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The age-associated reduction in propulsive power generation in walking

Jason R. Franz

Joint Department of Biomedical Engineering, University of North Carolina at Chapel Hill and North Carolina State University, Chapel Hill, NC, USA

Abstract

Propulsive power generation during push-off in walking decreases with advancing age. A common explanation is an accommodation for sarcopenia and muscle weakness. Yet, muscle strengthening often yields disappointing outcomes for walking performance. We examine the hypothesis that declines in force or power generating capacity of propulsive leg muscles cannot fully explain the age-related reduction in propulsive power generation during walking.

Keywords

Plantarflexor; biomechanics; gait; elderly; ankle; geriatrics; ultrasound

INTRODUCTION

The prevalence of mobility impairment among old adults (age 65+ years) is profound; 17%, 28% and 47% of people aged 65–74, 75–84, and 85+ years respectively report that difficulty walking interferes with their daily activities (1). Walking impairment in our aging population is presumably governed by complex, interdependent combinations of neurological, physiological, and biomechanical factors and are further exacerbated in the presence of more acute pathologies (29). In particular, biomechanical changes in elderly gait have garnered considerable scientific attention for nearly 50 years (30), in part because these may point to specific translational opportunities for prevention and rehabilitation. However, despite considerable research efforts, the sizeable percentage of people over age 65 that report being unable to walk 2–3 city blocks (~18%) has not improved in at least the last 20 years (2). Thus, there is both a critical need and a considerable opportunity for innovation in the biomechanical study of age-related gait changes and the translation of our findings to preserving and restoring walking ability in our aging population.

This article will review recent advances in our understanding of aging effects on the biomechanics of walking and their underlying mechanisms. We begin by summarizing the hallmark biomechanical features of elderly gait, including one of it not the most universal and clinically relevant, a reduction in propulsive power generation (i.e., that generated by the trailing limb during push-off). We then examine the hypothesis that declines in force

jrfranz@email.unc.edu, phone: (919) 966-6119.

or power generating capacity of propulsive leg muscles cannot fully explain the age-related reduction in propulsive power generation during walking (Fig. 1). Based on our findings and those of others, we will present evidence that many old adults underutilize their available muscular capacity for generating propulsive power in walking with important translational implications. We then present promising new areas of study toward a more complete understanding of the biomechanical origins of compromised push-off performance in aging, including our recent findings regarding the role of plantarflexor muscle-tendon coordination. Finally, based on the available literature, we offer several recommendations for positively affecting walking ability in our aging population.

THE BIOMECHANICS OF ELDERLY GAIT

The effects of advanced age on the biomechanics of walking are well described in the literature, including the nicely articulated summaries of Winter et al. (1990) and McGibbon (2003). In brief, these authors (29, 44) and others (9, 11–13, 25, 28, 39) most often point to a reduction in mechanical power generated by the plantarflexor muscles during the push-off phase of walking as an important and functionally limiting impairment in elderly gait. Indeed, in young adults, the plantarflexor muscles generate 70–80% of the mechanical power needed for forward propulsion and swing initiation and are thereby critical for modulating speed and step length in walking (32). Consequently, the slower preferred speeds and shorter steps frequently ascribed to old adults follow at least in part from the precipitous 11–35% decline in plantarflexor power generation (9, 11–13, 25, 28, 39, 44) and corresponding ~26% decline in total trailing limb propulsive power generation (11) during push-off. These functional changes are highly relevant, as preferred walking speed ultimately predicts independence, number of hospitalizations, health care costs, and even lifespan (19, 34). Moreover, and as we elaborate below, the functional relevance of reduced propulsive power generation in elderly gait may extend beyond its potential role in reducing step length and slowing preferred walking speed.

Walking economy, measured as the rate of oxygen consumption per unit distance, deteriorates considerably with advanced age. Old adults consume oxygen 15–20% faster than young adults during walking. On average, approximately one-third of this increase can be explained by increased activity in the antagonist leg muscles of old adults (20, 33). However, a complete explanation for this reduction in walking economy has remained elusive. When plantarflexor power generation during push-off is experimentally reduced in young adults, for example via ankle bracing, an increase in the use of more proximal leg muscles for power generation is accompanied by dramatic increases in metabolic energy consumption (22). Huang et al. (2015) recently found that for every unit reduction in trailing limb propulsive power generation during push-off, hip and knee power generation during single support increased by an average of one unit and metabolic power by more than two units. This indirect evidence suggests that the age-related reduction in walking economy may be at least in part biomechanically mediated by unfavorable increases in proximal muscle recruitment that accompany reductions in plantarflexor power generation during push-off. Indeed, when walking at the same speed as young adults, numerous studies find that old adults rely more on proximal leg muscles for power generation, involving the hip extensors in early stance, knee extensors during single support, and/or hip flexors in terminal stance (7, 9, 12, 13, 25, 28, 29, 39).

With their simultaneous presentation, the redistribution to more proximal leg muscles for power generation in walking with age is generally considered a neuromuscular compensation to offset reduced plantarflexor power generating capacity in old adults. However, the observation that old adults generate less plantarflexor power in walking compared to young adults is not sufficient to conclude that these biomechanical changes emerge from a reduction in the force or power generating capacity of these propulsive muscles. In an early test of this hypothesis, Judge et al. (1996) reported that, compared to walking at their preferred speed, old subjects failed to generate more plantarflexor power when they increased walking speed to maximum. Though the authors do acknowledge the small sample of subjects, Judge et al. (1996) drew from their data a conclusion that continues to resonate through the biomechanics literature - that old adults walking at their preferred speed generate near maximal plantarflexor power. Indeed, the easiest explanation for the age-related reduction in propulsive power generation during walking is that old adults are constrained, even during normal walking, by the functional consequences of sarcopenia and plantarflexor muscle weakness. In the following section, we propose that those functional consequences alone cannot fully explain the reduction in trailing limb propulsive power generation during walking in old adults.

THE UNDERUTILIZATION OF PROPULSIVE CAPACITY IN WALKING

Inspired by the seminal works outlined above and many others, our ongoing studies examining aging effects on the biomechanics and muscular actions of walking predominantly focus on understanding the prevalence of and mechanisms governing age-associated reductions in propulsive power generation during walking. In some of our relatively recent contributions to these efforts, we have used an uphill walking paradigm to systematically increase the propulsive demands of walking and investigate the multi-scale biomechanical effects in groups of healthy young adults and otherwise healthy adults aged 65+ years (11–13). If old adults' propulsive power generation, in particular from the plantarflexor muscles, were near maximum during level-ground walking, then uphill walking would either present an insurmountable challenge, or would elicit remarkable compensatory biomechanical differences compared to young adults.

Consistent with earlier findings, old adults in our studies exhibited significant propulsive deficits compared to young adults during level ground walking, including reduced whole-body propulsive forces, trailing leg power generation, and ankle power generation during push-off. However, despite the emergence of reduced propulsive power generation during level ground walking, and despite 30–37% less isometric leg strength than young adults, old subjects retained a significant capacity to enhance metrics of propulsive power generation to walk uphill. Compared to level walking, old adults increased peak propulsive force by 69%, trailing leg push-off work by 115%, positive ankle work during push-off by 44%, and plantarflexor muscle activities by 75–136% to walk uphill at 9° (Fig. 2) (11–13). Moreover, and most surprisingly, increases in ankle and trailing limb power generation were nearly identical in magnitude between old and young adults, suggesting that both groups responded similarly to the increased propulsive demands of uphill walking (e.g., positive ankle work, old: +0.09 J/kg, young: +0.08 J/kg, p=0.85). Consequently, governed foremost by age-related differences during level walking, relative increases in these metrics for old adults during uphill vs. level walking were larger than those exhibited by young adults. Specifically, compared to level walking, young adults walking uphill at 9° averaged only 30% greater positive ankle work and 60% greater positive trailing leg work during push-off. Although in contrast to Judge et al. (1996), these observations are consistent with more recent studies demonstrating that old adults, even those with mobility impairment, can indeed enhance propulsive power generation, including power generated by the plantarflexor muscles, to walk faster over level ground (18, 28, 36, 39).

Cumulatively, these observations suggest that old adults may underutilize their available capacity to generate propulsive power when walking at preferred speeds. As a logical extension of our primary hypothesis, this would imply that old adults may retain the muscular potential to enhance propulsion during push-off, but lose the ability to instinctively recruit, or purposefully elect not to recruit, propulsive leg muscles to the extent observed in young adults. In a follow-up to these experiments, we recently used real-time visual biofeedback to more directly test whether old adults retain a considerable but underutilized reserve capacity for generating propulsive power during level walking (14).

We invited old adult subjects (n=8, age: 72 ± 4 years) to walk on a treadmill at a comfortable speed while watching a computer monitor displaying, in different conditions, their peak propulsive ground reaction force or mean gastrocnemius muscle activity during push-off, updated in real-time as an average every two steps. We encouraged subjects to increase their step-to-step values to match target lines representing 20% and 40% larger propulsive forces or MG muscle activity, and compared these values to reference data collected in young adults (21 ± 2 years). Walking normally, old adults in that study exerted 12.5% smaller peak propulsive forces than young adults ($p<0.05$). However, despite this apparent deficit, we discovered that biofeedback targeting the propulsive reserve of old adults predictably and significantly enhanced peak propulsive forces and plantarflexor muscle activities (Fig. 3). For example, using propulsive force biofeedback, a target 20% increase elicited peak propulsive forces in old adults that were indistinguishable from those in young adults (p=0.87) accompanied by a 42% increase in gastrocnemius muscle activity compared to normal walking. Also compared to normal walking, old adults averaged up to 26% larger peak propulsive forces and 50% greater gastrocnemius muscle activity to match the +40% target. Using EMG biofeedback, old subjects increased their gastrocnemius activity during push-off by 19% and 30% to match the +20 and +40% targets, respectively. Consistent with our hypotheses, these data suggest that old adults with propulsive deficits are not explicitly limited in their capacity to increase forward propulsion during level walking. Thus, the widespread reduction in propulsive power generation in old adults walking at their preferred speed must be governed by more than the age-related decline in force or power generating capacity of propulsive leg muscles.

MECHANSIMS UNDERLYING AGE-RELATED DECLINES IN PROPULSIVE POWER GENERATION

Like most physiological changes due to aging, the reduction in propulsive power generation during walking is presumably multifactorial, emerging from a combination of governing factors. Some factors, such as muscle weakness and reduced flexibility, have garnered significant attention and been the focus of clinical intervention. Others, such as altered triceps surae muscle-tendon coordination, are relatively recent discoveries. Although not exhaustive, in the following sections we briefly summarize a series of plausible and potentially interdependent mechanisms that may contribute to the age-associated reduction in propulsive power generation in walking.

Muscle force-generating capacity.

We have proposed that declines in force or power generating capacity of propulsive leg muscles alone cannot fully explain the age-related reduction in propulsive power generation during walking. However, sarcopenia is a pervasive consequence of aging and is often associated with functional declines in strength that may contribute in part to biomechanical gait changes (5). Several studies (3, 35, 37) have used a concept defined by some authors as functional capacity utilized (FCU) to investigate these contributions. The FCU is computed, for muscles crossing a given leg joint for example, as the ratio of the net muscle moment, power, or EMG activity during walking to maximum values assessed during isometric or isokinetic contractions using a dynamometer. Curiously, FCU calculations for the propulsive plantarflexor muscles during walking often exceed 100%, even for healthy young adults. Very recently, Kahn et al. (2015) concluded that measures obtained during isolated plantarflexor strength testing lacked predictive relevance to the emergence of inter-individual differences in propulsive power generation in walking (26). One explanation is that plantarflexor muscle contractile behavior during walking is highly dynamic and may not be well represented by isometric or isokinetic conditions. Silder et al. (2008) did find that maximum isokinetic plantarflexor moments accounted for only 25% of the variance in plantarflexor power generation for old adults walking at their preferred speed. These findings are in general agreement with the earlier findings of Bassey et al. (1988), who reported that plantarflexor strength accounted for only 17% of the variance in old adults' preferred walking speed (4). Most recently, Hortobagyi et al. (2016) used an elegant design of cohorts including relatively "strong" and "weak" old and young adults to reveal that leg muscle weakness explained up to 39% of the redistribution to more proximal leg muscles for power generation in walking (21). Intuitively, muscle-force generating capacity may play a larger role in age-associated declines in propulsive power generation when muscular demands for propulsion are increased. Indeed, Silder et al. (2009) reported that their correlation between strength and plantarflexor power generation in walking increased to 52% for old adults walking at speeds faster than preferred. In summary, accounting for declines in muscle force-generating capacity alone, a significant portion of the variance in propulsive power generation in old adults during walking is left unexplained.

Hip Extension Flexibility.

Kerrigan et al. (e.g., 1998) have been a strong proponent of reduced hip extension flexibility as a functionally limiting impairment in elderly gait, one that indirectly contributes to old adults generating less ankle power than young adults walking at the same speed. Their conceptual premise arises from the increased prevalence of subtle hip flexion contractures in our aging population. As summarized by McGibbon et al. (2003), hip flexor tightness in old adults would limit peak hip extension range of motion during the late stance phase of walking, thereby reducing step length and thus propulsive power generation and preferred walking speed. More recently, in a collaboration led by Dr. Kerrigan, we implemented a double-blind, randomized controlled trial to determine whether a supervised, 10-week hip flexor stretching program would improve gait biomechanics in cohorts of 82 healthy and 74 mobility-impaired old adults (e.g., 43). In these studies, static evaluations revealed that hip flexor stretching significantly and predictably increased the passive range of hip extension available to old adults by an average of 22% ($p<0.01$), whereas no change was observed in control groups. While promising, only a small subset of old adults presenting with reduced hip extension range of motion prior to treatment increased their peak hip extension and step length during walking. Moreover, improvements in hip extension range of motion following treatment were not accompanied by increases in ankle moment or power generation during push-off. One interpretation of these findings is that many old adults failed to instinctively utilize newfound improvements in hip extension range of motion during walking, which led to invariant propulsive leg joint kinetics. In contrast, by quantifying passive contributions to joint moments in walking, Silder et al. (2009) concluded that age-related differences in leg joint kinetics do not arise as a result of increase passive hip joint stiffness in old adults. Therefore, the contribution of hip extension flexibility to age-associated changes in propulsive power generation remains equivocal.

Muscle-tendon adaptation.

Conventional gait analysis has yielded tremendous insight into the age-associated reduction in propulsive power generation during walking. More recently, advances in the use of ultrasound imaging are rapidly accelerating our understanding of the complexities of muscle and tendon dynamics *in vivo* during human movement and changes thereof due to aging. Narici and Maganaris (2007) present an eloquent summary of aging effects on muscle and tendon architecture and material properties, particularly those of the propulsive plantarflexor muscles via ultrasound imaging (31). Regarding their functional relevance, Stenroth et al. (2015) identified several plantarflexor muscle-tendon properties, for example gastrocnemius fascicle length and Achilles tendon stiffness, that were independently associated with performance on the 6 min walk test in people aged 70–81 years (40).

Our recent contributions to these efforts have focused on investigating *in vivo* Achilles tendon (AT) behavior during walking and its relevance to reduced triceps surae mechanical performance due to aging (16, 17). The AT is a complex structure, consisting of distinct fascicle bundles arising from each triceps surae muscle that may act as mechanically independent structures (41). Compared to young tendons, old tendons are thought to exhibit a reduced capacity for inter-fascicle sliding, potentially arising from a proliferation of collagen cross-linking and inter-fascicle adhesions (42). Consistent with observations in isolated tendon, our use of motion capture-guided ultrasound imaging and novel 2D speckle tracking has revealed that old adults exhibit smaller differences in AT tissue deformations during walking than young adults between regions of the tendon presumed to arise from the gastrocnemius and soleus muscles (Fig. 4) (See (17) for a comprehensive summary). Based on these age-associated changes in tendon deformations, we suspect that old adults are susceptible to a loss of mechanical independence of the gastrocnemius and soleus muscles. Perhaps consequently, we find that more uniform AT deformations most strongly correlate with age-related reductions in ankle moment (R^2=0.40, p<0.01) and also correlate, albeit to a lesser extent, with peak ankle power (R^2=0.15, p<0.01) and positive work during push-off (R^2=0.19, p=0.01).

How might Achilles tendon deformations influence propulsive power generation in walking? Our cumulative evidence suggests that altered tendon deformations do not necessarily preclude old adults from deliberately increasing plantarflexor muscle activities or power generation when walking faster, uphill, or with biofeedback. However, the gastrocnemius and soleus muscles do exhibit markedly different fascicle kinematics during the stance phase of walking and contribute differently to forward propulsion and vertical support (10, 24). Thus, if gastrocnemius and soleus muscle actions are unfavorably coupled via age-related changes in the AT, old adults may be unable to optimally modulate relative levels of propulsion and vertical support during push-off. Indeed, our recent model predictions suggest that adhesions in the Achilles tendon of old adults may act to redistribute mechanical performance from the gastrocnemius to the soleus muscle in a manner consistent with changes in muscle fascicle kinematics (17). Thus, for the same neural excitation, a reduced capacity for inter-fascicle sliding in the aging Achilles tendon may preferentially influence the triceps surae’s ability to generate forward propulsion during walking, an important function of the gastrocnemius muscle. Unfavorable shifts in gastrocnemius or soleus muscle fascicle lengths and velocities with aging could also yield a greater metabolic cost of generating a given ankle moment or power. These changes could subsequently yield an instinctive reduction in propulsive power generated during the push-off phase of walking despite the availability of propulsive reserves. However, while promising, our imaging results and model predictions thus far require future experimental validation, likely including comparative studies combined with multi-scale imaging and image-based modeling techniques.

Dynamic balance control.

What if reductions in propulsive power generation, rather than driven by age-related musculoskeletal constraints, are instead governed by potentially purpose-driven changes to preserve walking balance in response to altered neural control? Winter et al. (1990) framed their seminal review largely in this context – that the hallmark biomechanical features of elderly gait, including reductions in propulsive power generation, reflect the adoption of a safer, more stable pattern of movement. Indeed, old adults are at an exceptionally high risk of debilitating falls, and may opt to change their gait to abate those risks. To our knowledge, only Kerrigan et al. (27) explicitly compared leg joint kinetics in walking between old adults with and without a history of falls while controlling for walking speed. Those authors found that old adults with a history of falls generated 22% less ankle power during push-off than old adults without a history of falls when walking at similar speeds. However, using a conservative statistical approach, this difference did not reach significance.

The largest biomechanical difference between old adults with and without a history of falls reported by Kerrigan et al. (2000) was that fallers walked with more pronounced increases in hip joint moments and power generation during the stance phase. Some evidence suggests that proximal leg muscles, such as those crossing the hip joint, are under greater feedforward (i.e., predictive and insensitive to afferent information) control than the more distal plantarflexor muscles (8). Age-related falls risk, while most certainly multifactorial, may arise at least in part from sensorimotor decline and a preferential loss of feedback control of distal leg muscle forces (38). We have used these ideas to suggest that old adults' reliance on more proximal leg muscles during walking may arise in part from a shift toward the preferential use of a feedforward recruitment strategy (12). Complementary evidence from other studies suggests that old adults may be most susceptible to distal sensorimotor decline near the instant of push-off, the phase in which the control of inter-joint coordination is most compromised by aging (23). However, old adults do retain the capacity to enhance their propulsive power generation and appear to do so when faced with overriding task requirements, such as walking faster, uphill, or with biofeedback. Thus, the underutilization of propulsive capacity during walking by old adults suggests that there may be a tradeoff between propulsive power generation and walking balance control. However, while in line with the context provided by Winter et al. (1990), the presence of this tradeoff requires more rigorous experimental validation, possibly through the use of sensory or mechanical perturbations during walking and future studies using biofeedback to modulate propulsive power generation.

IMPLICATIONS AND FUTURE DIRECTIONS

Evidence suggests that declines in the force or power generating capacity of propulsive leg muscles in old adults cannot fully explain age-associated reductions in propulsive power generation during the push-off phase of walking. Thus, despite the functional consequences of sarcopenia and leg muscle weakness, many old adults appear to retain a significant but underutilized capacity for generating forward propulsion in walking. This new hypothesis has clear implications for the prevention and/or treatment of age-related mobility loss. While resistance training exercises are often prescribed and consistently improve muscle strength and mitigate sarcopenia, strengthening alone generally fails to directly translate to improved propulsive power generation or improved speed in walking (6). This is perhaps not altogether surprising; muscle strengthening alone may only act to further increase the already sizeable propulsive reserve available to old adults in walking. Indeed, techniques to quantify the extent to which one underutilizes their propulsive capacity in walking could be a valuable diagnostic tool. Similarly, hip flexor stretching, although evidence-based, leads to improvements in flexibility that are not consistently accessed by old adults during walking to enhance propulsive power generation or walking speed (43). Together, these findings suggest that the age-associated reduction in propulsive power generation during walking, despite limiting walking speed and perhaps incurring a metabolic penalty compared to young adults, is highly resistant to change.

Here, we present several recommendations based on the available literature for positively affecting walking performance in our aging population. First, rehabilitative approaches for age-related mobility impairment should go beyond resistance training and stretching alone, toward intuitive and more direct means to elicit favorable biomechanical adaptations in walking. For example, real-time biofeedback during walking that targets impairments in propulsive power generation in old adults can effectively and predictably enhance plantarflexor muscle activities and propulsive ground reaction forces during walking. Our ongoing work seeks to determine if these improvements are retained and translate to, for example, increased preferred walking speeds and improved walking economy. For sedentary and/or frail old adults, the functional limitations imposed by leg muscle weakness and/or hip flexion contracture may be more acute. Therefore, we recommend that in these groups, more conservative therapies such as resistance training or hip flexor stretching be coupled with innovative techniques to encourage improved utilization of newfound strength or flexibility gains. Second, investigating the functional relevance of inter-fascicle adhesions in the aging Achilles tendon may inform preventative or restorative therapies to better maintain mechanical performance of the plantarflexor muscles in old age. These may include the potential for activities such as running to prevent the onset of inter-fascicle adhesions or physical therapy to promote independent actuation of the gastrocnemius and soleus muscles. Finally, equally important to asking how we can improve various biomechanical aspects of walking in old adults is asking whether we should intervene at all. An important future contribution will be experimental evidence regarding tradeoffs between propulsive power generation and walking balance control. It seems highly plausible that therapies that enhance forward propulsion in walking can elicit favorable and functionally relevant biomechanical changes in elderly gait but, beyond some threshold, at the expense of dynamic balance.

CONCLUSIONS

Through the integrative use of quantitative motion capture, electromyography, dynamic *in vivo* imaging, and computational modeling, we and others continue to investigate the prevalence of and mechanisms governing age-associated reductions in propulsive power generation during walking. In contrast to some conventional perspectives, we now hypothesize that many old adults underutilize their available muscular capacity for generating propulsive power in walking, which may have important diagnostic and translational implications. Despite having been the focus of research efforts for more than 50 years, there remains considerable opportunity for innovation in the biomechanical study of age-related gait changes toward translation of our findings to preserving and restoring walking ability in our aging population.

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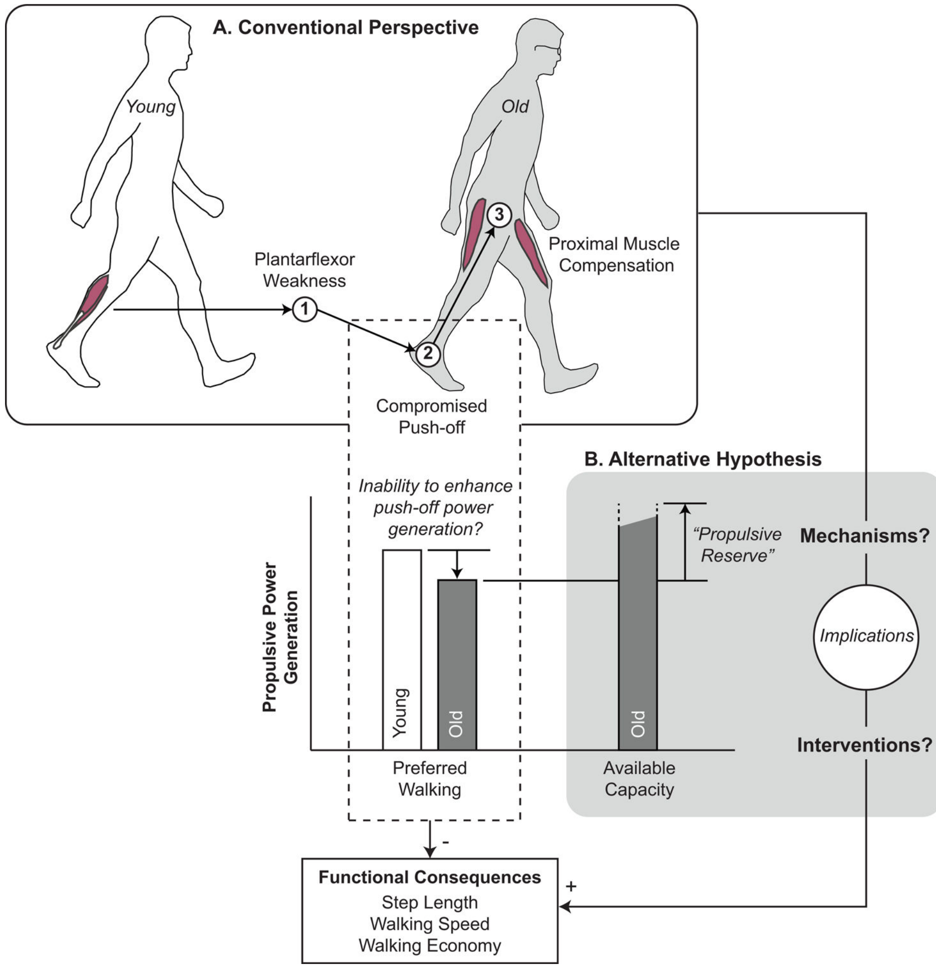

Figure 1.

(A) The easiest explanation for the age-related reduction in propulsive power generation during walking is that old adults are constrained, even during normal walking, by the functional consequences of sarcopenia and plantarflexor muscle weakness. (B) In contrast, we hypothesize that declines in the force or power generating capacity of propulsive leg muscles alone cannot explain the age-associated reduction in propulsive power generation during the push-off phase of walking. Based on our findings and those of others, a logical extension of this hypothesis is that many old adults underutilize their available muscular capacity for generating propulsive power during push-off in walking with important translational implications.

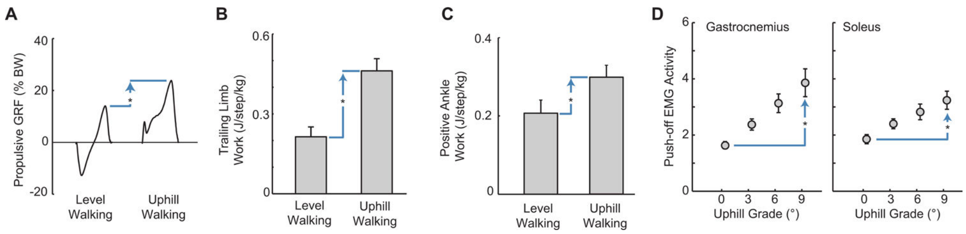

Figure 2.

In a series of studies (11–13), we used an uphill walking paradigm to systematically increase the propulsive demands of walking and investigated the multi-scale biomechanical effects in groups of healthy young adults and otherwise healthy adults aged 65+ years. Despite the emergence of reduced propulsive power generation during level ground walking, and despite 30–37% less isometric leg strength than young adults, old subjects in these studies retained a significant capacity to enhance metrics of propulsive power generation to walk uphill. Compared to level walking, old adults could increase (A) peak propulsive force by 69%, (B) trailing leg push-off work by 115%, (C) positive ankle work during push-off by 44%, and (D) plantarflexor muscle activities by 75–136% to walk uphill at 9°. Uphill walking in panels A-C refer to a 9° grade. EMG signals in Panel D are normalized the average values during a level walking stride.

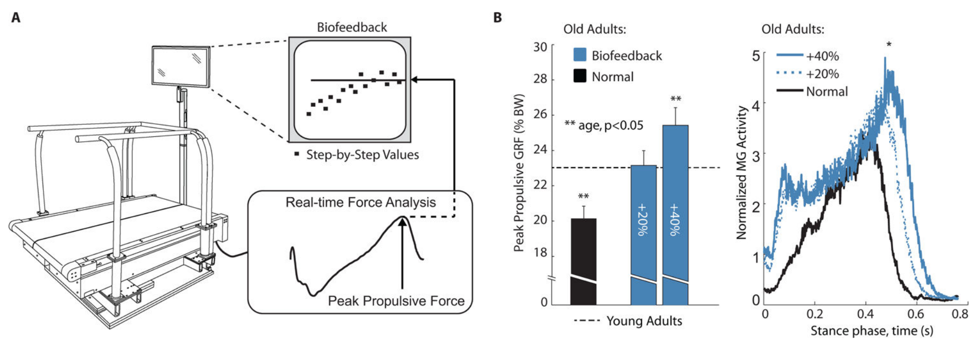

Figure 3.

(A) We designed and implemented a custom biofeedback system, based on real-time ground reaction force measurements, to target the propulsive reserve of old adults and enhance their propulsive power generation in walking. (B) The use of biofeedback encouraged old adults to exert propulsive forces that were equal to (i.e., +20% target) or greater than (i.e., +40% target) those of young adults walking at the same speed. These changes in the peak propulsive forces of old adults were accompanied by significant increases in plantarflexor muscle activities during push-off. Adapted from (14).

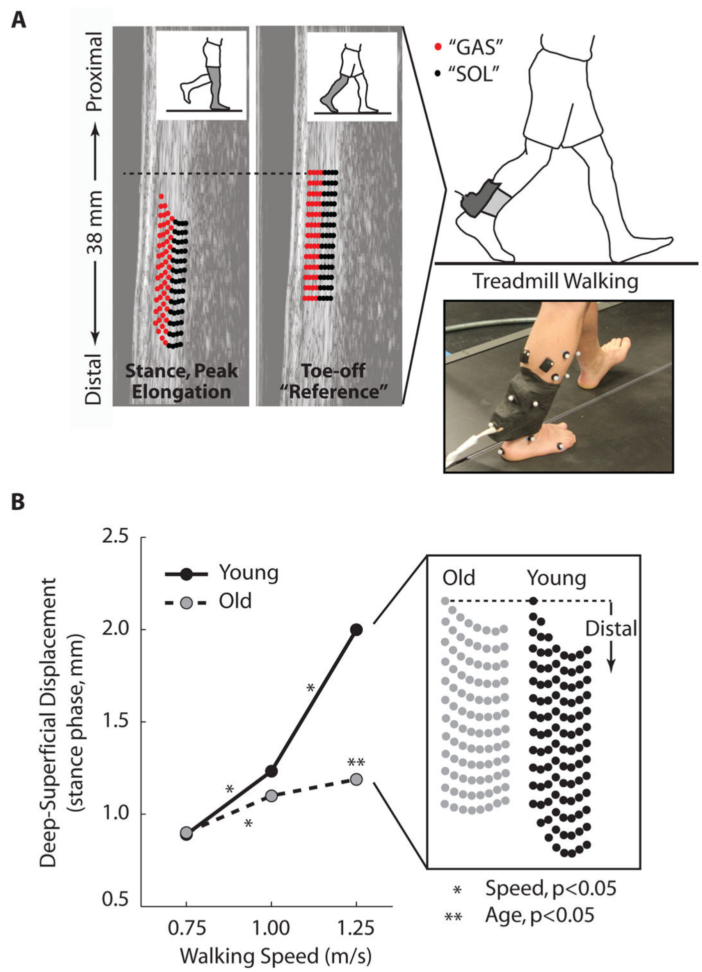

Figure 4.

(A) We used dynamic ultrasound imaging and a custom 2D speckle tracking algorithm to quantify localized in vivo deformations of the Achilles free tendon in groups of young and old adults (15, 17). The Achilles tendon is comprised of distinct bundles of fascicles arising from the medial and lateral gastrocnemius ("GAS") and soleus ("SOL") muscles that may act as mechanically independent structures (41). (B) During walking, the AT of young adults exhibits behavior indicative of sliding between adjacent tendon fascicles, evidenced by kinematic differences between superficial and deep regions of the tendon presumed to arise from the gastrocnemius and soleus muscles, respectively. Old adults exhibit smaller differences in tissue deformations between these tendon regions, which may arise from a proliferation of collagen cross-linking and inter-fascicle adhesions observed in isolated tendon preparations.