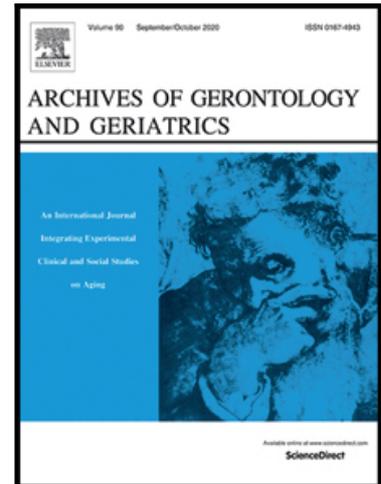# Journal Pre-proof

Variability in spatial and temporal gait dynamics during aging: a narrative review on the role of the neural system

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Highlights

- Aging increases spatial and temporal gait variability primarily due to neural system decline affecting motor control and balance.
- Structural brain atrophy, neurotransmitter depletion, and sensory degradation collectively impair gait stability and adaptability in older adults.
- Neuroimaging and mobile brain/body imaging studies reveal that older adults recruit additional cortical resources to compensate for reduced gait automaticity.
- Multimodal interventions combining physical and cognitive training can improve gait regularity and stability by promoting neural and functional adaptations.

Variability in spatial and temporal gait dynamics during aging: a narrative review on the role of the neural system

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Abstract

Gait dynamics, encompassing both spatial and temporal parameters, undergo significant changes with aging, often leading to increased gait variability and, consequentially, a higher risk of falls. While cognitive and musculoskeletal factors have been demonstrated to contribute to these alterations, the role of the neural system is crucial and yet not fully understood. This review aims to synthesize the existing evidence on the age-related deterioration in locomotor functioning, with a specific emphasis on the neural mechanisms involved. Besides summarizing appropriate measures to quantify gait variability, several neural factors including cortical, neurotransmitter, and sensory system degeneration, are explored as key contributors to the observed changes in locomotion during aging. Additionally, the review discusses the potential use of diverse interventions to enhance gait variability during aging to reduce the risk of falls. By elucidating the complex interplay between aging, gait dynamics, and neural function, this review underscores the importance of targeted interventions aimed at preserving neural health to maintain gait stability and reduce fall risk in the aging population. The findings suggest that further research is needed to develop and refine strategies for the early detection and prevention of gait-related impairments linked to neural decline.

Keywords: Gait, variability, aging, walking, motor control

1. Introduction

Human locomotion is a complex motor skill requiring the integration of sensory information coupled with an adequate motor output allowing stable navigation on different terrains. Generally, a typical healthy gait pattern is characterized by sequential footfalls generated by the central nervous system (CNS). Throughout the lifespan, this automated motor skill is learned during childhood but during aging mobility decline is a major concern as many components of the sensorimotor system degrade and thus shift motor control from an automatic task to a more conscious and cognitive task. This decline in locomotor functioning inherently decreases quality of life as well as independence during everyday life (Freiberger et al., 2020; Shafrin et al., 2017) which ultimately increases the burden and reduces levels of self-determination in older age (Freiberger et al., 2020).

Not surprisingly, the assessment of gait performance is part of several clinical testing batteries to assess either age-related dysfunction such as in sarcopenia (Cruz-Jentoft et al., 2019), or pathological severity levels during Parkinson's disease (Lindholm et al., 2018), dementia (Verghese et al., 2007) or stroke (Dos Santos et al., 2023). Understanding the neural demands of mobility as well as their change during the aging process is crucial for explaining the deterioration of mobility in older adults. A major factor in this decline is a reduced adaptability of the sensorimotor system. Previous research has demonstrated decreased sensorimotor adaptability in both the upper limbs (Anguera et al., 2011; Vandevoorde & Orban de Xivry, 2019) and lower limb locomotor tasks (Vervoort et al., 2020) of older adults. Different regions of the CNS are believed to contribute to various aspects of mobility (Fettrow et al., 2023; Lee & Kim, 2022), and these contributions may change with age. The consequences of a decline in gait performance and increased variability include an elevated risk of falling as well as fear of falling (Beck Jepsen et al., 2022) which often leads to the avoidance of walking and thus to personal isolation and decreased participation in community activities (Thomas et al., 2022).

The aim of this review is to summarize the existing scientific evidence on gait variability during aging as well as underlying neural mechanisms and the involved structures. A narrative review approach was chosen because the literature on gait variability and neural system function in aging is conceptually broad and methodologically diverse. Studies in this area employ heterogeneous designs, populations, and measurement techniques, making systematic synthesis challenging. A narrative review allows for comprehensive mapping of the existing evidence, identification of key concepts, and clarification of definitions and research gaps. This approach provides an essential foundation for future, more targeted systematic reviews or meta-analyses.

2. Quantifying gait variability

Gait characteristics have historically been quantified by average spatiotemporal parameters such as velocity, stride-length and step-time (Hausdorff et al., 1998). More recent evidence indicates that gait variability is a unique and superior marker of gait impairment compared to indices such as gait speed (Hausdorff, 2009; Verghese et al., 2006). Gait variability can be defined as the physiological variability, i.e., stride-to-stride fluctuations in walking, and is considered to reflect disruptions in intrinsic motor or postural control during walking resulting from age-related decline in the central and peripheral nervous systems. As outlined by Moon and colleagues (2016), increased temporal gait variability (e.g. stride-time variability) and anterior-posterior spatial gait variability (e.g. step-length variability) reflect loss of gait rhythmicity, while altered medial-lateral spatial variability (e.g. step-width variability) is associated with diminished balance control (Brach et al., 2008). The study of gait variability, achieved through instrumented gait analysis, provides the opportunity to quantify an abundance of parameters in locomotion and the changes with aging, and to assess the efficacy of therapeutic interventions and rehabilitation (Hausdorff, 2005; Marusic et al., 2015; Pradhan et al., 2015). The capability to quantify gait variability is therefore widely recognized as a diagnostically useful and clinically meaningful parameter (Kroneberg et al., 2018), particularly

to assess overall gait function in aging populations. At present, several methods are available for estimating gait variability, each with its own advantages and disadvantages. The following section provides a brief overview of these method types, with more detail provided in Table 1.

Temporal and spatial methods are some of the most widely used methods, and are well-established in clinical practice as they are easy to administer and interpret. However, such methods (e.g., step and stride length and time variability) provide little-to-no information on the underlying mechanisms of gait variability (Hausdorff, 2005). By comparison, kinematic measures provide a more detailed and comprehensive analysis of gait, including how different joints and muscles contribute to gait, and enable assessment of individual joint variability (Winter, 2009). Examples of kinematic methods include joint angle variability and segmental coordination variability; however, a potential key limitation of these methods is that they require specialized equipment such as 3D motion capture systems, which are not always readily available in clinical settings. Kinetic methods, such as ground reaction force variability and joint moment variability, provide data on the forces involved in gait, offering greater insight into muscle function, balance and stability during gait, and are often combined with kinematic measures for a more comprehensive analysis of gait variability (Mohammed et al., 2011). However, these methods also require specialized equipment (e.g. force plates), and data quality can be significantly affected by external factors such as footwear. Similarly, center of pressure measurement methods (e.g., center of pressure path and velocity variability) are often used to assess balance and stability during gait, providing valuable insight on postural control (Mehdizadeh et al., 2021). These methods provide data on dynamic stability during gait, which is particularly useful for assessing fall risk in aging populations.

Several more complex methods can provide further insight. Examples include 'nonlinear dynamics' which provides more in-depth data concerning the underlying dynamics and

complexity of gait, and has been used successfully to detail how aging affects variability during gait (Buzzi et al., 2003). These methods are generally more robust to data noise and measurement error (e.g., entropy analysis), however they typically require large datasets and advanced mathematical and computational knowledge. Frequency domain analysis methods (e.g. harmonic ratios) enable analysis of the rhythmicity, smoothness and symmetry of gait, which is useful in conditions associated with aging where gait rhythm and/or symmetry is affected (e.g., Parkinson's disease and stroke survivors) (Tamburini et al., 2015). While it is not the purpose of this review to provide an in-depth overview and critique of different methods to quantify gait variability, it is clear that each method can provide unique and important insights into different aspects of gait variability. Importantly, clinicians will often use a combination of methods to obtain a comprehensive picture of gait variability.

Table 1. Overview of methods to quantify gait variability.

Category	Example methods	Advantages	Disadvantages
1. Temporal and Spatial Measures	i. **Stride Time Variability**: Measures the variability in the time taken to complete a stride. It is often quantified as the standard deviation or coefficient of variation of stride times across multiple strides. ii. **Step Time Variability**: Similar to stride time variability but focuses on the time between consecutive steps. iii. **Step Length Variability**: Quantifies the variability in the distance covered by each step. iv. **Stride Length Variability**: Measures the variation in the distance covered between two consecutive footprints of the same foot.	• Simple to calculate and interpret. • Well-established in research and clinical practice, thus it is easier to compare results across studies. • Directly related to gait performance and easily linked to functional outcomes such as speed and step consistency.	• Provide little/no information on underlying mechanisms, i.e. motor control processes or coordination • Sensitive to measurement error - minor inaccuracies in step or stride detection can significantly affect variability estimates. • Often highly dependent on contextual factors such as walking speed, limiting the generalizability of findings.
2. Kinematic measures	i. **Joint Angle Variability**: Assesses the variability in joint angles (e.g., hip, knee, ankle) during the gait cycle. It can be analyzed using techniques like standard deviation or more advanced statistical methods. ii. **Segmental Coordination Variability**: Evaluates the variability in the coordination between different body segments during gait, often using cross-correlation techniques or vector coding.	• Provide a detailed and comprehensive analysis of movement patterns and coordination of different body segments during gait. • Enable understanding of how different joints and muscles contribute to gait variability • Enable assessment of individual joint variability	• Requires specialized equipment (e.g., motion capture systems) and advanced analysis techniques, which can be costly, time-consuming and may not be readily available in all clinical/research settings. • Errors in data collection impact reliability of gait variability measures.
3. Kinetic measures	i. **Ground Reaction Force (GRF) Variability**: Analyses the variability in the forces exerted by the ground on the foot during walking. Variability in GRF can indicate inconsistencies in weight transfer and balance. ii. **Joint Moment Variability**: Measures the variability in the moments (torques) at the joints during gait, which can reflect changes in muscle control or coordination.	• Provide data on the forces involved in gait, offering insights into muscle function, balance and stability. • Useful in the diagnosis and monitoring of diseases that impact muscle control and joint function, e.g., arthritis or Parkinson's disease. • Can be combined with kinematic measures for a more comprehensive analysis of gait.	• Requires specialized equipment (e.g., force plates) and advanced analysis techniques, which can be costly, time-consuming and may not be readily available in all clinical/research settings. • External factors such as footwear can significantly impact data quality.

4. Centre of pressure (COP) measures	i.	**CoP Path Variability**: Examines the variability in the path of the center of pressure under the foot during walking. This method is often used to assess balance and stability during gait.	• Directly related to balance control making it particularly useful for assessing fall risk aging populations. • Enables detail on dynamic stability during gait. • High sensitivity to changes in postural control compared to other methods.	• Requires specialized equipment (e.g., pressure sensors) and advanced analysis techniques, which can be costly, time-consuming and may not be readily available in all clinical/research settings. • Processing and analyzing data can be complex and requires specialized software. • May not provide much insight into other aspects of gait variability aside from balance and stability.
	ii.	**CoP Velocity Variability**: Quantifies the variability in the velocity of the CoP movement, providing insights into postural control.		
5. Nonlinear Dynamics and Complexity Measures	i.	**Approximate Entropy (ApEn)**: Measures the regularity and predictability of gait time series data. Lower values indicate more predictable and less variable gait patterns.	• Provides data and deeper understanding of the underlying dynamics and complexity of gait. • Methods (e.g., entropy analysis) are generally more robust to noise and measurement errors compared to traditional variability measures. • Sensitive to changes in motor control that occur in pathological conditions.	• Requires advanced mathematical and computational knowledge. • Results can be difficult to interpret • Requires large datasets to accurately estimate complexity measures, which can be a limitation in clinical settings with time constraints.
	ii.	**Sample Entropy (SampEn)**: Similar to ApEn but more robust, providing a measure of the complexity and irregularity of gait patterns.		
	iii.	**Detrended Fluctuation Analysis (DFA)**: Analyzes long-range correlations in gait time series, providing insights into the fractal-like nature of gait variability.		
	iv.	**Lyapunov Exponent**: Assesses the sensitivity of the gait system to small perturbations by measuring the rate at which initially close states diverge over time, indicating the stability of gait.		
6. Frequency-Domain Analysis	i.	**Power Spectral Density (PSD)**: Analyzes the frequency components of gait variability. This method can help identify periodicities in the gait cycle and how variability is distributed across different frequency bands.	• Useful for analyzing the periodicity and rhythmicity of gait, which can be important in conditions like Parkinson's disease where gait rhythm is affected. • Harmonic ratios provide detail concerning the smoothness and symmetry of gait, relevant for assessing recovery in stroke patients. • Offers a different perspective compared to time-domain analysis,	• Requires specialized knowledge in signal processing. • Requires very high-quality, consistent data. • May not fully capture non-periodic aspects of gait variability.
	ii.	**Harmonic Ratio**: Evaluates the smoothness and rhythmicity of gait by analyzing the ratio of harmonics in the frequency domain, often used to assess gait symmetry.		

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revealing aspects of gait variability
that may not be apparent otherwise.

3. Age related changes in gait variability

Gait speed has been recommended as a critical sign of physical performance in older persons; for example, decreases in gait speed of 10 cm/s are associated with higher falls risk in older adults (Verghese et al., 2009). In the context of gait variability, age-related changes refer to the differences in the predictability and consistency of gait patterns which are observed with increasing age (Verghese et al., 2009). Gait variability is considered a critical indicator of the stability and control of walking, and increased variability is often associated with a greater risk of falling (Callisaya et al., 2010). As humans age, several aspects of physical condition decline including muscle strength, balance and joint flexibility which, collectively, can contribute to increased gait variability. Unsurprisingly, gait speed is found to decrease with age at both usual and fast walking speeds, with more pronounced declines in the oldest adults partly due to a decreased stride length that is most evident at faster walking speeds (Magnani et al., 2019) (fig. 1), which is viewed as a compensatory mechanism for decreased stability (Gamwell et al., 2022). Greater variability in stride length, stride time and step width are typically observed in older adults (Callisaya et al., 2010; Osoba et al., 2019; Skiadopoulos et al., 2020), indicating a less stable and more inconsistent gait. Older adults typically exhibit longer stance times and shorter swing times during the gait cycle alongside increased time spend in double support (i.e. both feet on the ground simultaneously), which indicates a more cautious gait pattern that may serve as a strategy to maintain stability when walking. Existing data shows that older adults express even greater gait variability when performing dual tasks (e.g., talking while walking), which may indicate greater cognitive demand during gait, leading to less stable gait patterns (Gamwell et al., 2022).

Collectively, the available data demonstrates that spatial-temporal gait parameters are significantly affected by aging, with notable declines and greater variability in gait speed, stride length, step width and alterations in stance and swing times. These changes appear to become

more pronounced with increasing age, which may reflect a compensatory strategy for decreased strength, balance and coordination. Importantly, research has investigated how several key factors may influence gait variability in older adults, such as physical, cognitive psychological factors (Gamwell et al., 2022). Gamwell and colleagues reported that reduced strength and balance, reflecting a decline in overall physical function, were strongly associated with greater gait variability in that older adults with worse physical function showed more inconsistent and irregular gait patterns (Gamwell et al., 2022). Additionally, more variable gait patterns were observed in older adults with difficulties in attention and multitasking, suggesting that cognitive impairments, particularly in executive function, contribute to increased gait variability (Gamwell et al., 2022). Unsurprisingly, psychological factors such as fear of falling are found to be associated with increased gait variability, likely due to walking more cautiously. Arguably the most important conclusion from the study by Gamwell and colleagues is that such physical, cognitive and psychological factors interact in complex ways to collectively contribute to gait variability (Gamwell et al., 2022). Therefore, clinicians should consider all of these factors and adopted a multifaceted approach when assessing gait variability in older adults, and particularly when developing interventions to reduce and improve gait variability and stability, respectively.
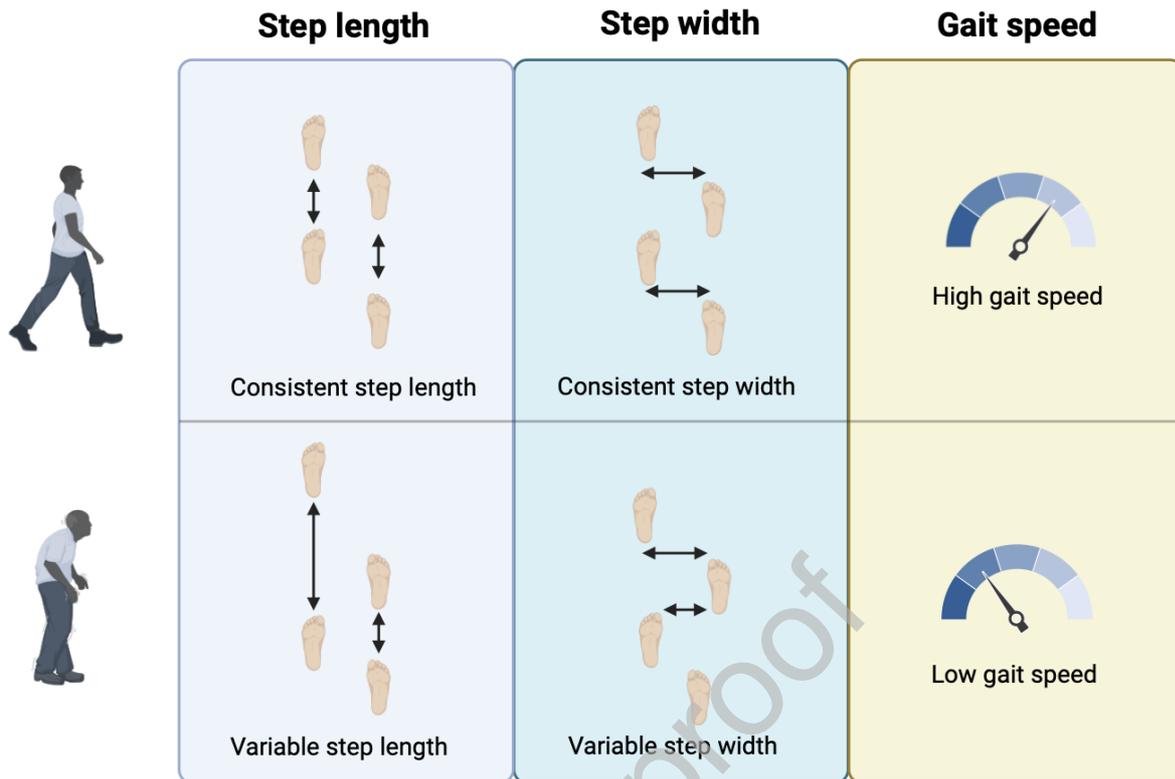
Figure 1 Exemplary changes in gait parameters with aging

4. Neural Mechanisms Involved in Gait Control

Age-related increases in spatial and temporal gait variability are primarily attributable to a complex interaction of structural and functional changes in the brain, sensory system declines, motor control impairments, and cognitive function deterioration. Besides metabolic alterations (Boyer et al., 2023; Palmer & Jensen, 2022) and changes in connective tissue properties (Mian et al., 2007; Stenroth et al., 2015) which frequently occur with aging and may have direct and indirect effects on gait control, it is well acknowledged that processes in neural degeneration play a fundamental role in the development of coordination deficits and higher variabilities in motor control (Sorond et al., 2015; Tian et al., 2017).

4.1 Cortical Alterations

4.1.1 Structural Changes

Various regions within the CNS have been shown to be involved in different aspects of mobility but have also been shown to experience measurable declines during the aging process.

A large body of scientific literature suggests that age-related structural brain atrophy occurs in an anterior-to-posterior pattern, with the frontal cortices demonstrating an earlier and faster atrophy compared other brain regions (Salat et al., 2004; Thambisetty et al., 2010). Especially, grey matter atrophy, which is particularly pronounced in the prefrontal cortex (Giorgio et al., 2010; Salat et al., 2004), may contribute to changes in executive functioning (Burzynska et al., 2012) and locomotion (Holtzer et al., 2014; Wilson et al., 2019) in older adults (fig. 2). With regard to gait and mobility, previous evidence indicates significant associations between a smaller sensorimotor and frontoparietal grey matter volume and a shorter step length and longer double support times in older adults (Rosano et al., 2008). These results were confirmed by Beauchet and colleagues (Beauchet et al., 2014), reporting that a higher gait variability (stride time) is associated with decreased parietal grey matter volume in healthy older adults. As a proxy of grey matter volume, cortical thickness has frequently been used in previous studies to estimate alterations in grey matter structure. Indeed, cortical thickness has also been shown to correlate with walking performance (Maidan et al., 2021; Ross et al., 2021), evidence is still limited to draw final conclusions about its association with gait variability during aging.

Furthermore, numerous investigations have explored the relationships between spatial gait variability and the structural and functional aspects of the hippocampus. Elevated spatial gait variability has been linked to diminished hippocampal integrity (Rosso et al., 2014), but not to neuronal function within the hippocampus (Zimmerman et al., 2009). The interrelationship between gait variability and hippocampal atrophy is still under debate with some studies demonstrating an association between a lower hippocampal volume and overall reduction in gait speed and step length (Allali et al., 2016; Callisaya et al., 2013) with aging, while on the contrary others revealed a positive association between a greater hippocampal volume and a greater (i.e., worse performance) stride time variability (Beauchet et al., 2015).

In accordance with grey matter changes, damage or loss of integrity of white matter microstructure, has consistently been demonstrated to be associated with variable gait patterns

and slow walking speed in older adults (Bolandzadeh et al., 2014; Starr et al., 2003; Verlinden et al., 2016). Especially during the aging process, white matter hyperintensities become more apparent, which have been found to facilitate motor decline (Silbert et al., 2008; van der Holst et al., 2018) by potentially disrupting neural communication between brain regions involved in motor control.

4.1.2 Electrical Activity

Beyond structural changes, functional brain dynamics provide a real-time window into gait control. Recent advances in mobile brain/body imaging (MoBI) have enabled the simultaneous recording of brain and body dynamics during human locomotion, which has greatly improved our ability to study gait dynamics under real-world conditions. MoBI typically combines high-density EEG with kinematic and neuromuscular measures (Marusic et al., 2023; Peskar et al., 2023; Protzak & Gramann, 2021; Richer et al., 2024) to capture the neural mechanisms that accompany gait variability and adaptation. Studies in young adults have repeatedly shown hallmark signatures such as beta-band desynchronization (a marker of active sensorimotor cortex engagement for motor execution) around heel-strike and increases in theta power (representing heightened cognitive effort and error-monitoring) during more demanding walking conditions, implicating sensorimotor, posterior-parietal and cingulate networks in stability and error monitoring (Jacobsen et al., 2022; Liu et al., 2024; Patelaki et al., 2023).

Although many foundational MoBI studies have focused on younger cohorts, recent work explicitly comparing age groups indicates these neural markers are highly relevant for understanding gait control in older people. For example, Salminen et al. (2025) recorded high-density EEG in younger and older adults walking at multiple speeds and reported that older adults—particularly those with lower mobility—showed greater theta synchronization in posterior parietal and cingulate regions and pronounced beta decreases with increasing speed, consistent with a shift toward greater cortical recruitment during gait in later life. Similarly, Protzak and Gramann (2021) demonstrated that during dual-task walking, older adults exhibited

attenuated alpha and beta power modulations compared to younger adults, suggesting reduced flexibility in motor resource allocation with age. These age differences suggest that the same MoBI signatures observed in young adults (beta ERD at foot strike; theta increases during challenging conditions) may reflect compensatory, and potentially maladaptive, increases in neural effort when observed in older or low-functioning participants. In line with this, De Sanctis et al. (2023) report that frontomedial theta and sensorimotor beta modulations during visually-perturbed walking are linked to cognitive risk: theta synchronization was stronger in higher-risk older adults while beta desynchronization was more evident in lower-risk participants, suggesting that oscillatory markers of MoBI correspond with cognitive status in old age.

Cognitive load and dual-task paradigms further support this interpretation: dual-tasking reduces central alpha/beta power and increases cadence variability (Vandenheever & Lambrechts, 2023) while individual differences in the ability to maintain cognitive performance when walking predict smaller increases in stride-to-stride variability and different frontal ERP profiles (Patelaki et al., 2023). These studies reinforce that frontal control networks become more engaged when walking demands increase or when automaticity declines, a pattern that is especially relevant to aging and fall risk.

4.2   *Neurotransmitter Changes*

In addition to structural changes in the brain, notable neurochemical differences exist between young and older adults, which have been directly associated with declines in motor performance in the elderly. Serotonin levels are reduced in older adults compared to younger individuals, particularly in regions such as the cingulate cortex and putamen (Gottfries, 1990). Data from a previous study highlight that altered serotonin transmission in older mice is associated with motor dysfunction (Sibille et al., 2007). To what extent this translates to human physiology is not clear.

More evidence, however, is available on the effects of dopamine. The aging brain experiences a notable decline in dopamine transmission levels (Kaasinen & Rinne, 2002). Research involving post-mortem brain analysis and molecular imaging via positron emission tomography (PET) has elucidated that this age-related decrease in dopamine transmission is multifactorial (Kaasinen & Rinne, 2002). Specifically, older adults exhibit reductions in the absolute levels of the neurotransmitter dopamine (Garnett et al., 1983), various dopamine receptors (Wang et al., 1998), and dopamine transporters (Rinne et al., 1998) compared to younger adults. In a study by Cham and co-workers (Cham et al., 2008), the authors showed that lower striatal dopamine transporter levels were associated with altered gait parameters as evidenced by reductions in speed, cadence, and single and double support durations. This suggests that the reduction of dopaminergic activity is directly linked to impaired motor control in older adults and thus also may substantially impact gait dynamics.

Often overlooked in early gait studies, the cholinergic system plays a vital role in the attention-gait interface. Acetylcholine, for instance, is essential for executive function and the filtering of sensory information during walking. Age-related cholinergic decline is strongly associated with slower gait and increased fall risk (Morris et al., 2019). In a previous study by Pelosin et al. (2016), the authors found that central cholinergic activity predicts changes in gait characteristics such as gait speed in older individuals prone to falling.
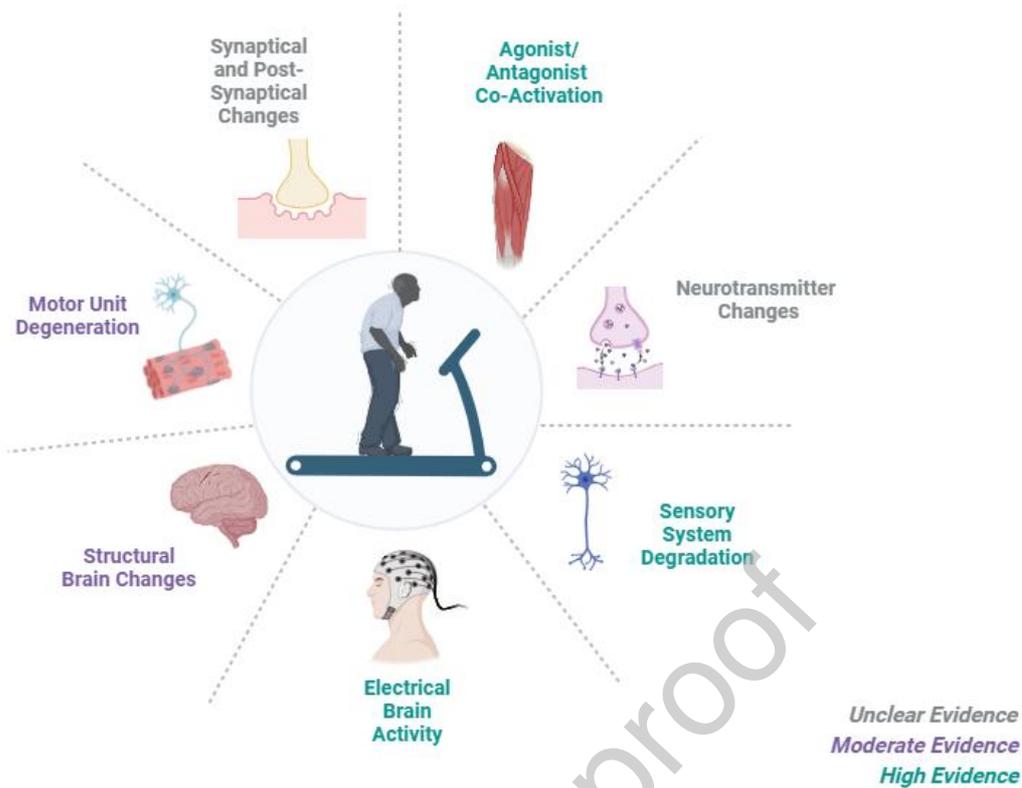
Figure 2 Overview of potential neural mechanisms of impairments in gait during aging. Text coloring indicates evidence level.

4.3   *Sensory System Degradation*

The capacity to maintain in a stable upright position during walking is essential for numerous daily activities and serves as a pertinent model for examining sensorimotor integration. Human locomotion necessitates appropriate sensorimotor integration in order to incorporate sensory inputs such as from the vestibular system, or visual and proprioceptive feedback and thus generate precisely tuned motor outputs (Wolpert et al., 1998).

Indeed, aging is accompanied by significant modifications in proprioception, visual and vestibular feedback leading to diminished sensitivity, acuity, and integration of sensory signals. These changes adversely affect postural control, decreasing its efficiency and potentially compromising an individual's functional gait performance.

Colledge et al. (1994) investigated the relative importance of vision, proprioception, and the vestibular system in maintaining balance across different age groups. Their findings indicated

that proprioception played a more critical role in balance maintenance than vision for individuals of all age groups. It is currently well acknowledged that aged individuals experience pronounced changes in proprioception and joint position sensation (Kaplan et al., 1985; Petrella et al., 1997). Underlying mechanisms involve both peripheral and central factors. On the peripheral level, an early investigation by Swallow (1966), conducted on human cadavers aged between 16 and 82 years, revealed a substantial age-related decline in the total number of nerve fibers within the anterior tibial nerve of the foot, along with a marked reduction in the proportion of large fibers in older subjects. Since Ia afferents are the largest peripheral axons, this suggests a reduction in the quantity of muscle spindle afferents, particularly Ia afferents, with advancing age. In a more recent publication, Vaughan and co-workers (Vaughan et al., 2017) corroborated these findings in mice, demonstrating that proprioceptive sensory neurons undergo degeneration with age, commencing prior to the atrophy of intrafusal muscle fibers. (Chung et al., 2005).

A frequently used methodological approach to evaluate the functional status of the monosynaptic reflex arc, in order to measure motoneuronal excitability, is the Hofmann (H)-reflex (Burke, 2016). Findings from numerous studies suggest that the H-Reflex is often reduced in older compared with younger individuals, facilitation and inhibition is less modulated (Piirainen et al., 2013) although these effects seem to be highly dependent on the functional task being performed during the experiments (Baudry & Enoka, 2009; Baudry et al., 2010; Orssatto et al., 2021). Further, advancing age has been shown to results in impairments in sensory input processing, characterized by myelin abnormalities, axonal atrophy, and decreased nerve conduction velocity (Ito et al., 2021; Neukomm & Freeman, 2014; Stålberg et al., 1989), as well as a decline in neuromuscular performance. Besides age-related deteriorations in proprioception, older individuals have frequently been demonstrated to have reduced visual acuity (Congdon et al., 2004) leading to impaired sensory input from the visual system. Similarly, vestibular dysfunction during aging and associated imbalance (Jahn, 2019)

has a major impact on dynamic movements and might be responsible for increased gait variability (Meng et al., 2023).

4.4 Motor Unit Degeneration

Age-related motor unit (MU) degeneration is considered a primary driver of gait dysfunction in the elderly, characterized by a progressive loss of alpha-motoneurons and the subsequent denervation of muscle fibers. These neuromuscular alterations (specifically the loss of fast-twitch units and reduced rate coding (Wages et al., 2024) directly impair the ability to generate rapid force (Wages et al., 2024), which is essential for the push-off phase of gait. Research has demonstrated that older adults possess fewer motor units, which are generally larger and slower, leading to motor unit reorganization (Brown, 1972; Deschenes, 2011; Stålberg et al., 1989; Verdú et al., 2000). Consequently, these age-associated changes in motor unit number and function significantly affect muscle force production and control.

4.5 Agonist-Antagonist Co-Activation

Muscular co-activation plays a pivotal role in enhancing joint stability during locomotion. In the scientific literature, an increase in co-activation is commonly described as a compensatory mechanism during aging to increase joint stiffness and thus stability (Hortobágyi & DeVita, 2000). Previous studies have demonstrated that aging is related to a significant increase in antagonist co-activation in the trunk and lower extremities during gait (Hortobágyi et al., 2009; Nagai et al., 2011). This increased co-activation was previously also linked to a gait speed, with higher co-activation in the lower extremities leading to lower gait speed levels in older individuals (Lee et al., 2017). Further, increases in co-activation have been shown to facilitate increases in walking energy cost (Hortobágyi et al., 2009).

4.6 Synaptic and Post-Synaptic Impairments

Decreased efficiency of neuromuscular transmission within the neuromuscular junction (NMJ) might have considerable impact on coordinated muscular activation which is essential for stable walking. Substantial evidence indicates that alterations in endplate morphology and NMJ remodelling occur with aging, preceding the loss of fast motor units. Typically, the neurotransmitter release at the postsynaptic membrane of the NMJ exceeds the minimum required amount, creating a safety factor that ensures effective transmission even during high-demand conditions such as fatiguing contractions (Wood & Slater, 2001). Under normal conditions, the NMJ facilitates a direct and immediate transmission of action potentials from the motor neuron to the muscle fiber. However, with aging, this reliability diminishes (Wood & Slater, 2001), likely due to both morphological and physiological age-related alterations and remodelling of the NMJ (Hepple & Rice, 2016). Both animal and human experiments show that with aging, the pre-synaptic structures undergo degenerative changes characterized by axonal denervation and remodelling (Fahim & Robbins, 1982) as well as altered sprouting (Smith & Rosenheimer, 1982). Additionally, NMJ represent a decreased number of pre-synaptic vesicles and nerve terminals (Rosenheimer, 1990) and show substantial degeneration of endplates (Gutmann & HanzlÍKovÁ, 1966; Rosenheimer, 1990). Morphologically, both the nerve terminal area as well as the number of post-synaptic folds are reduced with aging resulting in functional impairments in the post-synaptic response (Gonzalez-Freire et al., 2014). Until now the majority of evidence is still based on animal data, which highlights the importance of human studies in order to draw more reliable conclusions on NMJ alterations during human aging.

4.7   *Cognitive-Neural Interplay*

Age-related changes in cognitive function play an important role in modulating the neural control of gait and contribute substantially to increased spatial and temporal gait variability. Dual-task (DT) interference on gait is consistently greater in individuals with cognitive impairment compared with cognitively healthy older adults, and increasing task complexity

further exacerbates gait deterioration (Montero-Odasso et al., 2012; Muir et al., 2012; Theill et al., 2011). Moreover, the magnitude of DT-related gait disruption scales with the severity of cognitive impairment, with individuals with Alzheimer's disease exhibiting more pronounced gait impairments than those with mild cognitive impairment (Muir et al., 2012). Neuroimaging studies provide converging evidence for shared neural substrates underlying cognition and gait control, demonstrating that white-matter hyperintensities, focal brain atrophy, and subcortical structural changes are independently associated with both gait disturbances and cognitive dysfunction (Amboni et al., 2013; Gouw et al., 2006; Kafri et al., 2013). In particular, alterations in prefrontal, frontoparietal, and sensorimotor regions, as well as disruptions in interhemispheric and subcortical connectivity, have been linked to reduced gait speed, altered stride parameters, and impaired executive performance, supporting a common neural basis for cognitive and motor decline during aging (Amboni et al., 2013; Rosano et al., 2012).

4.8   Pathological conditions

From a clinical perspective, distinct aging-related neuropathologies further illustrate how specific neural system alterations differentially affect gait dynamics. In Parkinson's disease, degeneration of dopaminergic pathways within the basal ganglia disrupts the automatic regulation of movement, resulting in characteristic increases in temporal gait variability, impaired rhythmicity, and reduced adaptability to environmental demands (Bohnen et al., 2022; Wilkins et al., 2020). In contrast, gait disturbances in Alzheimer's disease and related dementias are more strongly associated with cortical atrophy and cholinergic dysfunction, particularly within frontal, parietal and hippocampal regions implicated in attention and executive control (Beauchet et al., 2019; Kim et al., 2025; Olazarán et al., 2012). These changes are commonly linked to increased spatial gait variability and impaired navigation, reflecting deficits in higher-order cognitive processing rather than primary motor execution. Together, these disease-

specific patterns highlight the importance of considering both cognitive function and underlying neural pathology when interpreting gait variability in aging populations.

5. Evidence-based interventions to improve gait performance

As a consequence of the high variability in stepping parameters during aging, several studies found a significant association with a higher risk of falling or fear of falling (Hausdorff et al., 2001; Lockhart et al., 2021; Maki, 1997; Mishra et al., 2022; Thaler-Kall et al., 2015; Verghese et al., 2009). In light of the subsequent complications following fall events (Schonnop et al., 2013) as well as the public health burden of fatal and non-fatal falls (Florence et al., 2018), countermeasures to improve gait performance and thus prevent falls are urgently needed. Although the occurrence of falls has previously been described as a multifactorial phenomenon (Wallis et al., 2022), gait parameters (esp. gait speed) seem to play a key role in predicting falls in older adults as highlighted in a recent umbrella review (Beck Jepsen et al., 2022)

Given a diverse array of factors contributing to an accelerated decline in gait variability (i.e., proprioception, balance, strength (Bogen et al., 2020; Hamacher et al., 2019)) with advancing age, the majority of studies have focused on multi-factorial interventions in order to address multiple risk factors simultaneously (Brach & Vanswearingen, 2013). In a study by Sauvage and colleagues (1992), the authors combined both strength and endurance training on gait performance in older men and found significant improvements in stride length and gait velocity. These findings were confirmed by another study in n=424 older adults, demonstrating that a multi-modal physical activity intervention (duration ~1.2 years) facilitates substantial improvements in walking speed as compared to the control group receiving health education (The, 2006). In a recent meta-analysis, the effectiveness of sensor-based interventions on gait performance in older adults were assessed. Interestingly, the findings demonstrated that sensor-based interventions were at some domains even better than traditional physical exercise interventions in improving gait speed (Mao et al., 2024). Lastly, the importance of cognition as

a mediator of gait variability must not be neglected. Given that strong evidence suggests a clear association between cognition and gait variability in aging, several studies have incorporated dual- or multi-task exercises into their intervention programs. The results indicate the combination of exercise and cognition training seems to be a strong combination to improve stride-to-stride variability in older adults (Ali et al., 2022).

A precise mechanistic explanation for these improvements following multi-modal exercise regimens remains speculative. While exercise interventions have been shown to facilitate neuroplasticity in several brain structures (Hötting & Röder, 2013), decrease brain atrophy (Li et al., 2017) and have strong effects on dopamine production (Marques et al., 2021), cognitive interventions may improve gait via certain cognition domains such as memory and attention (Holtzer et al., 2006). However, disentangling the specific mechanisms (cognitive vs. physical exercise) underlying such improvements proves challenging, given the intertwined effects of physical interventions on cognitive and motor domains.

6. Future Directions

Generally, an increase in gait variability presents the inability of our neural control system to adequately fine tune stride-to-stride fluctuations during human aging. Although numerous observations have already revealed the severe consequences of age-induced changes in gait (Hausdorff et al., 2001; Lockhart et al., 2021; Maki, 1997; Mishra et al., 2022; Thaler-Kall et al., 2015; Verghese et al., 2009), future work should concentrate on uncovering the neural mechanisms that underlie changes in gait patterns which helps to develop tailored interventions and therapeutic strategies. Neuroimaging techniques, such as functional MRI and PET scans, alongside neurophysiological methods like (mobile) electroencephalography (EEG) (Richer et al., 2024) and molecular marker-based assays, should be leveraged to map the neural activity associated with gait variability in aging populations. Longitudinal studies are particularly important to track neural changes over time and correlate them with gait performance.

Moreover, studies should consider the influence of neurodegenerative diseases, such as Parkinson's and Alzheimer's, on gait variability, as these conditions often exacerbate gait disturbances (Beauchet et al., 2008; Zanardi et al., 2021). Similarly, the assessment of stride-to-stride fluctuations could also help as a prognostic factor for cognitive impairment (Tuena et al., 2023). Integrating machine learning and computational modelling to predict gait variability based on neural and biomechanical data could also enhance the precision of diagnostic and therapeutic approaches (Zhou et al., 2020). To move the field forward, research should prioritize: 1) Causal Validation: Using non-invasive brain stimulation (e.g., tDCS) to determine if modulating the prefrontal cortex directly reduces stride-time variability and 2) Bio-marker Development: Identifying whether specific MoBI signatures (e.g., frontal theta) can predict future fall risk before clinical symptoms appear.

Additional information

Competing interest

None of the authors has a competing interest.

Author contribution

All authors contributed to the conception or design of the work. CC and LH performed the acquisition and analysis of data for the work. All authors contributed to the interpretation of results. CC and LH drafted the work and all authors revised it critically for important intellectual content. All authors approved the final version of the manuscript.

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Declaration of interests

☒The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

☐The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: