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Neuro-mechanical control of movement and coordination: a new perspective based on somatic equilibrium points

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Abstract

Despite more than hundred years of research since Sir Sherrington's studies on reflexes, his questions are still somehow unanswered. On what anatomical stage do the play of spinal reflex interaction take place? What are the physiological properties of this anatomical substrate? In this paper, we address these questions in light of the most advanced theory of motor control and the anatomical discoveries on the fascia that are changing how we think about control of action and perception. There are two sides of the problem: the neurological (reflex) connections that are at the base of movement, and the anatomical substrate that regulates and coordinates the movement. We recently advanced a hypothesis on how these two elements are connected and how they interplay. Here we further explain the concept of the *somatic equilibrium point* – SEP – and its central role in movement control and coordination. It is our belief that the concept of SEP explains how the neuro-mechanical control of movement is organized at peripheral level. At this level, intrafusal and extrafusal muscle fibres are combined in myofascial units, organized in anatomical directions. Myofascial units are closed systems whose behaviour can be affected by neural (voluntary) control or changes in external forces. SEPs represent the intrinsic equilibrium of the myofascial units, and are connected through the continuum of the fascia so that mechanical transfer of tension from segment to segment pre-adjust muscle fibers length and hence their excitation level. This is how coordination between segments is achieved. Finally, we suggest SEPs create the neurological representation of the referent configuration for action, and configurations are linked to the architecture of the fascial system.

Keywords: reflex; proprioception; sensorimotor; muscle spindle; fascia; human.

Introduction

Explaining how movement is controlled has always been an objective of scientists since the studies of Sherrington on monosynaptic reflexes, however at these days there is still debate on "*if and how"* reflex threshold is adjusted and controlled in a feedforward (anticipatory) way (Dimitriou, 2022; Dimitriou & Edin, 2010). It is known that monosynaptic reflexes are enhanced by direct facilitation of α-motoneurones (Bussel, Morin, & Pierrot-Deseilligny, 1978), and by increase in spindle activity induced by γ-activation (Rossi-Durand, 2002). Burg, Szumski, Struppler, and Velho (1974) found an increase of spindle activity in relaxed muscles during contraction of remote muscles and thought, therefore, that γ-fibre activity was responsible for the enhancement of tendon reflexes. On the contrary, Hagbarth, Wallin, Burke, and Löfstedt (1975) have shown that the spindle activation is always accompanied by a very slight contraction of skeletal muscle fibres, which implies α-activation. Aside from the methodological differences, this controversy can be explained by the existence of a closed system incorporating both elements and the concurrent effect of the fascial tension on both alpha and gamma activation. That is, within the closed system, the neurological control is intrinsically related to the basal tension of the connective tissue that surrounds single muscle fibers (endomysium), fascicle (perimysium), single muscle belly (epimysium), as well as groups of muscles (aponeurotic fascia).

Many motor control theories explain movement control and coordination only from a neurological point of view, as a result we have seen the theorization of concepts such as the central patterns generators (Marder & Calabrese, 1996), efference copy (Bridgeman, 1995) and optimal feedback control (Todorov & Jordan, 2002). Any theory based on computational models rely on abstract concepts that although helpful in describing motor behaviour, they do not explain the anatomical connections that make movement initiation and coordination possible. The referent control theory proposed by Feldman and champions (Feldman, 2015), is rooted on strong physiological knowledge and respects biological laws; unlike other control theories, it explains control based on the regulation of parameters, and allows measurable variables (i.e. muscle force, joint kinematics) to emerge during the movement. However, even this theory accredits the control of physical parameters (i.e. initial muscle length) primarily to central inputs. In this paper, we will try to contribute to the referent control theory by introducing the possible role of the connective tissue (fascia) in changing those important parameters. We previously introduced the concept of SEP, the somatic equilibrium point (Garofolini & Svanera, 2019), as the link between the motor muscle system and the fascial system. We now present the implication of such element in explaining how movement is generated, and more importantly, how changes in parameters are regulated by the fascial system and its neuroanatomical connection to the muscle system.

Organisation of movement in spatial directions

In the traditional view, muscles are independent elements so that each muscle has a specific action on a joint. For instance, the brachialis is regarded as a mono-articular elbow flexor activated by a neural input that causes the muscle to contract and the joint to flex. From here the idea that the CNS controls activation pattern and force generation of each muscle in the body. However, studies on primates have shown that not only the central nervous system knows nothing about muscles (Beevor, 1903) but it does not know anything about the movement to execute either (Giacomo Rizzolatti et al., 1988; Gentilucci Rizzolatti & Gentilucci, 1988). When an action is planned, neurons of the pre-motorial cortex area discharge based on the intention (an abstract idea, such as grasping) irrespectively of which part of the body (hand or foot) is used to perform the action (Gentilucci

Rizzolatti & Gentilucci, 1988). Weinrich and Wise (1982), also found the neurons of the pre-motorial cortex area to be organized in spatial directions, so that a group of neurons is active only when an action is performed in a specific direction.

Moreover, stimulation of a part of the homunculus in the motor cortex, does not produce activation of a single muscle (Bear, Connors, & Paradiso, 2020; Shumway-Cook & Woollacott, 2007); on the contrary, such stimulation results in the activation of multiple fibers distributed within multiple muscles along an axis in an anatomical region. Georgopoulos, Caminiti, Kalaska, and Massey (1983); Georgopoulos, Lurito, Petrides, Schwartz, and Massey (1989) found that motor cortical cells possess directional preference and directional spread, generating movements in particular directions. These evidences reiterate the idea that at the level of the CNS actions are organized according to the spatial planes and not in individual muscles (English, Wolf, & Segal, 1993; Fogassi et al., 1996; Giacomo Rizzolatti et al., 1988). At peripheral level, there is evidence for preferred sensory direction for the population of afferents (Aimonetti, Hospod, Roll, & Ribot-Ciscar, 2007; Bergenheim, Ribot-Ciscar, & Roll, 2000). We argue that a directional organisation at central level, and a proprioceptive coding at peripheral level, will necessarily have a similar correspondence at muscle fibers organisation (Figure 1).

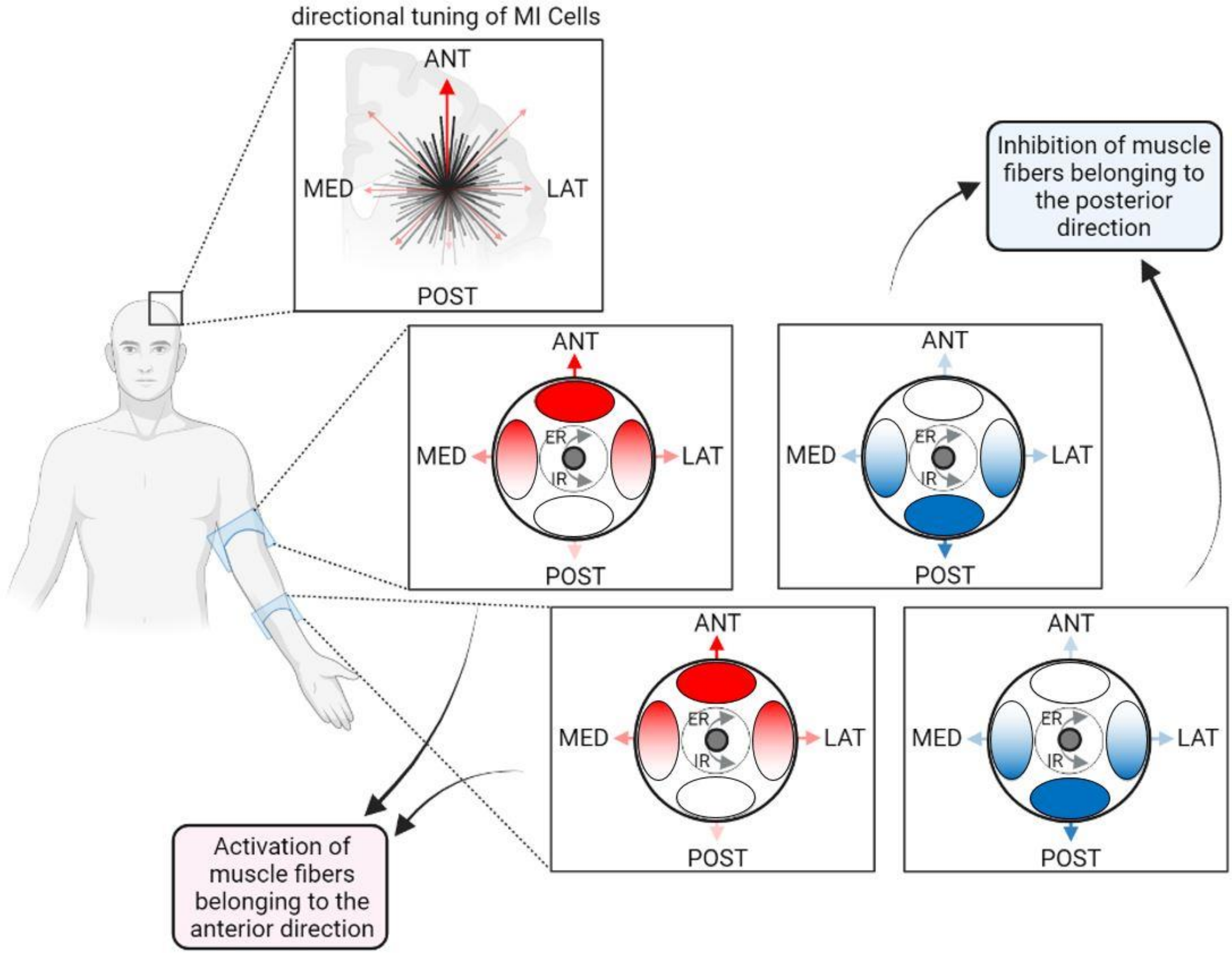

Figure 1. Voluntary forward motion of the arm. *The motor cortex compute a vectorial representation of movement direction in spatial coordinates (population vector hypothesis), where a population vector is defined as a "weighted vector sum of contributions of directionally tuned neurons" (Georgopoulos et al., 1989). The activity of a given population of motor cortical neurons peaks for a particular movement direction. Neural activation result in alpha motorneuron activation at peripheral level. Only the muscle fibers that belong to the same motor direction will be active. Muscle activation in the anterior direction will have a neurological effect (reciprocal inhibition) on the antagonist muscles, but it will also stretch the intermuscular septum (mechanical effect) activating Golgi tendon organs of the antagonist (posterior direction) resulting in inhibition.*

Therefore, a forward (antepulsion) motion of all limb segments is achieved by contraction of muscle fibers belonging to the anterior motor direction. If the movement happens in a pure plane (i.e. forward direction on a sagittal plane) all ipsidirectional motor units (distributed in multiple muscles) will be activated. To allow movement to occur, the muscle fibers belonging to the posterior direction will be inhibited by mechanical activation of the Golgi tendon Organs - autogenic inhibition- (Pierrot-Deseilligny, Katz, & Morin, 1979). The contraction of motor units of a segment will stretch the fascia in a proximal and/or distal direction interconnecting the myofascial units of antepulsion (L. Stecco, 2016). Myofascial units are defined as composed of a neural element (alpha, gamma and muscle spindles afferents Ia,II), a fascial element (coordinating ipsidirectional motor units through activation of muscle spindle and Golgi tendon organs), a muscular component (extrafusal muscle fibers generating force), and a sensory component (mechano receptors within the fascia surrounding joints and within ligaments, i.e. Pacini and Ruffini organs). Myofascial units should be seen as closed systems whose state can be changed by neural descending inputs or external forces (Figure 2).

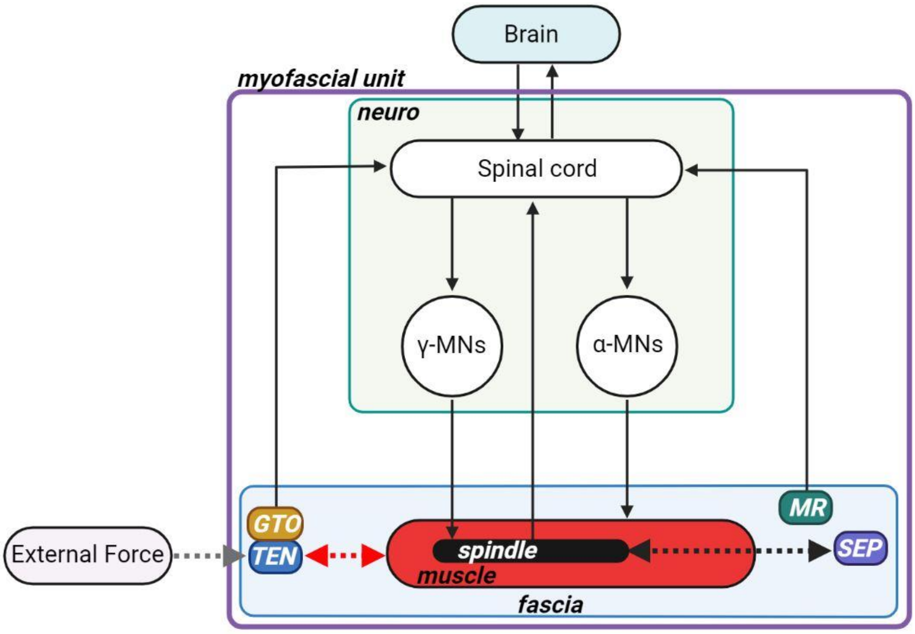

***Figure 2. Simplified neuro-myo-fascial unit circuitry underlying motor control of action**. The neural element is composed of alpha, gamma and muscle spindles afferents Ia,II. The fascial element coordinates ipsidirectional motor units through activation of muscle spindle and Golgi tendon organs (GTO). The muscular component is composed of the extrafusal muscle fibers generating force, and a sensory component, mechanoreceptors (MR) within the fascia (i.e. Pacini and Ruffini organs).*

Connections between sequential myofascial units pre-activate the primary endings of the muscle spindles evoking excitatory post-synaptic action potentials in alpha motor neurons moving adjacent segments. If movement happens on multiple planes (i.e. composition of directions) than motor unit activation will depend on the stretch on the fascia and the consequent activation of the muscle spindles belonging to these directions (Carla Stecco, 2014).

Somatic equilibrium point

Brief history and basic concepts

One of the recurrent element in all curative therapies developed through the centuries is the recognition of specific points on the human body. If how these points are treated differs depending on cultural beliefs and historical periods, their location has been always the same. There are traces of these points on the mummy of a man (Otzi) who lived some time between 3350 and 3105 BC. On his body there were 61 tattoos most of them located next to, or directly on acupunctural areas that are used today (Singh, Ernst, Lanza, & Vicentini, 2008). These are similar to the Marma points of Ayurveda (Lad, BAMS, Anisha Durve, & AP, 2008) and to the trigger points (Hong, 2000). More recently, Dr Luigi Stecco, Italian physiotherapist, found in his practice that these points were located on the connective tissue (fascia) and some of these points (called "Centre of Coordination" – CC) were strictly related to movement coordination and organisation (L. Stecco, 2016). Luigi's children have been bringing forward Luigi's work, investigating the role and functions of connective tissue from a mechanical point of view, demonstrating how the fascia is not simply a passive tissue for filling and containment, but how it plays a role in the interaction between the CNS, the body, and the environment (Carla Stecco, Macchi, Porzionato, Duparc, & De Caro, 2011). We embraced Stecco's concept of CC but we insert it into a neuro-mechanical context. Whilst CC are seen as physical points where tensional forces converge changing fascia density, we envision these points (we call them SEP) to represent the dynamic equilibrium between connective tissue, nervous system, and muscular tissue (Garofolini & Svanera, 2019). Balance does not refer here to the simple mechanical tension between intrafusal and extrafusal fibers. But it is the result of (i) the mechanical tensions of the intrafusal fibers on the fascia; (ii) the tension of the extrafusal fibers on the fascia; (iii) the activity Ia-II which allows an increase in the tension of the extrafusal fibers (through alpha activation); and (iv) the activity Ib which allows a decrease in the tension of the extrafusal fibers (through alpha inhibition). Therefore, both mechanical and neurological systems collaborate to maintain the state of equilibrium. In this example – Figure 3, the epimysial fascia is the container, whilst the muscle is the content. The SEP represents the point of convergence of all forces acting on the container (fascia); that is, forces from the content (extrafusal fibers), forces from the external load (tendon), and forces from intrafusal fibers. The effect of all these forces depend physiologically on the fascia properties (viscosity). Muscles spindles play a vital role in reacting to changes in container-content relationship. The gamma motorneurons sets the sensitivity of spindles by changing the length at which intrafusal muscle fibers will be active (see below "Parametric control"). SEP tends to the minimum possible activity (below membrane threshold) of the afferents Ia-II and Ib (Figure 3A). The equilibrium is maintained by three compensatory (feedback) mechanisms:

- Ia-II activation due to central facilitation of alpha motorneuron (Figure 3B). Following a slow muscle contraction there is an increase in the tension of the muscle (content) which causes a direct increase in the tension of the fascia (container). This happens thanks to the muscular insertions on the fascia (Fan et al., 2018; A. Stecco, Gilliar, Hill, Brad, & Stecco, 2013; C. Stecco et al., 2013; C Stecco et al., 2007). As long as the ratio between content and container tension remains constant (determined by the sensitivity of the spindles - gamma activity - and viscosity of the fascia), this compensatory mechanism will be silent. On the other hand, when the tension of the container exceeds a certain threshold value, it causes the stretching of some muscle spindles and the subsequent activation of the afferents Ia-II, compensating for the tension discrepancy between container and content.

- Ia-II activation due to stretch of the muscle spindles (Figure 3C). When external perturbations increase the tension on the fascia, as occurs in the stretch reflex (Corden, Lippold, Buchanan, & Norrington, 2000). By stretching the fascia, (and therefore increasing the tension of the container-fascia on the content-muscle) the muscle spindles are activated and Ia-II afferents activate the alpha motorneuron. This increases the tension of the content to maintain tensional equilibrium.

- Ib activation due to alpha excessive motorneuron activity (Figure 3D). If the tension of the content increases excessively, as in continuous and massive muscle contractions, the Ib afferents are activated by stretching of the Golgi tendon organs (Houk & Simon, 1967; L. Stecco, Basmanjian, & Day, 2004). This mechanism inhibits the tension of the content on the container, through the inhibition of the alpha motorneuron, bringing the system back into equilibrium.

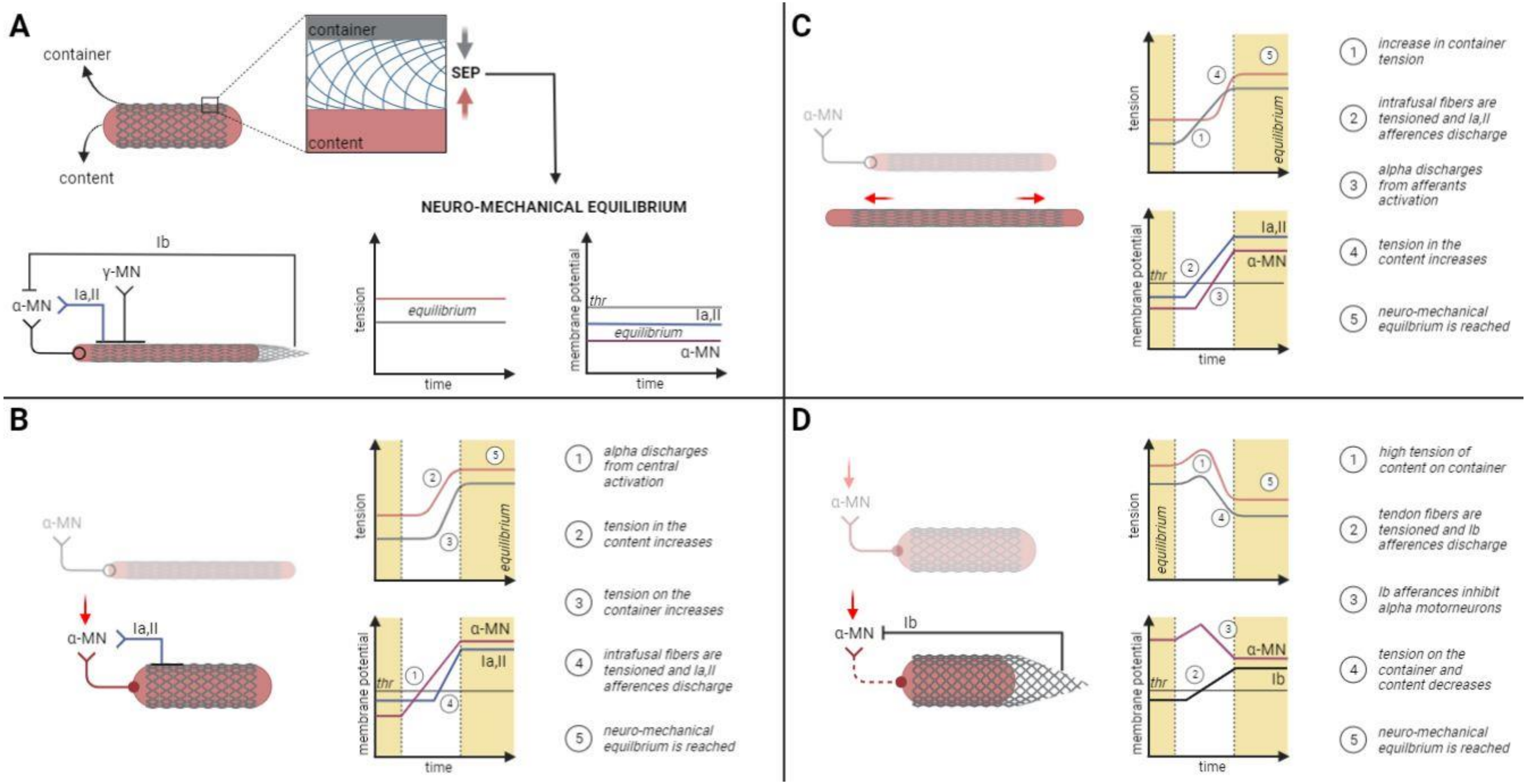

Figure 3. Container-content relationship. ***(A)*** *SEP represents the neuro-mechanical equilibrium between content (muscle) and container (fascia). This means tensional as well as neural equilibrium.* ***(B)*** *Ia-II activation due to central facilitation of alpha motorneuron.* ***(C)*** *Ia-II activation due to stretch of the muscle spindles.* ***(D)*** *Ib activation due to extrafusal fiber excessive tension*

Emergence of movement

To explain how we envision the central and the peripheral nervous systems work to generate and control movement, we present a neuroanatomical framework that integrates all elements (Figure 4).

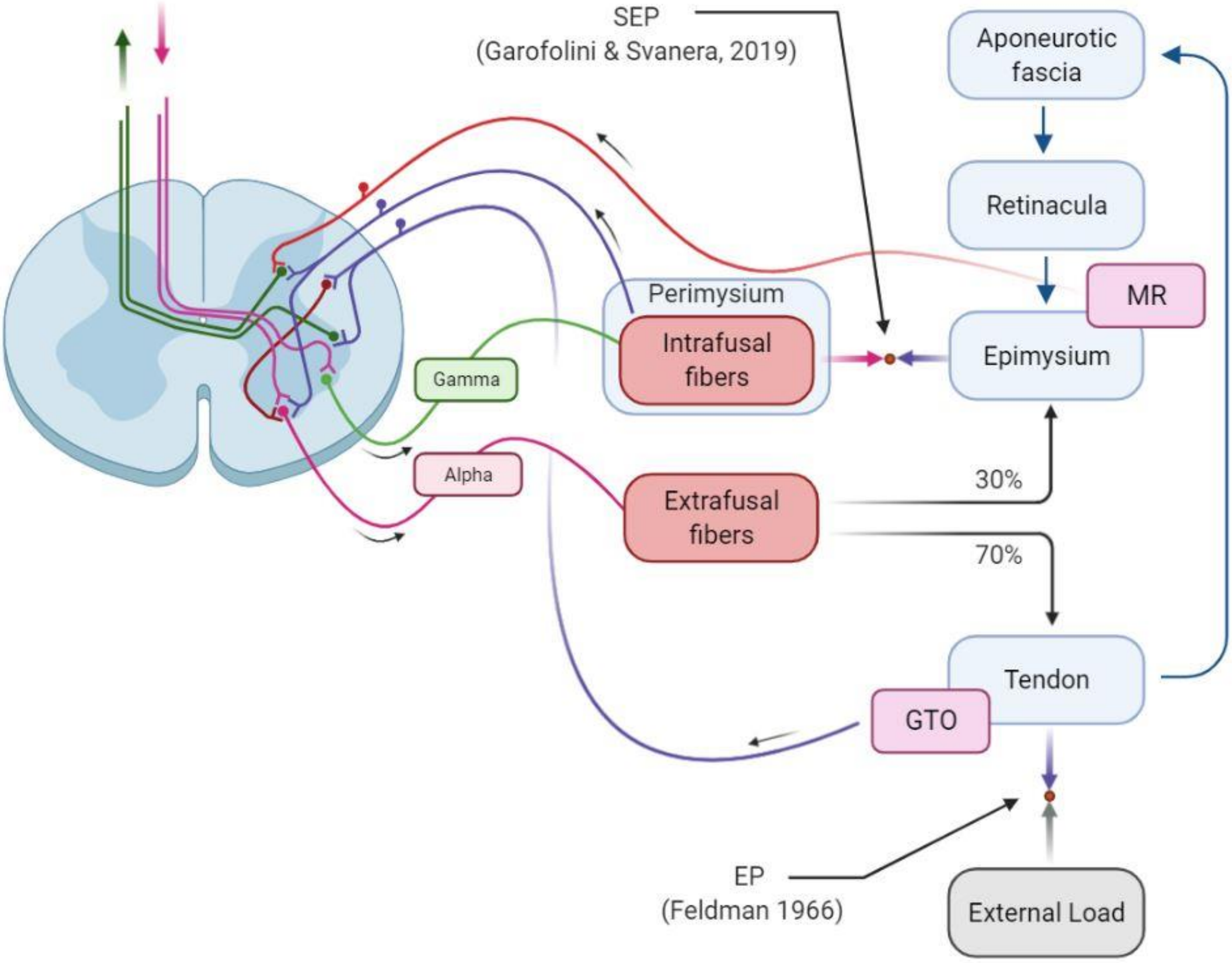

Figure 4. Theoretical framework. *Somatic equilibrium points (SEPs) represent the homeostatic internal state (internal equilibrium) given by the interaction between the intrafusal fibers and the epimysium (internal load represented by the partial tension of the extrafusal fibers on the fascia, tension of the tendon on the fascia, and by the fascial density). This dynamic equilibrium is sensed by mechanoreceptors (MR) that inform the higher hierarchical system about the position of the body segments in space and the state of the muscles associated with the body segment. Similar to the equilibrium point theory (EP; Feldman (1966, 1986)) that describes the equilibrium between the tension developed by the extrafusal muscle fibers and the external load, an internal equilibrium point between intrafusal fibres' tension and the internal load is assumed. Multiple sensors are present within the fascial system, such as mechanoreceptors and Golgi Tendon Organs (GTO), while the former are sensitive only to linear stretch (tension), the latter activate depending on joint angle as well, so that inhibition is regulated based on the intrinsic muscular lines of force.*

Voluntary movement is not only stimulus-induced, but autonomous generation of neural activity is also present. While this is represented in mathematical terms using recurrent neural networks (Sandamirskaya & Schöner, 2010), the anatomo-physiological components of such action are not explained by these computational models. Autonomous generation of neural activity is explained anatomically by the tendinous insertions on the aponeurotic fascia which connect the proximal and distal muscular forces (C Stecco et al., 2007). Partial forces generated in a segment passively stretch the muscle spindles (intrafusal fibers) in the other segments allowing for synchrony between myofascial units arranged along a sequence (Garofolini & Svanera, 2019). The primary endings of the spindles are very sensitive to muscular stretching and evoke excitatory post-synaptic action potentials in alpha motor neurons to discharge at a frequency that is proportional to the velocity.

Parametric control

Based on the equilibrium-point hypothesis, now advanced to the theory of indirect, referent control of action and perception (Feldman, 2015), the brain can control motor actions only indirectly, by changing neurophysiological parameters that may influence, but remain independent of, biomechanical variables (Feldman, 2019; Feldman, Levin, Garofolini, Piscitelli, & Zhang, 2021). Prof Feldman eloquently explains how sensory and central influences are integrated in neurons having a fundamental nonlinearity, electrical threshold, i.e., a specific membrane potential that is necessary to exceed to recruit neurons. In the presence of afferent feedback, central electrical changes in the membrane potential (ΔV) of alpha MNs are converted into changes in the spatial threshold ($\Delta\lambda$) at which the MN begins to be recruited. Tension on the SEP will influence the length at rest of extrafusal fibers. Thus, when the alpha MN is activated only the extrafusal fibers at a length equal or greater than a threshold length (lambda - λ) will contract (Feldman, 2015). Similarly, because muscle spindles are embedded into the perimysium, whenever a gamma impulse activates the intrafusal muscle fibers this stretches both the fascial framework (i.e. epimysium) and the equatorial plate of the spindle. Only the intrafusal fibers that are at a length equal or greater than a threshold length (phi - φ) will be activated and generate tension (Figure 5). The stretch of the fascial framework allows regulation of responses from the sensitive termination (i.e. mechanoreceptors). Therefore, voluntary movement is achieved by active (central) changes in myofascial units' parameters (λ and φ), which will allow emergence of neurophysiological responses aimed to regain equilibrium between content and container.

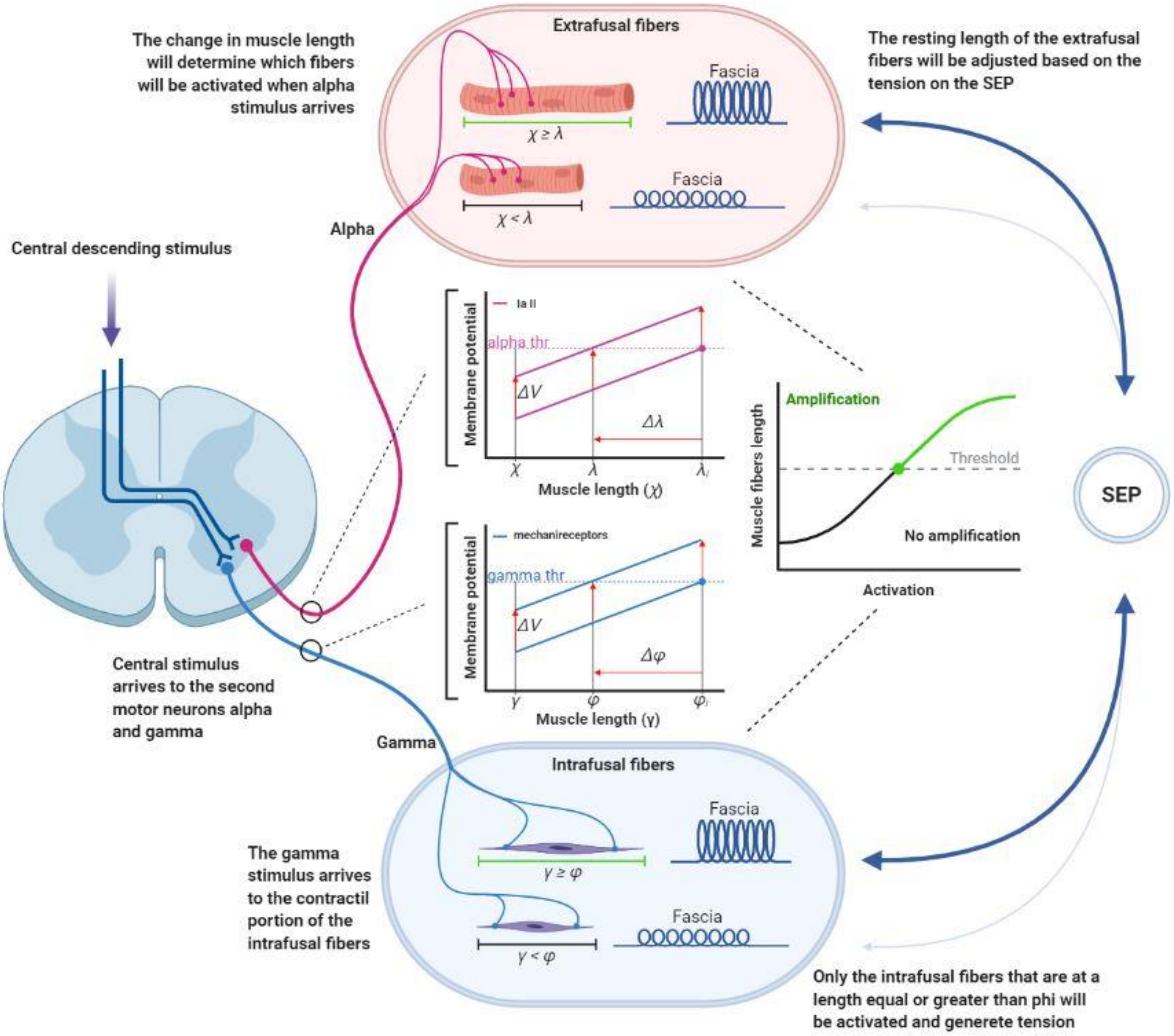

Figure 5. Parametric control of action. *Membrane potential for both alpha and gamma motor neurons is changed by central descending stimulus, this results in a shift in parameters (lambda and phi). Only the extrafusal and intrafusal fibers at a length greater than the correspondent parameter will be activated and their action amplified. SEP defines the length of intra and extrafusal fibers at rest, thus playing a crucial role in defying which fibers, and when they will be active.*

Thermodynamical equilibrium of the myofascial units

Biological systems follow biological laws (i.e. thermodynamics); the energetic level of each component in the system (i.e. muscle fibers, represented as dots in Figure 6) depends on intrinsic characteristics, such as growth state, fiber type and genetic heritage. The state of the system (and its components) is defined by an energetic landscape (tension on the fascial system; black line in Figure 6A) whose tension is defined by the activity of the muscle spindles; the somatic equilibrium points (SEPs) are points along the energetic landscape where tensions converge. A change in SEP's energetic level influences not only intra and extrafusal fibers length but also the tension on other SEPs that belong to the same functional direction. A condition of equilibrium will be reached when the system reaches a global minimum of the free energy; this condition does not assume that all muscle fibers are at rest (i.e. no muscle contraction) but rather that no external energy inputs are required to maintain the system (i.e. no neural inputs are required). This can be referred as the equilibrium point of the system, see Feldman (1986). Equilibrium is dynamic, meaning that the internal structures continuously exchange with the environment, and their reversibility is crucial for the system to find and remain in its most stable configuration**.**

For a given movement, the shape of the energy landscape depends on parameters, such as lambda and phi (cf. Figure 5). As a result, the position of the global minimum can change for different sets of these parameters. However, it is often the case that the system is not in thermodynamic equilibrium. This may be due to task (i.e. weight carried) and environmental constraints (i.e. gravitational field) or internal constraints, i.e. fascial densification (Pavan, Stecco, Stern, logna Prat, & Stecco, 2016). In a non-equilibrium state, extrafusal muscle fibers can lay in a local minimum of the energy landscape (green points in Figure 6). Its time evolution depends on the shape of the energy landscape around the minimum, and two situations can be envisaged. If the energy barrier for a pathway leading to the thermodynamic equilibrium is low enough, that is, the landscape can easily change its shape as a function of fascia elasticity (or its inverse, stiffness), the system will slowly adapt to a more stable structure. The system is in a metastable state. Note that multiple metastable configurations can exist. On the other hand, when the energy barrier is much higher, the system will remain captured in the local minimum for a period of time. This state is commonly referred in motor control theories as a strong attractor state (Ros, J Baars, Lanius, & Vuilleumier, 2014), or in chemistry as a kinetically trapped state (Yan, Huang, & Tang, 2016); physiologically this is explained by a restructuring of the fascial tissue (Pavan et al., 2016). By changing its density, the fascia changes the geometrical structure of its architecture. In pathological cases, rehabilitative intervention (i.e. fascial manipulation) have to be undertaken to ‘‘help’’ the system to escape its trap (Kalichman, Lachman, & Freilich, 2016; Pintucci et al., 2017; Rajasekar & Marchand, 2017).

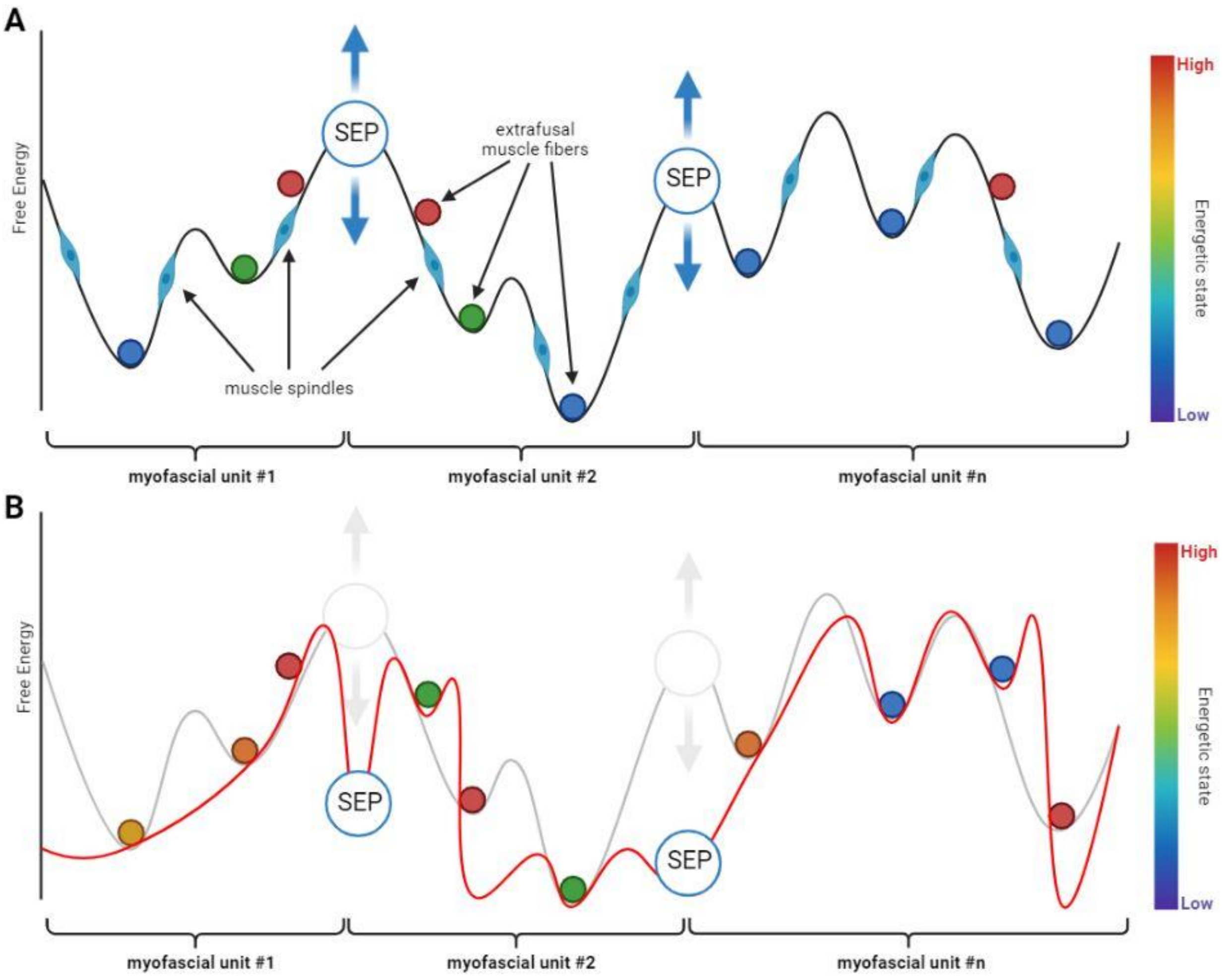

Figure 6 Example of energetic organisation of a functional direction. (A) *The energetic state of the extrafusal fibers of myofascial unit depends on the free energy landscape of the system and the tension at the SEP.* ***(B)*** *Muscle spindles function to modify the landscape to facilitate a change in energetic state of the extrafusal fibers. Mechanically, a change in SEP's energetic level will also influence the energetic state of the extrafusal fibers.*

Connecting the points: Referent configuration and SEPs

Finally, we try to combine the referent configuration theory (Feldman, 2015), with anato-physiological knowledge of the fascial system (L. Stecco, 2016) and with the SEP hypothesis (Garofolini & Svanera, 2019). The referent configuration is the idealistic configuration of the body (or segments, or muscle length) at which it will reach equilibrium. For instance, imagine to grasp an object, i.e. a cup, and lift it, the final referent configuration (spatial position) of the fingers will "penetrate" the cup; this allows the development of forces adequate to hold the cup and lift it. The forces generated will be proportional to the difference between the actual (real) position of the fingers and their referent position.

The referent body configuration can be related to the tensional force on the fascial system that maintains a certain degree of muscular tension and a silent state of the Ia, II and Ib afferences (or minimal activation). Anatomically it makes sense to talk about a referent configuration not only for each body segment but also for each spatial direction. We describe (and perceive) movement in reference to our body position; thus there are movement on the sagittal plane (ante and retro), frontal plane (medial and lateral), and on the horizontal plane (internal and external). There is evidence that muscle fibers are grouped following the same principle (English et al., 1993). The fascia connects together those muscle fibers, within different muscles and along different segments, which belong to the same functional direction (i.e. anterior movement - ante) so that they are coordinated in their action. For instance, a forward movement of the lower limb (ankle flexion, knee extension, and hip flexion) involves the myofascial units of ante-coxa, ante-genu, and ante-talus - Latin words for hip, knee, and ankle joints - (L. Stecco, 2016). The contraction of the ante-coxa myofascial unit determines a proximal traction of the iliopectineal ligament through the action of the psoas minor muscle, and a distal traction through the action of the vastus medialis muscle. During knee extension (ante-genu) the quadriceps expansion pulls the crural fascia proximally, while contraction of the dorsiflexion muscles of the foot stretch the fascia distally. The insertion of the foot muscles on the tendons of the leg muscles synchronize the action of ankle flexion with that of the foot. Each myofascial unit may act independently (segmental motion), however, when the effort in one myofascial unit increases the local muscular contraction will propagate both proximally and distally, involving the myofascial units of an entire sequence. If movements are along two ‘pure’ directions then a diagonal will be active; more complex movements compose spirals. At each level of the hierarchy, the number of directions, the complexity of the movement (i.e. number of segments), and movement flexibility (i.e. degrees of freedom) increase (Figure 7A).

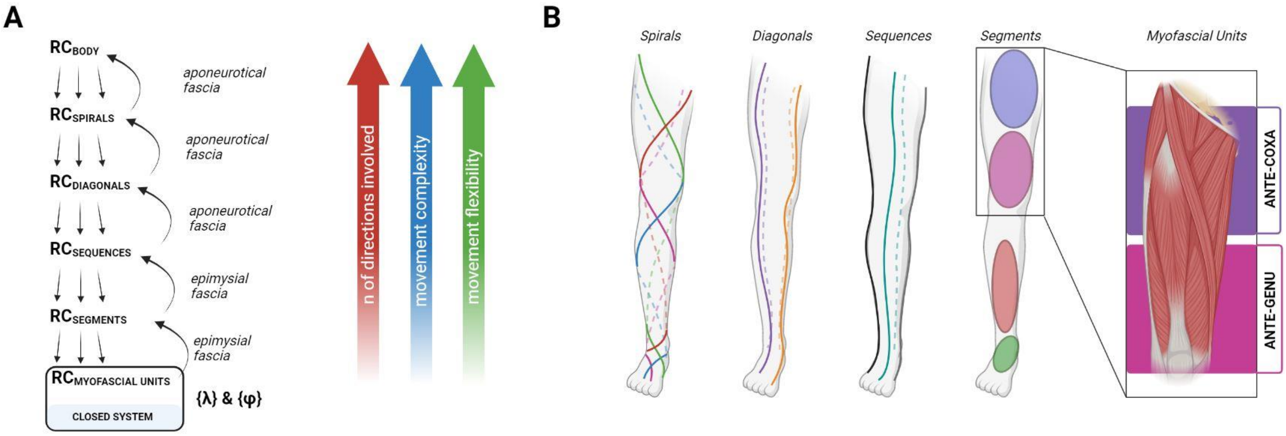

***Figure 7. Integration model*. *(A)* A reference configuration exists at each level of the hierarchy. Each lower level has more elements than the higher level. At the lowest functional level there are the myofascial units, which are closed systems whose function is dictated by parameters λ and φ. *(B)* Example of the spirals, diagonals, sequences, segments, and myofascial units of the lower limb.*

It is worth notice that each referent configuration has a real substrate of connective tissue along which mechanical forces are transmitted (Figure 7). Therefore, the referent configuration for action can be defined by the tension along the fascia and more specifically on the energy level of each SEP that belong to that level of the hierarchy.

Conclusion

Taking the recent studies on the anatomy of the fascia (Carla Stecco et al., 2011); the studies on the directional activity of neurons in the primary motor area (Georgopoulos & Carpenter, 2015); and the theory of motor control based on equilibrium points (Feldman, 2015), we have developed the hypothesis of a system based on somatic equilibrium points - SEPs. In summary, SEPs are:

- Physical equilibrium points of a complex system (body);
- The product of all the tensional forces on the fascia: convergence of forces from (i) the extrafusal fibers, (ii) the external load (tendon), and (iii) the intrafusal fibers.

- Points of neuro-mechanical equilibrium: minimal activity of the Ia,II and Ib fibers at the minimal mechanical tensions between content and container. Equilibrium is reached when the tension of the internal load is balanced with the tension of the intrafusal fibers, such that the muscle spindles are in a state of neurological silence (i.e. at the minimum possible neurological activity of Ia, II, and Ib).

We presented how changes in equilibrium within single myofascial units is attained by active changes in parameters, or through changes in environment (i.e. external forces). Using the analogy of content-container relationship, we explained how the close system maintains equilibrium and reacts to changes in state. We provided an explanation of how myofascial units are linked and coordinated at different levels, and how this organisation allows the emergence of movement with no need for central programs.

Competing interests statement

The authors declare that no competing interests exist.

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