

Muscle Spindles and Locomotor Control-An Unrecognized Falls Determinant?

Marks Ray

Marks Ray, Department of Health, Physical Education, Gerontological Studies and Services, School of Health & Behavioral Sciences, City University of New York, York College, USA and Department of Health and Behavior Studies, Columbia University, Teachers College, USA

Correspondence to: Marks Ray, Department of Health and Behavior Studies, Teachers College, Columbia University, Box 114, 525W, 120th Street, New York, NY 10027, United States.

Email: rm226@columbia.edu

Telephone: +1-212-678-3445

Fax: 1-212-678-8259

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ABSTRACT

BACKGROUND: Historically, evidence muscle spindles might be involved in locomotion was provided by their presence in tetrapod antigravity muscles associated with posture and locomotion. Later, Brodal (1962) noted muscle spindles in all muscles of locomotion. To unravel the complexity of the muscle spindle and its role in human locomotor control many investigators have since conducted lesion and/or anaesthesia studies in subhuman species and human contexts.

QUESTIONS: How strong is the evidence linking muscle spindles to normal human locomotion and its control? Can a case be made for an association between muscle spindle dysfunction and falls injuries?

METHODS: All relevant publications in the leading electronic databases were searched using the key terms muscle afferents, falls, gait, locomotion, muscle spindles. There were numerous related listings, but here only selected reports are examined and discussed because the articles had to be linked in some way to the key question driving the research.

RESULTS: Evidence supports a key role for muscle spindles in the control of human locomotion, and by analogy to falls related injuries.

CONCLUSION: Future work to explore the role of muscle spindles in the context of falls that occur when walking is warranted.

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Key words: Falls; Gait; Locomotion; Muscle Afferents; Muscle Spindles; Walking

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INTRODUCTION

Falls injuries among the older population are a major health care burden in an aging society. Predicting who is at risk for falls, and future falls is a very important health topic in this respect. Among the risk factors for falls are various forms of sensorimotor control deficits that often result in gait disturbances and that can precede falling incidents. Among these sensors are specialized stretch-sensitive mechanoreceptors called muscle spindles, which are found in all muscles of locomotion^[1], and appear uniquely suited to convey sensory feedback from the limbs to the spinal cord locomotor circuits and central nervous system pathways with which they have intricate connections through their group Ia and group II sensory endings. Their sensitivity in turn can be modulated by ongoing inputs from supraspinal or central neuronal mechanisms, making them ideally suited to enable desirable gait adaptations in response to changing environmental contexts^[2]. To further examine the degree to which muscle spindles and their sensory connections are implicated in locomotion and its control, many studies 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]. Others have focused on examining the role of muscle spindles in adaptive walking in the face of varying external perturbations^[5]. Others have noted that the large array of muscle spindle receptors^[6] that provide inputs into the sensorimotor system also supply the cerebellum, involved in balance control^[7].

The rationale for specifically examining the role of the muscle spindle in the context of locomotor control in general, is hence supported by evidence of: a complex set of efferent pathways that appear to influence muscle spindle sensitivity^[8,9], the presence of many intricate connections between muscle spindle arrays and the spinal cord generator complex and their ability to convey updated informational inputs in advance of any required adjustments needed for movements to be carried out in a timely and safe way in the face of unexpected locomotor perturbations. Their ability to respond differentially to muscle length variations, as well as velocity signals is also consistent with their documented role in the control of human walking^[10], as is their ability to 'smooth' out irregularities in movement trajectories by permitting symmetric and consistent responses, which do not yield following initial stretch^[11]. Able to provide sensory input via two types of afferent nerve fibres to the spinal cord and central nervous system^[3], and to receive motor inputs from the central nervous system and spinal cord via gamma motoneurone, the muscle spindle pathways appear to provide a unique neural mechanism for controlling bipedal locomotion^[3]. Conversely, deafferentation is found to produce complex abnormal movement patterns of the hind limbs^[12].

In sum, consistent with the needs of the organism, muscle spindles and their sensory nerve endings that provide length- and position-dependent sensory inputs to the spinal cord and central nervous system appear to be highly important structures in the context of locomotor control. They and their intricate connections appear to be able to provide the spinal cord central pattern generator responsible in part for locomotion, with timely information about unexpected external conditions that could impede this process, as well as the magnitude and nature of these movements^[13]. Their inputs to the central nervous system may in turn be used to control their overall sensitivity through an array of very specifically organized static and dynamic fusimotoneurons, which constitute a separate constellation of spinal cord motor outputs, thus enabling an organism to produce accurate and timely outputs for the limbs in the face of ever changing environments, and terrains^[14,15]. However, it seems surprising that very few links have been made between these highly complex structures and their function in the context of falls injuries, even though the complete loss of muscle spindles appears to seriously compromise the regularity of locomotion and the step cycle^[16].

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 falls, few attempts have been made in general to elucidate a distinct role for muscle sensory receptors in the context of falls injuries 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, related 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 implicated in providing stability during the stance phase of the gait cycle in bipedal gait. Although

animal models may not represent the role of muscle spindles during human locomotion, those using chronically implanted anaesthetized cats and passively imposed stretch to estimate fusimotor activity patterns^[17,18] or electrically stimulated decerebrate preparations^[19-21] have been helpful for providing important insights into the link between muscle spindle sensory inputs and locomotion^[22] and were thus included in the review. All selected papers had to address the key study question, and be published as full length research articles. The quality of the articles was supported by the nature of the journal and the reputation of the laboratory and research groups in this specialized field. All types of research were deemed acceptable if they focused on the topics of muscle spindle and their association with walking. Relevant articles on falls injuries were selected from the very sparse data base that exists on associations between deficits in muscle spindle pathways and falls. Excluded were those studies on muscle spindles that dealt largely with anatomical details, biochemistry and genetics, measurement strategies to identify functional properties, and foreign articles. For the key words, numbers of papers and data bases examined see table 1 below.

RESULTS

Major findings

The literature search revealed 60 related works, mostly dealing with muscle spindles and aspects of locomotion. No study was found linking these topics to falls injuries specifically. Regarding muscles 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^[22].

Loeb and Hoffer^[23] suggested that muscle spindle afferent inputs do have a major role to play in the control of locomotion because they help to generate smooth energy efficient automatic movements that can be refined in response to perturbations during locomotion. 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.

The powerful role of muscle spindles in locomotor control has been further evidenced in fictive preparation studies, where sustained

Table 1 Search Strategy for Current Review.

Data Source	Keywords	Years Covered	Number Articles
Academic Search Complete	Muscle spindles and locomotion	2001-2015	33
	Muscle spindles and falls	2002-2015	22
PUBMED	Muscle spindles and locomotion	1965-2015	136
	Muscle spindles and falls	1975-2015	19
	Muscle spindles and locomotion	1964-2015	296
Scopus	Muscle spindles and falls	1956-2015	110
Web of Science	Muscle spindles and locomotion	1972-2015	198
	Muscle spindles and falls	1991-2015	80

stimulation was applied to brainstem mesencephalic locomotor region in decerebrate animals. These studies suggested 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 can enhance and reset locomotor activity^[25], stimulation of the leg muscle afferents during fictive locomotion appeared to modulate locomotor phase duration, as well as speed, and gait stability^[26]. According to Hasan and Stuart^[27], muscle spindles in active, agonist muscles are able to help foster locomotor stability, because their feedback during stance consistently heightens motoneurone activity, and does so, regardless of walking system studied.

Research also shows that in addition to its role in stability control during locomotion, the negative relationship between the contractile activity in one muscle and the spindle afferent output from its antagonist during walking movements is of high import in enabling the organism to carry out these reciprocal movements, in a timely way^[28]. Indeed, whereas, some of this regulatory information may come from other sources, or may be of minor import in day to day non-varying walking situations, the presence of stretch sensitive nerve endings in the key muscles of locomotion appears to provide 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 walkers path^[27].

In addition to the aforementioned studies, some research has been forthcoming to examine if muscle spindles can mediate both intra as well as interlimb coordination processes that are needed during gait. In this regard, although Dimitrou^[28] did not study locomotion, this group found muscle spindles are able to modulate the desired outputs to the moving as well as the stationary limb due to their ability to convey ongoing information on position, both initial, subsequent and final, while remaining sensitive to efferent inputs and prevailing activity of the antagonistic muscles. That is, once one movement in the gait cycle has occurred, the muscle afferents can respond by helping to initiate a subsequent movement that is consistent with the magnitude of force needed to ensure stability, safety and efficiency. Work by Prochazka *et al*^[6] has shown that fusimotor drive during locomotion can be altered during unpredictable and novel movements or if the organism inadvertently deviates from their stereotypical stepping cycle, for example if they encounter a slippery surface^[3] and there is a need to avert falling, slipping, or tripping. That is, the muscle spindle afferents can help recalibrate the locomotor system accordingly.

Further support for this idea that there is a well-articulated association between components of the muscle spindle pathways and locomotion was provided by Taylor and Donga^[9] who recorded the presence of a strong fusimotor drive during active, rather than passive movements during locomotion. These researchers specifically concluded that during normal locomotion dynamic gamma efferent inputs sensitize or prime primary afferents in such a way as to enable them to detect departures from the trajectory of the intended movement. The needed compensatory mechanisms can thus be generated in advance of contact with the ground or obstacle provided the organism is otherwise healthy with an intact neuromotor system.

In addition, Grillner and Rossignol^[30] suggested receptors signaling limb position along with those signaling extensor muscle unloading^[31], such as muscle spindles are highly important, if not essential regulators of normal locomotor movements. This group specifically showed that muscle spindle sensory endings are not only very sensitive to changes in length, or position, but that even a simple

movement such as slowly extending the hip at the end of stance is able to initiate a new step-cycle in co-ordination with the opposite limb. In contrast, locomotion of one limb of the chronic spinal cat could be blocked by holding it in a semi-flexed position.

Murphy and Martin^[32] who examined recordings of fusimotor activity from dissected nerve filaments to the triceps surae muscle in a decerebrate cat revealed neurons that fired continuously throughout the walking sequence, as well as neurons which were deeply modulated, in parallel with alpha activity. According to Rossingel *et al*^[33], this type of neural feedback mechanism potentially helps to ensure that the locomotor system has a wider rather than a limited operating range, whilst heightening its accuracy and stability. Kamibayashi *et al*^[34] too found the inputs to the spinal cord during gait from the muscle spindles were phase-dependent, and as such contributed differentially to the activation of muscles used in gait. As suggested by Nielsen and Sinkjaer^[35] this intrinsic sensori-motor system enables the organism to move smoothly and efficiently and to adapt to unpredictable disturbances, thus allowing for timely corrections that may prevent falling, slipping, or tripping. Although disputed to some degree by findings of Loeb *et al*^[36,37] who studied the activity of muscle afferents during walking in two different muscle groups of the cat in the face of fusimotor blockade, corrective actions while walking on a narrow beam seemed to be accompanied by transient increases in dynamic fusimotor drive^[38]. Similarly, Wetzel, Atwater, Wait, and Stuart^[39] found that deafferentation of the left hind limb caused a deficit in its normal locomotor rhythm as well its force production. In addition, the intact limbs exhibited the same deficits. The force deficits were found when the extensors should have been most active. Another finding was that during swing, the deafferented limb failed to attain its normal position above the surface of the belt.

Recent evidence further reveals the mean firing rates of all muscle afferents in the step cycle are high^[40] and that important contributions to locomotor control in the intact animal are probably made, in part, by the spindle network to shape the amplitude, duration and timing of ipsilateral extensor activity during over-ground locomotion^[41]. Hiebert, Whelan, Prochaska, and Pearson^[42] concluded that as the flexor muscles lengthen with stance, their spindle afferents act to increasingly inhibit the spinal centers responsible for generating extensor activity thus facilitating the onset of the swing phase of the gait cycle, while during task specific activities during treadmill walking, the ankle extensor spindle reflexes were implicated^[43].

Sparby *et al*^[44] has further shown how muscle afferent feedback allows oscillations to the central pattern generator structures to occur at a wider range of drive values than the range over which oscillations occur without feedback. They specifically noted stronger feedback led to faster oscillations and argued that this implied it may be possible to restore locomotion even if the supra-spinal drive to the

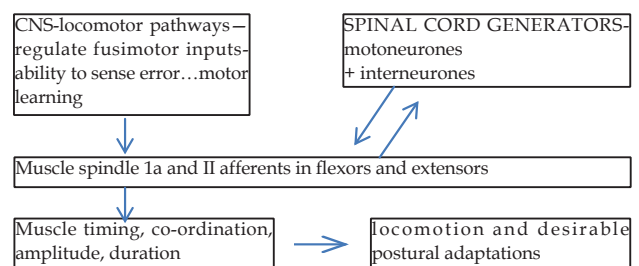


Figure 1 Hypothetical associations between muscle spindle actions in parent muscles involved in the locomotor pathway and postural adaptations. Adapted from: [12,13,35-37,38,42].

Table 2 Studies that have examined linkages in the muscle spindle locomotor pathway over the last 20 years.

Authors	Substrate	Conclusion
Akay <i>et al</i> [49]	Mouse locomotion under modified proprioception	Locomotion degrades in response to elimination of muscle spindle proprioceptive inputs. The degradation results in loss of joint coordination and alterations in actions of flexor and extensor muscles
Aoi <i>et al</i> [75]	Neuromusculoskeletal model	Sensory signals at the hip contribute to producing robust walking in face of disturbances
Enjin <i>et al</i> [22]	Mouse model	Reduced 1a afferent inputs to motoneurons during provoked movements may reduce undesired exaggerated muscle output
Guertin <i>et al</i> [41]	Decerebrate cat	During real locomotion, extensor spindle afferents may serve as an excitatory reflex system helping to shape the amplitude, duration, and timing of ipsilateral extensor activity. Increased or unexpected activation of group I extensor or plantar foot afferents during locomotion could help to compensate for increased loading of the limb
Hulliger[38]	Experimental simulation studies	1a sensitivity and dynamic gamma-drive while low in walking movements dramatically increase in tasks of increasing difficulty or unfamiliarity such as landing from falls
Loeb and Hoffer[36]	Cat thigh muscles	At the peak of fusimotor blockade spindle afferents activity decreased, along with decreases in stance and swing phases of walking at different stages of the progressive fusimotor blockade
Markin <i>et al</i> [59]	Neuromechanical model	Afferent feedback adjusts the central pattern generator pattern generator function to match limb dynamics and kinematics, thus fostering stability during walking. Increasing the degree of afferent inputs to spinal generator may occur following locomotor training eg in cases with spinal injuries
Perrault <i>et al</i> [60]	Decerebrate paralysed cat	Length-sensitive group II fibres, or spindle secondaries may act to regulate the duration and onset of flexor and extensor activity during real locomotion. Unexpected or enhanced activity of flexor secondaries during swing would promote a switch of the step cycle to stance
Takeoka <i>et al</i> [55]	Mouse model after spinal cord injury	Muscle spindle feedback is implicated in locomotor control and function
Yu <i>et al</i> [63]	Human model	Vibration of the ankle extensor when stepping alters the force distribution of the muscles when walking and stepping over obstacles. During the swing phase of gait, primary endings in the ankle extensors play a key role in mediating posture and stability

Box 1 Summary of Key Aspects of the Muscle Spindle Pathways as Related to Locomotion.

1. Some group II muscle afferents from muscles such as the quadriceps which respond to small stretches have been found to synapse monosynaptically on interneurons in the 4th lumbar segment.
2. Many of these interneurons, directly impact lower lumbar motoneurons and possibly other interneurons involved in locomotor control.
3. These L4 spinal interneurons may also receive facilitatory or inhibitory inputs from other primary afferent endings, as well as joint and cutaneous afferents, which collectively contribute to information on the rate of change of muscle length and the resulting position of the limb.
4. L4 interneurons with group II input may also be excited by nerve impulses from cortico-rubral, reticulo and vestibulo-spinal tract fibres, mono or polysynaptically and their inputs may be influenced by the magnitude of depolarization of the interneurons by their segmental afferents and are likely to contribute to the desired ankle extensor activity required during stance [64]. Of the descending inputs that converge from the mesencephalic locomotor region onto the L4 interneuron-group II afferent complexes, and are implicated in locomotion, are those from the cuneiform nucleus.
5. The group II axon-L4 interneuron synapses are monoaminergic and they therefore act in a similar manner to the facilitatory actions of the monoamines within the descending mesencephalic locomotor system, perhaps alternating with it. (Their action is retarded by serotonin and noradrenaline).

spinal cord is disrupted or injured. Other relevant observations are highlighted in table 2, Box 1, and figure 1.

DISCUSSION

Muscle spindles, the most commonly observed sensory structures located in mammalian muscles^[3] appear to be highly significant in all phases of the locomotor cycle. They appear to provide an effective source of sensory signals that can influence several features of normal locomotion^[2,40]. By contrast, adverse kinematic and kinetic profiles have been demonstrated if muscle spindle networks are rendered dysfunctional, disrupted or destroyed artificially or by injury, or disease^[3]. Insofar as this situation would have implications for the prevention and rehabilitation of many locomotor disorders, Wu and Henry^[45] undertook to examine the intracellular effects of dorsal root ganglia neurons following hind limb weightbearing measures of anaesthetized healthy and osteoarthritic rats. This demonstrated changes in hind limb stance among the osteoarthritic rats in terms of the functional properties of the muscle afferent neurons that were examined. It was thought the observed differences in spindle afferent inputs in the osteoarthritic model could be helpful for understanding the disease process, as well as intervening upon this. This finding, while limited in its generalizability, is interesting in light of other evidence that suggests oligosynaptic reflex pathways can be recalibrated to assist functional recovery of locomotor control after

injury^[19] and that group II afferents do make a small contribution to tonic muscle activity during stance and when walking across different terrains^[46]. On the other hand, the presence of weakness in the hip abductors and extensors in adults with medial compartment knee osteoarthritis, may not only increase tripping risk when encountering obstacles due to the excess demand made upon these muscles, but weakness itself may alter muscle spindle stretch sensitivity and timing due to the close relationship between extrafusal muscle fibers and spindle discharge^[47]. As well, the presence of altered muscle spindle sensory feedback, for example, those consequent to age related muscle and nerve structure changes^[48] is likely to further alter normal reciprocal patterning of the leg muscles during locomotor behavior^[49].

Dimitiuo and Eden^[50] showed that signals in human muscle spindle afferents during unconstrained wrist and finger movements can predict future kinematic states of their parent muscle. They also showed that the discharges of type Ia afferents are best correlated with the velocity of length changes in their parent muscles and that their discharges vary depending on motor sequences in a way that cannot be explained by the state of their parent muscle alone. This led the authors to conclude that muscle spindles can act as "forward sensory models": that are affected both by the current state of their parent muscle as well as by efferent (fusimotor) control, and their discharges represent future kinematic states.

Other findings clearly show muscle spindles respond to passive muscle stretch and are thus in a position to provide feedback to the central nervous system. In contrast, patients who have a complete absence of muscle spindles do not exhibit these responses^[51]. Their relationship to gait and its control is further revealed by the ataxic gait identified in patients who have no functional muscle spindle responses^[16], and deafferentation studies, among others. For example, Wu *et al*^[45] who examined whether enhanced feedback from thigh afferents improved locomotor output in human spinal cord injury, found an important contribution of sensory information from the thigh muscles and during stimulation there were enhanced hip and knee extension and flexion torque responses during the stance and swing phase of the gait cycle.

In this regard, Elloway *et al*^[3] concluded that the wide ranging response range of muscle spindles that can be differentially activated by the magnitude of prevailing dynamic gamma efferent feedback potentially helps to raise the sensitivity of primary muscle spindle afferents and their ability to detect departures from the trajectory of the anticipated movement. However, since their optimal efficiency depends on the presence of intact supraspinal control mechanism^[57,58], when this pathway is impaired, the resultant decreased ability to produce the degree of coordination required during locomotion to successfully prevent a slip or trip if encountering obstacles or unexpected surface variations may result in a fall^[59]. Arguably, therefore, if the schematic representation depicted in Figure 2 is valid, older people with aging sensory systems, cognitive deficits, sensorimotor disturbances, as well as muscular dysfunction may hence be quite prone to incurring falls during level walking activities, especially out of doors, or if the interior is unfamiliar or an external barrier to safe locomotion. In particular, based on the aforementioned research findings, 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 addition, the complex interactions involved in the control of gait at the muscle spindle level imply any subnormal or delayed interaction between muscle afferent inputs and outputs during gait coupled with muscle weakness is likely in turn, to adversely impact locomotion, in general, 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^[53].

While this is a relatively unexplored area of orthopedic practice, so the aforementioned ideas are generally only speculative, additional indirect evidence for this aforementioned viewpoint has been provided by results of Crozara *et al*^[54] who found the ability to produce joint torques, plus motor readiness are strong predictors of falls among older women. Moreover, in experiments that unload muscle and where muscle spindles go slack, group Ia and group II afferent activity decreases abruptly, muscle activity of the muscle in question declines as a whole, and in those with a loss of large diameter primary afferents, walking is significantly impaired^[35]. As well, data show reflex activity can be delayed in the presence of muscle damage or fatigue^[61], and that this could compromise the neural control of stability during locomotion needed to avert falling^[62]. Akira *et al*^[71] found that ice immersion, which is a method of reducing muscle spindle function, had a significant impact on the walking velocity of young adult males, suggesting a possible link between muscle spindle function and a decrement in walking ability, a well-accepted falls determinant. Additional related research suggests it is morphological changes of muscle spindles

that are implicated in the impaired ability of the older individual to compensate for balance threats^[72]. Mi *et al*^[73] who found vibrating the ankle muscles of the left lower limb while stepping over an obstacle was able to change center of mass (COM) behavior on both the anterior/posterior and medial/lateral planes felt that by providing information on the movement of the body's COM with respect to the support foot the primary endings of the muscle spindles of the ankle play a significant role in controlling posture and balance during the swing phase of locomotion.

Consequently, although more research is needed to verify the ideas presented in this brief, it seems likely that efforts designed to normalize and maximize muscle spindle inputs in both lower limb extensor and flexor muscle groups where these are dysfunctional will prove helpful in the overall approach to falls prevention among the elderly, as both appear essential for optimal rhythmic and stable timely forward motion. It also seems that in the aging individual with a declining neuromuscular system, locomotor training to maximize sensorimotor integration and balance during gait may be extremely helpful^[63]. This is because, theoretically, either or both approaches could facilitate appropriate muscle activation patterns, and their response speed, as well as balance control during walking, hence possibly preventing the incidence and magnitude of some fall injuries attributable to misstepping when walking, and their detrimental consequences.

As stated by Pearson^[12], muscle afferent feedback can not only contribute to the ability to walk normally, but more particularly to appropriate adaptations during different walking conditions or precision tasks^[49,55,64,65]. As outlined in this brief, evidence shows muscle spindles are important because 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. Since these properties can change, adaptive mechanisms that can optimize muscle activation patterns are essential^[12]. However, as a result of age-associated deterioration in proprioceptive sensibility, as well as situations that alter muscle receptor inputs and motor outputs, an increased risk of fall can be anticipated^[74].

CONCLUSION

Muscle spindle pathways appear to regulate spinal and central nervous system networks and effective locomotor adaptations depend on the integrity of this neural circuitry. 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 spindle afferents. Since defects in this process may explain the presence of a heightened fall risk in individual's with neuromuscular deficiencies and others^[66,67], as well as why walking trajectories of fallers who have tripped are more extensive than those who have slipped^[68], this paper examined what we know about muscle spindle activity in the context of locomotion for purposes of advancing our understanding of the nature of falls injuries among older adults and others. Although the current hypothesis has not been put to any adequate test, the available data do imply that an improved understanding of the link between muscle afferents, and their behavior as this affects locomotor activity can potentially help to predict who is at risk, and explain why exercise can reduce falls injuries in some cases, but not others. The data may also enhance the important role of assessing the motor control pathways among those deemed vulnerable to sensory loss or sensory impairments, given the ubiquitous health recommendation to walk, regardless of health condition, and findings

that many environmental hazards exist that increase the proclivity to falling^[69,70,72,74].

CONFLICT OF INTERESTS

There are no conflicts of interest with regard to the present study.

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Peer reviewers: Andrea Cereatti, PhD, Polcoming Department, Bioengineering Unit, University of Sassari, Viale Mancini 5, 07100, Sassari, Italy.