

Movement: How the Brain Communicates with the World

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Voluntary movement is a result of signals transmitted through a communication channel that links the internal world in our minds to the physical world around us. Intention can be considered the desire to effect change on our environment, and this is contained in the signals from the brain, passed through the nervous system to converge on muscles that generate displacements and forces on our surroundings. The resulting changes in the world act to generate sensations that feed back to the nervous system, closing the control loop. This Perspective discusses the experimental and theoretical underpinnings of current models of movement generation and the way they are modulated by external information. Movement systems embody intentionality and prediction, two factors that are propelling a revolution in engineering. Development of movement models that include the complexities of the external world may allow a better understanding of the neuronal populations regulating these processes, as well as the development of solutions for autonomous vehicles and robots, and neural prostheses for those who are motor impaired.

Introduction

The way the nervous system generates movement has been studied formally for about 150 years. Earlier work was based on anatomical observations: the way the brain and spinal cord were shaped and how one place in the system appeared to be connected to another. This, combined with careful observation of motor deficits and corresponding lesions of system structures, was the foundation of motor neurology. The introduction of electrical stimulation in animal models added another dimension to motor systems experimentation. Along with targeted lesions of different system components, these were the underpinnings of the original theories of motor control. Although the complexities of relating anatomical structures to specific aspects of behavior were well recognized by motor control pioneers, results of lesion and electrical stimulation experiments were viewed primarily in terms of fairly discrete connectivity pathways that are now referred to as “circuits,” with the implication that they operate in a way that is similar to their engineered counterparts, such as computers. More recently, experimentalists have been using technology that enables the simultaneous recording of action potentials from many neurons while natural movements are performed. Conventional concepts of discrete circuits working with distinct functionality have been challenged by experimental results that show that many neurons are active together, with a large population throughout the neural axis generating similar signals used for movement generation. This evolution in the field of motor control offers new insights for understanding purposeful behavior, as well as suggestions for new design principles that could be implemented in engineered systems.

Movement—Reflex and Volition

Traditionally, movements have been divided into those subserving reflexes and those associated with purposeful action. Volitional movement is the result of cognitive processes, which lead to the exertion of some action on the world. These processes are not clearly defined or understood, making it difficult to develop concrete, rigorous models to describe the way they operate. Although the resulting physical movement can be measured well and task-related neural activity can be recorded and correlated to the movement, in the absence of well-identified drivers of neural activity, the meaning of an association between any given neural pattern and the task will be open to debate.

Reflexes

In contrast to volitional movement, reflexes seem especially amenable to the modeling approach used by engineers. Instead of a process that begins with intention, the generation of reflexive movement starts with sensation. A given stimulus (input) elicits a set motor action (output). As described by Sherrington at the turn of the 19th century, these movements are stereotypical and generated by neuronal action that takes place in an orderly fashion beginning in the spinal cord, with elaboration by groups of neurons in progressively “higher” neural structures such as the hindbrain, midbrain, and cerebral cortex. Sherrington arrived at this hierarchical scheme by surgically separating these different structures and studying the remaining reflexive behavior. He found that each level could be characterized by inputs and outputs, allowing system identification procedures whereby mathematical transfer functions were used to predict outputs given an input. This gave rise to the use of linear system approaches (a linear equation that describes how output results

from input) in the 1960s and 70s to describe reflex inception. One of the first attempts in this regard was modeling the stretch reflex, based on the workings of the crayfish stretch receptor (Borrellino et al., 1965). The process of transforming a physical stretch into a train of impulses in the afferent fiber was considered to take place as a set of steps, each of which could be modeled with a transfer function (the input-output equation) (Loewenstein et al., 1963; Terzuolo and Washizu, 1962; Washizu and Terzuolo, 1966). The same principles were subsequently applied to the mammalian stretch receptor (Poppele and Terzuolo, 1968; Roberts et al., 1971). Stretching the muscle (by other muscles or external forces) activates the receptor which, in turn, excites the muscle that contains it, causing the muscle to shorten, effectively counteracting the stretch to maintain stability. Thus, reflexive movements act on the principle of feedback, where the output of the system is used to modify its input. In this case, the feedback is negative because the stimulus invoking the reflex is a lengthening of the muscle and the response, muscle contraction, shortens it.

The use of linear systems analysis was also fundamental to studies of the vestibular ocular reflex (Robinson, 1981), which functions to stabilize images on the retinas when the head accelerates. Based on the same principle as the stretch reflex, this system uses negative feedback to move the eyes in the direction opposite of the head movement. In this case, head acceleration from the semicircular canals of the vestibular system was considered the system input, which is transformed to velocity and position used to activate the extraocular muscles. We can see that these examples of negative feedback conform to basic engineering principles. However, even these basic reflexes are constantly modified by the context in which they occur. For instance, in mammals, the sensitivity of sensory muscle spindle receptors is regulated by gamma motoneurons, which change the stiffness of the receptor itself. The gamma motor neurons are controlled by supraspinal structures, which are influenced by the setting or context in which the subject is situated. Essentially, the gamma system adjusts the gain of stretch receptors to accommodate a predicted range of sensations that will be encountered. Similarly, the vestibular-ocular reflex is modified by output from the cerebellum, which can change the gain of the reflex. Donning a pair of bifocals is an everyday illustration of how feedback systems are readily modified. The glasses act as prisms that displace the world so that a given eye movement no longer results in the same shift of vision. After learning, the gain (ratio of output to input) of the vestibular-ocular reflex is adjusted rapidly to compensate for this change as soon as the viewer peers through alternate lenses.

Reflex Action and Volitional Movement

Reflexes are effective during volitional movement, and they contribute to the successful production of an intended action. In laboratory experiments using instructed tasks, movement intention is, at least partly, specified. The idea of “motor set” experiments in the mid-70s and early 80s was to separate a volitional component of the task (instruction) from that which was more related to the mechanics of the movement (reflex). This logic was followed in experiments (Evars and Tanji, 1974) in which monkeys were trained to move to a target in response to a rapid displacement (“go” signal) of the handle they were

holding. A target light served as the instruction and indicated which of two directions to move before the go signal. Although the handle displacement was the cue to move, its direction had no behavioral meaning. Two types of neuronal responses were found in motor cortical neurons. An early response (20 ms) after the handle perturbation was correlated with the direction of the rapid displacement. A later pattern of discharge corresponded to the direction of the instructed movement (40–50 ms) but was unrelated to the perturbation direction. The first response was deemed to be reflexive and due to afferent input elicited by the perturbation (since it carried directional information unrelated to the subsequent behavior), while the second was considered more volitional in that it was target related. The subject’s response, as registered by the onset of muscle activity, began 70 ms after the perturbation, and the movement began 20 ms later. The same paradigm was used to study responses in the cerebellum (Strick, 1983) with the idea that the early and late neuronal responses in the motor cortex may be mediated by the cerebellum. Recordings in the dentate nucleus showed that neurons changed their firing rates in a way that was dependent both on the cued target and the direction of the imposed perturbation. This dual dependency is interesting, since the mechanics needed to move the arm to the target depend on the initial position of the arm (which was altered by the perturbation) and the position of the target. Even though the perturbation direction had no behavioral meaning, the direction of the prior perturbed displacement had to be accounted for when generating the subsequent forces needed to make the volitional movement. These experiments defined components of the control signals that may contribute to the generation of volitional movement.

Reaching as Volitional Movement

Volitional movement is, by definition, the intended execution of an action. These movements are often considered to be singular events, even though, in real-world behavior, they take place in a continuous cycle of action-intention-action (Johansson and Flanagan, 2008). Nonetheless, because this chain is sequential, there are delays between intention and action and then between action and registration of that action via sensation. The first delay requires the intention to be predictive; the second means that sensory feedback cannot function in real time. This suggests that there are distinct phases of the task that may be controlled differently. During a reach for an object, the path of the hand is divided into two components; the first is a rapid displacement of the hand to the vicinity of the object, followed by a series of smaller “submovements” (acceleration-deceleration) of the hand until the target is reached (Meyer et al., 1982; Schmidt et al., 1978). The initial component, which covers about 80% of the distance, is on the order of 200 ms, whereas the second component takes slightly less time. Before and during the reach, the eyes are fixed on the target. Because the minimal time for a visually mediated movement to take place is estimated to be in the range of 190–200 ms (Beggs and Howarth, 1972; Cordo, 1987; Keele and Posner, 1968; Newell and Houk, 1983), it follows that the first phase of the movement is essentially over before a visual correction could be effective; this phase is often referred to as “ballistic” because it was thought to take place in the absence

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