Trends in Neurosciences

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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.

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.

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

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Box 1. Sensory 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 servo control 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].

Glossary

Choice reaction time (CRT): the time required to generate a motor response when there are multiple potential actions.

R1, R2, R3 responses: phases of electromyographic (EMG) activity generated after a mechanical load is applied to a joint or limb. For the arm, R1 begins at ∼25 ms, R2 begins at ∼50 ms, and R3 at ∼75 ms after the onset of the perturbation.

Simple reaction time (SRT): the time required to generate a motor response that is preplanned and launched by a small sensory stimulus.

Triggered reaction (TR): a motor response that is preplanned and launched by a large sensory stimulus (mechanical perturbation or loud sound).