

**Research Article***Copyright © All rights are reserved by Ray Marks*

Locomotor Oriented Muscle Stretch Receptors and Falls Risk in Later Life: Is There a Clinical Connection?

Ray Marks**Research, Osteoarthritis Research Center, Box 5B, Thornhill, ONT L3T 5H3, Canada*

***Corresponding author:** Ray Marks, OARC Clinical Research and Education Director, Ontario L3T 5H3, Canada

Received Date: December 11, 2025

Published Date: December 18, 2025

Abstract

Over many decades, evidence stretch sensitive muscle receptors termed muscle spindles might be involved in diverse aspects of locomotor control was provided by very intricate anatomical studies and the notable presence of muscle spindles in all muscles involved in locomotion. In unravelling the complexity of the muscle spindle sensory motor mechanisms and their role in human locomotor control and mechano-transduction processes it appears their dysfunction could offer one explanation for the high rates of falls in the older adult population that often leads to a high degree of disability, especially in those suffering from muscle atrophy, osteoarthritis, and overall declining neural data processing efficacy. Herein, after reviewing most of the available evidence linking muscle spindles to locomotion and its control, it appears increasing research evidence points to a possible key role for muscle spindles degeneration or dysfunction in acute as well as secondary falls related injuries and events. We conclude that periodic muscle reflex testing of vulnerable older adults may expose such a risk and if so, intervened upon accordingly to avert many undesirable mobility outcomes. In particular, further benefits may accrue if fallers in the emergency room are examined as soon as possible to establish any ongoing need for sensorimotor training and falls protection directives.

Key words: Aging; falls; gait; injury; locomotion; muscle spindles; prevention

Introduction

Older adults who experience a high rate of falling as well as possible immeasurable suffering and a loss of independence thereafter, continue to pose an ever increasing and major health care burden in all aging societies. Associated with high premature death or fatality rates, many previously unimpaired elders and the impaired who survive this particular injury may experience progressive associated mobility and independence losses that may require placements in assisted living centers [1,2]. Also associated with neuromusculoskeletal system declines and related gait

abnormalities, falls may lead to the presence of pain and possible muscle mass losses, ligament instability, muscle fat mass increases, and the risk of recurrent falls, and one or more bone fractures.

Hence predicting who is at risk for falls, and future falls as well as efforts to avert falls is a highly important health topic in this respect and among the risk factors for falls, we believe various forms of sensorimotor deficits that often accompany aging and resultant gait disturbances can precede falling incidents and are likely to be significant falls determinants in this respect. In particular, small

encapsulated muscle stretch sensors known as muscle spindles located in all muscles of locomotion and others appear designed to inform the central nervous system about the contractile status of each muscle as well as having a strong motoneuron and muscle responsiveness influence [3]. In particular, these muscle spindles that are activated when the muscle housing them is stretched and ordinarily and accurately convey information on muscle length, speed of stretch, and limb position to the central neural networks then generate the most optimal locomotor movement and postural responses by assessing the amplitude, velocity, and frequency of the overall sensory discharge. However, this functional network may yet fail to do this optimally if the spindle receptors are rendered dysfunctional or undergo age related attrition and if so, can potentially be expected to induce and yield abnormal static and dynamic locomotor motor responses in the stretched muscle, as well as possible postural instability, and an undesirable falls risk or actual injurious falls event.

Borne out by many preclinical studies that have examined the role of muscle spindle inputs in modulating spinal cord central pattern generator outputs to primary muscles, as well as their synergists [3,4] or examined mechanisms of adaptive walking in the face of varying external perturbations [5], many concur that the large array of muscle spindle receptors that provide inputs into the sensorimotor system and also supply the cerebellum are involved in balance and locomotor control [6,7]. They also have the ability to mediate movement and position sense and coordinated movements that may all fail to protect against falls if degraded.

It is of interest in our view however to examine falls in the elderly as an occurrence that is explainable and may be widely linked to a complex set of afferent and efferent interconnected pathways that originate in the muscle spindle and appear to influence muscle tone and contractile behavior and functional output sequences. Moreover, if this idea is valid, it offers a path towards advancing any required muscle adjustments or adaptations needed for locomotor movements to be carried out in a timely, low energy cost, stable, and safe way to be primed accordingly before any event [8-10]. Conversely, if ignored, deafferentation or declines in intrafusal fibre structure and function that can occur in degenerative joint conditions such as osteoarthritis may greatly impair timely spindle activity that potentially engenders non harmonious locomotor movement patterns and responses that could predispose to serious falls [4, 8-12].

Indeed, as one key sensory modality, the muscle spindle appears essential for ensuring gait will be self-organizing and optimally emergent without any risk of falling. Yet, in the population most affected by falls incidents and risk, older adults who may well undergo declines in their dynamic sensitivity to muscle stretch may lose their ability to generate well-coordinated locomotor movements, and allied or supportive functions [13]. This latter group concluded in particular that the deterioration of proprioceptive sensory neurons that innervate the muscle spindle nuclear bag fibers responsible for dynamic sensitivity may prevent the generation of optimally efficient coordinated movements and

movement sequences in the aged, together with a predictable functional decline of the extrafusal muscle. That is, while their intricate connections appear to provide the spinal cord central pattern generator responsible in part for locomotion with timely information about unexpected external conditions, thus enabling an organism to produce accurate, stable, and timely outputs for the limbs in the face of ever changing environments, and terrains, the failure of this mechanism may prove devastating not only in the face of unanticipated perturbations but on the neuromotor system in general [8, 14-16].

Nevertheless, these associations may be overlooked more often than not [16] and especially where the foot does not clear the ground during the swing phase of walking as a result [17,18]. It is also shown that the complete loss of muscle spindles appears to seriously compromise the regularity of locomotion and the associated step cycle, as well as balance if its cerebella inputs are impaired [19-21]. That is, although the presence of any dysfunction in the muscle spindle and/or its neural pathways could consequently be expected to produce gait disturbances or suboptimal placements of the foot that could lead to a loss of adaptive walking that leads to falls, few attempts have been made in general to elucidate and report on a distinct role for muscle sensory receptors in the context of falls injuries among older adults that mostly occur due to slipping or tripping. As a result, although independent studies on muscle spindles and their varied functions are quite numerous, the clinical implications derived from these studies for advancing falls injury prevention and identifying subject risk is highly limited.

Methods

To provide some insight into whether falls injuries incurred during walking may be ascribed in selected cases to deficiencies in the muscle spindle structures and/or their diverse neural connections, data housed in key repositories were searched and examined. The key topics sought were related to the role of muscle spindles in the control of intralimb and interlimb movement patterns during gait, and whether muscle spindles are further implicated in stability during the stance phase of the gait cycle and may result in a fall if they fail to function.

The Specific Themes Examined were:

- a) Whether muscle spindles have an impact on the quality and safety of regular walking activities.
- b) Whether older adults with muscle receptor deficits will be at high risk for falls, but that can be targeted successfully.

The Specific Theme Examined was

Whether muscle spindles have an impact on locomotion in the elderly and by analogy on falls risk in this group.

Excluded from the detailed descriptive analysis were studies conducted in a language other than English or were proposals or incomplete articles. The studies presently reviewed included observational, as well as prospective or case-controlled studies where muscle spindles were examined in any substrate. The review

is largely limited to brief summaries of key points, as the research extends over many decades. The goal was to derive implications for community dwelling older adults who wish to remain independent in their own homes, but may fall and be sent to emergency rooms.

Results

Key Findings

The literature search revealed increasing numbers of works dealing with muscle spindles and aspects of locomotion and more recently with falls and fall injuries specifically. Regarding muscle spindles and their effects, several studies supported the view that muscle spindle inputs are helpful in resetting the normal locomotor pattern in times of perturbation because they are able to convey ongoing information about the magnitude and rate of muscle stretch to interneurons and motoneurons, but their failure may lead to increasing challenges in the day to day ability of the organism to walk safely and without effort [22,23].

Among the numerous citations detailing some causative aspect of falls injuries and/or falls injury determinants in the older adult population are:

- a) Dizziness, pain, selected pain/psychoactive medications, and visual impairments.
- b) Vestibular and various co-morbid disorders such as diabetes.
- c) Reduced muscular strength and endurance.
- d) Impaired gait, and poor balance.
- e) Impairments in cognitive function and postural reflexes.

Knellwolf et al. [18] who studied the responsiveness of muscle spindles in the short muscles of the foot to stretch and related joint movements while standing found that while only 27% were spontaneously active in the unloaded condition, and 50% during unsupported free standing, they fired up to rates of 67% during transient foot contact. As a result, the researchers concluded that group 1a as well as group II muscle afferents can faithfully encode changes in the body's center of pressure during spontaneous or evoked postural sway, and this is indicative of its vital functional contribution in maintaining and responding in a robust manner to perturbations at the foot in the context of varying upright positions.

Loeb and Hoffer [22] consequently suggested that it is indeed muscle spindle afferent inputs that are of high import to recognize as falls determinants or mediators as they have a major role to play in the control of locomotion and the generation of smooth energy efficient automatic movements as well as in response to perturbations. More specifically, this group found the extensor or anti-gravity muscles, which are mostly active while lengthening or when the muscle is contracting nearly isometrically are able to produce muscle spindle afferent inputs that result in an energy-efficient mechanism for the generation of large forces with a low work output. Loeb and Hoffer deemed this mechanism to be consistent with the need of the organism to maintain a non-accelerating forward motion, in

which the body weight must be transferred from side to side, but is able to be modulated to accommodate applied loads and their rates of change with changes in gait speed. In contrast, muscle spindles in the flexors which were usually deemed to shorten actively and rapidly against minimum loads such the inertial mass of the limbs were said to foster a relatively constant motor pattern, rather than a changeable one, because they were found much less dependent on gait speed than the extensors.

Deng et al. [23] propose muscle afferents when stretched or experiencing tension changes can activate antagonistic muscle pairs about each joint in the sagittal plane when intact. This system works effectively to influence the setting and spinal circuits involved in regular or perturbed walking control motions, but may be altered in the face of any prevailing deafferentation associated situation and the impact of age on muscle afferent structures and function. However, where present the powerful role of muscle spindles in locomotor control is consistently evidenced in fictive preparation studies, where sustained stimulation is applied to brainstem mesencephalic locomotor region in decerebrate animals. These tend to suggest that during the extension phase of locomotion, disynaptic reflexes evoked from group I ankle extensor muscle afferents simultaneously activated hip, knee and ankle extensor motoneurons, thus increasing force production necessary to support the body during stance [24]. Moreover, consistent with the idea that muscle spindles are highly implicated in locomotor control efforts, data reveal they can enhance and reset locomotor activity patterns, stimulate or impact the relationship between spinal proprioceptive input patterns and neuromuscular control strategies of leg muscle spindles and hence serve to modulate locomotor phase duration, as well as speed, and gait stability [25-27].

Research also shows that muscle spindles enable the organism to carry out reciprocal movements in a timely way [28], while providing the central nervous system with an up dated set of inputs during on-going activities [29] that may not only be crucial for producing optimal stability, but also for exhibiting resistance to obstacles placed in the walker's path [27]. In this regard, muscle spindles must however be able to sense limb position accurately, the nature of any prevailing muscle movement or non-movement, and desired movement speed factors that underpin the desired movement or non-movement of a limb during reciprocal walking to avert any falls risk [28]. That is, muscle spindles must be able to sense as well as provide well-modulated timely neural inputs and linkages that must be recalibrated as indicated, for example if a slippery surface is encountered to avert harm and destabilization [30-35] and provide the optimal degree of kinaesthesia and control of bodily movements and spinal motoneuron pathways that determine contraction responses. The sensory information that can thus activate muscle synergies in a coordinated way or may fail to do this or produce stable walking in the older adult if muscle spindles are degraded by age [13]. If so, the locomotor muscles usually activated to prevent falling may fail to do so in a timely protective manner [8,10].

Alternately, to avert walking challenges, muscle spindle inputs and outputs must be physiologically intact and primed in a timely modulated manner to avert both fatal and nonfatal injuries [36], including those of the musculoskeletal system, the central nervous and sensory systems. Fallers who experience a fall induced loss of independence may well be forced into nursing home admittance and a low life quality. As well, fearfulness of falling in the future might cause social withdrawal and disengagement, in addition to imposing a heavy social and financial strain on the fallers' family, community health services, and economy [36]. Reducing the magnitude of falls injuries and their consequences is indeed a key geriatric health issue and one where several convergent influences might impact the timely function of reactive muscle responses during gait that lead to falls. These factors include, but are not limited to deficient muscle strength, confusion, sensory losses, poor postural control or balance impairments, especially in those of higher ages [1-3,6,35,36].

However, despite efforts to offset falls risk among the elderly [6], the specific mediating influence of the motor system efferent and afferent pathways embedded in extensive numbers of muscles subject to aging and muscle mass losses remains understudied and relatively unacknowledged. That is, a converging research base implies optimal muscle spindle function potentially impacts locomotor control profoundly and may be helpful or even crucial in offsetting falls risk among the elderly in the face of locomotor challenges [8]. This idea remains a topic that is rarely studied with regard to the influence of proprioceptive factors on balance capacity in general in the older adult population, and rarely in the contact of falls.

Before continuing to base public health as well as private practitioner falls prevention recommendations on inconsistent or incomplete consideration of research findings, it is our view that many problems associated with falls, and their meager intervention outcomes can benefit from a current review of muscle spindle related literature and insights. In particular, they can be applied to potentially understand and thereby offset falls risk in the aging adult, thus helping to avoid management errors and omissions that could be highly costly to the individual as well as society [37-40,50]. In sum, a large number of muscle spindles may decline with age, as may their primary and secondary endings, both sensitive to changes in muscle length and velocity, [4,14].

Discussion

Many decades of study have shown falls injuries are highly disabling in the older population. In other studies muscle spindles, the most commonly observed sensory structure located in mammalian muscles [3,10] constituting a key group of proprioceptors underpinning somatosensory signalling and transduction and its impact on movement synergies has an enormous impact on the emergent responses generated within the locomotor system [14]. However, even though this latter body of data show a possible linkage inherent to protective and functional motor outputs during gait, their degrading influences as far as falls

mediators are concerned is very poorly conceptualized or studied [2,40]. Indeed, even though adverse kinematic and kinetic profiles have been demonstrated in multiple locomotor simulation models if muscle spindle networks are rendered dysfunctional, disrupted or destroyed artificially or by injury, or disease [3] this situation would seem to have immense implications for the prevention and rehabilitation of many locomotor disorders this idea is not well articulated or integrated into practice. This is unfortunate because spindle afferent inputs in the osteoarthritic model alone could explain a fair number of falls experienced by those with knee joint disease even when they have replacement surgery and could be helpful for understanding those falls processes amenable to intervention, such as muscle weakness and atrophy. In addition, especially in the face of competing stimuli, muscle fatigue may decrease spindle stretch sensitivity and optimal response timing and muscle stabilizing synergies and thus certain groups may be at higher risk than others, for example those on chemotherapy or suffering from sleep disorders.

Age related pathological muscle and nerve structural changes are however likely to alter normal reciprocal patterning of the leg muscles during locomotor behaviour as well as the ability to detect departures from the trajectory of the anticipated movement in sizeable numbers of adults, especially in sedentary aging persons. Moreover, the individual may be less able to produce the degree of coordination required during locomotion to successfully prevent a subsequent slip or trip if they suffer from muscle fat encroachment and declines in muscle mass that affect spindle elasticity properties.

They may hence be quite prone to multiple injurious fall incidents when walking, especially out of doors, or if the interior is unfamiliar or an external barrier to safe locomotion. When faced with unexpected obstacles, or unanticipated changes in the ground surface of stairs they are even more likely to encounter falls that are injurious if they cannot activate the required compensatory strategies in a timely and force-efficient manner. In particular, any subnormal or delayed interaction between muscle afferent inputs, their links to the brain, cerebellum, or spinal cord and subsequent subnormal outputs during gait coupled with muscle weakness may have multiple cascading adverse effects on locomotion, in general, and on preserving muscle synergies that are designed for stabilizing purposes in the face of perturbations. For example, the individual may adopt a slower than desirable gait speed, which increases the chances of slipping, tripping and falling, among other gait disturbances, especially if vision or cognition or both are impaired [41-49].

Indeed, recent experimental manipulations have shown that information from the foot sole alone can have a widespread influence on balance, proprioceptive information, and gait. However, these interactions are not linear or easy to reverse because any generated reflex response to a balance perturbation implicates both the spinal and supra-spinal neural sites where sensory feedback is modulated. Additionally, other muscles, notably those of the neck and trunk that contribute to kinaesthesia and the sense of orientation in space can be diminished in the face of age-related

afferent input declines and density plus muscle strength losses, as can disruptions at the neuromuscular junction, and sarcopenia, muscle feedback and innervation mechanisms and compensation strategies critical for the control of upright posture, and safe walking ability. Declines in balance during standing and walking as well as defects in proprioception may thus be anticipated and need to be identified and treated proactively, rather than reactively to avoid altered muscle spindle derived proprioceptive signalling emergent motor programming deficits due to erroneous stimuli interpretations and impairing transmission capacity. Additionally, a role for age altered spindle anatomy as well as function, and poor position sense, direction plus speed attributes and reflexive sensitivity cannot be ignored [50-59].

According to Ito et al. [60] reduced proprioception including that due to muscle spindle deficits do tend to affect fall risk in the elderly, for example those who present with lumbar spondylosis and a decrease in trunk proprioception or lower leg impairments or both that may foster a decline in desirable sensory motor processes that can ensure postural stability. In comparing a group of no-falls-risk adults, their results showed the fall-risk group displayed a high relative lumbar spine proprioceptive weighting ratios that was possibly due to the over-dependence on inputs from muscle spindles in the calf muscles. Indeed, findings over time do tend to affirm a key role for muscle spindles in maintaining locomotor functions, and to assert neural control adaptations despite perturbations or obstacles. Data specifically show that sensory feedback from group Ia/II muscle spindle afferents regulate motor function and control in normal and perturbed walking. These sensory units that are speed and length sensitive can be readily impaired in later life [4, 61-66].

Applying this knowledge about the highly vital role of the muscle sensory system in gait control can potentially help us understand a generally unrecognized falls determinant that may prevail in vulnerable older adults. To this end, more careful neural based analyses and the use of AI and other diagnostics in this regard applied for purposes of dynamic postural control screening and possible falls risk reduction interventions appear indicated [67-73,77-84]. More knowledge regarding the molecular basis of muscle spindle function is still desirable however, as are efforts directed towards increasing our understanding of mechano transduction processes by muscle spindles and their link to associated injuries due to aging and disease. Exploring the nature of the mechanosensitive ion channel ASIC2 as a key component in proprioceptive sensing and regulation of spine alignment and the impact of muscle morphology on muscle afferent sensibility is also indicated [74-75].

This is because it seems likely that efforts designed to normalize and maximize deficient or suboptimal muscle spindle inputs in both lower limb extensor and flexor muscle groups where these are dysfunctional or weakened will prove helpful in the overall approach to falls prevention among the elderly than the presence of incomplete neural network input information and possible emergent erroneous movement impacts. On the other hand, locomotor

training or efforts to maximize sensorimotor integration and balance during gait may facilitate the transmission of appropriate muscle activation patterns, and thereby retard falling occurrences during walking, even under differing environmental constraints, [71]. As stated, many years ago by Pearson [12], inherent muscle afferent feedback mechanisms not only contribute to the ability to walk normally, but more particularly help to foster appropriate adaptations during different walking conditions or precision tasks. Their inputs are necessary for stable walking, and because accurate movements require a precise match between mechanical muscle properties and properties of the muscle's physical environment they should be primed accordingly if the older adult is weak or has possible neuromotor challenges [6]. Since these properties can change, adaptive mechanisms that can optimize muscle activation patterns may be efficacious and hence essential to contemplate and enact are indicated [12,76,85].

Since falls associated with osteoarthritis alone can magnify or induce a life time of suffering, it appears salient to encourage more emphasis on research in this regard in the human so that preventive strategies can be grounded in a strong cumulative solid evidence base, rather than in the realm of preclinical studies such as those presented here and depicted in references [26,39,41,46,61,65,81-85].

Conclusion

Despite a lack of definitive data linking some falls injuries in the older adult to muscle related sensibility attributes and their modulation during gait, and many design issues, until more research data emerges, our decade's long extensive and intensive evaluation and analysis lead us to conclude:

- a) Muscle spindle units and their associated input and output pathways, regulate an intricate integrated network of sensorimotor functions and responses, including locomotor responses.
- b) They determine in part, the efficacy of central nervous system, spinal, balance, and motor control feedback mechanisms, as well as the quality and efficiency of essential feed forward networks and locomotor stability attributes.
- c) Effective locomotor adaptations clearly depend on the integrity of the reactivity and sensitivity of the muscle afferents embedded in the primary locomotor implicated muscles.
- d) All phases of the gait cycle, including stance and swing, plus inter limb coordination appear to be influenced by the length, velocity and stretch sensitivity of muscle spindle afferents, their response efficacy, as well as the state of the final gamma motoneuron pathway and muscle status that controls the emergent muscle responses.
- e) Deafferentation, perturbations, or defects in any realm of these neural processes may explain an inability to respond protectively when walking, as well as the presence of a heightened fall risk in an individual of high age as well as those with neuromuscular deficiencies and others.

f) To enhance our understanding of the nature of human locomotion and its association with falls injuries among older adults and others, more evidence that links muscle spindle activity to locomotion in the human aging population in ecological settings as opposed to the laboratory setting and the study of subhuman non bipedal gait is needed.

g) Timely targeted falls prevention efforts that acknowledge the key role of the neurosensory system and its adaptive potential may help avert immense suffering, hospital and societal costs, and premature death rates, while fostering injury recovery, where and when necessary.

Practice Implications

Falls and their immense adverse impacts continue to increase unabated among older adults, and as such, remain a widespread costly health concern and one markedly impairing life quality, despite years of research and programs to avert falls risk in older adult communities. This is a highly underrepresented health issue in light of falls being commonly associated with the onset or perpetuation of longstanding pain, disability, independence losses, and premature deaths for many. Moreover, the outlook for older adults in this regard, remains bleak, and will likely worsen in our view unless due action is taken to avert this enormous public health challenge.

This however, demands more immediate attention to falls causative factors such as muscle spindle functional deficits and their implications for more timely, targeted preventive or mitigation strategies that can offset the risk for falling among the elderly. Based on our analysis and many years of related study we believe programs currently advocated to help the aging individual to avoid the partial or complete loss of personal freedom associated with falls, as well as excess rates of premature mortality, and morbidity, must in our view account for the role of muscle spindle networks and their integrity or face failure in finding appropriate strategies to prevent falls injuries or unanticipated environmental encounters.

Indeed, even though solid evidence awaits further study, we hypothesize clinicians can possibly help to mitigate some age related injurious falls by: a) conducting brief sensory motor tests and a concise falls history at the bedside and in the community at large, b) recommending further steps without delay, c) using artificial intelligence [AI] diagnostics to elucidate on any possible muscle structural anomalies, d) reviewing the faller's medical record for any risky medication intakes and disease status, e) recommending follow up home visits, possible home and footwear modifications, help to minimize fears and anxieties, assistance for elders who move to a new unfamiliar environment to become oriented, and educational and rehabilitation opportunities, as indicated. Active older persons with marked lumbar spine degeneration as well as knee instability who are obese or sarcopenic, those who suffer from neuropathy, and possible threat-induced emotions, and depend on opioids should be preferentially targeted.

Final Comments

a) Taken as a whole, and in light of what currently prevails, it appears that more insightful falls mitigation actions and practices that account for muscle sensory receptor status and their locomotor impacts and high costs are indicated.

b) What is needed and why, as outlined above, is a topic warranting considerable researcher and clinician attention and efforts to render falls prevention among the older population more efficacious, cost effective, and life affirming than not.

c) The importance of falls awareness and crucial role of their prevention to avert their diverse and possible noxious irreversible health consequences should be stressed and widely disseminated.

Funding

None.

Acknowledgement

None.

Conflicts of interest

No conflict of interest.

References

- Garnett MF, Weeks JD, Zehner AM (2025) Unintentional fall deaths in adults age 65 and older: United States, 2023. NCHS Data Brief (532): 1.
- Sharif SI, Al-Harbi AB, Al-Shihabi AM, Dana S Al-Daour, Rubian S Sharif (2018) Falls in the elderly: assessment of prevalence and risk factors. Pharmacy Practice 16(3): 1206.
- Kröger S (2018) Proprioception 2.0: novel functions for muscle spindles. Curr Opin Neurol 31(5): 592-598.
- Santuz A, Akay T (2023) Muscle spindles and their role in maintaining robust locomotion. J Physiol 601(2): 275-285.
- Severini G, Koenig A, Cajigas I, Nicholas Lesniewski-Laas, James Niemi, et al. (2023) Subsensory stochastic electrical stimulation targeting muscle afferents alters gait control during locomotor adaptations to haptic perturbations. iSciences 26(7): 107038.
- Schoene D, Gross M, Finger B, Nils Axel Lahmann, Kathrin Raeder, et al. (2025) Conventional and tablet-supported physical training to reduce falls and fall-related injuries in community-dwelling older adults: protocol of the randomised SURE-footed into the future Fall Intervention Trial (SURE-FIT). BMJ Open 15(11): e105969.
- Frigon A, Akay T, Prilutsky BI (2021) Control of mammalian locomotion by somatosensory feedback. Compr Physiol 12(1): 2877-2947.
- Dimitriou M (2014) Human muscle spindle sensitivity reflects the balance of activity between antagonistic muscles. J Neurosci 34(41): 13644-13655.
- Tamura D, Aoi S, Funato T, Soichiro Fujik, Kei Senda, et al. (2020) Contribution of phase resetting to adaptive rhythm control in human walking based on the phase response curves of a neuromusculoskeletal model. Front Neurosci 14s: 17.
- Banks RW, Ellaway PH, Prochazka A, Uwe Proske (2021) Secondary endings of muscle spindles: Structure, reflex action, role in motor control and proprioception. Experimental Physiol 106(12): 2339-2366.

11. Loram ID, Lakie M, Di Giulio I, Constantinos N Maganaris (2009) The consequences of short-range stiffness and fluctuating muscle activity for proprioception of postural joint rotations: the relevance to human standing. *J Neurophysiol* 102(1): 460-474.
12. Pearson KG (2004) Generating the walking gait: role of sensory feedback. *Prog Brain Res* 143: 123-129.
13. Kawai-Takaishi M, Hosoyama T (2025) Muscle spindle afferent neurons preferentially degenerate with aging. *Sci Rep* 15(1): 23946.
14. Macefield VG, Knellwolf TP (2018) Functional properties of human muscle spindles. *Journal of neurophysiology* 120(2): 452-467.
15. Niyo G, Almofeez LI, Erwin A, Francisco J Valero-Cuevas (2024) A computational study of how an α - to γ -motoneurone collateral can mitigate velocity-dependent stretch reflexes during voluntary movement. *Proc Natl Acad Sci U S A* 121(34): e2321659121.
16. Kröger S, Watkins B (2021) Muscle spindle function in healthy and diseased muscle. *Skelet Muscle* 11(1): 3.
17. Lavender AP, Balkozak S, Özyurt MG, Betilay Topkara, İlhan Karacan, et al. (2020) Effect of aging on H-reflex response to fatigue. *Exp Brain Res* 238(2): 273-282.
18. Knellwolf TP, Burton A, Hamman E, Vaughan G Macefield (2025) Firing properties of muscle spindle afferents in the intrinsic foot muscles and tactile afferents from the sole of the foot during upright stance. *Exp Physiol* 110(10): 1492-1510.
19. Nardone A, Corna S, Turcato AM, Marco Schieppati (2014) Afferent control of walking: are there distinct deficits associated to loss of fibres of different diameter? *Clin Neurophysiol* 125(2): 327-335.
20. Sato F, Tsutsumi Y, Oka A, Takahiro Furuta, Jaerin Sohn, et al. (2025) Projections from regions of the cerebellar nuclei receiving jaw muscle proprioceptive signals to trigeminal motoneurons and their premotoneurons in the rat pons and medulla. *Cerebellum* 24(4): 113.
21. Maris E (2025) Internal sensory models allow for balance control using muscle spindle acceleration feedback. *Neural Netw* 189: 107571.
22. Loeb GE, Hoffer JA (1981) Muscle spindle function during normal and perturbed locomotion in cats. In A. Taylor and A. Prochazka. (Eds.). *Muscle receptors and movement*. New York: Oxford University Press pp: 219-228.
23. Deng K, Szczecinski NS, Arnold D, Andrada E, Martin S Fischer, et al. (2019) Neuromechanical model of rat hindlimb walking with two-layer CPGs. *Biomimetics* 4(1): 21.
24. Simha SN, Ting LH (2024) Intrafusal cross-bridge dynamics shape history-dependent muscle spindle responses to stretch. *Exp Physiol* 109(1): 112-124.
25. Pearson KG, Misiaszek JE, Fouad K (1998) Enhancement and resetting of locomotor activity by muscle afferents. *Ann N Y Acad Sci* 860: 203-215.
26. Markin SN, Klishko AN, Shevtsova NA, Michel A Lemay, Boris I Prilutsky, et al. (2010) Afferent control of locomotor CPG: insights from a simple neuromechanical model. *Ann N Y AcadSci* 1198: 21-34.
27. Olson WP, Chokshi VB, Kim JJ, Noah J Cowan, Daniel H O'Connor (2025) Muscle spindles provide flexible sensory feedback for movement sequences. *Cell Rep* 44(11): 116452.
28. Abbott EM, Stephens JD, Simha SN, Leo Wood, Paul Nardelli, et al. (2023) Attenuation of muscle spindle firing with artificially increased series compliance during stretch of relaxed muscle. *BioRxiv*: 539853.
29. Bisio A, Biggio M, Avanzino L, Piero Ruggeri, Marco Bove (2019) Kinaesthetic illusion shapes the cortical plasticity evoked by action observation. *J Physiol* 597(12): 3233-3245.
30. Nichols TR (2024) Neuromechanical circuits of the spinal motor apparatus. *Compr Physiol* 14(5): 5789-5838.
31. Chacon PFS, Hammer M, Wochner I, Johannes R Walter, Syn Schmitt (2025) A physiologically enhanced muscle spindle model: using a Hill-type model for extrafusal fibers as template for intrafusal fibers. *Comput Methods Biomech Biomed Engin* 28(4): 430-449.
32. Dimitriou M (2022) Human muscle spindles are wired to function as controllable signal-processing devices. *Elife* 11: e78091.
33. Duman A, Azizi E (2023) Hindlimb muscle spindles inform preparatory forelimb coordination prior to landing in toads. *J Exp Biol* 226(2): jeb244629.
34. Kamibayashi K, Nakajima T, Fujita M, Makoto Takahashi, Tetsuya Ogawa (2010) Effect of sensory inputs on the soleus H-reflex amplitude during robotic passive stepping in humans. *Exp Brain Res* 202(2): 385-395.
35. Henry M, Baudry S (2019) Age-related changes in leg proprioception: implications for postural control. *J Neurophysiol*. 122(2): 525-538.
36. Xing L, Bao Y, Wang B, Mingqin Shi, Yuanyuan Wei (2023) Falls caused by balance disorders in the elderly with multiple systems involved: pathogenic mechanisms and treatment strategies. *Frontiers Neurol* 14: 1128092.
37. Spardy LE, Markin SN, Shevtsova NA, Boris I Prilutsky, Ilya A Rybak, et al. (2011) Adynamical systems analysis of afferent control in a neuromechanical model of locomotion: I. Rhythm generation. *J Neural Eng* 8(6): 065003.
38. Zhang Q, Liu T, Xie H, Haohua Zhang, Kuan Zhang, et al. (2025) Refined proprioceptive feedback framework for spatiotemporal mapping of spinal afferent input during gait in female knee osteoarthritis patients. *IEEE Trans Neural Syst Rehabil Eng* 33: 4614-4623.
39. Emonet-Dénand F, Laporte Y, Petit J (2001) Comparison of the effects of stimulating groups of static gamma axons with different conduction velocity ranges on cat spindles. *J Neurophysiol* 86(1): 533-535.
40. Proske U, Gandevia SC (2012) The proprioceptive senses: their roles in signaling body shape, body position and movement, and muscle force. *Physiol Rev* 92: 1651-1697.
41. Akay T, Tourtellotte WG, Arber S, Thomas M Jessell (2014) Degradation of mouse locomotor pattern in the absence of proprioceptive sensory feedback. *Proc Natl Acad Sci USA* 111: 16877-16882.
42. Dideriksen J, Negro F (2021) Feedforward modulation of gamma motor neuron activity can improve motor command accuracy. *J Neural Eng* 18(4).
43. Stephens JD, Ting LH, Cope TC (2025) Computing muscle mechanical state variables from combined proprioceptive sensory feedback. *Exp Physiol* 110(10): 1391-1400.
44. Sandbrink KJ, Mamidanna P, Michaelis C, Matthias Bethge, Mackenzie Weygandt Mathis, et al. (2023) Contrasting action and posture coding with hierarchical deep neural network models of proprioception. *Elife* 12: e81499.
45. Crozara LF, Morcelli MH, Marques NR, Camilla Zamfolini Hallal, Deborah Hebling Spinoso, et al. (2013) Motor readiness and joint torque production in lowerlimbs of older women fallers and non-fallers. *J ElectromyogrKinesiol* 23: 1131-1138.
46. Takeoka A, Vollenweider I, Courtine G, Arber S (2014) Muscle spindle feedback directs locomotor recovery and circuit reorganization after spinal cord injury. *Cell* 15(7): 1626-1639.
47. Yilmaz EO, Englitz B, Yucesoy CA (2025) Synergistic muscle activation impacts muscle spindles projecting to the mouse trigeminal mesencephalic nucleus. *J Neurophysiol* 134(5): 1453-1465.
48. Hill MW, Hosseini EA, McLellan A, Michael James Price, Stephen Ronald Lord, et al. (2020) Delayed impairment of postural, physical, and muscular functions following downhill compared to level walking in older people. *Frontiers in Physiology* 11: 544559.

49. Felicetti G, Thoumie P, Do MC, Marco Schieppati (2021) Cutaneous and muscular afferents from the foot and sensory fusion processing: physiology and pathology in neuropathies. *J Peripher Nerv Syst* 26(1): 17-34.
50. Mildren RL, Schmidt ME, Eschelmuller G, Mark G Carpenter, Jean-Sébastien Blouin, et al. (2020) Influence of age on the frequency characteristics of the soleus muscle response to Achilles tendon vibration during standing. *J Physiol* 598(22): 5231-5243.
51. Aoi S, Ogihara N, Funato T, Kazuo Tsuchiya (2012) Sensory regulation of stance-to-swing transition in generation of adaptive human walking: a simulation study. *Robotics and Autonomous Syst* 60(5): 685-691.
52. Avela J, Kyröläinen H, Komi PV, D Rama (1999) Reduced reflex sensitivity persists several days after long-lasting stretch-shortening cycle exercise. *J Appl Physiol* 86(4): 1292-1300.
53. Eschelmuller G, Inglis JT, Kim H, Romeo Chua (2025) Dual agonist and antagonist muscle vibration produces a bias in end point with no change in variability. *Exp Brain Res* 243(10): 204.
54. Yan Y, Antolin N, Zhou L, Luyang Xu, Irene Lisa Vargas, et al. (2025) Macrophages excite muscle spindles with glutamate to bolster locomotion. *Nature* 637(8046): 698-707.
55. Harrison JM, Podor B, Yans A, Victor F Rafuse (2025) Muscle derived BMP4 regulates morphology and function of endplates on extrafusal and intrafusal muscle fibers in adult mice. *J Neurosci*: e0707252025.
56. Wright RL, Peters DM, Robinson PD, Thomas N Watt, Mark A Hollands (2015) Older adults who have previously fallen due to a trip walk differently than those who have fallen due to a slip. *Gait Posture* 41(1): 164-169.
57. Mignardot JB, Deschamps T, Barrey E, Bernard Auvinet, Gilles Berrut, et al. (2014) Gait disturbances as specific predictive markers of the first fall onset in elderly people: a two-year prospective observational study. *Front Aging Neurosci* 6: 22.
58. Nichols TR (2024) Neuromechanical circuits of the spinal motor apparatus. *Compr Physiol* 14(5): 5789-5838.
59. Proske U (2023) A reassessment of the role of joint receptors in human position sense. *Exp Brain Res* 241(4): 943-949.
60. Ito T, Sakai Y, Nishio R, Yohei Ito, Kazunori Yamazaki, et al. (2020) Relationship between postural stability and fall risk in elderly people with lumbar spondylosis during local vibratory stimulation for proprioception: a retrospective study. *Somatosens Mot Res* 37(3): 133-137.
61. Ellaway PH, Taylor A, Durbaba R (2015) Muscle spindle and fusimotor activity in locomotion. *J Anat* 227(2): 157-166.
62. Oliveira Fernandes M, Tourtellotte WG (2015) Egr3-dependent muscle spindle stretches receptor intrafusal muscle fiber differentiation and fusimotor innervation homeostasis. *J Neurosci* 35(14): 5566-5578.
63. Santuz A, Akay T, Mayer WP, Tyler L Wells, Arno Schroll, et al. (2019) Modular organization of murine locomotor pattern in the presence and absence of sensory feedback from muscle spindles. *J Physiol* 597(12): 3147-3165.
64. Higurashi Y, Taniguchi Y, Kumakura H (2006) Density of muscle spindles in prosimian shoulder muscles reflects locomotor adaptation. *Cells Tissues Organs* 184(2): 96-101.
65. Yu M, Piao YJ, Eun HI, Dong-Wook Kim, Mun-ho Ryu, et al. (2010) Development of abnormal gait detection and vibratory stimulation system on lower limbs to improve gait stability. *J Med Syst* 34(5): 787-797.
66. Mayer WP, Murray AJ, Brenner-Morton S, Thomas M Jessell, Warren G Tourtellotte, et al. (2018) Role of muscle spindle feedback in regulating muscle activity strength during walking at different speed in mice. *J Neurophysiol* 120(5): 2484-2497.
67. Silva J, Atalaia T, Martins R, João Curado Silva, João Abrantes, et al. (2025) Effects of a 12-WEEK proprioceptive and strength exercise program on the gait biomechanical parameters of older adults. *J Bodyw Mov Ther* 45: 656-666.
68. Lin KC, Wai RJ, Chien Chang HY. (2025) AI-assisted dynamic postural control screening to improve functional mobility in older adult populations: quasi-experimental study. *JMIR Aging* 8: e73290.
69. Yamada M, Kojima I, Tanaka S, Hiroki Saegusa, Miho Nambu, et al. (2025) The Geriatric 10-Second Functional Capacity Test (Ger10-FCT): a practical and rapid screening tool for frailty, sarcopenia, and the risk of adverse health outcomes in older adults. *Geriatr Gerontol Int*.
70. Schoene D, Gross M, Finger B, Nils Axel Lahmann, Kathrin Raeder, et al. (2025) Conventional and tablet-supported physical training to reduce falls and fall-related injuries in community-dwelling older adults: protocol of the randomised SURE-footed into the future Fall Intervention Trial (SURE-FIT). *BMJ Open* 15(11): e105969.
71. Paramento M, Passarotto E, Agostini M, Emanuela Formaggio, Paola Contessa, et al. (2025) Multimodal analysis of postural control in adults at risk of falls. *Annu Int Conf IEEE Eng Med Biol Soc* 2025: 1-4.
72. Maas H, Noort W (2024) Knee movements cause changes in the firing behaviour of muscle spindles located within the mono-articular ankle extensor soleus in the rat. *Exp Physiol* 109(1): 125-134.
73. Jalaieddini K, Minos Niu C, Chakravarthi Raja S, Won Joon Sohn, Gerald E Loeb, et al. (2017) Neuromorphic meets neuromechanics, part II: the role of fusimotor drive. *J Neural Eng* 14(2): 025002.
74. Bornstein B, Watkins B, Passini FS, Ronen Blecher, Eran Assaraf, et al. (2024) The mechanosensitive ion channel ASIC2 mediates both proprioceptive sensing and spinal alignment. *Exp Physiol* 109(1): 135-147.
75. Rahmati SM, Klishko AN, Martin RS, Nate E Bunderson, Jeswin A Meslie, et al. (2025) Role of forelimb morphology in muscle sensorimotor functions during locomotion in the cat. *J Physiol* 603(2): 447-487.
76. Ackerley R, Samain-Aupic L, Ribot-Ciscar E (2022) Passive proprioceptive training alters the sensitivity of muscle spindles to imposed movements. *Eneuro* 9(1): eneuro.0249-0221.
77. Cronin, NJ, Klint RAF, Grey MJ, Thomas Sinkjaer (2011) Ultrasonography as a tool to study afferent feedback from the muscle-tendon complex during human walking. *J Electromyography Kinesiol* 21(2): 197-207.
78. Wyart C, Carbo-Tano M (2023) Design of mechanosensory feedback during undulatory locomotion to enhance speed and stability. *Curr Opin Neurobiol* 83: 102777.
79. Bartels EM, Harrison AP (2025) The use of acoustic myography to assess changes in muscle control with ageing in healthy subjects ranging 20 to 79 years. *J Muscle Res Cell Motil*.
80. Yamazaki K, Sakai Y, Ito T, Jo Fukuhara, Yoshifumi Morita (2024) Percentage of decline in individual proprioceptors in older adults. *J Phys Ther Sci* 36(9): 492-497.
81. Enjin A, Leão KE, Mikulovic S, Pierre Le Merre, Warren G Tourtellotte, et al. (2012) Sensorimotor function is modulated by the serotonin receptor 1d, a novel marker for gamma motor neurons. *Mol Cell Neurosci* 49(3): 322-332.
82. Guertin P, Angel MJ, Perreault MC, DA McCrea (1995) Ankle extensor group I afferents excite extensors throughout the hindlimb during fictive locomotion in the cat. *J Physiol* 487(1): 197-209.

83. Perreault MC, Angel MJ, Guertin P, DA McCrea (1995) Effects of stimulation of hindlimb flexor group II afferents during fictive locomotion in the cat. *J Physiol* 487(1): 211-220.
84. Hulliger M (1993) Fusimotor control of proprioceptive feedback during locomotion and balancing: can simple lessons be learned for artificial control of gait? *Prog Brain Res* 97: 173-180.
85. Kröger S (2025) Experimental physiology special issue: 'mechanotransduction, muscle spindles and proprioception'. *Exp Physiol* 10(10): 1383-1388.