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Spinal Reflexes

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Reading: Purves et al. (2008), Neuroscience, Chapter 1. Pages 12-13, and Chapter 16, pages 408-422

Goal : The goal is to understand the components and mechanisms of the myotatic(stretch) and inverse myotatic (Golgi tendon) reflex.

Introduction

The elements and their properties that constitute a reflex circuit are fundamental to our understanding of motor mechanisms. To the clinician. the presence, absence. and magnitude of a reflex provide the necessary ingredients for proper diagnosis and treatment. In today's lecture we will focus on spinal reflexes involving striated muscles. We will define a reflex as a simple motor action, stereotyped and repeatable, elicited by a sensory stimulus without the intervention of consciousness.

Before we delve into reflex mechanisms. it may be helpful to clarify the schema by which afferent and efferent nerves are classified. Afferent nerve fibers from receptors in the skin, joints, and muscles vary in size, degree of myelination, and conduction velocity. David Lloyd named the largest to smallest myelinated afferents I, II, and III, respectively, and named the small unmyelinated afferents IV. The size and conduction velocities of these fibers are shown in Table 1. He further subdivided the type I fibers into Ia's and Ib's, Ia's being slightly larger and faster than Ib's. This classification pertains to afferents from muscle receptors. Herbert Gasser came up with a different classification scheme for cutaneous afferents: A alpha, A beta, A delta, and C fibers and these correspond to the I - IV classification, respectively. Since there are no type I fibers from the skin, the A alpha designation is never used (or never should be used). There are only two categories of motor neurons, alpha (0-120 meters/sec) and gamma (50 meters/sec).

TABLE 1: Afferent Fiber Classification and Characteristics

Muscle Nerve	Cutaneous Nerve	Diameter (μm)	Velocity (m/sec)
I		13 - 20	80- 120
II	Aβ	6 - 12	35 - 75
III	Aδ	1 - 5	5 - 30
IV	C	0.2 - 1.5	0.5 - 2.0

Myotatic (stretch) Reflex

Figure 1: An important reflex is the myotatic (muscle stretch) reflex. It can be evoked by stretching any striated muscle. Stretching a muscle will evoke a contraction of that muscle---this is the myotatic reflex. How does it work? To answer this question, we need to delve into the properties of muscle receptors, muscle afferents and muscle efferents. Let's start with the muscle spindle (Fig. 1), a longitudinal structure several millimeters in length and less than a millimeter wide. It is embedded within the muscle and is oriented in parallel with the extrafusal (outside the spindle) muscle fibers. Moreover, its ends are attached to these extrafusal fibers. There are about 50 to 150 spindles in a muscle. The number of spindles is directly related to the amount of control required of the muscle. For example, per unit of muscle, finger muscles have more spindles than back muscles.

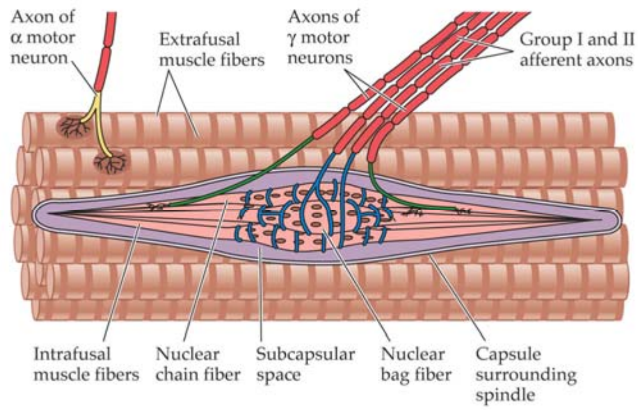

Figure 1: Muscle Spindle

Within the muscle spindle lie two types of receptors, nuclear bag and nuclear chain fibers. A typical muscle spindle contains about 2 nuclear bag and 5 nuclear chain fibers. Both fibers have contractile elements at their distal ends and both fibers are oriented along the long axis of the spindle. These two fibers are collectively called intrafusal (within the spindle) fibers. Nuclear bag fibers have a chubby, fluid-filled equatorial zone where many nuclei reside, while nuclear chain fibers are uniformly cylindrical in shape with nuclei distributed throughout its long axis, albeit concentrated near the central zone. These intrafusal fibers are afferently innervated by Ia and II nerve fibers, one each per spindle. The Ia fibers have annulospiral endings which coil around the central region of all nuclear bag and all nuclear chain fibers in a spindle. The type II afferents have flower-spray endings that innervate the pericentral regions of only the nuclear chain fibers. Due to their greater innervation and conduction velocity, Ia's are deemed primary, and II's are deemed secondary. Due to the parallel arrangement between the extra- and intrafusal fibers, stretching the muscle also stretches the intrafusal fibers. This is the adequate stimulus for activating the Ia and II afferent fibers. Thus, at this juncture, suffice it to say that the muscle spindle codes for muscle length.

We now have sufficient information to describe the myotatic reflex. A slow or brief stretch to a muscle results in a stretch to the muscle spindle. When stretched, the nuclear bag and nuclear chain fibers activate the primary (Ia) and secondary (II) afferents (see Fig. 2 and 3).These afferent signals then enter the spinal cord via the dorsal root. Upon entering the cord, a single Ia fiber synapses directly (monosynaptic) on all the homonymous alpha motor neurons that innervate the muscle from which the afferents arose. The Ia also activate alpha motor neurons of synergistic muscles, but in a

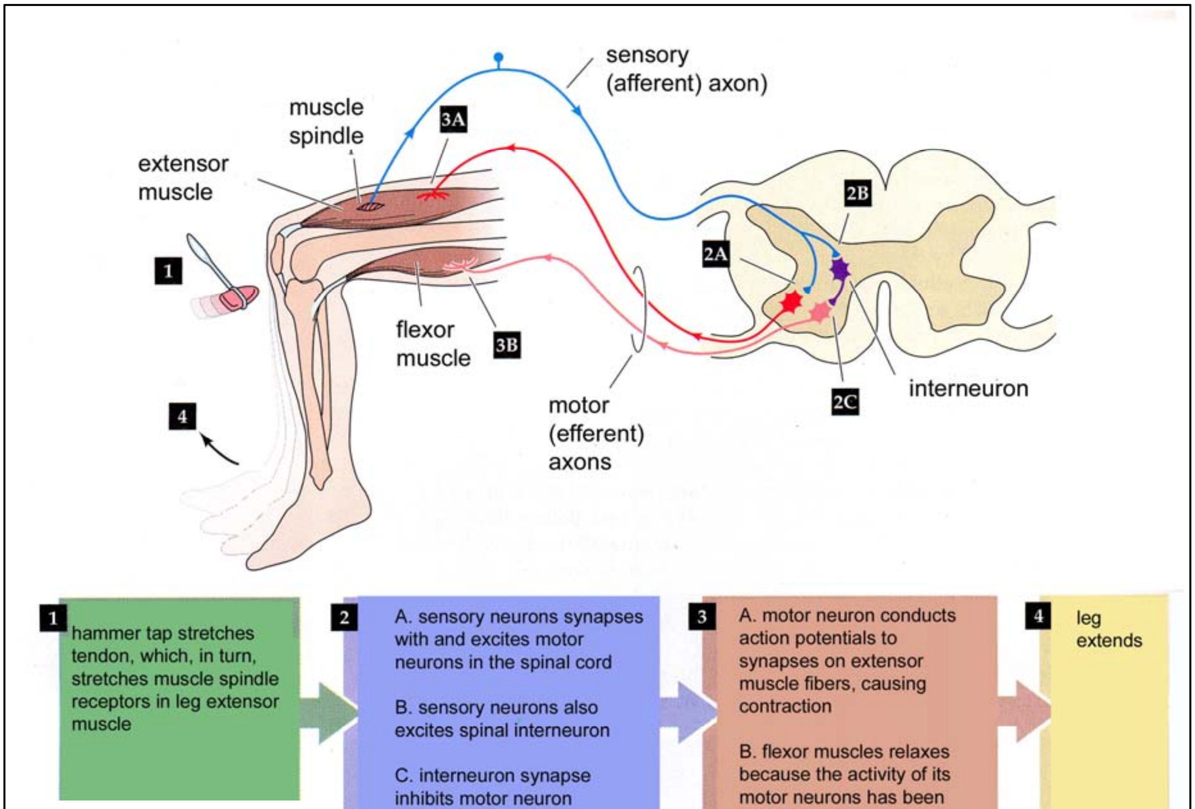

Figure 2. Myotatic Reflex

less powerful way. Recent findings suggest that some type II fibers also monosynaptically innervate alpha motor neurons. Also note that a collateral of the Ia axon synapses on an interneuron that in turn inhibits the motor neurons that innervate the antagonistic muscle. For example, the Ia afferents from the muscle spindles of the rectus femoris muscle, in addition to monosynaptically innervating the alpha motor neurons which drive this muscle, also deactivates through an inhibitory interneuron, the alpha motor neurons which innervates the antagonistic (e.g., semimembranous) muscle. In this way, when a muscle is stretched, the antagonistic muscle is deactivated. This illustrates the principle of reciprocal innervation. The axons of the alpha motor neurons leave the spinal cord via the ventral root and innervate the extrafusal muscle fibers from which the afferents arose, as well as synergistic muscles. Voila, the muscle contracts, completing the reflex arc, i.e., stimulus (stretch) - response (contraction). Since the myotatic reflex can be evoked by a

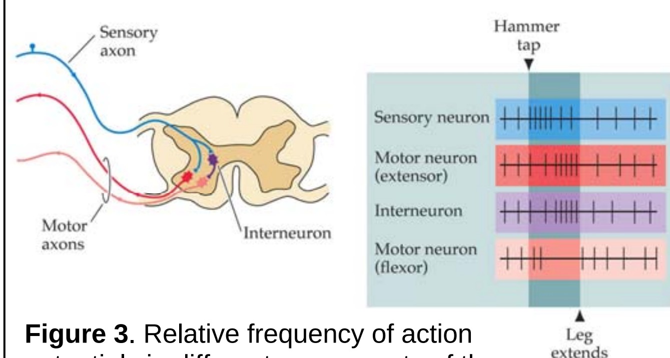

Figure 3. Relative frequency of action potentials in different components of the myotatic reflex

brief or a slow stretch, two components are suggested. The strong, short lasting, phasic response to brief stretch, e.g., evoked by tapping the patellar ligament, is mediated by the nuclear bag fibers. The weaker, longer lasting tonic response is mediated by the nuclear chain fibers. Thus, functionally, the nuclear bags are important in correcting for abrupt changes in muscle length, while nuclear chains are important for maintaining muscle length (e.g., as in posture). The Ia's could provide both types of information since their endings innervate both nuclear bag and chain fibers.

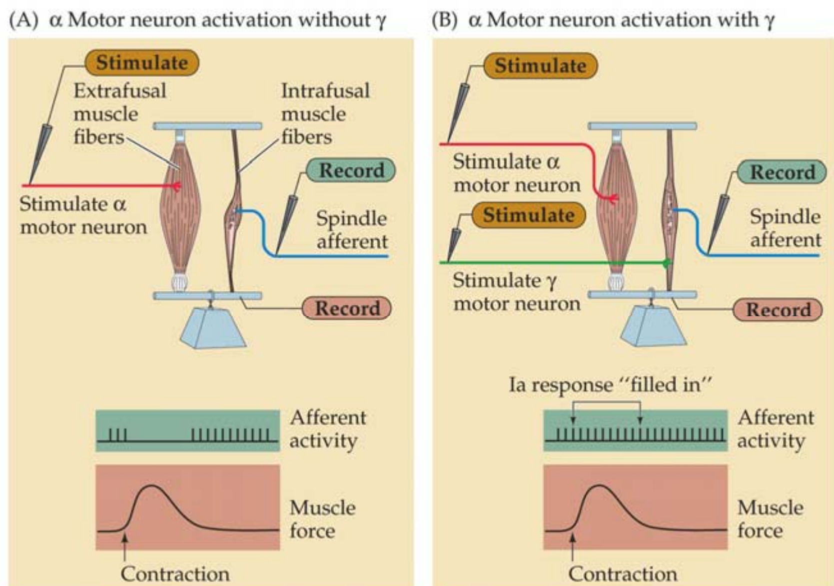

Figure 4 The role of gamma motor neurons in regulating the responses of muscle spindles

The stretch reflex can be evoked at different muscle lengths. How is this achieved. The answer is that the primary afferents in addition to synapsing on alpha motor neurons, also synapse via interneurons onto smaller gamma motor neurons. The axons of gamma motor neurons innervate the contractile elements on the distal poles of the intrafusal fibers (see Fig. 1). This efferent innervation has the effect of stretching the central region of the intrafusal fibers, thus activating the primary (Ia) and secondary afferents (II). In this way, the muscle spindle can adjust its sensitivity over a wide range of muscle lengths (see Fig. 4). Thus, spindle receptors transmit information about the length of the spindle relative to muscle length.

Although the patellar or knee-jerk reflex is a convenient way to demonstrate the myotatic reflex, realize that this reflex is continuously operating. For example, the myotatic reflex plays a major role in standing. Gravity stretches the quadriceps. This activates the Ia afferents, which in turn activate the quadriceps muscles via a monosynaptic connection to the alpha motor neurons. This loop keeps on repeating itself, thus providing continuous tone to the quadriceps muscles. Thus, the myotatic reflex is a mechanism for muscle tone, a necessary condition for standing.

The alpha and gamma motor neurons that innervate extrafusal and intrafusal fibers, respectively, are synaptically mediated by primary afferents (Ia's) as well as descending inputs from higher centers. Spinal cord injuries can result in the inactivation of gamma motor neurons, either directly through damage, or indirectly through an alteration of their excitatory inputs. In either case, the intrafusal fibers can no longer contract and hypotonia is the result. This is because changes in muscle length can no longer adequately stretch the flaccid muscle spindle to activate the primary and secondary endings. Another consequence of spinal cord injury is the removal of inhibitory influences on gamma motor neurons. In this case, the primary and secondary afferents are continuously activated. The muscle is now continuously activated (hypertonia) and the muscle spindle is super sensitive to stretch. Tapping the patellar ligament results in an exaggerated reflex. The lower leg swings vigorously forward and on the way down, due to inertia, the muscle is again stretched resulting in another myotatic reflex. This repetitive triggering of the myotatic reflex in hypertonic muscles is called clonus.

To summarize, the myotatic reflex is elicited by stretching a muscle. It is a reflex contraction to stretch. The myotatic reflex is the basic mechanism of muscle tone and plays a critical role in posture and movement. The afferent segment is the primary fibers (Ia) with annulospiral endings which coil around the nuclear bag and nuclear chain receptors. These Ia's carry information about dynamic (phasic) and static (tonic) changes in muscle length. The role of the secondary afferents is less well understood, but they seem to convey information only about static muscle length. The function of efferents to the intrafusal fibers is to adjust the length of the muscle spindles relative to the length of the muscle. In this way, the myotatic reflex can operate independent of muscle length. The myotatic reflex is local because it is restricted to the muscle from which its afferents arise. The reflex is rapid, stimulus-locked, finely graded with stimulus intensity, and capable of being sustained. The myotatic circuitry includes a disynaptically mediated inhibition to the antagonistic muscle, producing reciprocal innervation.

Inverse Myotatic (Golgi tendon organ) Reflex

The other major muscle receptor is embedded in the musculotendinous sheath and is called the Golgi tendon organ (see Fig. 5). The Golgi tendon organ is a slender capsule about 1 mm in length and 0.1 mm in diameter. Each capsule is anatomically in series with about 10-20 extrafusal muscle fibers. The number of Golgi tendon organs is usually somewhat lower

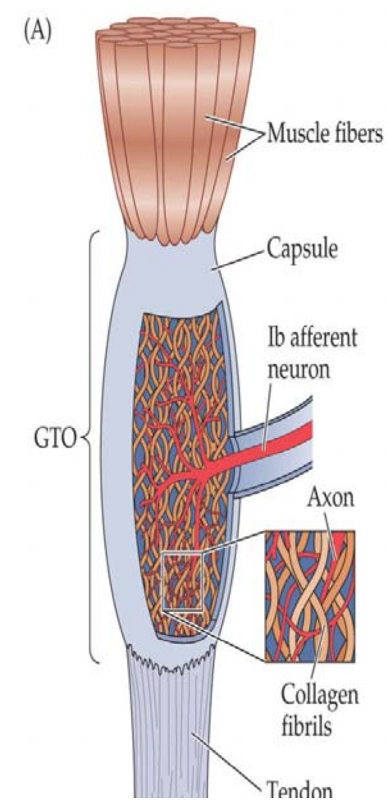

Figure 5. Schematic of the Golgi tendon organ is activated by muscle contraction

than muscle spindles in a given muscle.

What is the role of the Golgi tendon organ? While the muscle spindle is designed to detect muscle length, the series organization of the Golgi tendon organ makes it ideal for detecting muscle tension. This is because during passive stretch, the muscle fibers are much more elastic than the tendinous sheath (see Fig. 6). Thus, the muscle spindles are stretched, but there is minimal stretch applied to the Golgi tendon organ. In contrast, when the muscle contracts it becomes inelastic and stretches the tendon, thus activating the Golgi tendon organ (see Fig. 7). Because the myotatic reflex is activated by muscle stretch

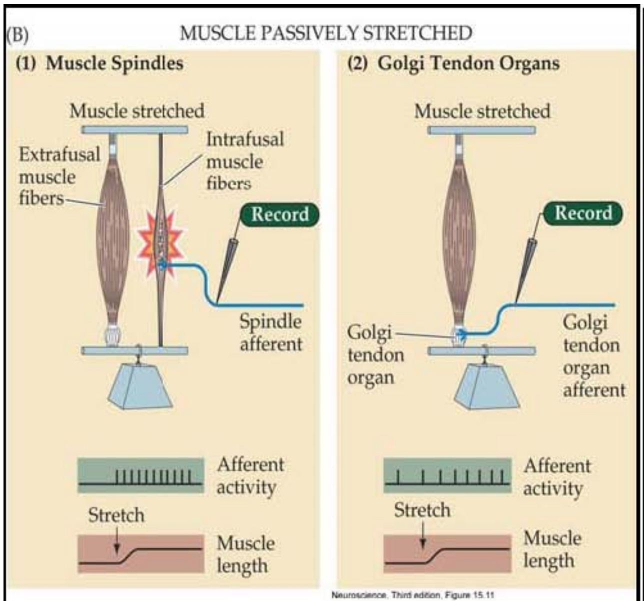

Figure 6 . Comparison of spindle and Golgi tendon organ afferents when muscle is passively stretched

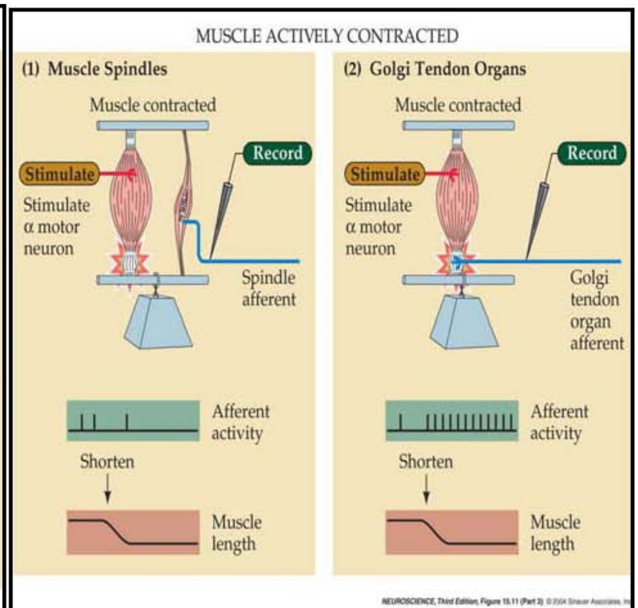

Figure 7 . Comparison of spindle and Golgi tendon organ afferents when muscle is actively contracted

(shortening), the Golgi tendon reflex is often called the "inverse myotatic reflex". So, we have two systems, one that monitors and maintains muscle length (myotatic or muscle spindle system) and another that monitors and maintains muscle force (inverse myotatic or Golgi tendon organ system).

Each Golgi tendon organ is innervated by a single 1b fiber. Thus, in general, these fibers have a slightly slower conduction velocity than the 1a fibers of muscle spindles. These 1b fibers have there cell bodies in the dorsal root ganglion and in the cord synapse via an interneuron (disynaptic) onto alpha motor neurons (see Fig. 8). Activation of a single Ib result in inhibition of many, if not all, homonymous motor neurons and excitation of many, if not all, motor neurons of the antagonistic muscle. Thus, the inverse myotatic reflex also shows reciprocal innervation, but its action is the reverse of that of the myotatic reflex.

As shown above, the Golgi tendon organ has a high threshold to passive stretch. This high activation threshold was the basis for the now obsolete idea that the specific function of tendon organs was to prevent muscle damage in situations of high muscle tension (e.g., lifting heavy weights). Accordingly, this high threshold idea was wrongly used to explain the Clasp knife reflex. The evidence against this idea was based on the finding that the Gogi tendon organ is exquisitely sensitive (i.e., low threshold) to muscle contraction and even the activity of a single motor unit was sufficient to activate this receptor.

In sum. information regarding muscle length and muscle force are provided by the muscle spindle and Golgi tendon organs, respectively. These two reflex systems are functionally tightly coupled (Fig. 9). When the bicep is stretched, the spindle is activated leading to relaxation of the triceps and contraction of the biceps. This, in turn, is the adequate stimulus to activate the Golgi tendon organ that leads to contraction of the triceps and relaxation of the biceps. Such synergism between the two reflex systems results opposing forces about a joint and is useful for stabilizing motion about a joint (e.g., maintenance of steady posture against gravity, as in standing).

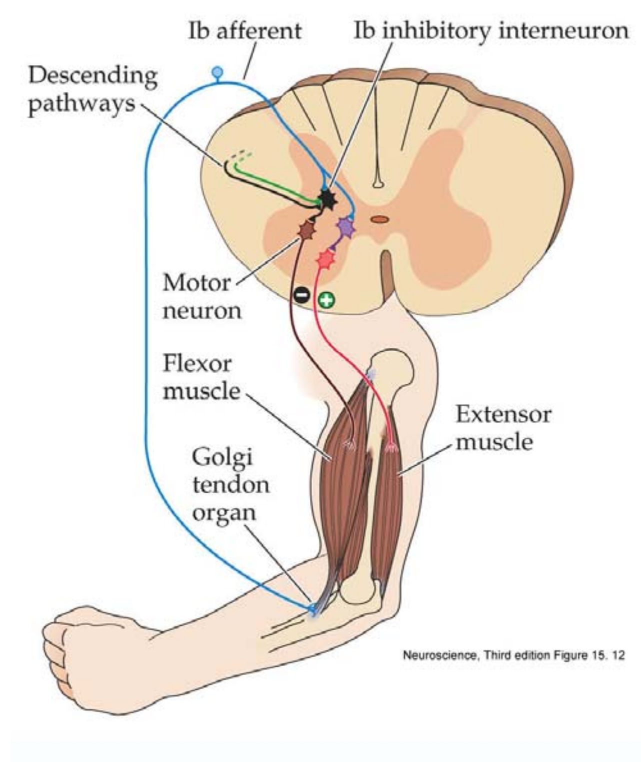

Figure 8. Example of a Golgi tendon organ circuit

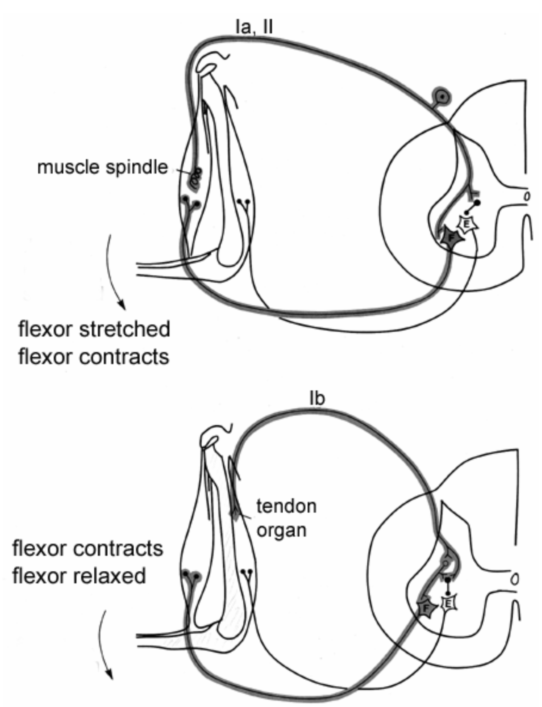

Figure 9: Stretch and tension reflexes work in concert

Information from muscle spindle and Golgi tendon organs is not exclusively used for the spinal reflex circuitry. Information from these receptors reaches all levels of the nervous system and is used to signal limb position, muscle status and to plan motor movements.

Other Important Considerations

It is important to remember that the function of muscle spindle and Golgi tendon organ afferents is not solely for mediating spinal cord reflexes. These afferents also travel upstream and inform the cerebellum and cortex about the state of the musculature. For example, collaterals of Ia and Ib afferents participating in the myotatic and GTO reflex also synapse in Clarke’s column. The output axons of Clarke’s column then form the dorsal spinocerebellar tract. Collaterals of these Ia’s also travel in the dorsal column and synapse in the lower medulla in nuclei related to the gracilis and cuneatus. From there they travel with the medial lemniscus to synapse in the thalamus. The thalamic output then goes to the cortex.