The University of Connecticut
Graduate School
Meds 371
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Spinal Motor Neurons

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Reading: Purves et al. (2008: 4th edition), Chapter 16.

Goals: The primary goal is to understand the relationship between motor neurons in the spinal cord and the type of muscle they innervate. This entails a basic understanding of the motor neuron pool, motor units, muscle fibre types, and the size principle. The student also should understand the concept of recruitment and rate coding as it applies to the control of muscle tension.

Introduction

This lecture concerns the anatomical and physiological properties of spinal motor neurons, the muscles they innervate, and their interrelationships. Muscles range in speed from those engaged in controlling rapid eye movements to those involved in standing; in force, from the delicate touch of a pianist's fingers to the brute force of a boxer's fists. Are these functions handled by the same type of motor neurons and muscle fibers? An old notion was that muscles are composed of homogeneous muscle fibers, i.e., a muscle is a muscle, is a muscle. Thus, the variety of motor responses are due to differences in nervous innervation. However, research in the past few decades have revealed different types of muscle fibers and motor neurons. It seems that different types of muscle fibers are innervated by only a certain type of motor neuron. Furthermore, the muscle fiber-motor neuron units show functional specializations. The material for this lecture is primarily based on the work of Elwood Henneman and his colleagues.

Motor neuron pool: A muscle is controlled by approximately 10-1000 motor neurons which are arranged in a column in the ventral horn of the spinal cord. The neurons that provide the drive for a particular muscle is called the motor neuron pool. Thus, each muscle in the body is innervated by a distinct motor neuron pool and that there is a functional organization of the different motor neuron pools. Figure 1 illustrates how motor neuron pools are identified. In this example, a retrograde neuronal tracer was placed in the left medial gasrocnemius muscle and the right soleus muscle, both of which serve to elevate the heel. The motor neurons that innervate these muscles can then be identified in the ventral horns of the spinal cord. Note that the two motor neuron pools overlap in rostro-caudal domain but are separated in the dorso-ventral domain.

Motor unit: This concept goes back to 1925, when Liddel and Sherrington defined the motor unit as the smallest functional unit that can be controlled by the nervous system. The motor unit is comprised of a motor neuron and all the muscle fibers it innervates (see Fig. 2). The number of motor units for a given muscle equals the number of neurons in the motor neuron pool.

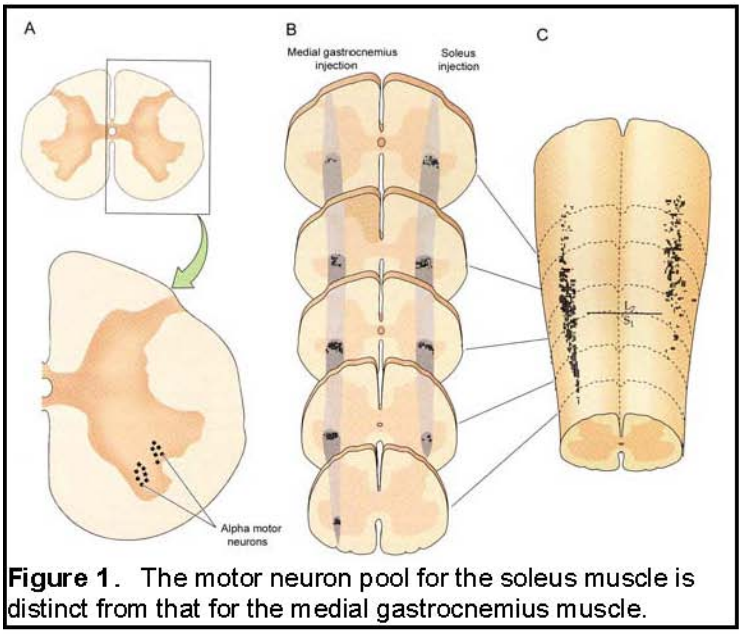

Figure 1. The motor neuron pool for the soleus muscle is distinct from that for the medial gastrocnemius muscle.

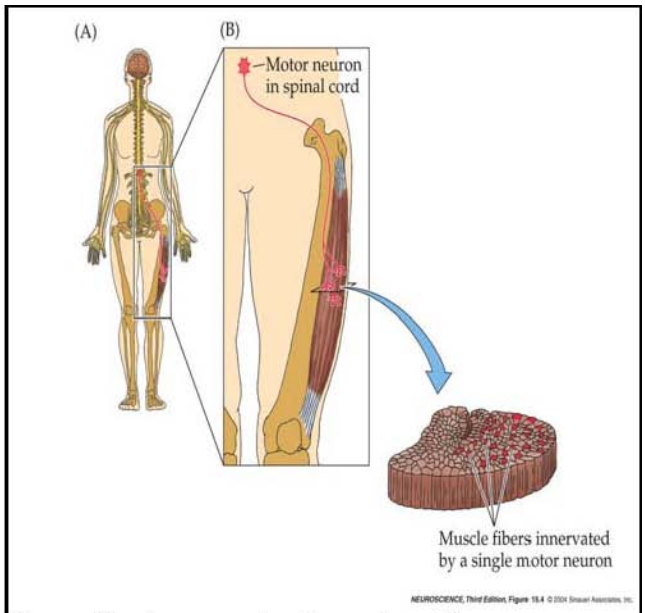

Figure 2. An example of a motor unit

Muscle Fiber Characteristics.

Muscle fibers are conveniently divided into three types. The small muscle fibers are called "red" muscle fibers because they have a rich capillary bed, rich myoglobin content and plentiful mitochondria. These fibers rely upon aerobic metabolism and thus do not fatigue easily. The large muscle fibers are called "pale" because they have a sparse capillary bed and are sparse in mitochondria. These muscles depend upon stored glycogen for energy and thus are susceptible to fatigue. In between these two types are the "intermediate" muscle fibers, so named because they have characteristics that lie between the two extremes. Some muscles (e.g., medial gastrocnemius) have all three types of muscle fibers, whereas other muscles (e.g., soleus) have predominantly one type.

Properties of Motor Units.

Conduction Velocity: Figure 3 is a diagram of the experimental set-up used to measure conduction velocity of motor units. To measure conduction velocity, the whole nerve to the muscle is stimulated and the time of arrival of the antidromic action potential at the recording electrode is measured. Since the distance between the stimulating and recording electrode is known, the conduction velocity can be calculated using the formula: Velocity = distance/time.

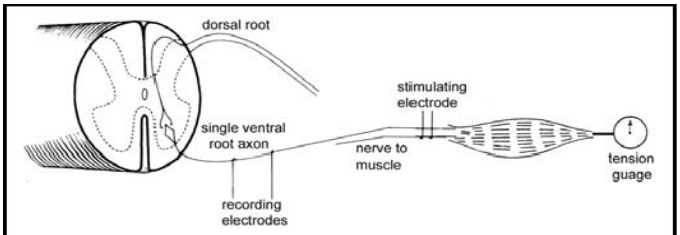

Figure 3: Experimental preparation used to measure conduction velocity.

Measuring conduction velocities in many motor units indicated that motor units could be conveniently divided into three groups, fast, slow, and intermediate. Since axonal diameter is directly related to cell body (soma) size, this grouping indicates that fast motor units have large somas, slow motor units have small somas, and motor units with intermediate conduction velocities have somas that are intermediate in size.

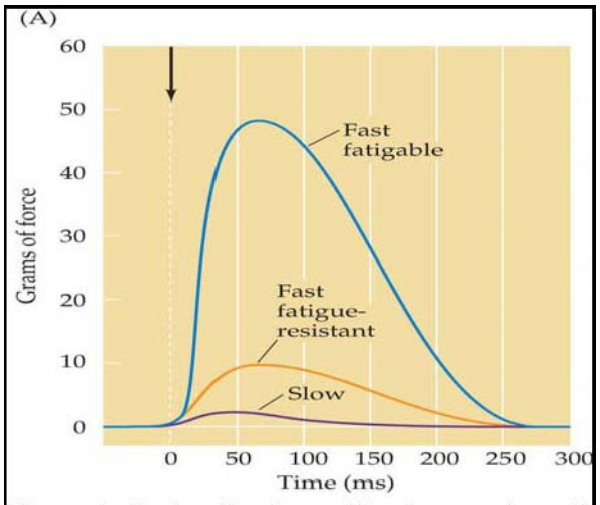

Figure 4 Contraction time of the three motor unit types

Contraction Time: In these experiments, a single stimulating pulse is delivered through the recording electrode and the time to the peak of a muscle twitch (measured with a with a tension gauge) is recorded (see Fig. 3). Again, doing this over many motor units indicates that contraction times can be divided into fast, slow and intermediate and correlate well with those that have fast, slow and intermediate conduction velocities. Figure 4 displays the contraction times of the fast (fast-fatigable), slow (slow-nonfatigable), and intermediate (fast-fatigue-resistant) motor units. These experiments also indicated a motor unit activates only one type of muscle fiber. If each motor unit contained several fiber types, contraction times would differ very little. Since there are large differences within a given muscle, it is most likely that a motor unit innervates muscle fibers with the same contraction speed.

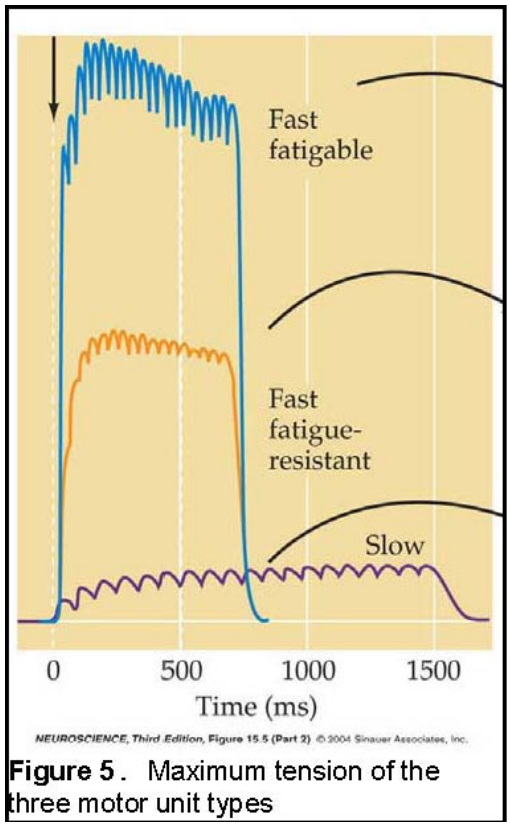

Figure 5. Maximum tension of the three motor unit types

Maximum Tetanic Tension: The purpose of these experiments is to determine if motor units differ in their force of contraction. Electrical pulses are delivered through the recording electrode at high rates to cause a fused tetanus and the tension gauge is used to measure the muscle tension. Figure 5 compares the tensions generated by the slow (small), fast fatigue-resistant (intermediate), and the fast fatigable (large) motor units.

Susceptibility to Fatigue: In these experiments, the motor unit is stimulated at high rates

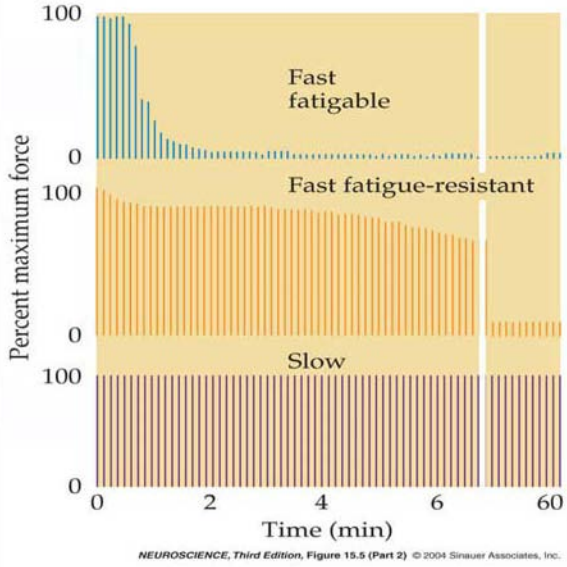

Figure 6 Differences in the fatigability of the three motor unit types

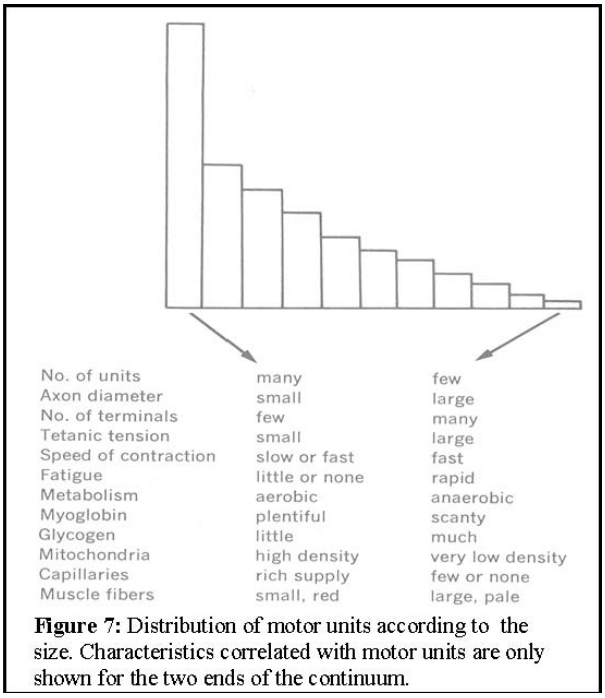

Figure 7: Distribution of motor units according to the size. Characteristics correlated with motor units are only shown for the two ends of the continuum.

through the recording electrode and the tension over time is measured. Figure 6 shows that the slow motor units do not fatigue at all, whereas the fast fatigable motor units can hold their maximum tension for only a minute or two.

Innervation Ratio: One way to determine the how many muscle fibers a motor neuron innervates is to stimulate a single motor neuron at slow rates for a prolonged period of time. This results in the depletion of glycogen stores in the muscle fibers that can be histologically identified using the appropriate stain. Using such methods, it has been shown that large motor units can have innervation ratios as high as 1:750, while small motor units have innervation ratios as low as 1:39. The lower the innervation ratio, the greater the motor control.

Figure 7 plots the distribution of motor units according to their size and their corresponding features. It conveniently summarizes the experimental evidence presented thus far.

Functional Organization of Motor Units.

What is the functional significance of these correlations? Before this question can be answered, it is necessary to examine the excitability threshold of these motor units. A convenient method for discharging motoneurons is to stretch a extensor muscle in a decerebrate preparation. In such cases the stretch reflex is greatly exaggerated resulting in motor neuron discharge and muscle tension. Figure 8 shows a schematized response of 3 motor units recorded from ventral root filaments of the sacral cord. As stretch is initiated, the response of one motor unit (1) is evident. A further increase in stretch activates a

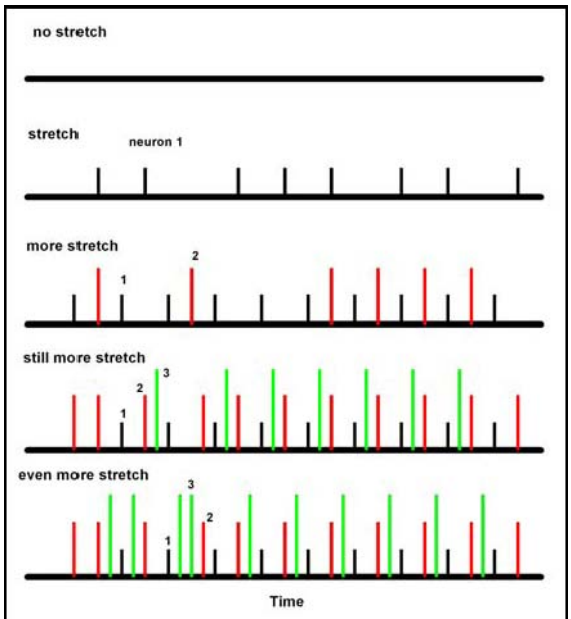

Figure 8. Recruitment of motor neurons according to size

second action potential (2) that is larger than the first. A further increase in stretch recruits a third motor neuron. Since the amplitude of extracellularly recorded action potentials is directly related to the diameter of the axon, and axon diameter is directly related to the size of the soma, these results indicate that motoneurons are systematically recruited according to their size. Thus this recruitment order is known as the "size principle".

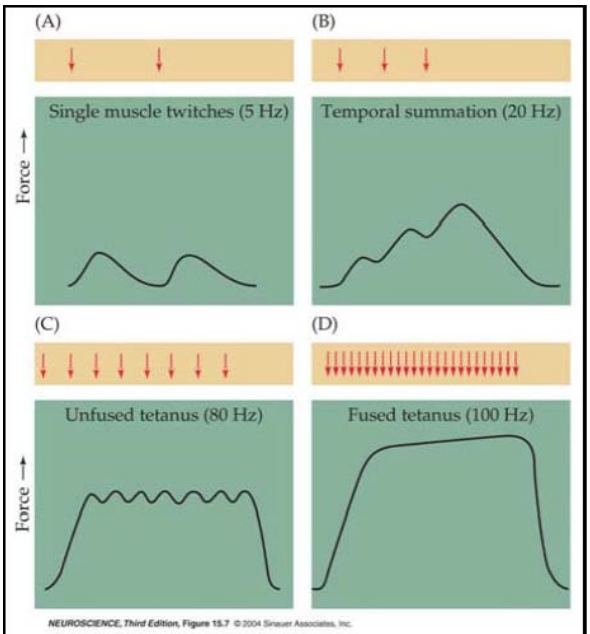

Figure 9: rate coding

Another way that the CNS controls muscle tension is by increasing the firing rate of the motor neuron. This mechanism is called "rate coding" and is illustrated in Fig. 9. A short electrical pulse applied to an axon evokes a single action potential. When the interval between action potentials (arrows) is long, the time course of the contraction and relaxation of the muscle (twitch time) can be clearly seen. As this interval between action potentials becomes shorter and shorter, the twitches begin to fuse and increase in tension. At very short intervals, i.e., high discharge rates, it reaches a plateau of maximum tension. Thus, an individual motor unit can control muscle tension by varying its firing rate.

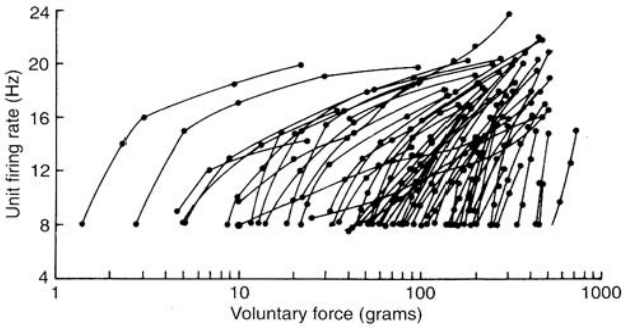

Figure 10: The Size principle and rate coding illustrated from recordings from 60 motor units in the extensor digitorum communis muscle of the human hand as the subject generates more and more force through his middle finger (After Monster and Chan, J. Neurophysiol., 1977, 40: 1434).

Figure 10 is an illustration of the size principle and rate coding at work in the motor units that control the extensor digits in the human hand. As the subject increases the force of his middle finger, motor units are recruited in an orderly way (size principle) and each motor unit increases its firing rate (rate coding). In this way, both mechanisms work in concert to achieve precise control of grading muscle force.

A simple neural circuit for how the size principle and rate coding might operate to control muscle force is illustrated in Fig. 11. Let's say for example that a weight needs to be picked up and involves the bicep muscles. Information about the state of the bicep muscle is transmitted as a continuous stream to the cortex via the appropriate 1a and 1b fibers (muscle spindles and Golgi tendon organs) traveling in the dorsal column system. The cortex realizes that the muscle force is inadequate and initiates a stream of action potentials that travel in an axon of the corticospinal tract that innervate the motoneurons that control the bicep muscles. Due to the size principle, this stream activates the motoneurons in a graded way beginning with the smaller, lower threshold motoneurons. The resulting increase in muscle force is again conveyed to the cortex and if it is still not sufficient to lift the weight, the

cortex increases the firing rate of the appropriate corticospinal axon. Consequently, higher and higher threshold motoneurons will be activated until the force is sufficient to lift the object.

A way of summarizing the key features of this lecture is presented in Figure 12. Here, motor units were recorded in the medial gastrocnemius muscle of a cat while it performed a variety of motor behaviors. The "slow" motor units activate small, dark muscle fibers, have low activation thresholds and are slow to achieve maximum contraction. However, they can maintain this contraction for long period of time (e.g., hours) and are well suited for low maintenance activities such as standing. The "fast, fatigue resistant' motor units activate small to intermediate muscle fibers, have a higher activation thresholds than "slow" units, and are quick to achieve maximum contraction. Moreover, these motor units can generate more force than "slow" units. These "fast, fatigue resistant" motor units were activated when the cat was walking or running slowly. Finally, "fast fatigable" motor units activate the large, pale muscle fibers, have the highest activation thresholds, generate the highest force, but can only do so for a short period of time (e.g. a few minutes). These motor units were activated when the animal engaged in strenuous activities (e.g., galloping and jumping). The anerobic metabolism of large pale fibers explains why such strenuous activity cannot be sustained for long periods of time.

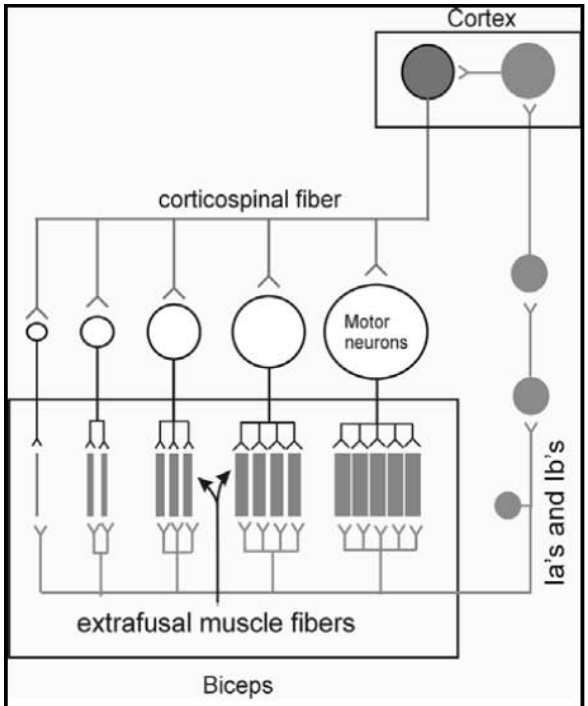

Figure 11: A simple neural schematic of how the Size principle might operate.

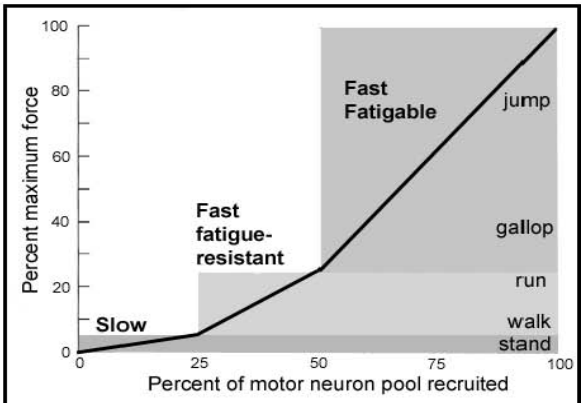

Figure 12: The recruitment of motor neurons in the cat medial gastrocnemius muscle under different behavioral conditions. Slow motor units provide the tension required for standing. Fast-fatigue-resistant units provide the additional force needed for walking and running. Fast fatigable units are need for the most strenuous activities. (Adapted from Purves et al., Neuroscience, 1997, p. 97.)