The Neuropnysiology of Tone: The Role of the Muscle Spindle and the Stretch Reflex

The excitability of the stretch reflex is used as a measure of tone. The muscle spindle is the receptor for the stretch reflexes which may be phasic or tonic in nature. This paper provides a theoretical background through an overview of published studies as a basis for the understanding of the contribution of the muscle spindle to both the phasic and tonic stretch reflexes.

HELEN CAMERON-TUCKER

Helen Cameron-Tucker, B Phty.(Hons.), is a Senior Tutor in the Department of Physiotherapy, University of Queensland.

Physiotherapists are concerned with the analysis of movement One of the factors involved in governing normal movement is normal muscle tone, one definition of which is presented by Wyke (1976) as being the tension obtaining at any one moment between the origin and insertion of each muscle. Tone is assessed clinically by testing and observing the excitability of the phasic and tonic stretch reflexes. An understanding of the normal neurophysiological basis of these reflexes is necessary if the pathological behaviour is to be appreciated.

Stretch Receptors in Muscle

Wyke (1976) presents a triad of mechanisms which determine muscle tone or tension: elastic properties of tendons, muscles and the connective tissue of fascial sheaths and intramuscular septa; visco-elastic properties of fibrillary protein in each muscle fibre; and the degree of motor unit activity. As motor unit activity is influenced by the excitability of the nervous system, it is this determinant which is capable of wide variation and is of paramount importance in the regulation of muscle tone.

The firing of a motor unit occurs in response to a stimulus acting upon the alpha motor neurone in the ventral grey matter of the spinal cord (Ganong 1973, Barr 1972). Liddell and Sherrington's (1924) experiments on decerebrate cats demonstrated that a muscle responds to a stretch stimulus with a

reflex contraction. This reflex firing of motor units occurred in the absence of other afferent stimulation and led Magoun and Rhines (1947) to conclude that a muscle must contain its own stretch receptors which discharge via afferents into the spinal cord. The reflex excitation of alpha motor neurones results in the firing of motor units and finally the muscle contraction observed by Liddell and Sherrington (1924).

The stretch sensitive receptors in muscle are now known to be the Golgi tendon organ and the muscle spindle, both of which have different rates. The muscle spindle is responsible for reflex contraction of the homonymous muscle, whereas the Golgi tendon organ acts to inhibit the homonymous reflex muscle contraction. (Fulton 1943, Eldred 1965, Matthews 1968, Matthews 1973).

The Golgi Tendon Organ

The Golgi tendon organ has been described as being a collection of nerve endings lying in series with the extrafusal muscle fibres at the musculotendinous junction at each end of the muscle. Due to this 'in series' arrangement, stretch of the muscle fibres and therefore the tendon to which the fibres attach, activates the Golgi tendon organ. (Eldred 1965, Ganong 1973, Matthews 1973).

Stimulation of this receptor causes relaxation of the muscle in which the

organ lies, a phenomenon described by Ganong (1973) as the 'inverse stretch reflex' or autogenetic inhibition. These events, depicted diagrammatically in Figure 1, occur because the Golgi tendon organ synapses with an inhibitory interneurone which in turn synapses with and inhibits the anterior horn cell of the agonist. At the same time, reciprocal excitation of the antagonistic muscle occurs (Ganong 1973).

Ganong (1973) stated that via autogenetic inhibition, the Golgi tendon organ has a protective function in that if the tension in a contracting muscle becomes too great the receptor is activated, causing the muscle to suddenly relax, and thus reducing the tension to safer levels. Jansen and Rudjord (1964) found that the amount of active muscular tension required to excite tendon organs is small in relation to the potential strength of the whole muscle and this led Matthews (1973) to abandon the hypothesis that Golgi tendon organs have a purely protective role. Matthews (1973) also noted that Golgi tendon organs can be excited by single motor units and therefore may be excited by only the muscle fibres attaching to the tendon on which the organ lies and not by other fibres. The Golgi tendon organ would then sample the contraction rather than taking a widespread average. Matthews (1973) concluded that the Golgi tendon organ functions as a contraction receptor, playing a con-
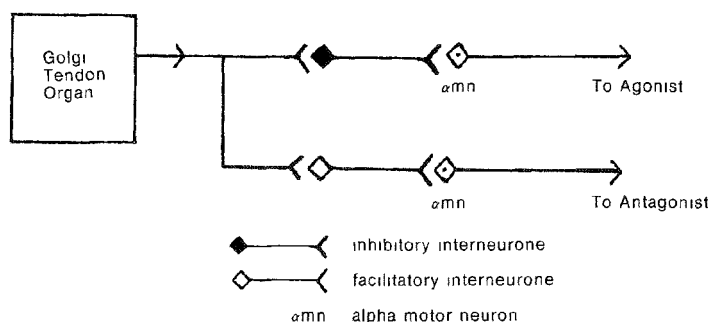
The Neurophysiology of Tone

Figure 1: Diagrammatic representation of autogenetic inhibition

tinuous part in the central regulation of muscle tone, rather than simply being reserved for use in emergencies.

The reflex connections of the Golgi tendon organ with the Alpha motor neurones of the agonist (autogenetic inhibition) and the functions ascribed to this receptor by Ganong (1973) (protective role) and Matthews (1973) (contraction receptor) indicate that this receptor could not be responsible for the reflex muscle contraction observed by Liddell and Sherrington (1924). Rather, the receptor responsible for the contraction of a muscle in response to stretch is now known to be the muscle spindle.

The Muscle Spindle

Eldred (1965) wrote that muscle spindles were first noted in growing muscles as small fibres with central nuclei. They resembled the fibres found in developing muscle fibres and were therefore thought to be sources of myogenesis and were termed 'muscle buds'. Eldred (1965) continued that in 1884 Mays suggested that the muscle spindle might be a sensory organ, a view supported by Cajal in 1888. Ruffini (1897) claimed that at least two types of sensory endings were discernible in mammalian spindles.

The muscle spindle is, in fact, a bundle of up to ten small specialized striated muscle fibres (intrafusal fibres), together with afferent and efferent nerve endings, enclosed in a connective tissue capsule (Matthews 1973). This capsule encloses the intracapsular space which extends about 1 mm on either side of the equator in living spindles (Boyd 1976). The intracapsular fluid within this space has a mucopolysaccharide constituent and is probably viscous (Eldred 1965). It is thought to insulate nerve endings from local mechanical disturbances (Matthews 1973).

According to Eldred (1965), the muscle spindle lies in an interfascicular cleft parallel to the extrafusal fibres and is usually near an intramuscular nerve and artery. This 'in parallel' arrangment means that the muscle spindle will be stretched at a similar rate and to a similar degree as the extrafusal fibres.

Brodal (1962) reviewed the work of researchers in the field of muscle spindle anatomy and physiology and noted that muscle spindles are located in all the muscles of locomotion, in the laryngeal muscles, muscles of mastication, the tongue, and in the extrinsic ocular muscles. Muscles used in delicate movements such as the muscles of the hand have a greater density of muscle spindles than do muscles used in coarser movements, such as the muscles of the trunk. The muscle spindles of any of these muscles have

a similar structure, as depicted in Figure 2.

Intrafusal Fibres

In 1956, Boyd identified two to three large intrafusal fibres and two to five small intrafusal fibres in the tenuissimuss muscle of the cat. Cooper and Daniel (1963) studied human muscle spindles and also identified two distinct types of intrafusal fibres based on the distribution of their central nuclei. The fibres lose their striations and appear to be non-contractile and less viscous in the nucleated region (Eldred 1965). These fibres are known as nuclear bag and nuclear chain fibres.

Nuclear Bag Fibres

Matthews (1973) described nuclear bag fibres as having a cluster or bag of nuclei lying two to three abreast at the spindle equator, with a few nuclei lying at the periphery of the fibre. According to Eldred (1965), some of these fibres pass beyond the connective tissue capsule as 'percapsular' fibres and are larger in cross section than the intracapsular fibres.

Two types of nuclear bag fibres, 'bag 1' and 'bag 2' fibres have been distinguished by Ovalle and Smith (1972) on the basis of their ATP ase staining reactions Bag 1 fibres have low staining reactions for ATP ase, whereas bag 2 fibres have medium to high staining reactions. ATP ase is the enzyme which hydrolyses ATP (adenosine-tri-phosphate), a high energy storing compound, to give ADP (adenosine-di-phosphate) free phosphate and energy (Ganong 1973).

The difference in the ATP ase staining reactions indicates a difference in the energy requirements of the bag 1 and bag 2 fibres This is further reflected in the number of mitochondria within each fibre. The mitochondria are often referred to as the 'power generating units' of a cell because it is here that the oxidative enzymes involved in the reactions providing energy for the cell are found (Ganong
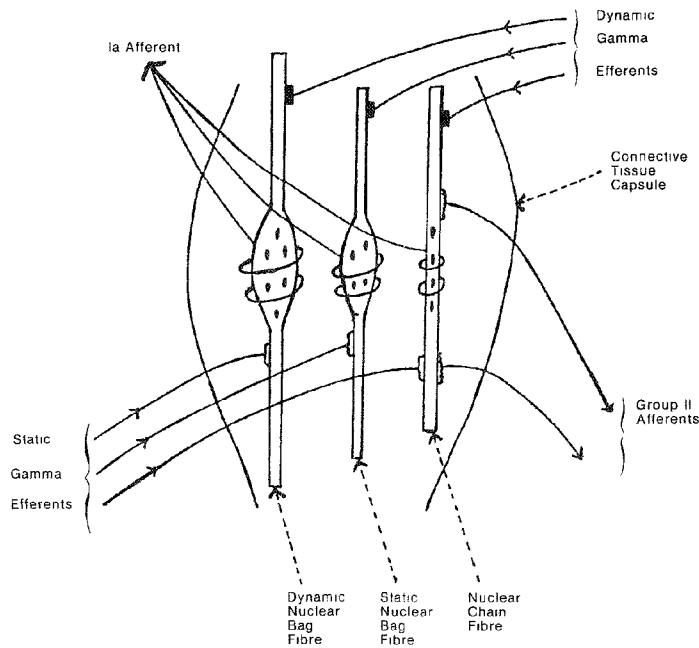
Dynamic
Gamma

Ia Afferent

Efferents

Connective
Tissue
Capsule

Group II
Afferents

Static

Gamma

Efferents

Dynamic
Nuclear
Bag
Fibre

Static
Nuclear
Bag
Fibre

Nuclear
Chain
Fibre

Figure 2 Structure of the muscle spindle (Adapted from Korten, 1972)

1973) The mitochondria are therefore concentrated in areas where energy requirements are high, and as ATP ase is involved in the energy producing reactions, it too is concentrated in structures requiring large amounts of energy It is therefore not surprising that Barker, Banks, Harker, Millburn and Stacey (1976) found that bag I fibres which have a low ATP ase staining reaction possess few mitochondria

Barker et al (1976) also found that bag 1 fibres often lack an M line (although one may be present in the poles), whereas bag 2 fibres have an M line throughout except in the area adjacent to the bag region. M lines are dark zones found in the middle of an A band which corresponds to myosin, a muscle protein When myosin is combined with actin, an-

other muscle protein, actomyosin results. Actomyosin is the unique complex responsible for the contractile properties of muscle fibres (Ganong 1973) According to Barker et al (1976), the appearance of an M line in intrafusal fibres is accompanied by increased mitochondria, increased sarcoplasm between myofilaments, and a better developed sarcotubular system, all of which indicate increased energy requirements or muscle fibre activity. From this it can be deduced that bag 1 fibres (which often do not possess an M line) and bag 2 fibres (which do possess an M line) differ in terms of energy requirements and therefore function. Boyd (1976) has found this to be the case

Boyd (1976) differentiated two types of nuclear bag fibres by studying the nature and time course of their con-

traction. Dynamic nuclear bag fibres (DNB) have a slow time course of contraction, whereas static nuclear bag fibres (SNB) have a fast time course. This could indicate that the energy requirements of DNB fibres are less than those of the SNB fibres, and that perhaps the DNB fibres are equivalent to the bag 1 fibres and the SNB fibres to the bag 2 fibres. Support for this conclusion has been given by Laporte (1979) in a review of the work of physiologists in this area

The majority of bag 1 fibres (or DNB fibres) respond to stimuli from dynamic efferents whereas bag 2 (SNB) fibres respond to static stimuli (Laporte 1979). Coupled with the lower energy requirements and slower time course of contraction, this suggests that DNB fibres participate in the reflex control of dynamic or phasic movement On the other hand, SNB fibres which have higher energy requirements and a fast time course of contraction appear to be involved in eliciting static or tonic muscle activity.

Nuclear Chain Fibres

The small intrafusal fibres identified by Boyd (1956) have their central nuclei lying in a single file or chain in the central region, with a few nuclei at the poles, and are known as nuclear chain (NC) fibres (Matthews 1973). These fibres are attached to the connective tissue capsule of the spindle; that is to say, they are intracapsular (Eldred 1965).

According to Barker et al (1976), the nuclear chain fibres have high staining for ATP ase, possess a well-developed M line, prominent mitochondria, increased interfibrillary sarcoplasm, and a well-developed sarcotubular system. Nuclear chain fibres also have more glycogen than do bag 2 fibres which, in turn, have more glycogen than bag 1 fibres. (Glycogen is the substance utilized in the production of ATP, and is therefore part of the energy producing cycle (Ganong 1973).) This suggests that the energy requirements of NC fibres are high,

The Neurophysiology of Tone

and appear to be similar to those of SNB fibres. The similar energy requirements and the demonstration that NC fibres as well as SNB fibres respond to static stimuli (Boyd, Gladden, McWilliam and Ward 1975) indicates that NC fibres participate with SNB fibres in reflexly controlling tonic muscle activity

Tandem Spindles

Muscle spindles usually have both nuclear bag (DNB and SNB) and nuclear chain fibres, although spindles with only one type of nuclear bag fibre have been found (Barker et al 1976). Cooper and Daniel (1963) found that the human lumbrical muscles have only nuclear bag fibres whereas Cooper et al (1955) reported that human extraocular intrafusals rarely have a nuclear bag formation

Barker and Gidumal (1961) reported the presence of transitional forms of intrafusal muscle fibres where a bag fibre in one spindle continued through to the next spindle as a chain fibre. Boyd (1960) wrote that true tandem spindles with continuous intrafusal fibres are rare, although spindles may have overlapping ends. However, Barker et al (1976) discovered in one of their experiments a tandem spindle with a bag 1 (DNB) fibre continuing in the next spindle as a NC fibre. The functional significance of tandem spindles remains unclear.

Sensory Endings and Afferents

Eldred (1965) presented four criteria to be considered in the classification of muscle spindle afferents. These are the number of sensory endings present in the spindle, the position of the ending along the length of the intrafusal fibre, the structure of the ending, and the size of its axon. With this in mind, the sensory endings and their afferents may be divided into two groups. Ruffini (1897) described two types of sensory ending — an annulospiral and a flower spray ending. Boyd (1956, 1957) noted that the annulospiral, or primary ending as it

is now called, is located on nuclear bag and chain fibres, whereas the flower spray or secondary receptor is found only on NC fibres.

Primary Ending and Group Ia Afferent

Each muscle spindle has only one primary ending, branches of which coil around every intrafusal fibre. This sensory ending is continuous with a single large myelinated rapidly conducting Ia afferent axon which is 12-20 μm in diameter (Eldred 1965, Matthews 1973).

(a) Location and Sensitivity to Stretch

The primary ending spirals round the central equatorial region of the intrafusal fibres where they lose their striations and appear to be non-contractile and offer less viscous resistance to stretch (Eldred 1965, Matthews 1973). Some of the nuclear bag fibres on which primary endings are located are percapsular, passing beyond the connective tissue capsule of the spindle to attach to tendon and endomysium. These attachments, if stretched, would directly stretch the primary ending whether or not the muscle spindle had been stretched. This means a similar degree of external stretch is needed to activate the primary ending (Eldred 1965) Hunt (1955) has found the threshold value of stretch needed to activate primary endings in soleus muscle to be 3 gms. As Eldred (1965) pointed out, this sensitivity to small changes in tension is important because a muscle is capable of changing length considerably without altering tension very much. If the primary ending was not extremely sensitive to stretch, this change in muscle length at low tensions would go unnoticed. Matthews (1973) discussed the sensitivity of the primary ending to stretch, noting that not only is it sensitive to change in length of the muscle, but it shows a high sensitivity to the velocity at which the stretching occurs.

This static sensitivity (responsiveness to change in length) and dynamic

(velocity) sensitivity of the primary ending is not surprising when it is considered that the receptor is found coiled around the less viscous equator of the intrafusals where the resistance to stretch is less In addition, the primary ending is found on the bag 1 (DNB) fibres which respond to dynamic stimuli and is also coiled around the bag 2 (SNB) and NC fibres which respond to static stimuli.

(b) Discharge Pattern

A study of the discharge pattern of the primary ending also reveals its dynamic (phasic) and static (tonic) sensitivity At the beginning of muscle stretch, the primary ending shows a burst of discharge (phasic activity) which gradually falls to a steady maintained level (tonic activity) appropriate to the new length of the muscle (Eldred and Tokizane 1955) Matthews (1973) claimed that the primary ending can 'reset' itself so that its high sensitivity to stretch transfers itself to a new muscle length, preventing the endings from becoming saturated Szumski (1974) added that when the stretch is released (or a muscle relaxes), the fibres recoil (or lengthen) and the primary ending again discharges (phasic activity) during this movement Eldred and Tokizane (1955) noted that there is a pause in primary firing following release of passive stretch or cessation of muscle contraction

(c) Central Connections

The information about the stretch of a muscle is conveyed by the Ia afferents to the central nervous systems (CNS) In the CNS there are supraspinal pathways and spinal cord connections. The supraspinal pathway is the dorsal spinocerebellar tract which activates the cerebellum and ultimately influences muscle tone via a cortico-cerebellar-cortical loop and then via the descending cortico-spinal tracts (Noback 1967, Barr 1972)

At a spinal cord level, the Ia afferent has a monosynaptic facilitatory synapse with the anterior horn cell (alpha motoneurone) of the muscle in which

the spindle is located (in this explanation the homonymous muscle is termed the agonist), a polysynaptic facilitatory synapse with the alpha motoneurones of the agonist or synergist, and a disynaptic inhibitory synapse with the alpha motoneurones of the antagonist (Ganong 1973, Scholz and Campbell 1980) Interneurones mediate the Ia facilitation and the Ia reciprocal inhibition in the poly- and disynaptic pathways respectively and are themselves influenced by the descending supraspinal pathways (Hultborn 1976). These central connections of the primary ending and its Ia afferent are depicted diagrammatically in Figure 3.

The reflex response of muscle to stretch has also been found to be phasic or tonic in nature. Lance and McLeod (1975) defined the phasic stretch as a synchronous motor neurone discharge caused by a brief stimulation of muscle spindles or their afferent nerve pathways. This reflex is seen clinically as the tendon jerk. The time course is such that the reflex must be monosynaptic (Lance and

McLeod 1975). The dynamic sensitivity of the primary ending, the phasic nature of its discharge, its continuation with the rapidly conducting Ia afferent fibres which monosynaptically excite alpha motoneurones, and its location on dynamic nuclear bag fibres indicate that the primary ending of muscle spindles is the receptor involved in the reflex control of phasic muscle activity.

The tonic stretch reflex, on the other hand, is one in which a stimulus produces a prolonged asynchronous discharge of motor neurones causing sustained muscle contraction for the maintenance or alteration of posture. The length of the time course is such that more than one synapse has been suggested. That is to say, it is polysynaptic. Clinically, this reflex is elicited by passively stretching a muscle (Lance and McLeod 1975). The primary ending is also activated by change in length per se of muscle fibres (static sensitivity), is located on SNB fibres and NC fibres, may discharge tonically, and has polysynaptic facilitatory synapses with alpha mo-

toneurones, rendering it significant in the maintenance of muscle tone by the tonic firing of motor units.

In summary, the primary ending and Ia afferent of muscle spindles is both a dynamic and a static receptor, controlling muscle tone via the monosynaptic phasic stretch reflex and the polysynaptic tonic stretch reflex.

Secondary Ending and Group II Afferents

The second afferent from muscle spindles reminded Ruffini (1897) of a wreath of flowers because of its structure. It was historically known as the 'flower spray' receptor but is now referred to as the secondary ending. According to Matthews (1973), the structural difference between the primary and secondary ending is well marked in the cat but not in man. Under the electron microscope, both human spindle receptors are closely applied to the intrafusal muscle membrane and appear the same except for their size.

There are usually from one to five secondary endings per spindle, although some small spindles have been found not to contain any. When several secondary endings are present, each is continuous with its own afferent axon, but endings in nearby muscle spindles may join the axon of an ending from another spindle (Eldred 1965).

Eldred (1965) explained that the secondary endings are continuous with the myelinated group II afferent axons which have a diameter of 4-12μ. As the group II fibres have a smaller diameter than the group Ia afferents, their nerve conduction velocity is slower (Erlanger and Gasser 1924).

(a) Location and Sensitivity to Stretch

Boyd (1957) found that secondary endings are located on nuclear chain fibres, lying on either side of the primary ending; that is, lying juxtaequatorially. Hunt's (1954) experiments showed that the threshold for stretch for soleus muscle secondary endings is 19 gms. This is much higher
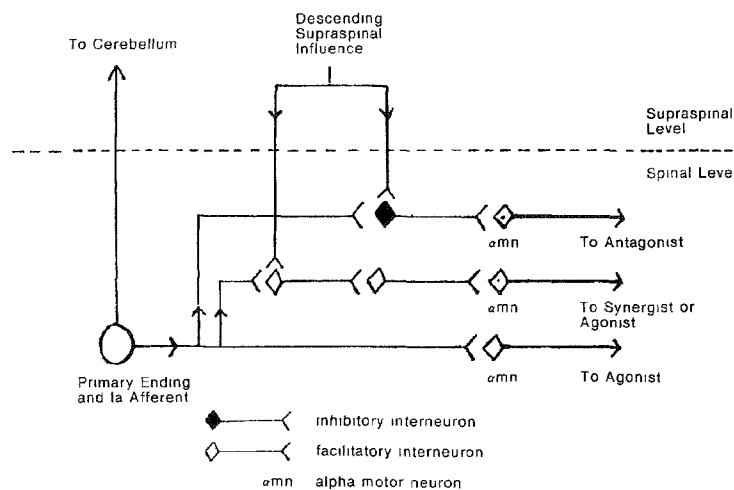

Figure 3: Diagrammatic representation of Ia afferent projections

The Neurophysiology of Tone

than that of the primary ending, indicating that the secondary ending is not as sensitive to stretch as the dynamic primary ending. Eldred (1965) noted that the location of secondary endings on nuclear chain fibres contributes to its lower stretch sensitivity. The nuclear chain fibres are intracapsular, attaching to the connective tissue capsule of the spindle. According to Eldred (1965), this means that the secondary endings would be affected by extrafusal muscle stretch only if this first lengthened the capsule. Furthermore, the juxtaequatorial region of the nuclear chain fibres where secondary endings are located is moderately well striated, offering more viscous resistance to stretch. Boyd (1976a) noted that in the juxtaequatorial region, the nuclear chain fibres have 'kinks'. A greater degree of stretch would therefore be required to stretch out these kinks and activate the secondary endings.

The higher threshold to stretch of the secondary ending indicates that it is not so much the rate or velocity of stretch which activates the receptor, but the amount of stretch or change in length of the muscle fibre. Matthews (1973) reported this to be the case, stating that the greater sensitivity of the secondary ending to change in length per se of the muscle fibre renders it a static receptor.

(b) Discharge Pattern

Examination of the discharge pattern produced by secondary endings in response to stretch further indicates the static nature of this receptor. When activated, secondary endings show a greater discharge per change in unit length than do primary endings. At a constant muscle length secondary endings fire more regularly than primaries. That is, secondary endings exhibit a tonic discharge (Matthews 1973). Eldred and Tokizane (1955) reported that following release of passive stretch or muscle contraction, secondary endings (in contrast to primary endings) show barely any pause in

tonic discharge. This suggested to Eldred (1965) that the secondary ending behaves as a receptor of little adaptation and exhibits greater static or tonic sensitivity than does the dynamic or phasic primary ending. (It must be remembered, however, that the primary ending has static as well as dynamic sensitivity. To Eldred (1965) this indicated that the primary ending behaves as a dual receptor, showing slow (static) adaptation or rapid (dynamic) adaptation, depending on the nature of the muscle stretch.)

(c) Central Connections

Like the primary afferent, the group II axons convey information to the central nervous system via spinal and supraspinal pathways. The secondary afferent projects with the primary afferent to the cerebellum via the dorsal spino-cerebellar tract. At a spinal level, the reflex connections are different from those of the primary afferent and controversy exists as to the exact control the secondary ending has over muscle tone via its synapses in the spinal cord.

The classical concept of group II afferent action on motoneurones arose from the experimental work of people such as Lloyd (1946) who found that in spinal cats stimulation of the group II afferents facilitated flexor muscles and inhibited extensors on the same (ipsilateral) side of the body, regardless of the muscle in which the reflex originated. Due to its long central latency the reflex was thought to be polysynaptic, the effects being mediated by interneurones.

Burke and Lance (1973) studied the reflex effects of group II afferents in human subjects and their results agree with those of Lloyd (1946). Burke and Lance (1973) concluded that the facilitation of hamstrings (flexor) activity and the inhibition of quadriceps (extensor) activity in spastic human subjects was due to activation of the secondary ending by stretch. This view has been challenged by researchers

such as Matthews (1969) and Kanda and Rymer (1977) whose studies with vibration and muscle stretch showed that simultaneous vibration and stretch of a muscle did not result in the one occluding the other, but rather an increase in muscle tension which was greater than that produced by vibration or stretch alone. This led these authors to conclude that as the Ia afferent discharge was held constant by vibration, the observed increase in muscle tension with vibration and stretch must be due to activation of the secondary endings by the stretch. According to Matthews (1969), these findings suggest a role for the secondary endings together with the primary ending in producing the tonic stretch reflex.

The hypothesis that the secondary endings function with, and augment, the primary ending discharge, is supported by the experimental work of Chapman, Michalski, and Siguin (1979). Their work showed that 65 per cent of group II afferents gave an excitatory input to extensor motoneurones — a direct contradiction to the classical concept of group II afferent function. The remaining 35 per cent of group II afferents behaved in accordance with the classical concept and were inhibitory to extensor motoneurones. Chapman and his colleagues (1979) concluded that the secondary endings may not be a functionally homogenous group and that under normal circumstances the majority (65 per cent) of secondary endings reinforce the primary ending. However, in cases of neurological dysfunction such as spinal cord injury where there is little or no descending facilitation of extensor motoneurones, the action of the remaining 35 per cent of secondary endings may become apparent — that is, ipsilateral facilitation of flexors and inhibition of extensors.

Matthews (1969) also considered that the effects of secondary ending stimulation might depend upon the integrity of the CNS. As Matthews

(1969) observed, interneurones mediate reflex effects of secondary endings. Interneurones are susceptible to descending supraspinal influence and, in Matthews' (1969) opinion, may be 'switched on or off' following CNS damage. If those mediating autogenetic excitations were 'switched on', then the reflex effect of secondary ending stimulation by stretch would be facilitation of the muscle activity. That is, the secondary ending would reinforce the action of the primary ending. On the other hand, if the interneurones to extensor muscles were 'switched off' then the group II afferent would reflexly inhibit extensors whilst facilitating flexors. Matthews (1969) concluded that this concept of group II fibre reflex effects allows for a graded control of muscle tone from excitation to inhibition via the tonic stretch reflex. In a review of the literature, Urbscheit (1979) and Munson, Fleshman and Sypert (1980) agreed that the secondary endings are involved in the tonic excitation of antigravity musculature — often extensors — and have a diverse effect upon muscle tone, depending upon the integrity of the CNS.

The polysynaptic nature of the group II fibre reflex pathway was challenged when Kirkwood and Sears (1974) demonstrated in cats that afferent impulses arising from group II fibres monosynaptically excite motoneurones. This monosynaptic pathway for secondary endings does not mean that they are involved in the monosynaptic stretch reflex (MSR) or tendon jerk because, as Matthews (1964) pointed out, the secondary endings are not excited by the small rapid stretch of a muscle used to elicit the MSR whereas the primary endings are.

It appears that the control of tone by the secondary ending/group II afferent is complex. The recent data suggests that these receptors are not a functionally homogenous group. Part of the population of secondary endings reinforce the action of the primary ending in influencing muscle tone,

especially that of antigravity postural muscles, via the tonic stretch reflex. The remainder of secondary endings facilitate flexor tonus and inhibit extensor tonus on the ipsilateral side regardless of the muscle in which the reflex originated These effects are mediated by mono- or polysynaptic pathways and their expression ultimately depends upon the function and integrity of the CNS, which facilitates or inhibits interneurones in the polysynaptic pathway.

Efferents: Motor Control of the Muscle Spindle

The intrafusal fibres of the muscle spindle have been found to have their own nerve supply (Boyd 1961). If these motor efferents influence the excitability of the muscle spindle stretch receptor, then they could well be involved in the reflex control of tone.

The efferents to striated muscle arise from motoneurones located in the anterior or ventral horn of the gray matter of the spinal cord. They may be divided into two groups: the efferents which are greater than 12μm in diameter, arise from large alpha motoneurones, and supply extrafusal muscle fibres; and the smaller (8-12μm in diameter) gamma efferents innervating the intrafusal fibres (Matthews 1973). Eccles, Eccles, Iggo and Lundberg (1960) found that the gamma motoneurones of a muscle are located within the nucleus of alpha motoneurones supplying that muscle. They give rise to the gamma efferent, also known as the fusimotor fibre. As Matthews (1973) pointed out, the separation of fusimotor from skeletomotor control is not always distinct and a shared fusimotor-skeletomotor innervation (known as the beta fibre) has been found.

Boyd (1961) described two types of fusimotor fibres: the gamma 1 fibres which ended in plates on nuclear bag fibres; and the gamma 2 fibres which had diffuse trail like endings on nuclear chain fibres. This histological separation has been found to corre-

spond to a functional classification based on the response of the primary ending to stretch (Matthews 1973). Matthews (1962) found that stimulation of gamma 1 (plate) efferents increased the dynamic (velocity) response of the primary ending to stretch. Stimulation of the gamma 2 (trail) ending decreased the primary ending velocity sensitivity whilst increasing its static response. The two kinds of fusimotor fibres are now named dynamic or static efferents and correspond to the gamma 1 or gamma 2 fibres respectively (Matthews 1973).

Eldred (1965) discussed the controversy as to whether the dynamic and static gamma efferents supply a distinct type of intrafusal fibre. Earlier experiments (Boyd 1961) indicated that dynamic efferents supplied nuclear bag fibres and static efferents ended on nuclear chain fibres. Barker (1962) disputed this, stating that gamma efferents are not restricted to one type of intrafusal fibre and indeed one intrafusal fibre may carry both types of efferent.

Later experiments by Boyd et al (1975) demonstrated that whereas dynamic gamma efferents innervate DNB fibres, cross innervation exists between SNB and NC fibres. When the similar function of the SNB and NC fibres is considered, it is not surprising to find that both are innervated by static gamma efferents. Laporte's (1979) review of the literature on this subject showed support for the experiments of Boyd et al (1975) and also presented evidence to suggest that some DNB fibres are also innervated by static gamma efferents. However, as Matthews (1973) stated, the nuclear bag and nuclear chain fibres appear to have sufficient distinct motor innervation to result in distinct dynamic and static motor effects, resulting in a degree of independent reflex control of muscle activity.

Dynamic Gamma Efferents

The dynamic gamma efferents (2.5-4.0μm) terminates on the DNB fibres

The Neurophysiology of Tone

in discrete plate endings (Boyd 1961). The gamma plate endings lie towards the poles of the spindle and several may lie on any one nuclear bag fibre. The plate endings often arise from separate dynamic fusimotor fibres although one efferent may branch to supply several plate endings (Matthews 1973). Barker, Stacey and Adal (1970) have further subdivided the plate endings into 'p$_1$' and 'p$_2$' plates, the p$_1$ plates closely resembling the motor end plates on extrafusal fibres. Barker et al (1970) found that while a bag 1 (DNB) intrafusal fibre always had a p$_2$ plate, bag 2 (SNB) and NC fibres may also occasionally have a p$_2$ plate. These authors found that 90 per cent of p$_2$ plates ended on nuclear bag fibres and 10 per cent on chain fibres.

On this basis, stimulation of the gamma plate (dynamic) efferents would result in contraction of DNB, SNB and NC fibres. The primary ending coils around all intrafusal fibres, and would therefore be influenced by the dynamic gamma efferent. (Secondary endings also lie on NC fibres and are, according to Matthews (1973), controlled exclusively by static gamma efferents. Dynamic efferents excite only the primary endings). Dynamic gamma fusimotor discharge controls the velocity sensitivity of the primary ending to stretch (Matthews 1973). Via the primary ending connections with the alpha motoneurones, the dynamic fusimotor fibres are therefore involved in controlling the sensitivity of the phasic stretch reflex.

Static Gamma Efferents

Boyd (1961) decribed a diffuse ending from gamma 2 (static) efferents on nuclear chain fibres. Barker, Stacey and Adal (1970) named these terminations 'trail endings'. In contrast to the plate endings, the trail endings have no discrete point of termination. Instead, they are spread along the intrafusal fibre, lying on the juxtanuclear portion. The static gamma efferents are 1.2-2.0μm in diameter (Matthews 1973). As the static fibres

are smaller than the dynamic gamma efferents they have a slower nerve conduction velocity (Erlanger and Gasser 1927).

Although it was classically thought that static gamma efferents innervated NC fibres only, subsequent research in this area has shown that this appears not to be so. Boyd et al (1975) observed static efferents terminating on SNB as well as NC fibres. Barker (1976) agreed with the observations of Boyd et al (1975), adding that bag 1 (DNB) fibres also have some innervation by static efferents. Laporte's (1979) review on the intrafusal distribution of dynamic and static fusimotor fibres concluded that about one-third of DNB intrafusals are innervated by static gamma efferents. As Laporte (1979) wrote, Emonet-Denard, Laporte, Matthews and Petit (1977) suggested that the innervation of DNB fibres by static efferents could preserve their responsiveness to stretch when the dynamic system is not active as would be the case during strong static stimulation. According to Matthews (1973), the secondary endings on NC fibres respond only to static efferent stimulation. Matthews (1973) argued that the strong static effects resulting from the simultaneous excitation of NC and SNB fibres would mask the effects of stimulatng the DNB fibre.

It appears that the major effect of static gamma discharge arises from the SNB and NC fibres, resulting in excitation of the primary (static sensitivity) and secondary endings. Continuous or tonic firing of these receptors is brought about by the repeated firing of the static gamma motoneuron. The gamma motoneuron has many interneurones impinging on it. Via these interneurones the descending supraspinal tracts (such as vestibulospinal or reticulospinal tracts) are able to influence and maintain the tonic discharge of the gamma motoneuron (Barr 1972).

Primary endings on SNB fibres and secondary endings on NC fibres have

been seen to be the receptors of the tonic stretch reflex As the firing of these receptors is regulated by static gamma efferent discharge, the static gamma motoneuron with its efferent is important in the maintenance of the tonic stretch reflex and therefore in the control of muscle tone.

Beta Efferents

Adal and Barker (1965) observed individual motor fibres which branched to supply both intrafusal and extrafusal fibres These collaterals of alpha efferents, known as beta fibres, are intermediate in size between alpha and gamma fibres (Laporte and Emonet-Denand 1976). Based on the work of Erlanger and Gasser (1927) the beta fibres have a nerve conduction velocity between alpha and gamma fibres.

The presence of beta fibres has been well documented in amphibian (Katz 1946), reptilian (Proske 1969) and mammalian muscle spindles (Bessou, Emonet-Denand and Laporte 1965; Emonet-Denand, Jamie and Laporte 1975; and Boyd, Gladden, McWilliam and Ward 1977). Beta fibres to mammalian muscle spindles have been found to terminate on both nuclear bag and nuclear chain intrafusal fibres (Barker, Emonet-Denand, Harker, Jamie and Laporte 1976; Boyd et al 1977).

Primary endings have been seen to spiral around the three types of intrafusal fibre and contraction of these fibres by beta efferents would result in stimulation of the primary receptor. It is Post, Rymer and Hasan's (1980) view that beta efferents, by providing an additional means of spindle excitation, would ensure continued stimulation of intrafusals if fusimotor activity is largley completed before the threshold for extrafusal contraction has been reached. Beta activity therefore increases Ia afferent discharge on a background of gamma motoneuron activity, constituting a positive means of excitation for muscle spindles.

Phasic and Tonic Motor Units

It has been seen that the muscle spindle exerts dynamic/phasic or static/tonic control over muscle activity In 1956, Granit, Henatsch and Steg, followed by Granit, Phillips, Skoglund and Steg (1957), demonstrated that the alpha motoneurones in the ventral horn could be divided into two functionally different groups: phasic and tonic. Phasic alpha motoneurones responded only briefly to a tetanizing stimulus whereas tonic motoneurones showed a repetitive long lasting discharge following the stimulus. The efferent axon of the phasic motoneuron was found to be larger in diameter than the tonic axon According to the nerve conduction' velocity studies of Erlanger and Gasser (1927), the phasic axon would have a faster nerve conduction velocity This is in keeping with the faster dynamic muscle contraction resulting from phasic motoneuron discharge. In Rushworth's (1964) opinion, it is likely that in man, phasic motoneurones are involved in the tendon jerks or monosynaptic stretch reflex and tonic motoneurones in the maintenance of posture via the tonic stretch reflex.

The muscles themselves have been found to be made up of two functionally different types of fibres. Eccles, Eccles and Lunderg (1958) reported on the experimental work of Ranvier, 1874, and Kronecker and Stirling, 1878, who noted that 'red' striated muscle has a slower contraction time than 'white' muscle fibres. This functional differentiation of muscle fibre types was supported by the histochemical analysis carried out by Kugelberg and Edstrom (1968) These researchers found that the motor units of slow 'red' fibres have a high content of oxidative enzymes. The oxidative enzymes are stored in the mitochondria, or 'power house', of a cell and are involved in the metabolic reaction (breakdown of ATP) to produce energy (Ganong 1973). As Edstrom (1973) wrote, this oxidative metabo-

lism produces high levels of energy, making the 'red' fibres well suited for tonic work. Conversely, the fast twitch or 'pale' fibres which are low in oxidative enzymes (Kugelberg and Edstrom 1968) are easily fatigued and are suited for short bursts of phasic or dynamic activity (Edstrom 1973).

It would be reasonable to assume that slow 'red' motor units which fire tonically would be innervated by efferents arising from tonic alpha motoneurones and that phasic alpha motoneurones would supply fast 'pale' motor units Eccles, Eccles and Lundberg (1958) found this to be the case. These authors added that the correspondence between motoneuron and motor unit type occurs even with muscles which are supplied by an admixture of 'fast' and 'slow' motoneurones; that is, muscles which are involved in both phasic and tonic activity.

The Phasic and Tonic Stretch Reflexes

The differentiation between tonic and phasic function has been seen at a motoneuron, muscle spindle, and extrafusal fibre level. Muscle spindle discharge can be evoked in two ways One way is by stretching the tendon or the extrafusal fibres to which the tendon attaches and so imparting the
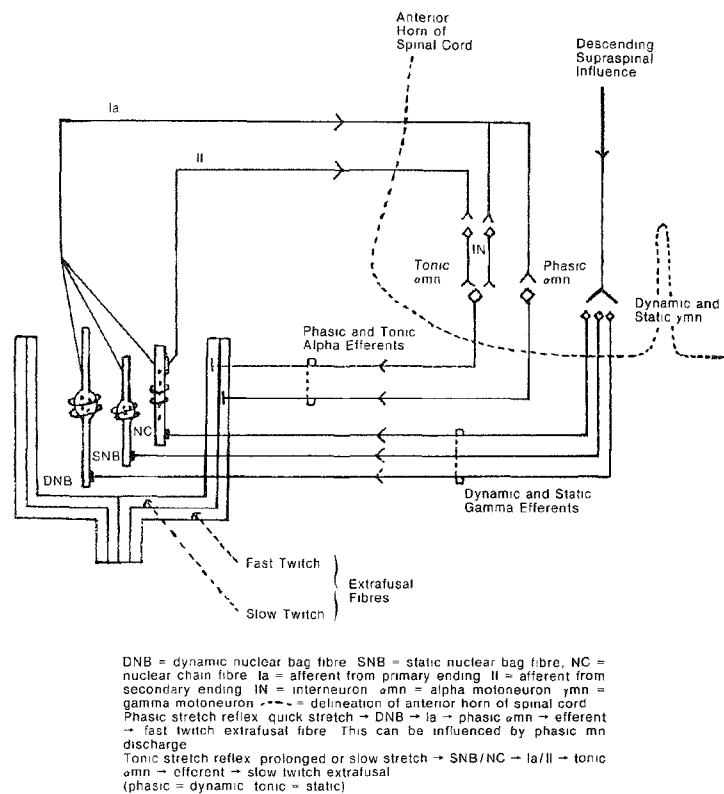

DNB = dynamic nuclear bag fibre SNB = static nuclear bag fibre, NC = nuclear chain fibre Ia = afferent from primary ending II = afferent from secondary ending IN = interneuron ⍺mn = alpha motoneuron γmn = gamma motoneuron -·-·- = delineation of anterior horn of spinal cord
Phasic stretch reflex quick stretch → DNB → Ia → phasic ⍺mn → efferent → fast twitch extrafusal fibre This can be influenced by phasic mn discharge
Tonic stretch reflex prolonged or slow stretch → SNB/NC → Ia/II → tonic ⍺mn → efferent → slow twitch extrafusal
(phasic = dynamic tonic = static)

Figure 4: Diagrammatic representation of the phasic and tonic stretch reflexes

The Neurophysiology of Tone

stretch to intrafusal fibres of the muscle spindle. A small rapid stretch, imparted to the DNB fibres results in separation of the coils of the primary ending, causing them to fire and generate an action potential. The rapidly conducting Ia afferent fibre conducts the impulses to the ventral horn of the spinal cord where there is a monosynaptic connection with phasic alpha motoneurones. The impulses then pass along the efferents to the white or fast twitch extrafusal muscle fibres and a contraction results. This is the phasic monosynaptic stretch reflex and is depicted diagrammatically in Figure 4.

A prolonged or slow stretch produces the tonic stretch reflex. The effects of a slow stretch largely excite the primary endings (static sensitivity) and the secondary endings lying on SNB and NC fibres. Impulses are conducted along group Ia and group II afferents to synapse in the spinal cord. Here, part of the population of group II afferents reinforce Ia afferent activity, with both afferents making polysynaptic connections with tonic alpha motoneurones. The tonic alpha motoneuron discharges, and contraction of 'red' slow twitch extrafusal fibres results.

The second way in which muscle spindles can be made to fire is via stimulation of the gamma motoneuron. Discharge of the gamma motoneuron causes contraction of the intrafusal fibres, subsequent distortion of the sensory (primary and secondary) endings and propagation of impulses along the group Ia and group II afferents to the spinal cord where synapses are made with the alpha motoneurones. In this way, the gamma motoneuron can influence alpha motoneuron dicharge and this is what is often referred to as 'driving the alpha motoneuron through the gamma loop'

Although dynamic gamma efferents innervate all the intrafusal fibres, the effect is only on primary endings, increasing their velocity sensitivity.

Therefore the primary endings on DNB fibres would be particularly affected by dynamic gamma efferent discharge Through these connections the dynamic gamma motoneuron influences the sensitivity of the phasic monosynaptic stretch reflex.

Static gamma efferents may also innervate all intrafusal fibres. The predominant effect of static gamma stimulation has been found to be contraction of SNB and NC fibres This distorts primary and secondary endings, increasing their static or tonic sensitivity, which can increase the sensitivity of the tonic stretch reflex The tonic discharge of alpha motoneurones through the static gamma loops helps to maintain normal muscle tone, particularly that of the anti-gravity postural muscles.

Conclusion

The muscle spindle plays a dominant role in regulating muscle tone via the phasic or tonic stretch reflexes These reflexes which provide the clay for normal tone, can be shaped or moulded by peripheral, spinal or supraspinal factors. Physiotherapists, through the application of specific treatment techniques, are able to alter muscle spindle activity, thereby shaping desired muscle tone and movement

References

Adal MN and Barker D (1965), Intramuscular branching of fusimotor fibres, Journal of Physiology, 177, 288-299

Barker D (1962), The structure and distribution of muscle receptors, in Barker D (ed), Symposium on Muscle Receptors 227-240, Hong Kong University Press, Hong Kong

Barker D and Gidumal JL (1961), The morphology of intrafusal muscle fibres in the cat, Journal of Physiology, 154, 513-528

Barker D, Stacey MJ and Adal MN (1970), Fusimotor innervation in the cat, Philosophical Transactions B, 258, 315-346

Barker D, Banks RW, Harker DW, Milburn A and Stacey MJ (1976), Studies of the histo-chemistry, ultrastructure, motor innervation, and regeneration of mammalian muscle spindles, Progress in Brain Research, 44, 67 87

Barker D, Emonet-Denand F, Harker DW, Jamie and Laporte Y (1976a), Distribution of fusimotor axons to intrafusal muscle fibres in cat tenuissimus spindles as determined by the glycogen-depletion method, Journal of Physiology, 261, 49-69

Barr ML (1972), The Human Nervous System, 2nd edition, Hagerstown Md, Medical Books Department, Harper and Row, New York

Bessou P, Emonet Denand F and Laporte Y (1965), Motor fibres innervating extrafusal and intrafusal muscle fibres in the cat, Journal of Physiology, 180, 649-672

Boyd IA (1956), The tenuissimus muscle of the cat, Journal of Physiology, 133, 35-36

Boyd IA (1957), The innervation of mammalian neuromuscular spindles, Journal of Physiology, 140, 14-15

Boyd IA (1960), The diameter and distribution of the nuclear bag and nuclear chain fibres in the muscle spindles of the cat, Journal of Physiology, 153, 23-24

Boyd, IA (1961), The motor innervation of mammalian muscle spindles, Journal of Physiology, 159, 7-9

Boyd IA, Gladden MII, McWilliam PN and Ward J (1975), 'Static' and 'dynamic' nuclear bag fibres in isolated cat muscle spindles, Journal of Physiology, 250, 11-12

Boyd IA (1976), The response of fast and slow nuclear bag fibres and nuclear chain fibres in isolated cat muscle spindles, Quarterly Journal of Experimental Physiology, 61, 203-253

Boyd IA (1976a), The mechanical properties of dynamic nuclear bag fibres, static nuclear bag fibres and nuclear chain fibres in isolated cat muscle spindles, Progress in Brain Research, 44, 33-66

Boyd IA, Gladden MH, McWilliam PN and Ward J (1977), Control of dynamic and static nuclear bag fibres and nuclear chain fibres by gamma and beta axons in isolated cat muscle spindle, Journal of Physiology, 265, 133-162

Brodal A (1962), Spasticity — Anatomical Aspects, Acta Neurologica Scandinavia, Supplement 3, 38, 9-40

Burke D, Lance JW (1973), Studies of the reflex effects of primary and secondary spindle endings in spasticity, in Desmedt JE (ed), New Developments in Electromyography and Clinical Neurophysiology, 3, 475-495, Karger, Basel

Chapman C, Michalski, Siguin (1979), The effects of cold-induced muscle spindle secondary activity on monosynaptic and stretch reflexes in the decerebrate cat, Canadian Journal Physiology and Pharmacology, 57, 606-14

Cooper, S, Daniel PM and Whitteridge D (1955), Muscle spindles and their sensory endings in the extrinsic eye muscles The physiology and anatomy of these receptors and of their connexions with the brain stem, Brain, 78, 564-583

Cooper S and Daniel PM (1963), Muscle spindles in man, their morphology in the lumbrical and the deep muscles of the neck, Brain, 86, 563 586

Eccles JC, Eccles RM and Lundberg A (1958), The action potentials of the alpha motoneurones supplying fast and slow muscles, Journal of Physiology, 142, 275-291

Eccles JC, Eccles RM, Iggo A and Lundberg A (1960), Electrophysiological studies on gamma motoneurones, *Acta Physiologica Scandinavia*, **50**, 32-40

Edstrom L (1973), Relation between spasticity and muscle atrophy pattern in upper motor neurone lesions, *Scandinavian Journal of Rehabilitative Medicine*, **5**, 170-171

Eldred E and Tokizane T (1955), Two patterns of afferent discharge from muscle spindles, *American Journal of Physiology*, **183**, 612

Eldred E (1965), The dual sensory role of muscle spindles, *Journal of the American Physical Therapy Association*, **45**, 290-313

Emonet-Denand F, Jamie L and Laporte Y (1975), Skeletofusimotor axons in hind-limb muscles of the cat, *Journal of Physiology*, **249**, 153-166.

Emonet-Denand F, Laporte Y and Matthews P (1977), On the subdivision of static and dynamic fusimotor actions on the primary ending of the cat muscle spindle, *Journal of Physiology*, **268**, 827-861

Erlanger J and Gasser HS (1924), Compound nature of action current of nerve as disclosed by cathode ray oscilloscope, *American Journal of Physiology*, **70**, 624-666

Fulton JF (1943), *Physiology of the Nervous System*, 2nd edition, Radford University Press, Virginia

Ganong WF (1973), *Review of Medical Physiology*, 6th edition, Lange Medical Publications, Canada

Grant R, Henatsch HD and Steg G (1956), Tonic and phasic ventral horn cells differentiated by post-tetanic potentiation in cat extensors, *Acta Physiologica Scandinavia*, **37**, 114-126

Grant R, Phillips CG, Skoglund CR and Steg G (1957), Differentiation of tonic from phasic alpha ventral horn cells by stretch, pinna and crossed extensor reflexes, *Journal of Neurophysiology*, **20**, 470-481

Hultborn H (1976), Transmission in the pathway of Ia inhibition to motoneurones, *Progress in Brain Research*, **44**, 235-255

Hunt CC (1955), Relation of function to diameter in afferent fibres of muscle nerves, *Journal of General Physiology*, **38**, 117-131

Jansen JKS and Rudjord T (1964), On the silent period and Golgi tendon organs of the soleus muscle of the cat, *Acta Physiologica Scandinavia*, **62**, 364-379.

Kanda K, Rymer WZ (1977), An estimate of the secondary spindle receptor afferent contribution to the stretch reflex in extensor muscles of the decerebrate cat, *Journal of Physiology* (London), **264**, 63-87

Katz B (1946), The efferent regulations of the muscle spindle in the frog, *Journal of Experimental Biology*, **26**, 201-217

Kirkwood PA and Sears TA (1974), Monosynaptic excitation of motoneurones from muscle spindle secondary endings of intercostal and triceps surae muscles in the cat, *Journal of Physiology* (London), **245**, 64-66.

Korten JJ (1972), The Regulation and Function of the Muscle Spindle, in Birkmayer W (ed), *Spasticity — a Topical Survey*, Chapter 12, Hans Huber Publishers, Berne.

Kugelberg E and Edstrom I. (1968), Differential histochemical effects of muscle contractions on phosphorylase and glycogen in various types of fibre Relation to fatigue, *Journal of Neurology, Neurosurgery, and Psychiatry*, **31**, 415-423

Lance JW and McLeod JG (1975), *A Physiological Approach to Clinical Neurology*, 2nd edition, Butterworths, London.

Laporte Y and Emonet-Denand F (1976), The skeleto-fusimotor innervation of the cat muscle spindle, *Progress in Brain Research*, **44**, 99-106.

Laporte Y (1979), On the intrafusal distribution of dynamic and static fusimotor axons in cat muscle spindles, *Progress in Brain Research*, **50**, 3-10

Liddell EGT and Sherrington CS (1924), Reflexes in response to stretch (Myotatic reflexes), *Proceedings of the Royal Society, London*, Series B, **96**, 212

Lloyd DPC (1946), Integrative pattern of excitation and inhibition in two-neurone reflex, *Journal of Neurophysiology*, **9**, 439-444

Magoun HW and Rhines R (1947), *Spasticity The Stretch Reflex and Extrapyramidal Systems*, Charles C. Thomas, Springfield, Illinois

Matthews PBC (1962), The differentiation of two types of fusimotor fibres by their effects on the dynamic response of muscle spindle primary endings, *Quarterly Journal of Experimental Physiology*, **47**, 324-333.

Matthews PBC (1964), Muscle Spindles and their motor control, *Physiology Review*, **44**, 219-288

Matthews PBC (1968), Receptors in muscle, *Physiotherapy*, **54**, 204

Matthews PBC (1969), Evidence that the secondary as well as the primary endings of the muscle spindles may be responsible for the tonic stretch reflex of the decerebrate cat, *Journal of Physiology*, **204**, 365-393.

Matthews PBC (1973), The advances of the last decade of animal experimentation upon muscle spindles, in Desmedt JE (ed), *New Developments in Electromyography and Clinical Neurophysiology*, **3**, 95-125, Karger, Basel.

Munson JB, Fleshman JW and Sypert BW (1980), Properties of single fibre group II EPSPs in triceps surae motoneurones, *Journal of Neurophysiology*, **44**, 713-725

Noback, CR (1967), *The Human Nervous System*, McGraw-Hill Inc., Tokyo.

Ovalle WK and Smith RS (1972), Histochemical identification of three types of intrafusal muscle fibres in the cat and monkey based on the myosin ATP ase reaction, *Canadian Journal of Physiology and Pharmacology*, **50**, 195-202.

Post EM, Rymer WZ and Hasan Z (1980), Relation between intrafusal and extrafusal activity in triceps surae muscles of the decerebrate cat: evidence for beta action, *Journal of Neurophysiology*, **44**, 383-404.

Proske U (1969), Electrophysiological analysis of responses from lizard muscle spindles, *Journal of Physiology*, **205**, 289-304.

Ruffini, A (1897), Observations on sensory nerve endings in voluntary muscles, *Brain*, **20**, 368-374

Rushworth (1964), Some aspects of the pathophysiology of spasticity and rigidity, *Clinical Pharmacology and Therapeutics*, **5**, 828-836

Scholz JP and Campbell SK (1980), Muscle spindles and the regulation of movement, *Physical Therapy*, **60**, 1416-1424.

Szumski AJ, Burg D, Struppler A and Velho F (1974), Activity of muscle spindles during muscle twitch and clonus in normal and spastic human subjects, *Electroencephalography and Clinical Neurophysiology*, **37**, 589-597

Urbscheit NL (1979), Reflexes evoked by Group II afferent fibres from muscle spindles, *Physical Therapy*, **59**, 1083-1087

Wyke B (1976), Neurological mechanisms in spasticity a brief review of some current concepts, *Physical Therapy*, **62**, 316-319