denote that a visual target was shifted during movement (target jump) or when it was illuminated to initiate a movement (reaction time [RT] tasks). Arrows for visual feedback examples denote direction of hand movement. S and F denote the start and final spatial goals, respectively. For online control of the goal, F1 is the initial target that is jumped to F2 during movement. The color scheme is the same as in Figure 1. Superscripts denote references related to each class or type of corrective response.

Termed the R1 response (see Glossary), occurs at ~25 ms and is generated at the spinal level. For locomotor or cyclical tasks including those involving the arms, these spinal responses can be task-dependent, and show changes in the magnitude and even sign of the response [14,15]. However, for other motor tasks, such as reaching or maintaining a fixed arm position, fast spinal responses have low gain reflecting load level and pre- perturbation muscle activity [16]. Thus, they do not display key features related to goal-directed motor corrections [17]. Spinal-level responses do display an ability to rapidly stop an ongoing corrective response [18]. For the purposes of the present discussion this R1 response is treated as a process below the level of the control policy. From this perspective, the control policy must consider any influences of this fast spinal feedback on motor execution, much in the same way that the control policy must deal with muscle and limb biomechanics. Why the motor system does not take greater advantage of this fast spinal feedback process is unclear, but may reflect the lack of processes to deal with sensory delays which can lead to instability [8].

Automatic Control
Controlling the Present Movement: Reaching the Current Goal

After the R1 spinal-generated response, a second phase of electromyogram (EMG) activity, termed the R2 response, occurs at ~60 ms following a limb disturbance ([17,19,20] for review). These motor responses are surprisingly complex, and reflect the physics of the limb and...
environment [21–27] including hand-held objects [28], the time or accuracy required to attain a goal [29,30], the properties of the goal such as its shape [31], and are present even for extremely small disturbances approaching the range of natural variability in movement [32]. Perhaps most surprising is that these fast motor responses even consider multiple strategies to avoid objects in the environment [33] (Figure 3A). These rapid goal-directed responses are also seen in bimanual motor tasks, but with an additional 10 ms delay, likely related to the need to communicate sensory information between the two sides of the brain [34–37].

Rapid goal-directed corrections following limb disturbances appear to be inconsistent with seminal studies suggesting that the motor system follows a desired trajectory when attaining a behavioral goal [38,39]. The classic study by Bizzi and colleagues [38] showed that a transient disturbance of the limb that pushed the hand towards a spatial goal generated a corrective response that returned the hand back to the position it would have been at in the absence of the perturbation. However, recent work demonstrates that such a corrective response can occur if

![Diagram](image-url)
Subjects are given a simple timing constraint [29]. In effect, subjects slowed their movement or even reversed movement direction so as to not arrive at the target before the specified time-period. When there was no timing constraint, subjects permitted the applied load to push their arm to the target. The presence of this timing constraint altered motor responses ~60 ms after the load was applied.

Taken together, these studies indicate that there is a key 60 ms task-dependent feedback loop in the motor system for online control that deals with factors related to how to move the limb (or body) to a specified goal. While the spinal cord may contribute to this process, the timing of these corrective responses implicates a transcortical feedback pathway, particularly through primary somatosensory and primary motor cortex [40, 41], although other cortical and subcortical brain regions are also likely to be involved [13].

Similarly, vision plays an important role for selecting and guiding motor actions. Many studies illustrate how shifts in the viewed position of the hand (such as a cursor on a computer screen) elicit rapid corrective responses to attain spatial goals [42, 43]. Such corrections are elicited at ~90 ms [7, 44] and consider factors such as target shape [45], hand-held objects [46], and whether the alteration in viewed hand position is transient or permanent [47].

An important issue to consider is how vision and proprioceptive feedback are integrated together [48]. Vision is conditionally involved in motor control because many motor actions can be performed without the use of vision. For example, blind subjects clearly have good motor skills [49, 50]. By contrast, loss of proprioceptive or cutaneous feedback can be devastating for control [51–53]. Visual feedback is relatively accurate but slow, whereas proprioceptive feedback is less accurate but fast [48]. This creates a natural trade-off between speed and accuracy for estimating where you move in the world. Figure 1B assumes that visual and proprioceptive information are integrated together to estimate the state of the limb which is then used for control. Further work is necessary to understand this dynamic multi-sensory integration process.

**Present Control: Defining the Current Goal**

The location of an object can abruptly change. For example, a squash ball may skim the side wall, altering its expected course. It has been shown that shifts in the location of a spatial goal generate a rapid motor response to redirect the hand towards the new location [44, 54–57], including appropriate changes in the motor responses to subsequent mechanical disturbances applied to the limb [58]. Corrective responses are not complete if the target jump occurs late during movement [59], likely due to a trade-off between stability and accuracy.

Interestingly, motor responses to a shift in the location of a spatial goal take slightly longer than a response to a shift in the viewed position of the hand during reaching [7]. Simultaneous shifts in hand feedback and the location of a spatial goal elicit a response at ~90 ms related to the former and a second response at ~110 ms related to the latter, respectively (Figure 4A,B). The feedback response for the latter is reduced when the target is shifted towards the hand because feedback gains are reduced as one approaches a spatial goal [7]. This difference in the timing between limb and goal feedback processing leads to a transient corrective response related to the limb when a cursor representing hand position and the spatial goal are shifted simultaneously in the same direction even though there is no need for a response at all (Figure 4O) [42].

Recent work highlights that, even when multiple potential targets are present before movement, mechanical disturbances to the limb generate a corrective response to an alternative goal at ~75 ms, slightly more time than the 60 ms taken for corrections related to limb motion [33].
Given that visual feedback is ~30 ms slower than proprioceptive feedback, the timing of these corrections to an alternative (already present) goal is similar to that observed for shifts in the location of a spatial goal (i.e., 15 versus 20 ms slower than limb-related feedback, respectively). Thus, for these conditions, there appear to be minimal savings of time related to the preparation of an alternative goal over responding directly to sensory feedback.

Interestingly, similar-sized motor corrections when reaching to a single large target elicit motor responses at 60 ms [31]. Thus, it appears that the fastest task-dependent feedback loop (R2) can only consider a single discrete goal. While this response at 75 ms to select an alternative goal could be viewed as a change in the control policy, I will assume here that it is simply updating the goal location in the ongoing reaching control policy. Another recent study found that corrective responses when tracking a moving target rather than a static target also required ~75 ms (Figure 3B) [29], suggesting that the internal representation of the target’s position was constantly updated in the control policy.

Recent studies that force subjects to move before one of two possible target locations is identified as the final target demonstrate that subjects move in a direction intermediate to the two potential targets [80,61]. This intermediate movement can be interpreted as a blend of two control policies, one for each potential target [62]. This appears to be inconsistent with the idea that online control policies normally consider a single discrete goal, even if multiple goals are present. However, even in this situation where one is forced to act without a clearly defined goal, one may still view this motor problem as a single control policy reflecting goal uncertainty [57], the presence of obstacles [33,57,60], timing constraints to attain the correct goal after it is identified, and potentially, transient increases in feedback responses immediately following target presentation [63].
Lee and Tatton [64] were the first to identify three peaks or epochs associated with muscle stretch responses (R1, R2, and R3 responses, although the original nomenclature used M1, M2, and M3 responses, respectively). The R3 response at 75 ms was only observed in a few subjects and there was no clear functional significance to this response. Because motor corrections associated with shifts in spatial goals require the same amount of time, it is possible that subjects that displayed an R3 response in Lee and Tatton assumed some type of new spatial goal when they responded ‘as rapidly as possible’ to the mechanical disturbance.

It is commonly assumed that the motor system computes a difference vector between the position of the hand and spatial goal so as to plan motor actions [65]. Differences in the timing of corrections related to the limb versus goal suggest that the hand and the spatial goal are treated separately, at least for online control (see [66]). With a specified spatial goal, a control policy on how to attain the goal is created and motor commands are generated by streaming sensory and internally generated feedback through the policy. Disturbances of the limb lead to rapid corrective responses in ~60 ms. If the goal location changes (or if an alternative goal appears to be a better choice), the ongoing control policy is altered to drive motor responses to the new spatial goal, and this process takes ~75 ms.

Selecting Upcoming Actions: Timing

Sensory signals are often used to initiate new motor actions, or help to initiate different phases of a task. The traffic light turning green provides a sensory signal that leads to lifting of our foot from the brake to the gas pedal. The lack of a sensory signal can also drive motor actions. For example, cutaneous afferents located on the digits elicit a brief burst of action potentials when a grasped object lifts off a table, thereby signaling the transition from the loading to the transport phase [67]. If the object is heavier than expected, and the lift-off does not occur at the predicted load force, the absence of the burst from these afferents elicits a further increase in grasp and load force to lift the object.

When the goal of an impending motor action is known, visual, auditory, and somatosensory stimuli can initiate a motor response of the arm because the sensory stimuli only specifies when to ‘go’ [68,69]. In these situations, muscle activity is generally observed at 100–120 ms, commonly termed simple reaction times (SRTs) [63,70]. This additional time suggests that there is a specific time-cost in initiating a new motor action beyond that used, and to employ sensory information to continue driving movement towards a given goal [71]. In this case, time is necessary to disengage a postural control policy and initiate a movement policy [72]. Before the initiation of a reach, corrective responses are directed back to the original hand position but, immediately before movement initiation, corrective responses become directed to the new spatial goal [63,73]. SRTs increase for more complex motor actions involving multiple phases or chunks [68,74], and can be elicited even if the sensory stimuli are not perceived [75].

Interestingly, SRTs can be reduced to 60–70 ms for large sensory stimuli [76–79]. In this case, the large mechanical disturbances applied to the limb appear to help to disengage the ongoing control policy and initiate the pre-planned control policy [72]. These triggered reactions (TRs) are flexible and goal-directed because they scale with the applied load [80], highlighting that TRs select a control policy and not a fixed motor response. Loud auditory stimuli can also elicit TRs [81,82], and visual stimuli can also elicit a stimulus-locked motor response at ~90 ms [83]. TRs are as fast as R2 and R3 responses related to online control of the limb and goal, respectively. However, TRs are functionally distinct because they involve a switch in the type of behavior, and thus control policy being performed, such as switching from maintaining a fixed posture to initiating a movement. As observed for SRTs, TRs can be delayed when there is an accuracy requirement [84].
Selecting Upcoming Actions: Identifying and Achieving Subsequent Goals

The selection of our next motor action can be a relatively simple or complex process. It can involve a vast array of perceptual and cognitive processes to select each action, such as driving a car on busy city streets where cars can quickly stop to parallel park or pedestrians randomly cross traffic. Such decisions cannot be preplanned but depend on sensory feedback to define the present state of the world.

Decision making and motor control have been commonly assumed to be separate processes, but recent work highlights a more intimate relationship between them [85,86]. Various factors influence our choice amongst them related to the value of potential goals, and the cost to attain them [85–87].

Motor decisions can be viewed as a single-step control problem in which the control policy identifies the next motor action based on the overall behavioral goal and the present state of the body and environment [88]. It can be a continual process in which sensory information is sampled continuously to decide when best to guide or alter the ongoing action to continue towards the overall behavioral goal [86].

The simplest selection process occurs when one of several potential stimuli is presented that instructs a subject to perform a specific motor response. The time to perform these tasks is commonly termed choice reaction time (CRT). The relationship between the sensory stimulus and motor response strongly influences the time required to generate these responses, termed “stimulus–response compatibility”. Congruent stimulus–response mappings are highly automatic, such as reaching to a visual stimulus which can occur in as little as 170 ms [89]. These times can vary as a result of many factors, such as the spatial distribution and number of potential targets [90], and stimulus intensity [69]. Notable is that these motor responses can be elicited without perceiving the visual stimuli [91], which suggests that volition is not necessary for this rapid selection of a spatial goal.

More complex stimulus–response mappings are learned through experience. For example, we learned in our parent’s car that a green light means to proceed through an intersection, red means stop and yellow means speed up. In this case, bottom-up sensory feedback automatically drives the selection of these motor actions, allowing us to perform other mental tasks such as carrying on a conversation or deciding if an alternative route with less traffic would be faster to reach the final destination.

For extremely fast motor actions, sensory feedback can be too slow to drive transitions between actions. Skilled typists can type more than 120 words per minute, which converts to a key stroke every 100 ms! It is clear that finger contact with a key cannot drive the transition to the next key stroke for such fast typing speeds, but that internal feedback processes can anticipate the timing and transition of key events [92]. Keystrokes for a word are blended together or connected as chunks [93,94], effectively creating a single continuous control policy. This does not mean that sensory feedback is ignored because it will continue to update the actual position of the body and also helps to identify errors in motor performance [95].

Non-Automatic Control

Novel Motor Skills

The sections above describe the use of bottom-up sensory feedback for highly skilled motor performance in which sensory signals can quickly guide and select motor actions with minimal attention or mental effort. However, attaining highly skilled performance takes time. Teenagers must learn how fast and far to turn the steering wheel when turning a corner or parking a car.
These novel motor actions often require explicit strategies or rules to associate sensory information to motor responses either for online control or for rapid selection of motor actions. These non-automatic control policies are initially quite distinct from automatic control policies, and can dramatically slow the use of sensory feedback for online control and motor selection (Figure 1B). Hick’s Law captures the fact that CRTs increase linearly with the logarithm of the number of stimulus–response pairings (Hick 1952). Many cognitive tasks, such as mental rotation, Flanker test, and Stroop test, are non-automatic control policies that transform sensory input to rapid motor responses that can typically take several 100 ms to complete.

The most difficult stimulus–response pairings occur when the sensory/motor response is opposite to or incongruent with the automatic response [96,97]. When visual feedback of the hand is reversed (i.e., hand movement to the left leads to cursor movement to the right), one must maintain this novel rule and also suppress the automatic motor response. Corrections for any errors can lead to an automatic corrective response at ~90 ms that increases the motor error, which is then followed by an appropriate corrective response at ~200 ms [98,99]. With some practice (100s of trials), subjects are able to suppress the automatic visuomotor response at 90 ms, but not the timing of the later appropriate corrective response [99].

The anti-saccade task is another common task to quantify non-automatic control, in which subjects must move in the direction opposite to that of a visual stimulus [100]. In this case, the oculomotor system must override the automatic response to look at the visual stimuli and generate a movement in the opposite direction. Similarly, reverse reaching tasks, in which a cursor moves in the opposite direction of hand motion, also require inhibiting the automatic motor response and generating a movement in the opposite direction [101]. An alternative strategy may be to simply delay movement initiation to avoid generating a motor action until the appropriate is selected [71]. The key point is that bottom-up sensory feedback drives the selection and guidance of these non-automatic sensorimotor actions.

**Motor Learning: Modifying and Speeding Up Bottom-Up Feedback Control**

Motor learning, such as when we learn to drive a car as a teenager, is a crucial aspect of voluntary motor control. Movements are initially inaccurate, slow and clumsy, and require considerable attention. With practice movements became fast, fluid, and more automatic, requiring less conscious effort to perform. While a review of all aspects of motor learning is beyond the scope of this article ([93,102] for review), a key to learning is modifying how sensory feedback is processed by the motor system.

As mentioned above, online feedback of the limb (R2) considers the physics of the limb and environment. When movements are performed with a novel load, online feedback corrections will be inaccurate because they do not consider the applied load. With practice, subjects alter this online control of the limb [103,104], including changes in motor responses starting in the R2 time epoch [105]. Further, the amount of adaptation during learning correlates with the amount of change in the long-latency motor response ([105], see also [46]).

Training can dramatically reduce the time required to associate sensory stimuli and motor responses for non-automatic control [69,93,97] and speed up the transition between different motor actions [93]. When one learns to type, there is a clear separation in the time between each key stroke. With practice, key strokes become much faster, with finger movements for each key stroke blurring together. Learning reduces the time to select key stroke for each letter and concatenates keystrokes creating chunks or control policies for entire words [93,94]. In effect, these tasks become more automatic, reducing top-down attention.
Neural Basis of Highly Skilled Motor Actions
A major challenge is now to map these functional feedback processes onto brain circuits. Sensorimotor circuits in cerebral cortex together with the basal ganglia and cerebellum clearly support our ability to perform highly skilled motor actions [65], although their use of sensory feedback for online control remains poorly understood. While broad frontoparietal circuits are implicated in the use of vision for online control [106], somatosensory feedback has generally been assumed to be limited to primary somatosensory (S1) and primary motor cortices (M1) at the cortical level. Neurons in primary motor cortex respond rapidly to mechanical disturbances of the limb [19]. Neural responses are task-dependent in that they are reduced when the animal is not engaged in a limb motor task [107], and also reflect knowledge of limb mechanics [108]. Primary motor cortex has also been implicated in the ability to rapidly select a new motor action [109,110]. However, recent work highlights that many of regions beyond M1 and S1 rapidly respond to limb disturbances and can alter their responses based on the behavioral goal [111]. This suggests that broad frontoparietal circuits commonly associated with goal-directed motor

Box 2. Reflexive and Voluntary Control
The fact that bottom-up sensory feedback is used in myriad ways to guide and select motor actions leads to the question of what is reflexive and what is voluntary [120]. The origin of the term reflex is centuries-old, initially based on observations on animals that were unconscious or recently dead [121]. These studies demonstrated many complex reflexes that can be elicited by sensory stimuli applied to the unconscious body, and that the spinal cord itself was capable of relatively complex motor responses.

At one extreme, some assume that a reflex must be fixed and immutable, eliciting the same response for a given sensory stimuli. Based on this definition, it is not clear that any response in a healthy, conscious, fully developed individual can be defined as a reflex, because even a tendon tap with a physician’s hammer is modifiable by the Jendrassik maneuver. At the other extreme, if reflexes are simply sensory events that lead to a motor response, then virtually all feedback responses outlined in Figure 1B, main text, would be defined as reflexes. Even cognitive processes can be viewed as reflexive [122]. If such a definition is used, then the entire motor system (including cognitive and perceptual processes) must be viewed as reflexes, which is untenable.

Instead, it may be best to relegate the idea of reflexes as motor responses that can only be elicited by pathology, early in development, or in unconscious/reduced preparations (the view of Clarac in [120]). Pathologies that interfere with the generation of automatic control lead to stereotyped responses. The tendon tap will remain an important clinical tool to assess the motor system, but it is important to recognize that the elicited responses include the voluntary decision by the subject to create a control policy to relax and ‘not respond’ to the hit of the hammer.

The term ‘voluntary’ is also problematic because it means many things to many people. The ability to avoid an obstacle when disturbed while reaching (Figure 3A in main text) seems to have some voluntary qualities, but can be performed in only 60 ms, with half of that time likely being due to transmission delays to and from cortex. Goal-directed reaching movements are commonly considered to be voluntary movements, but the actual involvement of volition to initiate these acts can be somewhat limited because CRTs can be generated even if the target is not perceived [91]. Alien hand syndrome, habits, sleepwalking and utilization behavior, where affordances of objects automatically initiate motor actions even though there is no desire to perform them, highlight how goal-directed motor actions can be performed without volition.

Some may argue that voluntary should refer to any skilled action such as reaching to a spatial goal or, perhaps, what is termed here ‘non-automatic control’, such as performing an anti-saccade task. While it is true that greater attention is required to perform non-automatic control policies, the corresponding motor responses are still extremely fast. Is such fast processing to generate a corrective response really voluntary? Subjects choose to perform a motor task that requires a non-automatic control policy, a novel rule on how to act for a specific condition (i.e., anti-saccade task, or mirror-reverse reaching in which visual errors to the right require motor correction to the right). Volition is required to maintain this non-automatic rule, and potentially to override or inhibit automatic motor responses. In this state, sensory feedback on whether the event occurred can then stream through this non-automatic control policy, leading to an appropriate motor response in as little as 200 ms. In other words, the subject voluntarily chose to perform the motor task. When actually engaged in the motor action (top-down goal selection), bottom-up sensory feedback or reactive control can drive the control policy. Volition is constantly updated on the status of motor actions, although potentially after they have occurred. Volition can ultimately make decisions on whether to stop attaining a goal or to allow the motor system to continue with its present goal. Admittedly, there is likely a complex interaction between voluntary and reactive control, leading to a degree of voluntariness for most situations.
actions likely participate in rapid feedback processing for motor selection and online control [13,112].

**Concluding Remarks**

The purpose of this article was to highlight a functional taxonomy related to bottom-up sensory feedback that supports motor function. This use of sensory feedback to drive goal-directed motor actions can be so automatic and fast that it questions what we call reflexive and voluntary (Box 2). Initially we require considerable top-down control to learn novel skills or associate sensory stimuli with the selection of a given motor action. With practice, these motor skills become automatic, reducing the need for top-down control by exploiting bottom-up sensory feedback whenever possible, leading to the ability to perform fast and agile motor actions with minimal mental effort (see Outstanding Questions).

**Acknowledgments**

I would like to thank members of the Limb Laboratory and Drs J.R. Flanagan and D. Munoz for constructive criticism on drafts of this manuscript. This work was supported by grants from the Natural Sciences and Engineering Research Council of Canada (NSERC) and the Canadian Institutes of Health Research (CIHR), and GSK-CIHR Chair in Neurosciences.

**References**


**Outstanding Questions**

Sensory delays vary across sensory modalities (vision versus somatosensory), but somatosensory delays also vary substantially based on the distance from the periphery to the CNS (i.e., face versus toes). How does the motor system deal with these variable delays when selecting and guiding motor actions?

How does learning convert non-automatic feedback processes into automatic feedback processes?

Are different classes of feedback processing, as described in this article, supported by similar or distinct cortical and subcortical neural circuits?
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