Introduction to Voluntary Movement

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Voluntary movement is the expression of thought through action. Virtually all areas of the central nervous system are involved in this process. The main flow of information may begin in cognitive cortical areas in the frontal lobe, or in sensory cortical areas in the occipital, parietal and temporal lobes. Ultimately, information flows from motor areas in the frontal lobe through the brainstem and spinal cord to the motoneurons. The basal ganglia and cerebellum have reciprocal connections with most of the structures listed above, and therefore play a supporting role.

One approach to understanding the neural control of voluntary movement is to consider the function of each of the structures involved (Fig. 1A). For example, the primary motor cortex is generally regarded as the main cortical area for providing descending motor command signals to motoneurons. However, the exact functions of other brain structures remain open for debate. Since diseases of the basal ganglia and cerebellum are relatively common, numerous functions have been proposed for these structures (e.g., movement initiation, error correction, etc.). One emerging perspective is that the basal ganglia and cerebellum do not have discrete roles in motor control and instead work via their interconnections with other subcortical and cerebral cortical structures (see Alexander et al 1986, Kelly and Strick 2003, Hoshi et al 2005).

A different approach to the study of voluntary movement is to consider the movement goals, strategies and algorithms for implementation, without direct reference to the neuroanatomy. Theoretical and computational studies have been aimed at providing a quantitative description of movement characteristics in order to gain insight to the neural code. Furthermore, flow chart models like the one shown in Fig. 1B have become increasingly sophisticated by incorporating hypothetical processes such as the use of efference copy. Hopefully, future studies will merge this functional approach with the more anatomical approach by establishing the exact neural mechanisms for implementing the key algorithms that are essential to sensorimotor integration.

Structures involved in voluntary movement

The ultimate output of the motor system is the activation of a motor unit (defined as a single motoneuron and the group of the muscle fibers contacted by its axon). Researchers have documented several consistent aspects to the patterns of motor unit activation used for voluntary hand and arm movement: 1) as muscle force is increased, small motor units tend to be recruited prior to large motor units (the size principle, Henneman et al 1965); 2) neighboring motor units within the same muscle can be
preferentially selected for different movements (such as arm movements in different
directions, Herrmann and Flanders 1998); 3) the motor system does not exert independent
control of each motor unit or of each muscle, instead groups of motor units across
different muscles show covariation in their recruitment patterns (see muscle synergies);
4) there is often inhibition of motor units with a mechanical action antagonistic to that of
the excited motor units (a classical phenomenon in motor control physiology known as
reciprocal inhibition).

The brain controls voluntary arm and hand movements by sending descending motor
commands to the pattern generating circuitry in the spinal cord. The primary motor
cortex is the cerebral cortical structure most directly responsible for activating this
circuitry and thereby controlling motor unit selection and recruitment. Although
premotor cortical areas also provide direct projections to motoneurons (see motor cortex
– output properties and organization), and somatosensory cortical areas also contribute
to the corticospinal tract, the primary motor cortex provides the most powerful projection
to the spinal cord for the control of voluntary hand and arm movements. There is a
complex mapping of hand and arm representations across the surface of the cerebral
cortex; it has been characterized as patchy and redundant (see motor cortex – hand
movements and plasticity). This pattern may be consonant with the number of different
types of voluntary movements that are possible and the inherent plasticity of the hand
motor control system (Fetz 1969).

The basal ganglia play a modulatory role in shaping the output of the cerebral cortex.
Because of the basal ganglia are organized into loops that run from cortex through
striatum through pallidum through thalamus back to cortex, they are positioned to assist
with the facilitation, shaping, and learning of movement. While modern investigations
have revealed that the basal ganglia also influence cognition and emotion, their
participation in motor control has received the greatest attention and may be their most
important function (see basal ganglia – motor function of). Deficits seen in humans
with Parkinson’s disease (degeneration of dopamine pathways from substantia nigra to
striatum) suggest that in healthy humans, the basal ganglia have a role in integrating the
activities of the many, diverse cortical and sub-cortical regions that are engaged in
implementing and adapting ongoing motor behavior.

The cerebellum is an intriguing and somewhat mysterious structure (see cerebellum –
motor function of). It is a key structure for processing sensory information from the
vestibular system, and for the control of eye movement. It is also important for voluntary
limb movement. An exquisite feature of voluntary movement is its flexibility and
adaptability, and the cerebellum, in conjunction with other sensory and motor structures,
is thought to play and important role in motor learning. Due to its interconnections with
the cerebral cortex and its involvement in motor learning, theorists have speculated that
that the cerebellum is the site of (or at least an important part of) the so-called internal
model, a functional construct which will be described in detail in the following section.

Processing algorithms for voluntary movement
Due to the complexity of the sensorimotor system, it may be useful to analyze its function without direct consideration of the specific anatomical structures involved. A class of voluntary movements that has been used extensively for this purpose is point-to-point reaching movements. In a reaching movement, the arm begins at rest with the hand in a specific initial location. A visual target appears and the hand must then be moved, in one simple motion, to stop at the specified final location. Observations about the characteristics of such movements have given rise to various motor control models, which generally provide a description of the sensorimotor transformation by proposing that the goal is to optimize a particular characteristic, like the smoothness of the hand trajectory or the amount of muscle activation (Flash and Hogan 1985, Uno et al 1989, Soechting et al 1995, Harris and Wolpert 1998). These models have provided valuable accounts of the types of kinematic (position and movement-based) and kinetic (force-based) parameters that are used by the control system.

Studies of reaching movements have also provided solid evidence for the simplest aspect of the flow chart shown in Fig. 1B. The simplest part of this model is the transformation from a visually presented goal (labeled “target”), through the “INTERNAL MODEL,” to the output command to contract arm motor units (labeled “movement”). This aspect of the internal model is called the inverse model because the visual target is specified in terms of its position or velocity (kinematic parameters) and the output is in terms of muscle force or change in force (kinetic parameters). Because the laws of physics generally describe the cause and effect transformation of force to movement (i.e., force equals mass times acceleration), the sensorimotor transformation of a kinematic goal to a muscle force is considered to be backwards or “inverse.” This neural mapping must take into account the mechanical characteristics of the arm and any object held in the hand, or else the reaching movement would miss its target. Numerous investigations (e.g., Shadmehr and Mussa Ivaldi 1994) have provided evidence that the brain can learn a new internal model within a few trials, even when the model must account for unusual patterns of elastic or viscous resistance to arm movement (rather than the more common situation where one learns to interact with a new object with unexpected inertial characteristics).

The goal of moving the hand from an initial location to a final location can be called a “motor error,” defined as the difference between the current and the target locations. Electrophysiological studies have shown that frontal and parietal cortical areas represent this motor error in terms of the direction or velocity of a reaching movement, not just the final target position (e.g., Moran and Schwartz 1999, Buneo et al 2002). Furthermore, the proper pattern of motor unit recruitment depends on both the initial and the final arm positions, as well as the other mechanical aspects of the arm and hand held object. Therefore the internal model must take into account the arm’s initial position as well as its final target position.

In studies of reaching from a stationary hand, head and body position to a stationary target, it is possible to regard the sensorimotor transformation as open-loop or feedforward (i.e., occurring without additional information about the hand or target location). However if the body moves (as in stepping while reaching) or the target moves
(as in tracking or drawing), the hand and target locations must be updated (see movement sequences). Models to describe such processes are more speculative than the initial proposal of a feedforward transformation through the inverse model.

Several lines of indirect evidence indicate that the sensorimotor system may contain a real-time estimate of the current arm and hand position during the course of a reaching, tracking, or drawing movement (Wolpert et al. 1995, Dassonville 1995). This may be accomplished by creating an “efference copy” (Fig. 1B) within the cerebral cortex, of the motor commands sent to the spinal cord (see also Shergill et al. 2003). It has been hypothesized that the efference copy information, which is in terms of muscle forces, goes back through the internal model in the opposite (forward) direction (right to left in Fig. 1B) in order to quickly produce an estimate of current hand position (the expected result of the current motor command).

If this is true, it is possible for the sensorimotor system to make an ongoing comparison of the target location and the current hand location (the “motor error” in Fig. 1B) during the course of a fast reaching movement. However, to use this mechanism for tracking a moving target, the representation of current hand position should be compared with a representation of current target location, which would need to be extrapolated from previously sensed target motion to make up for visual sensory processing delays. This hypothetical predictive extrapolation is indicated by a gray, smoothly curved arrow in Fig. 1B.

The initial motivation for proposing a quick efference copy feedback loop was the fact that sensory feedback may be subject to processing delays of as much as 100-200 ms. This is due to the numerous synaptic delays in the visual pathway, and also due to long axonal conduction times in the somatosensory system. If the current hand location was simply sensed using visual or somatosensory input, this sensory feedback information would arrive at the internal model too late to be used during an ongoing movement. However, as mentioned above, recent research on smooth pursuit eye movement has begun to provide evidence that smooth, natural target trajectories can be extrapolated (see eye-hand coordination). For example, a target velocity sensed on the retina could potentially be transformed to a representation of the most likely future target location via processing in motion sensitive cortical areas (Shibata et al. 2005).

It is not known whether the somatosensory cortical areas can perform a similar function, i.e., extrapolating a smoothly changing, familiar input to make up for the sensory delay. If so, it could make up for the time delay in tactile and proprioceptive feedback (as suggested by the gray smoothly curved feedback arrow in Fig. 1B). This would serve to produce an additional, somatosensory-based input to the forward model, which, along with the efference copy, would update current arm position (see Fig. 1B). Furthermore, it would provide the basis for a haptic comparison of the expected and actual somatosensory consequences of a hand movement (“error?” in Fig. 1B). This may be the mechanism that forms the basis of haptic perception.

Conclusions and future directions
In voluntary movement, collections of motor units are selected and recruited based on an ongoing evaluation of neural representations of current and target states. The transformation from goal to motor command must be processed using memories: the internal model and hypothetical mechanisms for sensory extrapolation are essentially memories developed through experience. Most prior research on this process has employed arm movements to visual targets, but one can think of more general examples as well:

Imagine a woman driving while singing along with the singer of a familiar song on the car radio. The driver’s voice is the immediate result of a complex sequence of motor unit activations and aspects of these patterns have become “hard wired,” genetically and through prior use of the pattern generating circuitry. The driver’s song does not lag the radio’s song by the amount of time that it takes to process the radio’s auditory information. This suggests that the radio’s auditory cues are filtered through the memories ingrained in the driver’s brain, to make up for the sensory delay. The driver is constantly listening to the radio but she can lead the voice on the radio and she can even finish the song after the radio goes off.

Common experiences such as this indicate the types of processes that must occur in sensory and motor areas (e.g., flexible patterns of motor unit recruitment and sensory extrapolation based on learning). The structures involved in some of these functions have been revealed mainly through cases of human brain lesions and disease, and studies using functional brain imaging in humans and electrophysiological recordings in animals. However, few studies have specified the neurophysiological basis of complex algorithms such as the use of efference copy and the recollection of memories. Thus there are many open questions for future research.

References


A. Schematic diagram of the main central nervous system structures involved in voluntary movement. Cognitive and motor cortical areas are in the frontal lobe; sensory and association areas are in the occipital, parietal and temporal lobes. The basal ganglia and cerebellum get input from the brainstem and spinal cord, and are interconnected with the cerebral cortex through the thalamus.

B. Schematic flow chart of the types of processing that must occur in the control of voluntary movement. Information about target location is combined with information about current location to form a motor error input command to the internal model. The output is the motor command to produce a movement. An efference copy of this command, representing the expected result of the movement, can be compared to sensory feedback, representing the actual result. The efference copy can also be used to update the representation of the current location. If the central nervous system can extrapolate in time, the information in the sensory input (gray, smoothly curved arrows), it would make up for delays due to synaptic transmission and axonal conduction.