Physiology of the Peripheral Motor System

Nicholas Cothros

The peripheral nervous system (PNS), which comprises all neural tissue outside of the brain and spinal (together these of course are the central nervous system, or CNS) consists of the autonomic nervous system and the somatic nervous system. As the name suggests, the autonomic nervous system is chiefly concerned with the control of bodily functions that are outside of conscious awareness and control, like sweating and blood flow. Neurons of the somatic nervous system (note that "soma" is the Greek word for "body") include motor fibres projecting to skeletal muscle and sensory fibres projecting from receptors found in the skin, viscera, muscles, and tendons. The somatic nervous system contributes to voluntary movement and the detection of stimuli that pertain to the body's physical state and position in space.

In the control of voluntary movement, a signal originating from the CNS travels through an alpha motor neuron, which in turn projects to a number of muscle fibres. The combination of a single alpha motor neuron and its muscle fibres is referred to as a "motor unit". The concept of the motor unit is the focus of the present review.

The upper motor neuron. Before considering the motor unit, it is important to review the pathway of a motor signal. During intentional movements, the command to move a skeletal muscle originates from the central nervous system (take for example the primary motor cortex). The neurons that carry these signals are upper motor neurons. Upper motor neurons connect to alpha motor neurons (also referred to as "lower motor neurons") via a number of different tracts. For example, some upper motor neurons travel through the corticospinal tract, or "pyramidal tract". This tract mostly contains motor axons. While the neurons that give rise to the pyramidal tract are in fact pyramidal neurons, this is not why the pyramidal tract is so named. Point in fact, many pyramidal neurons do not project their axons through the pyramidal tract. At the medullary level, the shape of the pyramidal tract resembles a pyramid.

Some upper motor neurons travel through the corticobulbar tract. This tract is much like the corticospinal tract, but it terminates in the medulla (once called the "bulb") and not in the spinal cord. This tract is also called the "corticonuclear" tract. Motor commands for head, neck and face muscles are carried via this tract.

Other upper motor neurons travel through the rubrospinal tract. This tract originates in the red nucleus of the midbrain. It descends through the brainstem tegmentum and ultimately through the spinal cord, along with the corticospinal tract. This tract underlies the control of a number of gross movements as well as a few fine movements.

The rubrospinal tract is thought to be a primitive counterpart to the corticospinal tract. The rubrospinal tract is relatively small in humans and much larger in non-human primates. In humans, the corticospinal tract is relatively large. It is perhaps no surprise that distal, highly dextrous muscles like those of the hand are heavily innervated by corticospinal tract neurons.

Humans and non-human primates differ in manual dexterity. These differences did not arise due to evolved changes in the motor effectors - the human hand and the hand of any non-human primate are essentially identical in terms of musculature and skeletal organization. Rather, great manual dexterity in humans is afforded by neural circuitry that is unique to the species.

The lower motor neuron. Upper motor neurons synapse onto alpha motor neurons (recall that these are also called "lower motor neurons"), whose nuclei reside in the brainstem and spinal cord. Even though the nuclei (be aware that the term "nuclei" is used here, as opposed to "ganglia", which is reserved for the PNS) of alpha motor neurons are in the CNS, they are deemed PNS neurons, given the extent of their axons into skeletal muscle. Brainstem alpha motor neurons project to face and neck muscles; spinal cord alpha motor neurons project to the rest of the body.

In the spinal cord, alpha motor neurons are located in the grey matter of the ventral horn. In particular, they are located in lamina IX, mostly in the medial portion of the ventral horn. This region is organized somatotopically. That is, the position of a given alpha motor neuron is associated with its target muscle. Alpha motor neurons in the medial portion of lamina IX tend to innervate proximal muscles. Those in the lateral portion tend to innervate distal muscles. Alpha motor neurons that innervate flexor muscles tend to reside in the dorsal portion, while those that innervate extensors tend to be located in the ventral portion. This flexor-extensor arrangement allows for efficient force generation and smooth motor control.

Fibres projecting to and from muscle. Alpha motor neurons originate from the brainstem and spinal cord and are myelinated and of relatively large diameter, allowing for fast conduction (note that maximum conduction velocity in a human alpha motor neuron does not far exceed 65 metres per second). Alpha motor neurons innervate extrafusal muscle fibres. The signal traveling through an alpha motor neuron initiates muscle contraction. Alpha motor neurons should not be confused with gamma motor neurons. These are smaller neurons that project to intrafusal muscle fibres. Intrafusal muscle fibres are the contractile elements within muscle spindles, which are sensory structures embedded in skeletal muscle that convey information about the state of the muscle.

There are two different fibre types that carry information from the muscle spindle. The Type Ia fibre signals the rate of change of muscle length. It also signals the static length of a muscle. The firing rate of the Type II fibre correlates with the length of a muscle. Information corresponding to muscle length is related to the position of an effector. Note that the Type II fibre is a non-adapting fibre. Unlike primary fibres like the the Type Ia, which transiently signal the events to which they are sensitive, secondary fibres like the Type II continually fire when they detect a sensory event to which they are sensitive. Type II fibres connect to nuclear chain fibres within muscle spindles. Type Ia fibres connect to both nuclear chain and nuclear bad fibres within muscle spindles.

Type Ia and II fibres are complemented by Type Ib fibres, which arise from Golgi tendon organs. Tendons are flexible, but inelastic cords of collagen tissue linking muscle to bone. The Golgi tendon organ is a sensory structure lodged in tendon. The Type Ib fibre signals muscle tension.

The motor unit. Originally described by Sir Charles Scott Sherrington, the motor unit is the combination of a single alpha motor neuron and the muscle fibres to which it connects. A muscle fibre is a muscle cell; it is the contractile unit of muscle. Some muscle fibres can reach lengths of 30 centimetres. The connection between an alpha motor neuron and a muscle fibre is called the "neuromuscular junction". When an action potential is elicited in an alpha motor neuron, its muscle fibres contract and generate force.

Motor units originating in the spinal column are arranged in columns referred to as "myotomes". The motor unit pool of a single muscle comes from several columns. This is an adaptive organization. In the event of spinal cord injury, the likelihood of losing all neural control of a muscle is reduced. For example, myotomes serving the quadriceps span

three segments of the cord (lumbar segments 2, 3 and 4). A lesion to L3 may not result in complete loss of neural control of the quadriceps.

Glycogen depletion methods have been used to elucidate the spatial extent of a motor unit's influence within a given muscle. This technique entails isolating an alpha motor neuron axon and stimulating it for hours at high frequency, thereby exhausting its supply of glycogen. Slicing the muscle and staining it histologically for glycogen reveals muscle fibres that are depleted of glycogen. This helps draw a connection between the axon of a motor neuron and its muscle fibres. In human biceps muscle, a motor unit covers an area of 8 to 10 millimetres in length.

Motor unit numbers and innervation ratios. The number of muscle fibres per motor unit varies throughout the body, as does the number of motor units per muscle. This reflects the control requirements of different effectors. Take for example the extraocular muscles, which control eye movements. Each of these muscles is innervated by some 3000 motor units. Each of these motor units encompasses a very small number of muscle fibres, seldom exceeding 10. A high number of motor units per muscle along with few muscle fibres per motor unit is an excellent combination for exquisite motor control. Eye movements are very precise and the eye, which is a small, light organ, requires very little force to overcome its inertia. The motor unit number and innervation ratio are thus perfectly suited for fine, delicate movements, which are precisely the sort that are needed for moving the eye.

Consider the gastrocnemius (calf muscle). A calf muscle is innervated by roughly 600 motor units. This is one fifth of the number of motor units corresponding to an eye muscle. Each motor unit connecting to a calf muscle innervates approximately 2000 muscle fibres. This arrangement is ideal for calf muscles, which are used for generation of great force. Calf muscles do not require rich motor commands, like the sort that are carried by large numbers of motor units, but do require many contractile elements. A low number of motor units per muscle along with many muscle fibres per motor unit is an effective combination for simple control of brute strength.

Motor unit categorization. Motor units vary in terms of a number of properties, like force production, susceptibility to fatigue, and certain metabolic characteristics. Consequently, there are numerous ways in which motor units can be categorized. Regardless of categorization convention, motor units generally vary along a spectrum, with fast-contracting, fatigue-prone motor units on one end of the spectrum and slow-contracting, fatigue-resistant motor units on the other end.

First, consider the slow units. These are *Type I* motor units (take care to not confuse this "Type I" with the muscle spindle "Type I" afferents described above). The muscle fibres of these motor units are red in colour and akin to dark meat in poultry. The fibres contain high levels of myoglobin (a red protein containing heme that carries and stores oxygen in muscles - functionally, it is hemoglobin for muscle). They are also supplied by a high number of capillaries and have a high number of mitochondria, the energy producing organelles in animal cells. When electrically stimulated, the motor units that connect to such fibres generate slow, low-force muscle twitches. They contract slowly, produce little force, and relax slowly. The muscle fibres pertaining to these slow units generate adenosine triphosphate (ATP, the universal fuel for cellular metabolism) aerobically (i.e. using oxygen) and are thus classified as "oxidative". These fibres split ATP slowly. Type I motor units are resistant to fatigue.

Now, consider the other end of the motor unit spectrum: the fast units. These are *Type IIb* motor units. To avoid confusion, be aware that there is another fast unit, the Type IIa

motor unit; it is considered further below. The muscle fibres of Type IIb motor units are white in colour and akin to white meat in poultry. Relative to the Type I fibres, these fibres contain low levels of myoglobin, they are supplied by few capillaries and have few mitochondria. When electrically stimulated, the motor units that connect to such fibres generate fast, high-force muscle twitches. They contract quickly, produce a lot of force, and relax quickly. They rely on glycolysis for generation of ATP and are thus classified as "glycolytic". These fibres split ATP quickly. Type IIb motor units are susceptible to fatigue.

Somewhere in the middle of the motor unit spectrum lies the *Type IIa* motor unit. As one might imagine, the Type IIa unit shares some features with Type I and Type IIb motor units. The muscle fibres of Type IIa motor units have moderate levels of myoglobin and mitochondria. When electrically stimulated, the motor units that connect to such fibres generate fast twitches, but not as much force as in the case of Type IIb units. They are both oxidative and glycolytic. Type IIa motor units are resistant to fatigue, but not to as great an extent as the Type I fibres.

Recall that there are numerous ways in which motor units can be classified. This is reflected in the different naming conventions, like "Type I" versus "slow" versus "oxidative". The Type I and II classification system is based how the fibres stain for Myosin ATPase. The system that uses names like slow, fast-fatigue-resistant and so on are based on the twitch characteristics of the fibres. If one classifies motor units according to twitch characteristics, then strictly speaking it is not appropriate to refer to a slow-twitch motor unit as an oxidative motor unit. However, the different classification systems overlap with one another considerably.

The size principle. The different types of motor units/muscle fibres are suited for different tasks. A Type I motor unit is able to maintain low levels of force for long periods of time and is thus suited for maintaining posture and for tasks that require endurance. A Type IIb motor unit is able to produce sudden, explosive force and is suited for tasks requiring fast movements, like sprinting or jumping.

A single motor unit projects to only one type of muscle fibre. However, individual muscles are composed of different fibre types, which means that different types of motor units project to a single muscle. Though it is the case that a single muscle will contain different muscle fibre types, like slow, fast and so on, the different types of muscle fibres do not cluster within a muscle. Rather, they are intermingled with one another. This intermingling is fairly diffuse. The muscle fibres coming from a single motor unit are spread throughout a muscle, allowing for the generation of force across a relatively large area of the muscle.

In order to generate a small force, it is only necessary to recruit Type I motor units. Generating large amounts of force quickly, however, would require recruitment of, say, Type IIb motor units. The recruitment of different motor units for different tasks is afforded mainly by differences in the size of the alpha motor neurons. This is referred to as the "size principle" and it was first described by Henneman.

Motor units are recruited in an orderly fashion, which is related to the size of the motor neuron cell bodies. To gain an understanding of the size principle one must appreciate Ohm's law. This law states that voltage is equal to the product of current and resistance. Voltage is an electromotive force or potential difference. Current is the rate of flow of electric charge. Resistance is the degree to which a substance opposes the passage of an electric current, thereby resulting in the dissipation of energy. A symbolic representation of Ohm's law is shown below.

$V = I * R$

The smaller the neuron, the greater the resistance. This is due to an increase in the density of channels in the cell membrane. For a given current (this is delivered by the central nervous system, via upper motor neurons), the small motor neurons will fire first, given their relatively high resistance. The high R multiplied by a given I will result in a higher V than in cases where R is not high. Along the motor unit spectrum, the slow units are the smallest and the fast units are the largest.

Additional motor unit properties. The activation of one motor unit results in a weak but distributed muscle contraction. Further recruitment of motor units results in stronger muscle contraction. According to the size principle, motor units are recruited in order of smallest to largest as the motor system calls for a progressively more forceful muscle contraction. The motor units that are recruited last are large, fast units whose muscle fibres cover the largest area within a muscle. The derecruitment threshold of a given motor unit is correlated with its recruitment threshold and so the size principle works in reverse during muscle relaxation.

The higher the frequency of firing, the higher the amount of force. This is "rate coding" and it is observed at the level of a single motor unit or the whole muscle. Increasing frequency results in there being not enough time for muscle fibre relaxation. As a result, the force production phases summate.

The onset of muscle fibre contraction requires a motor unit firing frequency of 5 to 7 Hz. The minimum sustainable contraction requires a train of 8 to 10 Hz. The maximum possible firing rate is between 20 and 40 Hz. A plot that describes firing rate as a function of force differs across motor units. The smallest motor units, which are recruited first are characterized by functions that initially are moderately steep and then gradually decrease in slope before reaching an asymptote. The largest units, which are recruited last, are characterized by very steep firing rate-as-a-function-of-force curves. Like the smallest units, they are recruited at a firing rate of 5 to 8 Hz, but they reach their peak force levels more quickly.

The above motor unit properties are further described by the "onion skin" phenomenon. It has been shown that the average firing rates of motor units during contractions of different force (for example, 30%, 50% or 80% of maximum voluntary contraction) are organized hierarchically. Motor units that are recruited first have higher average firing rates than motor units that are recruited later. When mean firing rates of motor units with different recruitment threshold are plotted one on top of the other for a contraction with a trapezoid force profile (i.e. an increase in force followed by a static hold phase, followed by a decrease in force), the resulting firing rate curves resemble an "onion skin." That is, for a given amount of force, the lower-threshold motor units fire at greater rates than the higher-threshold units.

Clinical applications. Some clinicians rely on sophisticated knowledge of the electrophysiololgical properties of the motor unit. Electromyography can be used to diagnose a number of different pathologies, including myopathies and neuronopathies, such as demyelination and axonal loss. Aberrations in the waveform of a motor unit potential and/or nerve conduction velocity indicate the presence of different pathologies.

Major Themes/Questions

- What is a motor unit?
- What is the significance of variations in the number of motor units per muscle and the number of muscle fibres per motor unit?
- How are different types of motor units used during different motor tasks?
- What role does the size principle play?