Muscles
A Tech Brief Prepared for the
Neurofuzzy Soft Computing Program
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Introduction

In studying the application of pulse-coded neural networks for bipedal locomotion, our biological model for neural organization is the network of neurons in the ventral horn of the spinal cord. This neural system meets our application requirements for involving large amounts of sensory input data, large numbers of coordinated output signals, and relative ease in determining whether or not our neural system is working. The ventral horn neural circuits were historically the first mammalian neural network systems to be studied in detail, and much of what we know about neural organization in the brain was first learned by studying spinal neuron organization.

The context that underlies ventral horn neural organization can probably best be explained by first understanding what it is that these neural networks evolved to control: muscles. Even though any bipedal mechanical test platform we are likely to build at some point is ipso facto going to involve electromechanical actuators and sensors, an understanding of muscle organization is useful in defining the input/ output organization and servo dynamics of a robotic platform. In addition, by casting our neural network design in such a biomimetic framework we open the door to the possibility of future applications of what we learn about ventral horn networks to applications in neural prostheses. The purpose of this tech brief is to review the organization of muscles and muscle systems.

Basic Terminology

Most of the technical terminology biologists use to describe muscle systems is familiar to us already, although the technical definitions of these terms may not be. The primary technical literature I have consulted for this brief consists of two elementary textbooks:

1) A. Vander, J. Sherman, and D. Luciano, *Human Physiology*, 7th ed., Boston, MA: McGraw-Hill, 1998;

2) N.A. Campbell, J.B. Reece, and L.G. Mitchell, *Biology*, 5th ed., Menlo Park, CA: Addison Wesley, 1999.

An individual muscle cell is called a **muscle fiber**. There are two general classes of muscle fibers, each of which contains three species of fibers. **Extrafusal fibers** are the muscle fibers that actually do the work of moving the bones to which the muscle is attached. **Intrafusal fibers** are small muscle fibers, generally surrounded by extrafusal fibers, that act as sensory transducers. Intrafusal fibers are incapable of producing motion, and their role is to provide a mechanical platform for sensory neurons that detect motion. They, plus the sensory neurons that attach to them, are often called **muscle spindles**.

A **muscle** is a group of parallel muscle fibers bound together by connective tissue. Figure 1 illustrates the basic structure of a muscle. A typical muscle usually contains at least four or five of the basic species of fibers (one or two types of extrafusal muscle fibers and all three types of intrafusal fibers), and often contains all six types. The properties of the muscle are determined by
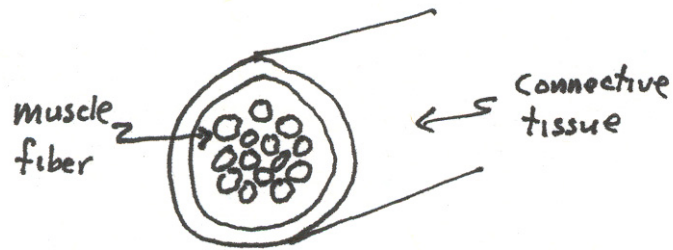
Figure 1: Illustration of basic muscle structure. The muscle filaments run in parallel throughout the length of the muscle. Muscle fibers are bound together within a connective tissue. Not shown are the connections to the tendons at each end.

the number and types of fibers it contains. Muscles work by contraction. When excited by motor neurons, excited fibers reduce their length.

A muscle is connected to bones by **tendons** at each end. Muscle fibers may be up to 20 cm in length (in large muscles), and tendons may likewise be very long. More than one muscle might be connected to the same tendon. An example of this is provided by the large tendon that connects the four quadriceps muscles in the front of the upper leg to the tibia (the front bone in the lower leg). The mature human body has more than 600 muscles connecting 206 bones.[1] The spine has 26 vertebrae, and spinal neurons are located in tissue residing on the segments of the vertebrae.

Although not directly related to our work, there is some other familiar terminology worth mentioning in order to set everything in proper perspective. **Ligaments** are fibrous elastic tissue that links bones together, typically in parallel arrangements. Like muscles, ligaments can stretch. **Joints** are bone structures that fit bones together end-to-end. **Cartilage** is glassy-smooth tissue in a joint that reduces friction between two bones when they move relative to one another. **Synovial fluid** is a watery secretion that lubricates joints.

Muscles are arranged in pairs for "opening" and "closing" the joint configuration of two bones. The muscle that "opens" a joint is called an **extensor** muscle. Any one of the quadriceps muscles is an extensor because these muscles are used to extend the leg. Opposing the extensor muscle is the **flexor** muscle, which acts to "close" the joint. An example here is the biceps muscle, one of muscles in the "hamstrings" (the group of big muscles in the back of the upper leg that attach to the fibula, the rear bone in the lower leg). The biceps muscle "closes" the knee joint when you bend your leg. Taken together, the extensor and flexor muscles form an **agonist-antagonist pair**. The agonist is the muscle that is being contracted; the antagonist is the muscle that would oppose this contraction unless it is relaxed.

Complex movements are performed by groups of muscles activated in a coordinated fashion. Such coordinated muscles are called **synergists**. For example, when the quadriceps femoris is relaxed and the gastrocnemius (a calf muscle running from the lower end of the femur bone to the heel of the foot bone) is contracted, your leg flexes. This happens when you are walking. However, if both the quadriceps femoris and the gastrocnemius contract, the leg does not bend and your foot is extended (i.e., you stand on your tiptoes). Because it is possible to execute this

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[1] It appears to be the case that at birth a human being has all the muscles he or she will ever have. However, the number of bones in an infant and young child is about 300. Many of these bones, such as most of the bones in the skull, will later fuse together, reducing the total number to 206.

movement when both muscles contract, the quadriceps femoris and the gastrocnemius are not an agonist-antagonist pair, but they are synergists to each other. By contrast, contracting the quadriceps and the hamstrings at the same time produces no movement, hence these groups are comprised of agonist-antagonist pairs.

Extrafusal Muscle Fibers

When most people talk about "muscle fibers" they are referring to the extrafusal fibers. These are the fibers that actuate movement. They are innervated by motoneurons (MNs), called alpha-motoneurons (α-MNs), that activate contraction by firing action potentials. These muscle fibers react to a single action potential with a brief, short contraction that produces a movement called a "twitch", hence these fibers are also sometimes called twitch fibers.

Extrafusal fibers are categorized according to the speed at which they contract, the chemical activities involved in producing the contraction, and the activity duration they can sustain before becoming fatigued. There are three categories of extrafusal fibers:

       1) slow-oxidative fibers (S-type);
       2) fast-oxidative fibers (FR-type);
       3) fast-glycolytic fibers (FF-type).

S-type fibers are small-diameter fibers that act slowly and are highly resistant to fatigue.[2] A single twitch in an S-type fiber can last longer than 100 ms in duration, which is very long compared to the 1 to 2 ms duration of a single α-MN action potential (AP). There is a latency on the order of tens of ms from the time of the action potential to the start of the twitch movement. Because they are small, an S-type fiber does not exert very much tension compared to the other types of fibers. However, because they are highly resistant to fatigue, S-type fibers are important in maintaining posture.

FR-type fibers are larger in diameter than S-type fibers but smaller than FF-type fibers. They are stronger than S-type fibers and have a much more rapid twitch response, reaching peak tension in a few tens of ms with a motion latency of less than 20 ms. Their rate of contraction is also much faster than S-type fibers, reaching peak twitch tension in about 35 ms. As a "rule of thumb", S-type fiber twitch lasts about 5 times longer than FR-type fiber twitch, but FR-type fibers can develop between 7 and 8 times higher peak tension.[3] They are very resistant to fatigue, although not as resistant as S-type fibers. (The "FR" designation stands for "fast, resistant to fatigue"). An FR-type fiber can maintain its tension for about three and a half minutes before it begins to show fatigue. It then shows a more or less linear drop in maintained tension, reaching a minimum "tension floor" of about 10% of peak tension after about 50 minutes. In contrast, S-type fibers can maintain their level of tension for well over an hour without noticeable loss.

FF-type fibers are generally the largest diameter fibers. They develop the highest maximum tension levels (roughly 2.5 times the maximum tension of FR-type fibers), have the shortest time to develop maximum tension, and they fatigue rapidly. (The "FF" stands for fast, fatigable). With regard to twitch contraction time, there is a great deal of overlap between FF- and FR-type fibers. The slowest FR-type fibers are 2 to 3 times faster than S-type fibers, and the fastest FF-type fibers are about 2 times faster than the slowest FR-type fibers.[4]

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[2] Muscle fatigue is defined as loss of tension due to repeated or maintained contraction.
[3] cf. V.B. Brooks, *The Neural Basis of Motor Control*, Oxford, UK: Oxford University Press, 1986, pg. 61.
[4] *ibid*.
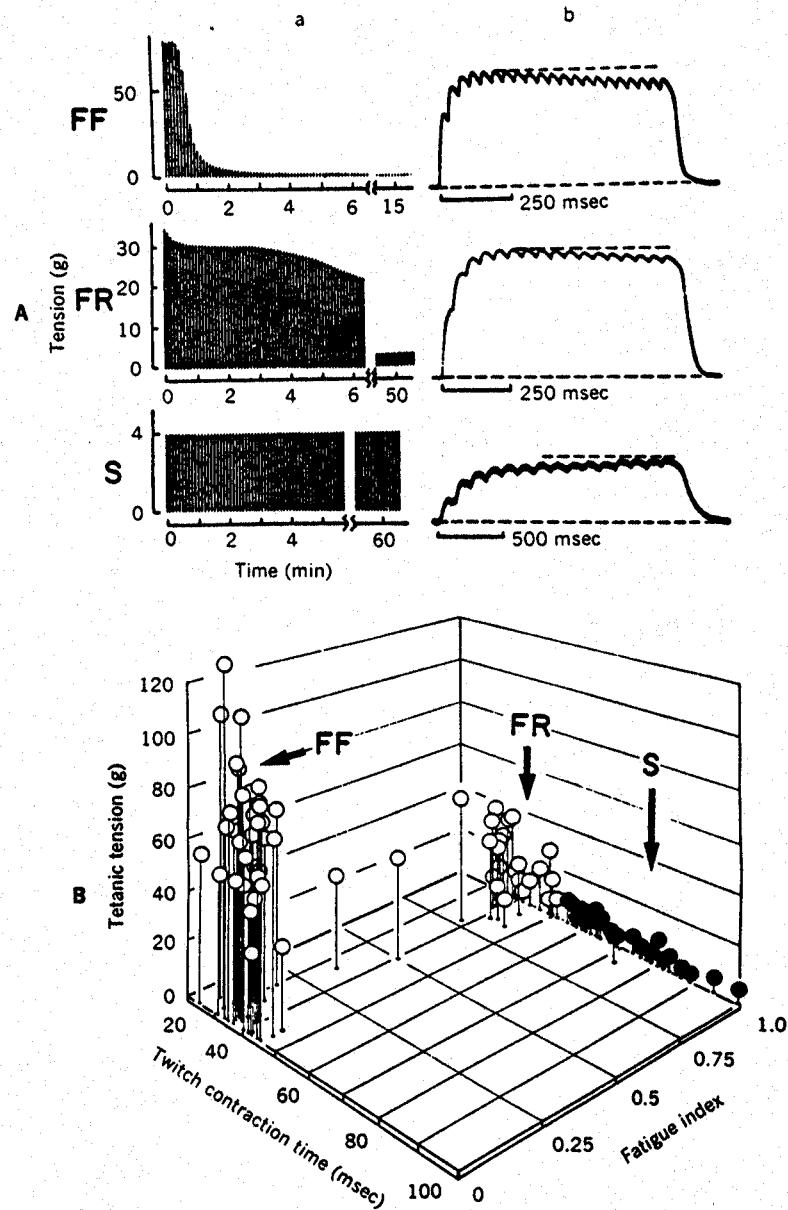
Fig. 4.3. Classification of motor units by muscle contractile properties, into types FF (fast-fatiguing), FR (fatigue-resistant) and S (slow) in medial gastrocnemius of the cat. (A) Tension records show onset of fatigue in column a, and in column b "sag" of tetanic tension below maximum marked by dashed line. (B) Three-dimensional plot relates tetanic tension (ordinate) to twitch contraction time and to fatigue index on left and right abscissae, respectively. (From Burke et al, 1973; in Henneman, 1980; and Burke, 1981b)

Figure 2: Properties of S-, FR-, and FF-type muscle fibers. (Figure is taken from Brooks, see footnotes 3, 4). The caption included above (Fig. 4.3) explains the measurements exhibited here.

FF-type muscle fibers fatigue much more rapidly than the other types. This is illustrated in Figure 2(A[a]) above. The minimum "base tension" level under fatigue in only a few percent of the peak tension level. Relative representative twitch contraction times are illustrated in Figure 2(B). Some FF-type fibers have twitch contraction times of under 10 ms.

For all fiber types there is a latency between the time an action potential is applied to the fiber and the time when muscle fiber tension is produced. Typically this latency is only a few ms (at least for the fast fibers). There is a longer latency between application of the AP and the beginning of the twitch motion. This is because sufficient muscle tension has to build up in order to overcome the load force of the limb. For a 60 ms twitch, a typical latency from AP to start of the twitch is about 10 ms (FF- and faster FR-type fibers); latency from AP to beginning of the rise of fiber tension is a few ms, and peak tension is reached in about 35 ms. After this, tension begins to fall off asymptotically (for the response to a single AP) for about another 100 ms. S-type fibers are, of course, much slower than this.

Muscle fibers integrate the effects of action potentials. This is illustrated in Figures 3 below. Figure 3(a) illustrates the case where subsequent APs (denoted by the black triangles) arrive after the twitch response from the previous AP has died out. The fiber relaxes completely between twitches and no summation effect is observed. In Figure 3(b) the third AP arrives before the second twitch has died out and a summation, resulting in a higher total tension, results. Figure 3(c) illustrates what is known as an "unfused tetanus". Here the AP firing rate is sufficiently high so that the fiber reaches its maximum tension. However, there is still a slight relaxation of the fiber between APs. Figure 3(d) illustrates the case where the AP arrival rate is high enough that the fiber has no chance to relax before the next AP stimulus. The fiber reaches and holds its maximum tension with no "jiggle" in the tension. This is called a "complete tetanus" response. The fiber is able to hold this level of tension until either stimulation ceases or fatigue sets in. Once the muscle fiber starts to fatigue, the tension it creates diminishes even if the stimulus continues. The maximum tension a fiber can develop is about 5 to 6 times greater than the peak tension developed during a twitch. As suggested by Figure 3(d), the summation of contractile excitations produces a tension vs. stimulus response that follows a sigmoidal characteristic.

The maximum tension a fiber can develop also depends on the length of the fiber. For all fibers there is some optimum length, I_o, at which it develops the maximum amount of tension. Figure 4 illustrates the tension vs. length characteristic of a typical extrafusal fiber. Within a range of about ±5% of I_o the fiber is capable of achieving its maximum tension. Beyond this range, the available fiber tension drops off owing to particular properties of the filaments that make up the muscle fibers. Beyond about ±30% contraction or extension, there is a catastrophic failure of the system as the muscle becomes separated from the bone.

Intrafusal Muscle Fibers

The intrafusal fibers can roughly be regarded as modified extrafusal fibers. Within a muscle they lie inside the bigger extrafusal fibers (hence the names for these two groups). Intrafusal fibers are too small and develop too little tension to participate in the actual movement of a limb. Rather, their main role is to provide a "support platform" for sensory neurons. These fibers also receive stimulus input from motoneurons, primarily the class of motoneurons known as gamma-motoneurons (γ-MNs). These fibers also contract under stimulation. However, since they are incapable of producing limb motion their contraction tends to take place at the ends of the fiber while the central portions of the fiber stretch. This center portion is where the sensory neuron ending wraps around the fiber. This region is called the **muscle spindle**. Stretching the muscle spindle causes the sensory neuron to increase its firing rate; reducing the length of the muscle spindle causes the sensory neuron to decrease its firing rate.

There are three principal categories of intrafusal fibers: Bag1, Bag2, and chain fibers. Bag1 fibers support a single type of sensor, known as a group Ia sensory neuron. Bag2 and chain fibers can support two types of sensors, the Ia and another type called a group II sensory neuron.
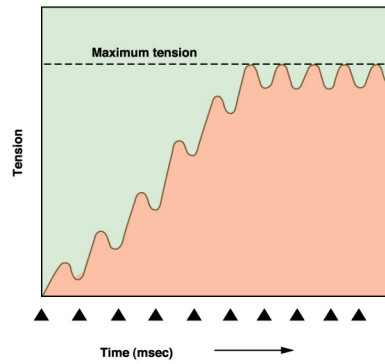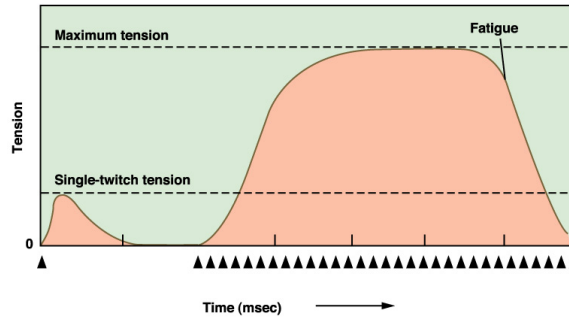
(a) Single twitches
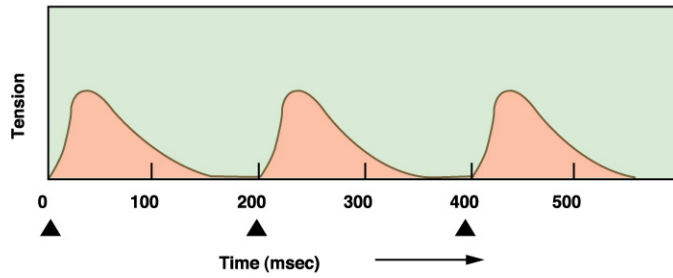
(b) Summation
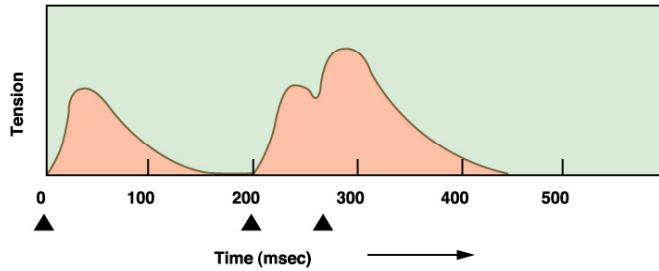
(c) Summation leading to unfused tetanus

Maximum tension

(d) Summation leading to complete tetanus

Maximum tension

Fatigue

Single-twitch tension

Figure 3: Summation of contractions. This figure illustrates how the arrival time of APs at the muscle fiber affects the contractile tension developed. See text for explanation. (Pictures are courtesy of Dr. Dee Silverthorn, *Human Physiology*, 2nd ed., Prentice-Hall, 2001).
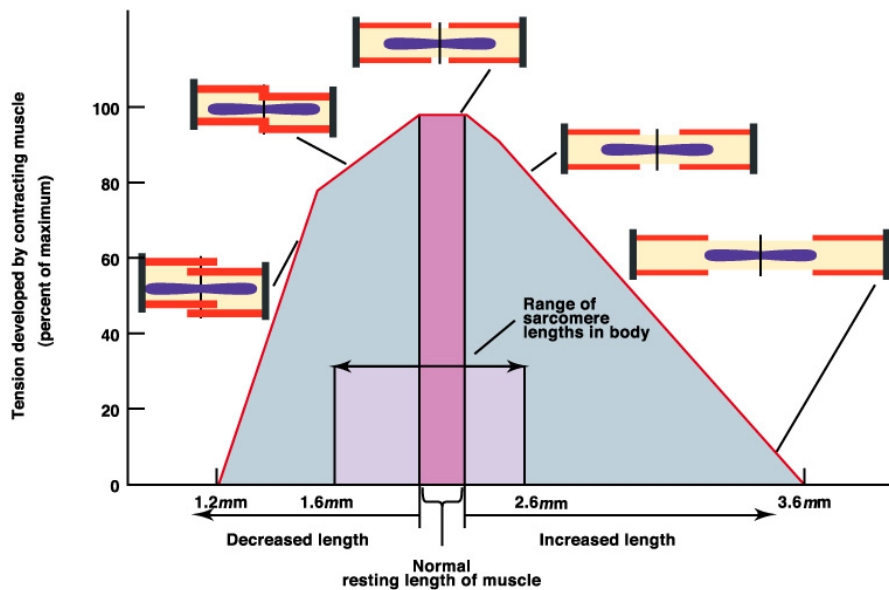
Figure 4: Tension vs. fiber length properties. The optimum fiber length, I_o, for most fibers occurs when the fiber is at its normal resting length. Within about ±5% of this length the fiber is capable of producing its maximum tension. Stretching or contracting the fiber by more than this amount but within a range of about ±20% of I_o reduces the amount of tension the fiber can produce. Contracting the fiber within the range from ±20% to ±30% produces an increased rate of maximum tension loss due to filaments in the fiber reaching their minimum compressible length. Although the figure seems to imply that the maximum tension can be smoothly reduced to zero, in fact this is not true. For contraction or extension above about ±30% of I_o separation of the muscle from the bone occurs. (Picture courtesy of Dr. Dee Silverthorn).

Group Ia sensors are primarily velocity-sensitive sensors (although they also produce a lesser response to changes in the length of the muscle spindle). Group II sensors are primarily length-sensing sensors. Group Ia muscle spindles are often called "primary endings", while group II muscle spindles are often called "secondary endings." These are also often referred to as "dynamic" and "static" spindles, respectively, since the two types of spindles respond primarily to velocity and length, respectively.

It is appropriate here to mention that extrafusal fibers also support a sensor, called the Golgi tendon organ (GTO), that responds to tension. The sensor for a GTO is called a group Ib sensor. The GTO is located at the junction where the extrafusal fiber meets the tendon. It participates in the muscle control "servo system" and also serves to help protect the muscle fiber from being dangerously stretched or contracted.

Up to the present time I haven't yet found very much quantitative information on the properties of the intrafusal fibers. Bag1 and Bag2 fibers differ in the linearity of their characteristic stretch and relaxation responses. Bag1 cells are less linear than Bag2. They are more elastic and more viscous at the site of the primary spindle than at the site of the secondary spindle. This suggests that their dynamics might be that of two (nonlinear) lossy springs in series. The Bag1 fiber exhibits mechanical "creep" after being stretched, lasting about 1 to 2 seconds after it hits its mechanical yield point. I am still looking for more detailed sources to shed some light on the specific properties of these fibers.

Motor Units

A single extrafusal fiber is innervated by only one alpha-motoneuron. However, a single α-MN can innervate a large number of extrafusal fibers. An individual extrafusal fiber is generally not strong enough by itself to cause limb movement, and so the fact that a single α-MN can stimulate multiple fibers (which collectively <u>can</u> cause a motion) leads to the formation of **motor units**. A motor unit is defined as a single α-MN and all the extrafusal fibers it innervates. A motor unit is always made up of only one particular type of fiber, i.e. all S-type fibers, or all FR-type fibers, or all FF-type fibers.

Motor units differ in the number of fibers they contain. To a first approximation, the total tension developed in a motor unit is the sum of the tensions developed by the individual fibers. Small motor units therefore permit fine control of tension. Large motor units are only capable of course control of tension. Whole-muscle tension and speed control depends on the total number of motor units activated, the type of fiber in each motor unit, and the firing rates of the different α-MNs (which sets the amount of tension developed in its motor unit). This is an important point to consider in studying neural motor control. There can be a large number of motor units in any given muscle, and to some degree these different motor units can be "recruited" independently (so far as the lower-level neural networks of the spinal cord are concerned). The combinatorics of motor unit activation permits a large ensemble of possible whole-muscle activation dynamics.

Figure 5 below illustrates the basic idea of a motor unit. In addition to providing a mechanism for a great deal of control over applied muscle force and speed, recruitment of individual motor units also provides a means for combating the effects of muscle fiber fatigue. Muscle fibers recover from fatigue after a rest period. The length of the rest period they require depends on the duration and intensity of their previous activity. High-frequency but brief stimulation is accompanied by rapid recovery after a brief rest. Fatigue that develops slowly with
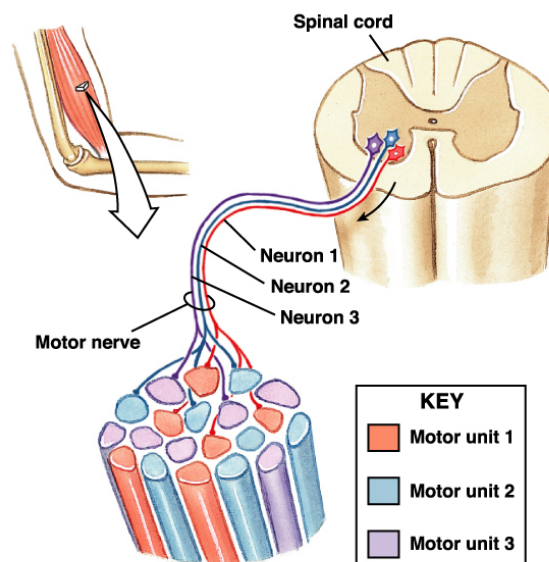
Figure 5: Illustration of multiple motor units. Each unit has its own α-MN and different numbers and types of fibers. (Picture courtesy of Dr. Dee Silverthorn).

low-intensity, long-duration exercise may require up to 24 hours before the muscle fiber recovers completely. Muscles that hold the body upright and maintain posture are almost always partially contracted (low-intensity, long-duration operation), and in order to avoid fatigue in these muscles, the nervous system alternates activation among the various motor units making up this muscle.

Sensorimotor Muscle Organization

Operation of a muscle involves both the collective of activated motor units and the sensory function of the intrafusal muscle fibers. The basic organization is illustrated in Figure 6. In this
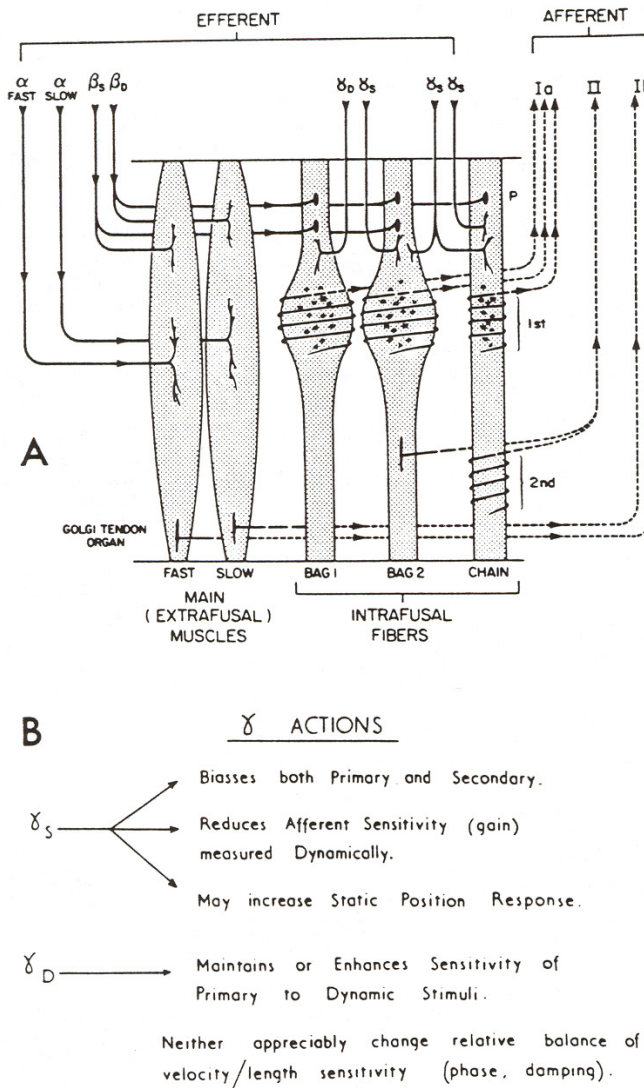

Fig. 4.8. Muscle sense organs. (A) Diagram of sensory and motor connections of mammalian extra-fusal (α) muscles and intrafusal (γ) fibers, as well as skeletofusimotor (β) fibers that innervate extrafusal and intrafusal muscle fibers. Static and dynamic β and γ fibers have subscripts S and D, respectively. Plate endings, P; 1st, primary; 2nd, secondary. (B) Summary of static and dynamic fusimotor actions that may be currently deemed to be of functional importance. [(A) From Brooks, 1984; (B) from Matthews, 1981b]

Figure 6: Basic sensorimotor muscle organization. The extrafusal fibers represent the parallel combination of a number of motor units. See text for additional explanations.

figure the muscle fibers each represent a parallel combination of motor units (extrafusal fibers) and muscle spindles (intrafusal fibers). Each motor unit or muscle spindle is activated by its own motoneuron (α-MN or γ-MN). The fast fiber depicted in the schematic represents either FF- or FR-type extrafusal fibers. Although the figure only depicts one fast extrafusal fiber, it is to be understood that both types may in fact be present, depending on what motor units are being stimulated by α-MNs.

Motoneuron signals from the spinal cord to the fibers form what are called "efferent" pathways. As shown in Figure 5, all motoneurons reside in the ventral horn of the spinal cord and project their axons to the muscle fibers they innervate. Sensory information flowing back to the spinal cord is by means of sensory neuron axon "tails" that wrap around the intrafusal fibers. These form what are called the "afferent" pathways leading back to the cell body of the sensory neurons, which project their signal to the ventral horn of the spine and to synapses with spinal cord interneurons. There are three types of efferent pathways:

1) α-MN pathways, which control the extrafusal fibers of motor units;
2) γ-MN pathways, which provide the main control signals for intrafusal fibers;
3) β-MN pathways, which provide a reference stimulus common to both fiber classes.

The existence of β-MNs in the primate spinal cord is a relatively recent discovery, prior to which it was thought that alpha- and gamma-motoneurons were the only motoneurons in mammals. β-MNs are thought to be an evolutionary hold-over from reptiles and amphibians (which use only one type of neuron to co-excite both extrafusal and intrafusal fibers). β-MN organization and function is not yet well understood, but it is believed that their role is to provide the intrafusal fibers with stimulus information that allows these fibers to "track" what is going on in the extrafusal fibers they monitor, thereby making it possible for the intrafusal fibers to detect deviations from the "expected" contraction of the extrafusal fibers due to mechanical load variations. Current thinking holds that dynamic β-MNs are brought into play during weak muscle contractions by allowing the brain to adjust the sensitivity of the muscle during the activity of slow postural muscles. Static β-MNs are active during fast muscle contractions, and so are thought to help maintain the sensitivity of the muscle spindles during movement.

It is thought that β-MNs receive a positive feedback signal from the group Ia afferent pathway, although the functional consequences of this pathway are as yet unknown. My own guess is that this feedback loop might constitute a form of "sliding-mode control system" (sliding-mode control is a servo-control method sometimes used in the control of nonlinear systems). It is known almost beyond any doubt that the α-MNs are the principal motoneurons that drive extrafusal fibers. Note from Figure 6 that the motoneurons for each of the three efferent pathways are further subdivided into "fast and slow" α-MNs and "static and dynamic" γ-MNs and β-MNs. These designations refer to the type of fiber they stimulate.

The afferent pathways are also divided into three types based on the type of sensory information they convey back to the spinal neural network. These are:

1) Group Ia afferents, which carry primary muscle spindle (velocity) information;
2) Group II afferents, which carry secondary muscle spindle (length) information;
3) Group Ib afferents, which carry tension information from the Golgi tendon organs.

Note that Bag1 fibers provide only group Ia sensory information, while Bag2 and chain fibers provide both velocity (Ia) and length (group II) information. Chain fibers are known to contract

more rapidly than Bag2 fibers, and so this dual-sensory arrangement in Figure 6 might be thought of as constituting a kind of frequency-selective filtering of velocity and position information. The interplay between muscle fiber excitation and muscle spindle response is illustrated in Figure 7.
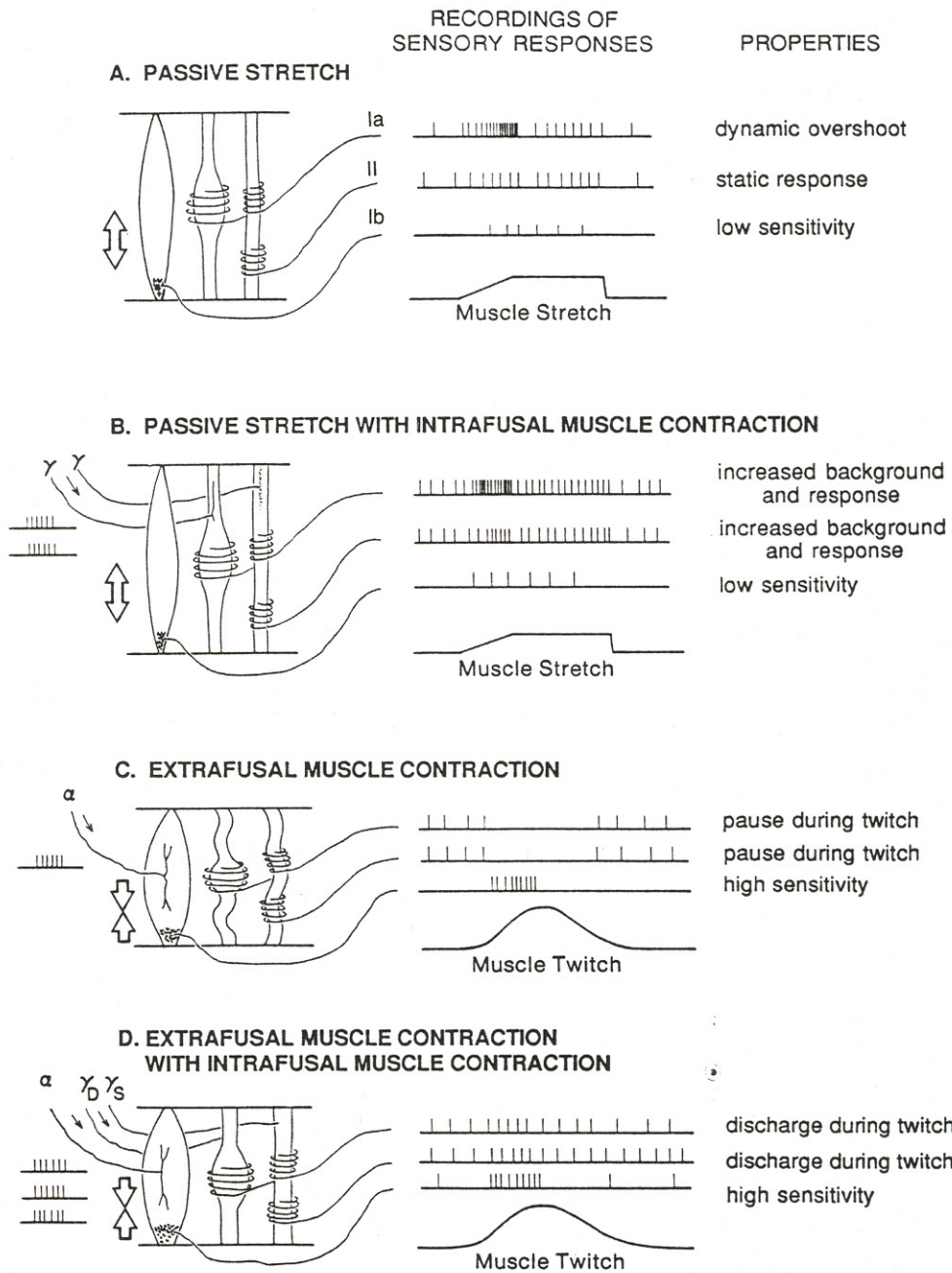
Figure 7: Muscle spindle and tendon organ response to muscle stretch, contraction, and intrafusal fiber excitation. Motoneuron excitations are shown on the left-hand side of the figures. Sensory responses for the three afferent pathways are shown in the center column. The right-hand side provides a commentary describing the key features of the responses. Note also the timing of the pulse patterns relative to the muscle stretch or twitch.

Additional References

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