

**ENERGY COST OF INDIVIDUAL LOWER LEG MUSCLES IN WALKING:
COMPARISON BETWEEN YOUNG AND ELDERLY MEN AT DIFFERENT
WALKING SPEEDS**

Patricio Pincheira

Patricio Pincheira

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Department of Biology of Physical Activity

University of Jyväskylä

Supervisors: Neil Cronin and Janne Avela

ABSTRACT

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The cost of transport (COT) in elderly subjects is increased in comparison to young adults, independently of the walking speed. The changes in the neuromuscular activity of the lower extremity muscles could explain this phenomenon. The objective of this thesis was to qualitatively compare the muscle activity pattern of the lower extremities between healthy young and elderly subjects, over a range of walking speeds in order to infer the contributions of individual muscles to changes in COT in both age groups.

26 participants were recruited (13 young aged 18-30; 13 old aged 70-80). Mean oxygen consumption was used to calculate COT and electromyography signals from 10 leg muscles were used to calculate the cumulative muscle activity per distance traveled (CMAPD) for each muscle, over seven walking speeds.

At the group level, COT was higher for most speeds in the old group, and qualitative analysis implies the same trend for CMAPD. Young and old had speed-dependent changes in COT occurring in parallel with changes in mean CMAPD of all tested muscles. At muscle level, in both groups most of the muscles exhibited higher CMAPD at speeds faster and slower than the energetically optimal, whereas soleus CMAPD was independent of speed. Proximal muscles such as vastus lateralis presented a higher correlation between CMAPD and COT. These results suggest that soleus CMAPD may be relatively independent of age. The metabolic cost of contraction in proximal leg muscles seems to make a relatively large contribution to changes in COT regardless of age.

Keywords: Cost of Transport, Muscle Metabolism, Electromyography, Aging.

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1. INTRODUCTION

A parameter that characterizes locomotion is the metabolic cost of transport (COT), which can be defined as the energetic cost needed to travel a given of distance. The COT strongly depends on walking speed: it is minimized at intermediate speeds of 4.5–5.4 km·h⁻¹ and rises rapidly as speed increases above or decreases below this optimum, showing a characteristic “U”- shaped curve. In elderly subjects even in those who are healthy and free from gait impairment, the COT is increased in comparison to young adults, although the U shaped COT versus walking speed relation is still evident. In addition to being less economical walkers, older adults generally exhibit a decline in muscle strength and maximum metabolic capacity. Thus, older adults perform activities of daily living at a higher level of effort relative to their maximum capability, which can lead to fatigue, reduced ability for physical activity and increased potential for accidents.

The mechanisms involved in this the age-related decrease in gait economy remains unclear. Several investigations have revealed that increased COT in the elderly is not related to mechanical parameters and that changes in the neuromuscular activity of lower extremity muscles are more likely to explain this phenomenon. Altered coactivation and increased electromyographic (EMG) activity around the knee and ankle joints has been found to be correlated with the increased COT in elderly subjects. However, there is a gap in the literature about how the activity of individual muscles activity is related to COT in both young and older populations.

A reasonable inference is that the majority of the increase in COT during locomotion, results from increases in the energy cost of active motor muscles. However, the distribution of energy consumption among and within these muscles remains unknown. Despite the obvious utility of measuring the energy use of the individual muscles during locomotion, technical difficulties have hampered these measurements. Direct approaches are invasive, technically demanding and mostly used in animal models. Indirect methods, commonly try to characterize muscle metabolism during walking using computational models. These approaches have revealed complex

patterns of energy use across the gait cycle. However, they are unable to accurately predict net and/or gross cost during walking, and there is an inherent difficulty in validating the individual-muscle predictions that are of primary interest.

An alternative option involves the use of Electromyography (EMG). Because EMG amplitude indicates the state of activation of the contractile element, it can provide a relative measure of muscle metabolism. Recently it has been demonstrated that this tool is capable of indirectly estimating the metabolism of individual muscles with high temporal resolution (Blake & Wakeling, 2013). Thus, the aim of this study was to estimate the energy cost of individual leg muscles comparing healthy young and elderly subjects, in an attempt to determine which muscle(s) contribute to walking speed dependent changes in COT. To achieve this objective, we used the integrated muscle activity per distance traveled (CMAPD), an EMG tool that provides a correlative indication of muscle metabolism. This information could shed light on the causes of increased COT in elderly walking. We hypothesized that higher COT in older adults would be related to higher CMAPD of some or all muscles across the range of speeds investigated, and that there would be different trends in the individual muscle CMAPD behavior when comparing between age groups.

2. MOVEMENT ECONOMY

One of the most robust characteristics of the everyday performance of motor skills is the propensity to complete the task with the least energy expenditure, being minimization of energy or work an organizing principle common to natural phenomena (Sparrow & Newell, 1998). Economical movements are those that achieve the task goal with relatively low metabolic energy expenditure for the given task demands, and it has been proposed that similar principles underlie the development of biological systems (Sparrow & Newell, 1998). From all possible movement sequences, humans and other organisms tend to adopt a coordination and control solution that is economical in terms of energy expenditure, to accommodate the task and environment constraints that are imposed (Sparrow & Newell, 1998). In this context, metabolic energy expenditure might provide insights into the organization of movement. Two possibilities were raised to account for the efficiency of movement skill: First, that metabolic energy expenditure per se is not regulated, but, rather, is minimized as a consequence of increased proficiency at a motor task (Miller et al. 2012); Second, that efficiency of performance may be viewed as a condition which specifies a priori a particular biokinematic organization of the organism (Sparrow & Newell, 1998). Nevertheless, the mechanisms of how organismal energy is optimized are still unclear.

2.1 Basic Definitions

2.1.1 Movement efficiency

Several definitions of efficiency have been used in the literature, commonly related with one particular motor task such as walking (Ingen Schenau et al. 1997). However is common to define efficiency as the ratio of mechanical work done to metabolic energy expended, (often expressed as a percentage) according to the formula:

$$\text{Efficiency} = W_{\text{tot}} / E$$

where W_{tot} is the total positive work (sum of *external work and internal work*) and E is metabolic energy expenditure.

Efficiency in this equation represents the amount of metabolic energy that is converted into work to meet task demands, with the remainder lost as heat (McArdle et al. 2010 p-208). However mechanical work is difficult to measure in most of the models (Ingen Schenau et al., 1997) mainly due to three reasons: 1) When it is computed from increments in the body center of mass and/or segment mechanical energies, it suffers from uncertainties: The internal and external work are not necessarily independent, and the degree to which they overlap in some motor tasks (e.g. walking) is unknown (Umberger & Martin, 2007). 2) Mechanical work calculated by treating the body as a point-mass (the product of body mass and distance traveled, divided by time) is insensitive to variations that depend on how the limbs are moved (Sparrow & Newell, 1998) 3) When it is computed with the positive and negative work done by each of the lower limb joint moments, it is not possible to resolve cocontraction of antagonistic muscles (Umberger & Martin, 2007). This whole means that the calculation of mechanical work is not straightforward. The denominator of the efficiency equation is metabolic energy expenditure. Metabolic energy is derived from food (mainly fat and carbohydrates), that is converted to chemical energy, which in turn is converted to mechanical energy through muscular contraction (McArdle et al., 2010 p-123; Sparrow & Newell, 1998). When energy is expended in muscular contraction, heat is produced, and the amount of heat produced by food metabolism is equivalent to the heat liberated by the body. In this process oxygen is consumed, that can be used as an indirect method for determining heat production, commonly through indirect calorimetry (McArdle et al., 2010 p-180)

2.1.2 Economy

Economy can be defined as the metabolic energy expended to achieve the task goal (Sparrow & Newell, 1998) or to maintain a constant velocity (McArdle et al., 2010 p-207). This concept is more useful than efficiency, because the complexity of accurately measure the mechanical work done (Miller et al., 2012; Umberger & Martin, 2007). Heat energy can be calculated on the basis of the volume of oxygen consumed and the type of food metabolized, therefore calculated by calorimetry and usually reported as oxygen consumption per unit of body mass (McArdle et al., 2010 p-241; Sparrow & Newell, 1998). Thus, the term economy is used to make comparisons in terms of oxygen consumption per unit of body weight for performing a given task (Sparrow & Newell, 1998). A subject with greater economy consumes less oxygen.

2.2 General considerations about movement economy

An organism's movements are characterized as emerging from the interaction of environment, task and organism constraints. Environment constraints are those external to the organism that impose metabolic energy demands directly rather than through the task (e.g. illumination, noise) (Sparrow & Newell, 1998). Organism constraints can be defined with respect to any perceptual, physical, or cognitive parameters and at any level of analysis (from behavioral to cellular) that impose physical limitations on the body's ability to perform mechanical work that meets task demands (Sparrow & Newell, 1998). Task constraints are classified in three types: rule-constrained tasks, in which the performer is constrained in achieving a task goal by rules that constrain the nature of the movement output (i.e. ball games); machine and implement constrained tasks, in which implements or machines are used, such as tools and vehicles; and biomechanically constrained tasks: when the motor response does not involve an implement, the biomechanical parameters that define the task are the constraints. (e.g. running, walking) (Sparrow & Newell, 1998). It is proposed, that

the process of movement adaptation is guided by minimum metabolic energy criteria, so that task and environment constraints are accommodated with minimum metabolic cost. In addition to intrinsic sensory information about the state of the body, informational support for metabolic energy regulation is provided by the task and the environment (Figure 1). (Sparrow & Newell, 1998)

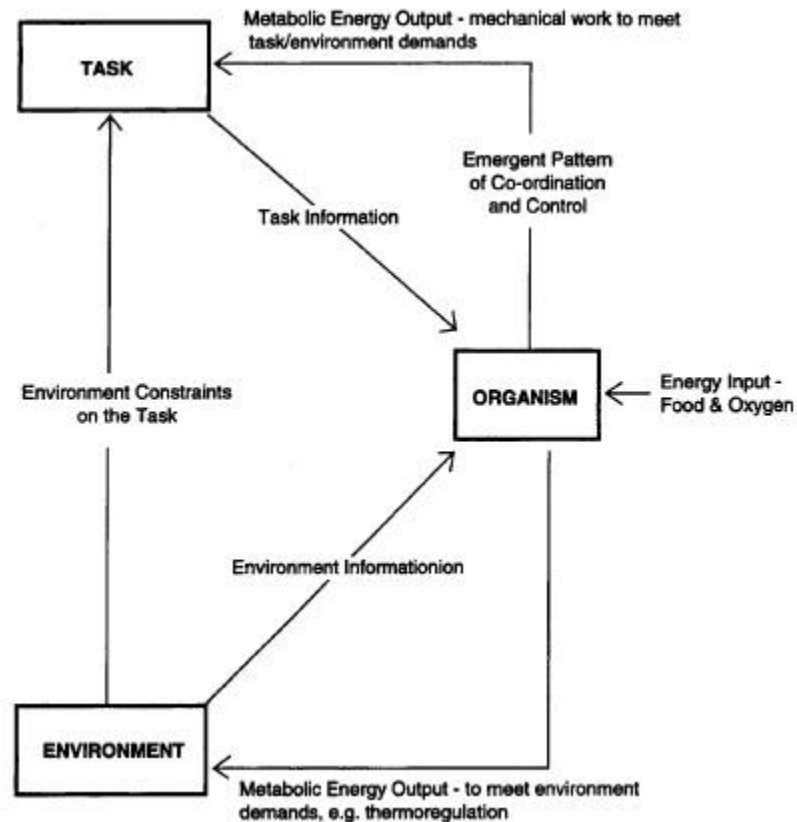


FIGURE 1. A constraints-based framework of metabolic energy expenditure and motor coordination and control (from Sparrow & Newell, 1998).

2.2.1 Self-optimization

It has been shown that in the short term, organisms adopt a movement pattern that minimizes metabolic energy expenditure. This process has been referred to as self-optimization, which suggests that economical movements can be established without augmented information about the performer's cardiorespiratory response to exercise

(Sparrow & Newell, 1998). Early studies by Cavanagh & Williams, (1982) in the effect of stride length variation on oxygen uptake during distance running, showed that the efficient patterns used by subjects during unrestricted running, indicate either an adaption to the chosen stride length through training or a successful process of energy optimization (Cavanagh & Williams, 1982). Tseh and colleagues (2008) demonstrates that specific biomechanical manipulations can produce substantive increases in the oxygen cost (VO_2) of submaximal running in female distance runners (Tseh et al. 2008). The two most likely explanations were either that humans are sensitive to metabolic cost and adopt a preferred pattern on the basis of such sensory information or that, preferred behaviors emerge from stability considerations (Sparrow & Newell, 1998). Even, some authors suggest a complementary relationship between energetic (physiological) and stability constraints in the adoption of a preferred strategy (Holt et al., 1995). However the question remains about the physiological processes that allow us to select preferred modes.

2.2.2 Movement economy and learning

Many theories of motor control suggest that movements are refined so as to minimize energetic cost (Finley et al., 2013). With practice, organisms learn to adapt movements in order to achieve the task goal with the least metabolic energy expenditure and therefore greater economy, because the relief from the distress associated with responding repeatedly. This is synthesized in the “Law of less effort” proposed by Hull (1943) (in Sparrow & Newell, 1998) “If two or more behavior sequences, each involving a different amount of energy consumption or work (W), have been equally well reinforced an equal number of times, the organism will gradually learn to choose the less laborious behavior sequence leading to the attainment of the reinforcing state of affairs” (Hull, 1943, p-294).. Recently, Finley et al., (2013) showed that motor learning robustly increases the economy of locomotion during split-belt treadmill adaptation, and demonstrated that reductions in metabolic power scale with the magnitude of adaptation are also associated with a reduction in muscle activity throughout the lower limbs (Finley et al., 2013).

2.2.3 The role of sensory information in movement economy

Sensory information from receptor organs, resulting from any posture or movement, is utilized to regulate movement economy, being interoceptors the most important sensory structures. Converging evidence indicates that interoceptive homeostatic afferent activity reflects all aspects of the physiological condition of all tissues of the body (Craig, 2003), being even capable of modify motor behavior (Casanova et al., 2013). Several interoceptors act during movement and physical activity. The cardiovascular center in the brainstem medulla, receives reflex sensory feedback from peripheral receptors in blood vessels, joints, and muscles. Chemoreceptors and mechanoreceptors within muscle and its vasculature monitor its chemical and physical state (McArdle et al., 2010 p-288). This input modifies either vagal (parasympathetic) or sympathetic outflow to bring about appropriate cardiovascular and respiratory responses to various intensities of physical activity. Activation of chemically sensitive afferents within the muscle's interstitium helps to regulate sympathetic neural activation of muscle during submaximal exercise. Metabolites produced primarily during the concentric phase of muscular activity stimulate this metaboreflex (McArdle et al., 2010 p-332). The organism could use this information to choose the least effortful coordination and control function. With practice, the selected control parameters are refined to attain the task goal with less metabolic energy expenditure related with the "Law of less effort" (Brener & Mitchell, 1989; Hull, 1943).

3. METABOLIC COST OF TRANSPORT

Locomotion is a unique feature of the animal kingdom. It allows individuals to socialize, find food or escape danger. Legged locomotion is not particularly efficient because the limbs need to be continually repositioned on the ground and the velocity of the foot falls to zero at each step (Saibene & Minetti, 2003). However, legs offer several advantages, making it possible to move on any kind of terrain, overcome obstacles, climb, etc. Human locomotion is characterized by two principal gaits, walking and running. The basic features of the two modes of progression are the same: each step presents one phase of stance and one of swing, but they differ as the leg controllers have two separate modes of operation for walking and running (Saibene & Minetti, 2003). The timing of the events in the cycles are different, the stance of each foot is longer in walking and shorter in running, although the swing shows the opposite trend. In walking there is always at least one foot on the ground, in running there is a period during which both feet are off the ground, and the amplitudes of the contractions of the flexor and the extensor muscles during the two phases of the step are different (Saibene & Minetti, 2003; Vaughan et al., 1992). While the goal of locomotion is progression in the forward direction, limb motion is based on the need to maintain a symmetrical, low amplitude displacement of the center of gravity of the head, arms, and trunk in the vertical and lateral directions. This conserves both kinetic and potential energy, according with the principle of biological 'conservation of energy' (Waters & Mulroy, 1999)

A parameter that characterizes any type of animal locomotion is the the Metabolic Cost of transport (COT), which can be defined as the energetic cost divided by distance traveled or speed (Waters et al., 1988). To compare subjects of different size, the COT is usually expressed as the quotient of net metabolic power divided by the product of speed times body weight (body mass times acceleration due to gravity).

The relationship between walking and running with the energy expended has been extensively studied since the early sixties (Cotes & Meade, 1960; Margaria et al., 1963). These studies have revealed that COT strongly depend on walking speed, which have been confirmed later (Cunningham et al., 2010; Fellingham et al., 1978; Holt et al., 1995). The COT is minimized at intermediate walking speeds of 4.5–5.4 $\text{km}\cdot\text{h}^{-1}$ (1.25–1.5 $\text{m}\cdot\text{s}^{-1}$) and rises rapidly as speed increases above or decreases below this optimum, showing a ‘U’-shaped curve (Figure 2) (Bramble & Lieberman, 2004). In other hand, the metabolic cost to run a given distance is generally recognized to be independent of speed in humans (Cunningham et al., 2010; Margaria et al., 1963) with the exception of one study by Steudel-Numbers & Wall-Scheffler, (2009) who found that individual humans have speeds at which running is significantly less costly than at other speeds (Steudel-Numbers & Wall-Scheffler, 2009).

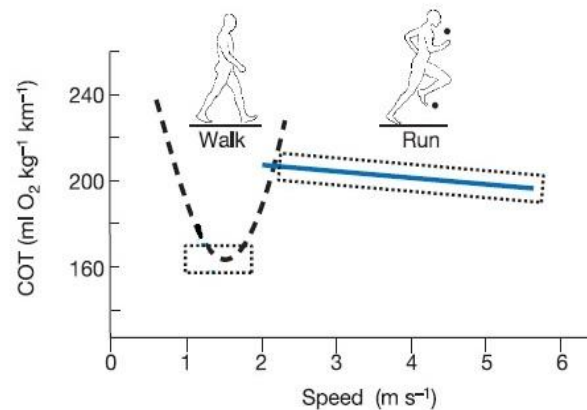


FIGURE 2. Metabolic cost of transport (COT) in humans. There is a U-shaped COT curve for walking, but the COT is essentially flat at running speeds. Preferred speeds (dotted rectangles) correspond to the most energy-efficient speeds being speed selection unrestricted in running. Note also that human running, involves synchronized movements of diagonally opposite appendages (dots) (Adapted from Bramble & Lieberman, 2004)

As previously mentioned, COT depends on walking speed. There are at least two reasons for this relationship (Carrier et al., 2011): 1) the force that a muscle generates decreases as its shortening velocity increases in a hyperbolic relationship; this means

that muscle's capacity to perform work and its energetic efficiency are highest at intermediate shortening velocities; and 2) during walking, the pendular transfer of kinetic and potential energy is greatest at intermediate speeds (Carrier et al., 2011; Cavagna et al., 1977). Thus, the observed energetically optimal walking speeds are consistent with the contractile physiology of skeletal muscle and biomechanics of terrestrial locomotion (Carrier et al., 2011)

3.1 Evolutionary specializations for minimization of COT

Humans have walked by at least 4.4 million years (Bramble & Lieberman, 2004; Ward, 2002), being minimization of energetic cost the primary goal of human walking (Alexander, 2002). Detailed analyses of the existing fossil samples and comparative studies with bigger apes revealed that through evolution humans have gotten many musculoskeletal specializations for bipedalism. Bramble & Lieberman, (2004) have nicely reviewed these modifications.

In contrast to apes, human legs have many long spring-like tendons connected to short muscle fascicles that can generate force economically (Thorpe et al., 1999), saving approximately 50% of the metabolic cost of running (Alexander, 1991), being the most important the Achilles tendon. Long legs benefit walking by increasing optimum walking speed, but they also increase ground contact time in both walking and running. The inverse of contact time has been found to correlate across species with the energetic cost of running (Alexander, 1980).

Humans have larger articular surface areas in most joints of the lower body in order to lower joint stress (Jungers, 1988). Another possible modification is the enlargement of the pelvis and calcaneal tuber, for resisting the stresses associated with running (Rose, 1984). Moreover, there are a number of derived features that enhance trunk stabilization including: expanded areas on the sacrum and the posterior iliac spine for the attachment of the large erector spinae muscles; and a greatly enlarged gluteus maximus (Rose, 1984). The latter muscle, whose increased size is

among the most distinctive of all human features, is strongly recruited in running at all speeds (Cavanagh, 1990).

Hominids possess many derived features related to heat dissipation, including elaboration and multiplication of eccrine sweat glands, reduced body hair, elongated body form (Ruff, 1991), and possibly an elaborated cranial venous circulation (Falk, 1990). Another derived feature is the tendency for mouth breathing (but not panting) during strenuous activity (Niinimaa et al., 1980). Considering all the evidence together, it is reasonable to hypothesize that humans evolved to travel long distances by both walking and running (Bramble & Lieberman, 2004) minimizing COT.

3.2 Mechanical parameters related to energetics of locomotion

As mentioned above, the interconversion of kinetic and gravitational potential energy as observed in an inverted pendulum, it is a mechanical method that is employed to minimize energy expenditure during terrestrial locomotion (Cavagna et al., 1977; Hoyt et al., 2006). Furthermore, the storage and recovery of energy in stretched elastic structures, (e.g. tendons) it is another method to increase locomotion economy. Biomechanists have shown that at low speeds, animals frequently utilize pendulum mechanics and at higher speeds they use spring mechanics. They refer to the gait that uses pendulum mechanics as a “walk” and the gait that uses spring mechanics as a “run” (Hoyt et al., 2006)

Most humans voluntarily switch to running at approximately $2.3\text{--}2.5\text{ ms}^{-1}$ which corresponds nearly to the intersection of the COT curves for walking and running (Alexander, 1991; Bramble & Lieberman, 2004; Margaria et al., 1963). At these higher speeds, running becomes less costly than walking by exploiting the spring mechanism that exchanges kinetic and potential energy differently (Figure 3). Elastic structures in legs and feet (collagen-rich tendons and ligaments) store kinetic and potential energy during the initial, braking part of the support phase, and then release as elastic strain energy through recoil during the subsequent propulsive phase

(Bramble & Lieberman, 2004; Ker et al., 1987). To use these springs effectively, the legs flex more in running than in walking: flexing and then extending at the knee and ankle during the support phase (Bramble & Lieberman, 2004).

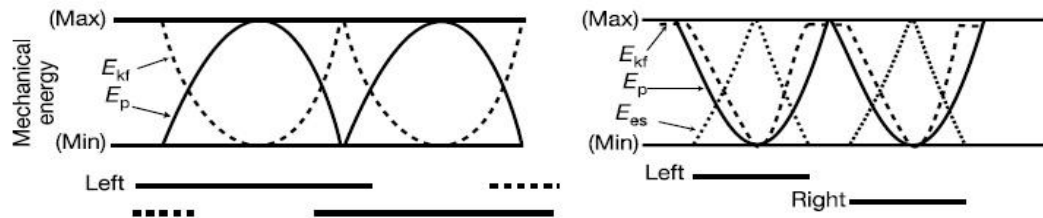


FIGURE 3. During walking (left), inverted pendulum mechanism exchanges forward kinetic energy (E_{kf}) for gravitational potential energy (E_p) between heelstrike and mid stance; the exchange is reversed between mid stance and toe off. During running (right), the mass-spring mechanism causes potential energy and kinetic energy to be in phase, with both energies declining rapidly to minimal between footstrike and Mid Stance. Leg tendons and ligaments partially convert decreases in potential energy and kinetic energy to elastic strain energy (E_{es}) during the first half of the stance, which is subsequently released through recoil between Mid Stance and Toe Off (adapted from Bramble & Lieberman, 2004).

Walking and running require metabolic energy expenditure for active contraction of muscle, largely associated with the production of work as muscle fibers actively change length. During these cyclical movements, the limbs often perform negative and positive work in succession, allowing elastic tendons to store and return energy (Dean & Kuo, 2011). However, the energetic cost of terrestrial locomotion cannot be explained just on the basis of mechanical work performed (Farris & Sawicki, 2012a; Hoyt et al., 2006), because work rate does not parallel metabolic rate with either speed or size (Kram & Taylor, 1990). Biewener and colleagues proposed that decrease in mean limb extensor mechanical advantage, and increase in knee extensor impulse during running, likely contribute to the higher metabolic cost of transport in running than in walking (Biewener et al., 2004).

Heglund and colleagues (1982) in their experiments with a wide range of terrestrial animals, showed that the rate at which animals consume energy during locomotion cannot be explained by assuming a constant efficiency between the energy consumed and the mechanical work performed by the muscles. They suggested that the intrinsic velocity of shortening of the active muscle motor units (MU) (which is related to the rate of cycling of the cross bridges between actin and myosin) and the rate at which the muscles are turned on and off are the most important factors in determining the metabolic cost of constant-speed locomotion (Heglund et al., 1982). This led to an alternative hypothesis that the time course of generating force and the cost of supporting body weight during locomotion were the major determinants of the metabolic cost of running (Kram & Taylor, 1990; Taylor et al., 1980). In many tasks, both muscle work and force might thus contribute simultaneously to overall energy expenditure, in proportions largely unknown (Dean & Kuo, 2011).

Alexander, (1991) reviewed the relationship between the mechanical performance of locomotion and its metabolic energy consumption, giving insights about how energy-saving mechanisms in walking and running act in different ways. They stated that: 1) the maximum shortening speeds of the muscles can be adjusted to their optimum values for the tasks required of them; 2) the moments exerted by the muscles at different joints can be adjusted to keep the ground force in line with the leg so that muscles do not work against each other; 3) the joints of the legs can be kept as straight as possible, minimizing muscle forces and work requirements 4) tendon and other springs can be used to store elastic strain energy and to return it by elastic recoil. Thus, muscles that are optimally adapted for their tasks in running should do positive work with constant efficiency (Alexander, 1991).

Finally, Komi and co workers have extensively studied how the stretch shortening cycle (SSC) can affect muscle mechanical output (Komi 2003 p-184, 2010 p-15). Normal movements of the skeletal muscles are performed in a sequence of preactivation (isometric), braking (eccentric) and concentric actions in this order (SSC of muscle function). The performance in the concentric phase is potentiated and/or made more economical by the behavior of the muscles during the preceding

eccentric phase of the cycle: stretch reflexes increase muscle stiffness during the eccentric phase of SSC, allowing an active muscle to perform a greater amount of work when shortening immediately after being stretched. This high muscular activation (stiffness) during the braking phase of SSC is a prerequisite for efficient storage of elastic energy in tendinous tissues during cyclic movements like walking, and running (Komi 2003 p-184, 2010 p-15).

3.3 Factors affecting economy during walking

Walking represents the major daily physical activity for most persons. It is an energy-cheap activity, with an energy requirement being only about 50% above that of the metabolism at rest (at $0.6 \text{ m}\cdot\text{s}^{-1}$ it is about $2.44 \text{ W}\cdot\text{kg}^{-1}$) (Saibene & Minetti, 2003). However, many factors can affect the economy during walking (Figure 4). In this part, the factors are briefly reviewed. These are grouped in environmental, task, and organism factors.

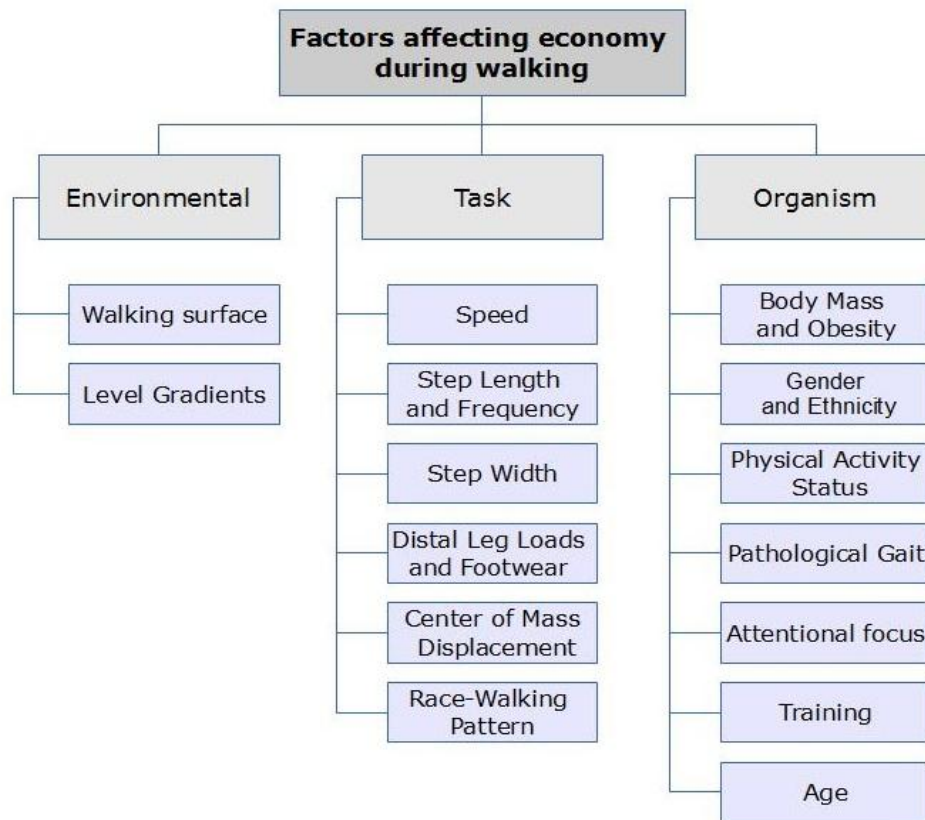


FIGURE 4: Factors affecting economy during walking

3.3.1 Environmental Factors

Walking surface

Similar economies exist for level walking on a grass track or paved surface. In contrast, walking in the sand requires almost twice the energy expenditure compared to walking on a hard surface because of sand's hindering effects on the forward movement of the foot and the added force required by the calf muscle to compensate for foot slippage (McArdle et al., 2010 p-210). Walking in soft snow triples energy expenditure compared with similar walking on a treadmill. Persons generate essentially the same energy expenditure walking on a firm, level surface or walking on a treadmill at an equivalent speed and distance. Such results lend support to laboratory data to quantify human energy expenditure in real-life situations (McArdle et al., 2010 p-210).

Level Gradients

Downhill walking is more economical than level or uphill walking (Minetti et al., 1993). Compared with walking on level ground, progressive negative grade walking decreases oxygen consumption down to a 9% grade for speeds of $5.4 \text{ km}\cdot\text{h}^{-1}$ (McArdle et al., 2010 p-210). However, the energy expenditure begins to increase at the more severe negative grades. Hunter et al., (2010) demonstrate that during extreme downhill, subjects do not take optimal advantage of the propulsion provided by gravity to decrease energetic cost, but instead prefer a more stable and costly gait pattern.

3.3.2 Task Factors

Speed

Several studies have revealed that COT strongly depend on walking speed (Cunningham et al., 2010; Fellingham et al., 1978; Margaria et al., 1963). Waters et al., (1988) investigated the energy-speed relationship of walking in 260 normal male and female subjects walking around a 60.5m circular outdoor track. Subjects were divided into four age groups (children, 6–12 years; teens; young adults, 20–59 years; and senior adults, 60–80 years). In each age group, the rate of oxygen uptake increased with the gait velocity.

Step Length and Frequency

Energy expenditure in walking is usually expressed as a function of walking speed. However, this relationship applies only to freely adopted step length-rate patterns. If walking speed is prescribed, humans prefer step frequencies and lengths that minimize energetic cost (Zarrugh & Radcliffe, 1978). Unlike most quadrupeds, humans increase speed during running mostly by increasing stride length rather than rate (Bramble & Lieberman, 2004). Preferred rate likely represents a compromise between mechanical power and mechanical efficiency in walking (Umberger & Martin, 2007).

Step Width

Donelan and colleagues (2001) demonstrated that humans appear to prefer a step width that minimizes metabolic cost. Their results showed that COT increased 45% for widths greater than the preferred value, and in 8% for narrower steps. The increases in these costs appear to be a result of the mechanical work required for redirecting the centre of mass velocity during the transition between single stance phases (step-to-step transition costs) (Donelan et al., 2001).

Distal Leg Loads and Footwear

A weight equal to 1.4% of body mass placed on the ankles increases the energy expenditure of walking an average of 8% or nearly 6 times more than with the same weight on the torso (McArdle et al., 2010 p-210). Adding an additional 100g to each shoe increases oxygen consumption during moderate running by 1% (McArdle et al., 2010 p-210). The cushioning properties and longitudinal bending stiffness of shoes also affect walking and running economy. A more flexible and softer-soled running shoe reduced the oxygen consumption (increased economy) of running at a moderate speed by 2.4% compared with a similar shoe with a firmer cushioning system, even though the pair of softer-soled shoes weighed an additional 31 g (McArdle et al., 2010 p-210). In a study of women walking in shoes with progressively higher heels, energy consumption did not increase significantly until heel height reached 7.62 cm, when many of the kinematic and kinetic variables also had been affected (Ebbeling, et al., 1994).

Center of Mass Displacement

Humans are capable of walking in a manner that will reduce center of mass (CoM) displacement. Increasing and decreasing vertical CoM displacement beyond subject's preferred range result in increases in the metabolic cost of walking, because of greater mechanical work performed at the hip, knee, and ankle joints (Gordon et al., 2009).

Race-Walking Pattern

Biomechanical evidence indicate about the same crossover speed - when running becomes more economical than walking - for conventional and competitive styles of walking (McArdle et al., 2010 p-211). However, competition walkers achieve high yet uneconomical rates of movement, unattainable with conventional walking, with a distinctive modified walking technique that constrains the athlete to certain movement patterns regardless of walking speed (McArdle et al., 2010 p-211). The athlete must maintain this gait despite progressive decreases in walking economy as exercise duration progresses and fatigue increases (McArdle et al., 2010 p-211).

3.3.3 Organism Factors

Body Mass and Obesity

There is a direct relationship between body mass and energy expenditure (Mahadeva et al., 1953). One can accurately predict energy expenditure of horizontal walking at speeds between 3.2 and 6.4 km•h⁻¹ for men and women who differ in body mass using standardized equations and tables (Hall et al., 2004; McArdle et al., 2010 p-209; Passmore & Durnin, 1955). The increased load of body weight with obesity also increases the rate of oxygen consumption when walking speed is held constant (Waters & Mulroy, 1999). In a group of severely obese women, the self-selected walking speed was slower and had higher VO₂ than normal weight control subjects (Mattsson et al., 1997).

Gender and Ethnicity

Mahadeva and colleagues (1953) conducted one of the first large-scale energy expenditure studies that focused attention on energy expenditure during walking and stepping at a constant speed (McArdle et al., 2010 p-215). They made observations on 50 men and women, aged 13 to 79 years, of diverse ethnic backgrounds, whose body mass ranged from 48 to 110 kg. Results showed a relationship between energy expenditure and body mass for each activity, but gender, ethnicity, and previous diet contributed little to predicting energy expenditure during walking and stepping (Mahadeva et al., 1953).

Physical Activity Status

Martin and colleagues (1992) measured the aerobic demands for 30 young and 30 old individuals representing sedentary and physically active groups, during treadmill walking at seven speeds ranging from 0.67 to 2.01 m•s⁻¹. All four age/physical activity groups displayed U-shaped speed-aerobic demand curves with minimum gross oxygen consumption per unit distance walked at 1.34 m•s⁻¹, but physical activity status had no significant effect on walking aerobic demand (Martin et al., 1992)

Pathological Gait

Waters & Mulroy, (1999) reviewed the results of energy expenditure studies performed in patients with specific neurologic and orthopedic disabilities. In summary, the O₂ cost per meter is directly related to the extent of the patient's gait disability. This rate indicates the physiological effort of walking at the selected speed. The use of upper extremity assistive devices (cane, crutches or walker) for weightbearing requires significant arm work, resulting in an elevated rate of energy expenditure (Waters & Mulroy, 1999).

Attentional focus

Schücker and colleagues (2009) examined whether the focus of attention can influence running economy (oxygen consumption at a set running speed). Trained runners had to focus their attention on three different aspects while running on a treadmill. For three consecutive 10-min periods, runners concentrated on the running movement, on their breathing, and on their surroundings. Results showed an increased running economy in the external focus condition in terms of the physiological performance (Schücker et al., 2009).

Training

Training level is a factor that can affect the economy of the movement (Lay et al., 2002; Saunders et al., 2004; Sparrow et al., 1999). Higher running economy in long distance runners is largely attributable to a lower vertical displacement of the center of mass, probably related to neuromuscular adaptations induced by long training (Saunders et al., 2004). Endurance training leads to increases in muscle's functional capacity as well as cardio-respiratory modifications, responses that invoke improvements in economy (McArdle et al., 2010 p-343; Saunders et al., 2004). Practice-related refinements to coordination and control can reduce the metabolic energy cost of performance associated with significant reductions in muscle activation (Lay et al., 2002).

Age

Waters et al., (1988) found that the energy cost for children at their customary slow, normal, and fast speeds was significantly higher than other age groups due to their higher rate of energy expenditure and slower gait velocity. Further, recent studies show that COT increases with age (Hortobágyi et al., 2011; Hortobágyi, et al., 2003; Malatesta et al., 2003). Martin et al., (1992) found a statistically significant age effect on walking aerobic demand, with old subjects (greater than 65 yr of age) showing an 8% higher mean aerobic demand than the young subjects.

4. MUSCLE METABOLISM DURING WALKING

Because skeletal muscle is the largest organ in the body, a reasonable inference is that the majority of the increase in metabolism during locomotion, results from increases in the metabolism of active motor muscles with smaller contributions from other tissues like the heart and respiratory system (Marsh & Ellerby, 2006). However, the distribution of energy use among and within these large muscles and the amount of energy used by accessory muscles remain unknown. (Marsh & Ellerby, 2006).

4.1 Muscle metabolism measurement techniques

Improving our knowledge of how muscles use metabolic energy to perform specific mechanical tasks during walking and running is central to our basic understanding of terrestrial locomotion (Umberger & Rubenson, 2011). Such information also has important clinical implications, as many gait disorders are characterized by an elevated cost of locomotion (Umberger & Rubenson, 2011; Waters & Mulroy, 1999). Despite the obvious utility of measuring the energy use of the individual skeletal muscles during locomotion, technical difficulties have hampered these measurements (Marsh & Ellerby, 2006; Umberger & Rubenson, 2011). In the following paragraphs, several techniques for muscle metabolism measurement are described, taking into account their respective advantages and drawbacks. Most of these techniques assume a direct relationship between muscle blood flow and metabolism, and can be divided in invasive and non invasive. Between the non invasive, the focus will be on electromyography.

4.1.1 Invasive methods for measure the muscle metabolism

Direct Fick Method

Direct Fick was the original method conceived in the late 1800's by Adolf Eugen Fick to measure cardiac output (McArdle et al., 2010 p-341). It is based on calculating the oxygen consumed over a given period of time, from measurement of the oxygen concentration of the venous and arterial blood (McMichael & Sharpey-Schafer, 1944). For do this at muscle level, it is necessary the introduction of a catheter with a manometer into large veins to measure arterial oxygen content, the oxygen content of venous blood emerging from the individual muscle, and the rate of blood flow to the same muscle (Wüst et al., 2011). For instance, it has been used to investigate if the activation of muscle oxygen consumption is caused by accumulation of ADP (Wüst et al., 2011). However, direct measurements of oxygen consumption of individual muscles during locomotion with this method are likely not feasible with current technology except under very limited circumstances (Marsh & Ellerby, 2006). Many hurdles stand in the way of these measurements, including the presence of numerous collateral branches in the circulation, which makes measuring the average venous oxygen content of blood from an individual muscle difficult (Marsh & Ellerby, 2006).

Microsphere technique

Measurements of blood flow in the active muscles, or portions of these muscles, can be made simultaneously using the microsphere technique (Buckberg et al., 1971; Marsh & Ellerby, 2006). Microspheres labeled radioactively or with a dye, are injected into the systemic circulation, usually via the left ventricle or left atrium. The microspheres mix with the blood and provide a tracer for the distribution of flow (Marsh et al., 2004). Thus, the number of microspheres that lodge in a particular volume of tissue is proportional to the blood flow to that tissue volume (Marsh & Ellerby, 2006). This technique have helped to reveal that swinging the limbs during walking and running requires an appreciable fraction of the energy used (measured as

blood flow) during terrestrial legged locomotion (Marsh et al., 2004). According to Armstrong & Laughlin, (1985) this technique has a potential to measure muscle fiber recruitment, but care must be taken about this use because other factors than local metabolic rate might play a significant role in determining blood flow (Marsh & Ellerby, 2006). Moreover, it cannot be used in humans.

Indicator dilution methods

Indicator dilution methods include thermodilution and dye dilution, useful methods for performing measurements of blood flow at rest and during maximal and submaximal exercise (Casey et al., 2008). They are based on the principle that infusate is diluted by blood with a corresponding change in color or temperature in proportion to blood flow: when the indicator substance is added to circulating blood, the rate of blood flow is inversely proportional to the change in concentration of the indicator over time (Casey et al., 2008). Thermodilution of iced saline - injected usually in the right atrium - can be used to measure regional blood flow with a constant infusion technique. In other hand, dye dilution uses the indicator dye indocyanine green and requires multiple blood samples to measure blood dye concentration with a photodensitometer (Casey et al., 2008). Peripheral injection of this solution can even allow simultaneous determinations of total cardiac output and regional muscle blood flow (Casey et al., 2008; Guenette et al., 2008). Like dye dilution, thermodilution requires expertise to use. However it does not require multiple blood sampling nor spectrophotometry, and is not complicated by recirculation of dye (Casey et al., 2008)

Muscle biopsies

Being the gold standard in the diagnosis of different myopathies (Haas et al., 2007), muscle biopsies has been used as well to measure the muscle metabolism before, during, and after exercise (Gaitanos et al., 1993). Commonly used in combination with other techniques as blood sampling or indirect calorimetry, several metabolic substrates like adenosine triphosphate, phosphocreatine, and glycogen (between

others) can be directly quantified to highlight the anaerobic or aerobic metabolic pathways (McArdle et al., 2010 p-582). However the use of muscle biopsy is not straightforward. Subjects evaluated might present problems with healing when performed repetitively (Rico-Sanz et al., 1999). Moreover, has been demonstrated that following exhaustive dynamic exercise, repeated muscle biopsy sampling can alter glycogen resynthesis for several days (Constantin-Teodosiu et al., 1996).

4.1.2 Non-Invasive methods for measure the muscle metabolism

Venous occlusion plethysmography (VOP)

The idea behind VOP is that when venous drainage from a body segment is briefly interrupted (when a pneumatic cuff is inflated), arterial inflow is unaltered and blood can enter but cannot escape (Wilkinson & Webb, 2001). Blood flow is measured as linear increase in segment volume over time, until venous pressure rises towards the occluding pressure (Casey et al., 2008; Joannides et al., 2006). Mercury-in-silastic strain gauges placed around the widest part of the limb where flow is to be measured are commonly used to detect changes in limb circumference and the calculation of the percentage increase in volume changes (Casey et al., 2008). However, this measurement during exercise can underestimate the true response to exercise (Casey et al., 2008).

Doppler ultrasound

This is a method for continuous determination of blood flow in conducting vessels that are the main suppliers of blood to a specified region (Casey et al., 2008). Blood flow is calculated by multiplying mean blood velocity by the cross-sectional area of the artery (Casey et al., 2008). Studies during dynamic leg exercise have led to observations that relative and absolute blood flow during exercise is reduced in conditions such as aging (Parker et al., 2008) and chronic heart failure (Shiotani et al., 2002). The most important limitation of this technique is the operator dependency of the measurement (e.g. isonation angle) (Merritt, 1987). Another limitation may be

that the Doppler measurements can only be made at rest and immediately after exercise (Osada, 2004; Ozcan et al., 2006).

Near infrared spectroscopy (NIRS)

NIRS is a non-invasive technique that gives information about the oxygenation of a tissue (Praagman et al., 2003). Muscle tissue is relatively transparent for light in the near infrared region. When the light is transmitted through, one part of it is absorbed, the other scattered. Being the absorption dependent on the amount of oxygen present, by measuring the absorption changes at three different wavelengths, these can be converted into the concentration of oxyhaemoglobin and deoxyhaemoglobin (Praagman et al., 2003). Recently, the recovery of muscle oxygen consumption after endurance exercise, measured with NIRS, has been used as an index of skeletal muscle oxidative capacity (Ryan et al., 2013). However, they require sophisticated and expensive equipment and analysis (Casey et al., 2008). In individuals with high subcutaneous fat deposition, the NIRS signal will be blunted compared to leaner persons due to the lower metabolic and blood flow rates in adipose tissue (McCully & Hamaoka, 2000).

Magnetic resonance imaging (MRI) techniques: Spectroscopy and Functional MRI

Magnetic resonance spectroscopy (MRS) is an application of magnetic resonance imaging that provides chemical information about tissue metabolites (Shah et al., 2006). Whereas conventional MRI detects the nuclear magnetic resonance spectra of water in tissues, MRS detects the resonance spectra of chemical compounds other than water, allowing for a true depiction of in situ chemistry (Shah et al., 2006). These compounds include intracellular phosphorus metabolites (i.e., phosphocreatine–PCr, ATP, and inorganic phosphate–Pi), and thus is the ideal tool for in vivo monitoring of the cell energy status and metabolism (Valkovič et al., 2013). Dynamic ³¹P-MRS during exercise and consecutive recovery reflect the maximal in vivo muscle mitochondrial output or capacity (Kemp & Radda, 1994; Valkovič et al., 2013). However, recently it has been shown that the non-localized acquisition of

mixed ^31P spectra from exercising and relaxed muscle groups significantly influences the results (Meyerspeer et al., 2012).

In other hand, muscle functional magnetic resonance imaging (mfMRI) is used to compare the relative involvement of different muscles recruited during exercise (Meyer & Prior, 2000). The method relies on the activity-induced increase in the “nuclear magnetic resonance transverse relaxation time” (T_2) of muscle water, which is caused by osmotically driven shifts of fluid into the myofibrillar space (Meyer & Prior, 2000). Exercise-induced shifts in T_2 values correlate with integrated electromyography activity (Adams, et al., 1992), force induced by electrical stimulation (Adams et al., 1993), and workload (Adams et al., 1992). However, some considerations must be made when interpreting mfMRI data. Because exercise-induced increases in T_2 depend on muscle fiber type, differences in T_2 values among muscles cannot be directly interpreted as a difference in muscle activation (Reid et al., 2001). Moreover like NIRS, they require sophisticated and expensive equipment and analysis (Casey et al., 2008).

Computational Modeling

Computational modeling involves generating computer simulations of locomotion, in conjunction with a model for predicting energy consumption in individual muscles (Umberger et al., 2003; Umberger & Rubenson, 2011). Because ATP hydrolysis is directly coupled to crossbridge cycling, a natural connection between mechanics and energetics exists in this type of framework (Bhargava et al., 2004). Umberger et al., (2003), developed a model for estimate muscle energy predicting the rate of heat production and the rate at which mechanical work is done, based on the activation and contractile state of the muscle. Miller et al., (2012) used this model to address if the nervous system prioritizes the COT itself for energy minimization, or if some other quantity (like muscular activity), is minimized and a low COT is a consequential effect. Their results revealed that minimizing activation predicted the most realistic joint angles and timing of muscular activity, suggesting a potential control strategy centered on muscle activation for economical running (Miller et al.,

2012). However, it has been shown that muscle energetics models yield to good predictions of net and/or gross cost for walking. Moreover, there is an inherent difficulty in validating the individual-muscle predictions that are of primary interest (Umberger & Rubenson, 2011).

Mechanical approach

The laws of mechanics and thermodynamics provide the necessary framework to link muscle force and work with the energetics of terrestrial locomotion (Umberger & Rubenson, 2011). Measurements of organismal energy consumption have been paired with biomechanical analyses providing important information on general links between locomotor mechanics and energetics (Umberger & Rubenson, 2011). For instance, Farris & Sawicki, (2012) examined the effects of walking and running speed on lower limb joint mechanics and metabolic COT in humans. During gait, they found that there was no difference in the proportion of power contributed by each joint (hip, knee, ankle) to total power across speeds, but changing from walking to running resulted in a significant shift in power production from the hip to the ankle, which may explain the higher efficiency of running at speeds above 2.0 ms^{-1} (Farris & Sawicki, 2012b). Nevertheless, mechanical approaching lacks the resolution necessary to establish these relations at the muscular level: there are difficulties in measuring muscle force and work in individual muscles during locomotion (Umberger & Rubenson, 2011).

Electromyography (EMG)

Activation signals from the central nervous system generate MU action potential trains. These are repeated continuously for as long as the muscle is required to generate force. As this excitation increases, a greater number of MUs are recruited and the firing rates of all the active MUs increases to generate greater force in the muscle (De Luca, 2006). The EMG signal is the electrical manifestation of the neuromuscular activation associated with a contracting muscle, current that propagates through the intervening tissues to reach the detection surface of an electrode located in the environment. (De Luca, 2006). Thus, the EMG signal is the spatial and temporal summation of all active MU action potentials (Figure 5) (De Luca, 1997).

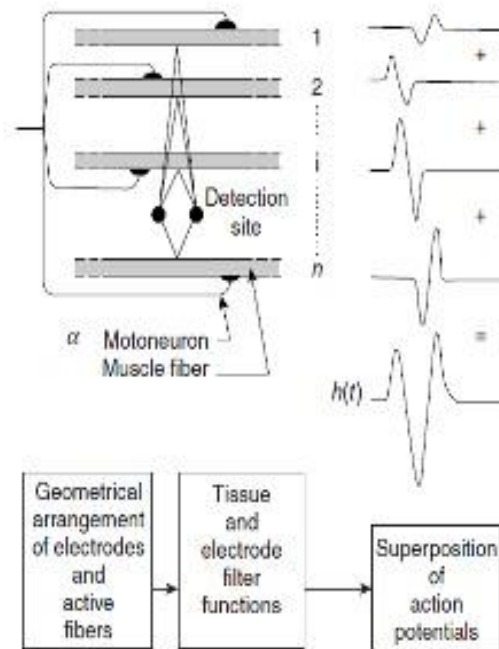


FIGURE 5. The EMG signal represents the superposition of all the action potentials in the capture volume of the electrode, and depends of the characteristics of the surrounding tissue and geometrical arrangement of the electrodes. Note that the position of the detection site relative to the motoneuron endplate affects the shape of the potential (from De Luca, 2006).

The amplitude of the surface EMG signal reflects muscle activation and has been related to force production in the “Force-EMG signal relationship” (De Luca, 1997; Lawrence & De Luca, 1983). As muscular force production increases, contracting muscles require more energy. Increased metabolic rates during exercise are primarily attributed to the energy supplied to the contracting muscles by aerobic and anaerobic sources (McArdle et al., 2010 p-123). Because of this, a closed-form and/or simple equation describing this force-EMG signal relationship would be desirable (De Luca, 1997) and extremely useful for describing muscle metabolism. However, the observation that the EMG signal amplitude generally increases as the force and/or contraction velocity of the muscle increases, only provides a qualitative indication of a relationship between the variables (De Luca, 1997). Many factors cause the relationship to be nonrigid (Figure 6), ranging from causative (e.g. electrodes configuration), intermediate, (e.g. signal crosstalk, volume capture) and deterministic (e.g. MU action potential characteristics) (for a detailed review, refer to De Luca 1997). Moreover, it has been shown that the myoelectric signal-force relationship is primarily determined by the muscle under investigation and is generally independent of the subject group and the force rate (Lawrence & De Luca, 1983). The relation between electrical activity and energy use is also influenced by the mechanical behavior of the muscle, because energy use varies with shortening speed and duty cycle (Marsh & Ellerby, 2006)

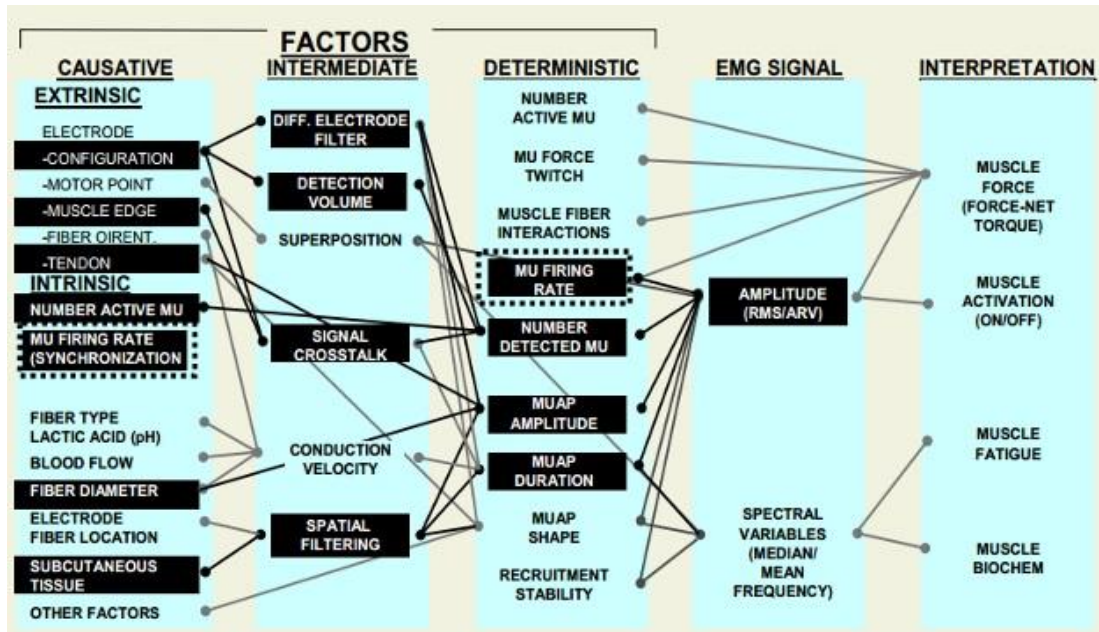


FIGURE 6 Schematic diagram of the factors that affect the EMG signal. The arrangement of factors is designed to demonstrate the flow of the influences and interactions among the factors. The segments highlighted in black show the interrelationship of factors affecting the EMG signal amplitude at the beginning of a contraction, that is when no fatigue is present. Factors which are active at this stage of contraction are shown. The time-dependent (fatigue influencing) factors that would be influential during a sustained contraction are not shown. (from De Luca, 1997).

Although EMG cannot provide direct measures of muscle force, work, or metabolism, increases in amplitude and/or duration of EMG indicate increases in activity of muscle fibers and, therefore, provide a correlative indication of muscle metabolism within the recording field of the electrode (Carrier et al., 2011). This was addressed by Praagman et al., (2003) who investigated the relationship between muscle's local oxygen consumption (e.g. VO_2 , determined by NIRS), external moments, and surface EMG during elbow movements. They found a linear relationship between EMG and VO_2 for the biceps brachii muscle in an isometric, 70% maximum voluntary contraction task, suggesting the relationship between EMG and muscle metabolism.

A combination of different studies in animal models (guinea fowl), revealed a relationship between EMG signal and muscle blood flow. McGowan and colleagues (2006) using sonomicrometry, oxygen consumption and fine-wire EMG, demonstrated that load carrying enhanced passive force production by increasing active stretching during walking and thus the metabolic cost of generating muscular force decreases with added load (McGowan et al., 2006). Matching this results with the work by Marsh et al., (2004) that measured muscle blood flow with the same model, provides the opportunity to make in vivo comparisons of loading-induced changes in muscle contractile dynamics and individual muscle metabolic energy use (Griffin, 2006). Their results showed that a fractional increase in muscle blood flow is nearly the same as the average increase in EMG intensity, which was also similar to the percent increase in organismal metabolism, suggesting a relationship between blood flow and EMG activity. However this was not uniform for all muscles evaluated, therefore this relationship should be interpreted cautiously (Griffin, 2006).

Following this concept, Carrier et al., (2011) used electromyography to evaluate 13 muscles of the back and legs during walking and running. Because humans are known to have energetically optimal walking and running speeds, they want to test if optimal speeds would also exist at the level of individual locomotor muscles. Using a new approach, they calculated the cumulative activity required from each muscle to traverse a kilometer (CMAPD), presenting the EMG mean amplitudes normalized to a travel distance of 1 km (Carrier et al., 2011). They found that activity of each of these muscles was minimized at specific walking and running speeds, but the different muscles were not tuned to a particular speed in either gait (Figure 7). The results of this study indicate that our locomotor muscles do not maximize the economy of locomotion, to improve performance in other motor behaviors.

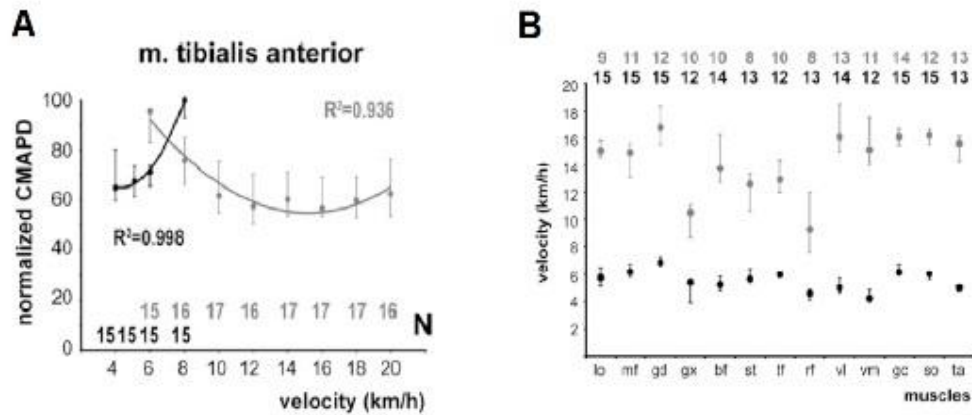


FIGURE 7. Example graphs of integrated muscle activity required to walk or run a kilometer (CMAPD) analysis. A) Median values of normalized CMAPD versus walking (black) and running (gray) across several speeds ($\text{km}\cdot\text{h}^{-1}$) for tibialis anterior muscle. Lines fitted to the data were derived from second-order polynomial least-squares regressions. Error bars represent the upper and lower quartiles. Sample sizes at each speed are listed along the x axes. Squared R value (coefficients of determination) is given. Note that CMAPD values resemble U shape curves. B) Median optimal walking (black) and running (gray) speeds for the 13 muscles evaluated. Error bars represent the upper and lower quartiles of speed. Sample sizes at each speed are listed at the top of the graphs. Note that all muscles evaluated have a different optimal walking velocity, where they are more economical. (Adapted from Carrier et al., 2011)

Recently, Blake & Wakeling, (2013) established a metabolic power-EMG relationship during non steady-state conditions. EMG and gas exchange were monitored during cycling at different workloads, and comparisons were made between breath-by-breath resolutions of metabolic power and total EMG intensity. Different weighting coefficients were also applied to the EMG for each muscle to analyze the effects of different muscles on metabolic power estimations. Results showed a significant correlation ($r = 0.91$) between estimates of metabolic power from EMG and gas exchange (Figure 8) and found that muscle weighting had a significant effect on metabolic power determination. This study demonstrates that EMG contains important information about the metabolic costs of muscle contractions and provides

good predictions of metabolic changes during non steady-state conditions. Further, EMG gives more immediate, higher temporal resolution predictions of changes in metabolic power than indirect calorimetry (Blake & Wakeling, 2013). In conclusion, all this information together shows that it is feasible to use EMG to evaluate individual muscle metabolism.

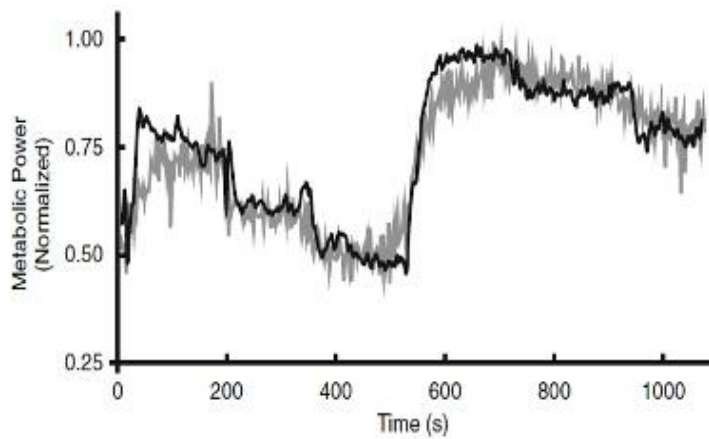


FIGURE 8. Metabolic power (grey) calculated from oxygen uptake and estimated metabolic power (black), calculated from the EMG signal of 10 leg muscles for one participant. (correlation of $r = 0.94$) (from Blake & Wakeling, 2013)

4.2 Key findings about muscle and lower limb metabolism during walking

4.2.1 Energetic costs of producing muscle force

The force generated by the muscle for propulsion seems to be the key factor related to his energy consumption during walking and running. Taylor et al., (1980) thought of muscles as 'biological machines' for converting chemical energy into force. It seemed reasonable to postulate that the rate at which muscles consume energy might be related to the magnitude of the integral of force over the time during which it is developed. Studies in quadrupedal species and humans during load carrying at different speeds, showed that the rate of energy utilization by the muscles of an animal as it moves along the ground at any particular speed, is nearly directly proportional to the force exerted by its muscles (Griffin et al., 2003; Kram & Taylor, 1990; Roberts et al., 1998; Taylor et al., 1980). Further, as much as 60% of the metabolic cost of a whole body movement can be attributed to the cost of generating muscular force (Dean & Kuo, 2011; Kram, 2011), mainly used in the stance phase of walking (Griffin et al., 2003).

Taylor and colleagues suggested that the cost of generating force is proportional to the rate of cross bridges between the actin and myosin cycle, and this rate increases in direct proportion to intrinsic velocity (Taylor et al., 1980). However, recently has been proposed that the mechanism for such a cost may be associated with sarcoplasmic reticulum ATPase activity (i.e., calcium transport), as opposed to the actomyosin interactions that produce work, because the former may become a limiting factor in the production of cyclical force at high frequencies (Dean & Kuo, 2011; Doke et al., 2005). Muscles with primarily slow fibers are preferentially recruited at slow speeds, and those with mostly fast fibers are preferentially recruited at faster speeds, whereas muscles with a mixed fiber distribution are recruited evenly across all speeds (Ellerby et al., 2005; Umberger & Rubenson, 2011).

Roberts et al., (1998), reported that 30 % of the increase in energy cost across the speed ranges is not explained by the linear relationship between energy cost and rate of force generation. A possible explanation is the change in the relative shortening velocity of the muscles across speeds, because a greater cross-sectional area of muscle would have to be activated to provide the same force as a result of the force–velocity relationship. Moreover, at higher walking speeds metabolic rate increases because faster, metabolically more expensive muscle fibers must be recruited to produce force (Roberts et al., 1998).

4.2.2 Energy cost of stance phase and leg swing.

Using simulation models, Umberger (2010) revealed that for a typical walking speed and stride rate, the single-limb support period of the stance phase represent the greatest percentage of the total muscular cost, while double-limb support and the swing phase were found to have similar, but lesser, relative costs. Accounting for the duration of the transitions between steps led to the conclusion that performing step-to-step transitions accounted for a little more than one-third of the net cost of human walking (Umberger, 2010).

Griffin et al., (2003) studied how stance phase determines the metabolic cost of walking. First, they indirectly assessed the metabolic cost of swinging the legs, and then examined the cost of generating muscular force during the stance phase, manipulating independently with increased loads just in the stance limb muscle actions. They showed that the work or force required to swing the legs relative to the center of mass does not appreciably change. Conversely, during stance phase, the active muscle volume required to generate force on the ground and the rate of generating this force accounted for > 85% of the increase in net metabolic rate across moderate speeds and most loading conditions. These data indicate that, regardless of the work that muscles do, the metabolic cost of walking can be largely explained by the cost of generating muscular force during the stance phase (Griffin et al., 2003).

Gottschall & Kram, (2003, 2005) presented similar results. Using the aid of horizontal forces, they investigated the reduction in metabolic rate that reflect the cost of generating propulsive forces during normal walking. Their EMG data indicate that generating horizontal propulsive forces constitutes nearly half of the metabolic cost of normal walking, with a major activity of medial gastrocnemius (Gottschall & Kram, 2003). In another study and with the same principle of external forces, they investigated the metabolic cost and muscular actions required for the initiation and propagation of leg swing during walking on a treadmill. They showed that just ~10% of the net metabolic cost of walking is required to initiate and propagate leg swing, with an important role of hip flexor muscles (Gottschall & Kram, 2005). Marsh et al., (2004) measuring blood flow to the hindlimb muscles in guinea fowl, estimated that in the swing-phase, muscles consume 26% of the energy used by the limbs, and the stance-phase muscles consume the remaining 74%, independent of speed. In humans, studies using mechanical approaches had revealed that moving the legs back and forth at a typical stride frequency of 0.9 Hz, might consume about one-third of the net energy needed for walking at $1.3 \text{ m}\cdot\text{s}^{-1}$ (Doke et al., 2005). The consistency of results in different species using very different methods strongly indicates that leg swing accounts for approximately 25% - 30% of the cost of locomotion, with the remaining 70% - 75% associated with stance phase muscle actions (Umberger & Rubenson, 2011).

4.2.3 Energy consumption across lower limb joints

Estimates of energy use in individual muscles also provide information on how energy consumption in locomotion is distributed across the major lower limb joints. Umberger & Rubenson (2011) provided a direct comparison based on human simulation results (Umberger, 2010) and muscle blood flow measurements in guinea fowl (Rubenson et al., 2006) because direct measurements of this kind are difficult in humans. Their results showed that the distribution of energy consumption seems to be similar across the hip, knee, and ankle for both experiments, mirroring the similar stance/swing phase costs in humans and birds (Figure 9) (Umberger & Rubenson,

2011). Hip muscles are the primary energy consumers, followed by the ankle plantar flexors, with knee extensor muscles consuming less energy. The remainder of the metabolic energy was consumed by muscles that primarily flex the joints, largely during the swing phase (Umberger & Rubenson, 2011). The relatively low costs incurred by knee extensor muscles occurred in the face of considerable cocontraction on the joint, which seems to be crucial for stabilizing the knee (Umberger & Rubenson, 2011). The plantar flexors seem to achieve this high overall mechanical efficiency by exploiting storage and release of tendon elastic energy and by performing work partly during deactivation, which is an especially economical mode of operation (Umberger & Rubenson, 2011).

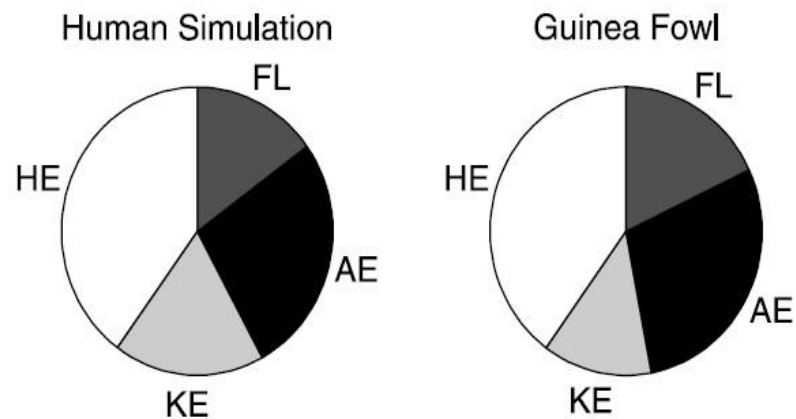


FIGURE 9. Distribution of muscle energy consumption across the major joints of the lower limb. Left panel: distribution of muscle energy consumption across muscle groups for a computer simulation of human walking (Umberger, 2010). Right panel: distribution of total hind limb muscle blood flow for running in the guinea fowl (based on Rubenson et al. 2006). HE (hip extensors), KE (knee extensors), AE (ankle extensors: plantar flexors in humans, combined ankle extensors and digital flexors in birds), and FL (flexors combined across all joints) (from Umberger & Rubenson, 2011).

Sawicki et al., (2009) studied the energy distribution based on joint work and organismal energy consumption during human walking. They estimated the net metabolic energy cost per stride, taking into account independent contributions of each of the lower limb joints to the overall metabolic energy expenditure of walking - apparent efficiency -, calculated with the help of a robotic exoskeleton (Sawicki et al., 2009). In accordance with Umberger & Rubenson observations, they showed that the hip had the higher energy demand, but being the ankle the most economical joint (Sawicki et al., 2009). They argue that a large portion of the mechanical work required for walking comes from muscles and tendons crossing the ankle joint. Thus, by storing and releasing elastic energy in the Achilles tendon during each step, humans greatly enhance the efficiency of ankle joint work far beyond what is possible for work performed at the knee and hip joints (Sawicki et al., 2009).

4.2.4 The role of the elastic components in muscle metabolism

During human gait, the storage and return of elastic energy in compliant structures is an important energy saving mechanism that may reduce the necessary muscle fiber work, and be an important determinant of the preferred gait mode at a given speed (Sasaki & Neptune, 2006). Elastic energy savings may reduce the amount of work that muscles must perform to power oscillatory movements of the body, such as in walking and running (Cavagna et al., 1977). For these locomotor gaits, kinetic and potential energy lost by the body can be recovered usefully by elastic structures, resulting in metabolic savings as high as 50% or more (Biewener, 1997).

Roberts et al., (1997) revealed that the stretch and recoil of tendon and muscle springs supply mechanical work while active muscle fibers produce high forces. They showed that during level running, there was near-isometric force production in the gastrocnemius muscle fibers and thus little work performed (Roberts et al., 1997). Thus, running economy is improved by muscles that act as active struts rather than working machines (Roberts et al., 1997). Ishikawa and colleagues (2005) and Lichtwark and colleagues (2007) found that the interaction between the muscle

fascicles and tendinous tissues plays an important role in the process of release of elastic energy (Ishikawa et al., 2007; Lichtwark et al., 2007). Calf muscle fascicles acted relatively isometrically during walking stance phase (Ishikawa et al., 2005), however during running the fascicles shortened throughout the stance phase, which corresponded to an increase in the strain of the series elastic elements (Lichtwark et al., 2007). These findings suggest that the elastic recoil takes place not as a spring-like bouncing but as a catapult action in natural human walking (Ishikawa et al., 2005). The elasticity of the tendinous tissues of different lower limb muscles improves the power output and efficiency of skeletal muscle (Ishikawa & Komi, 2004). Moreover, the stretch shortening cycle plays an important role in the effective use of this elastic energy (Komi 2003 p-184, 2010 p-15). However, the use of recoil energy is likely different in different muscles/MTUs, - not all of them have a long elastic tendon like the calf muscles/Achilles tendon - and that this may affect the metabolism of each muscle.

5. AGING EFFECTS ON NEUROMUSCULAR FUNCTION AND WALKING

Elderly group represents a growing segment in developed countries. In Europe, from 2008 to 2060, the median age is projected to rise 7.5 years and the share of people aged 65 years or over in the total population will increase 13%, with 151.5 million of elderly people living in 2060 (Giannakouris, 2008). The growth of the older population has resulted mostly from a general increase in the overall population size but is also strongly influenced by major declines in leading causes of mortality (Ferrucci et al., 2008). These demographic transformations reverberate in society, increasing medical care and social needs, which are expected to increase steeply in the years to come (Ferrucci et al., 2008).

The health status of older adults is a result of cumulative risk factor exposure, the progressive development of impairments with age, the interactions of underlying health status with acute precipitants of clinical outcomes, and underlying aging-related biologic changes (Fried, 2000). Limitations performing daily tasks - e.g., walking two to three blocks, transferring from the chair - that are essential for maintaining independence in the community (Manini, 2011), are related with these biology of aging. Over the past several decades, the scientific and medical communities have recognized that neuromuscular dysfunction is a debilitating and life threatening condition in older persons that impact on daily tasks (Manini & Clark, 2012). For example, falls is a major cause of morbidity and death in the elderly (Centers for Disease Control and Prevention (CDC), 2006) and in almost all incidences of falls, some aspects of locomotion have been implicated (Prince et al., 1997), with muscle's physiological and neurological changes associated (Manini & Clark, 2012). The objective of this chapter is to give a brief overview of neuromuscular changes associated with aging and the performance of walking.

5.1 Age-related changes in strength capacity

Muscular strength is typically maintained at peak levels until the fifth or sixth decade, after which accelerated losses occur, with strength decreasing approximately 50% by the age of 80 years (Sturnieks et al., 2008). Studies have reported reductions in leg strength of 28% in men and 38% in women aged in their sixties, compared to men and women aged in their twenties (Sturnieks et al., 2008). Peak torque production and rate of torque development also declines (Thelen, et al., 1996). Leg strength decrease by 1–2% per year, with a loss of leg power of approximately 3.5% per year (Skelton, et al., 1994). Lean body mass and muscle mass diminishes considerably between the ages of 20 and 80 years, with an average 40% loss of muscles area and a similar loss of the number of fibres (Sturnieks et al., 2008).

Age-related reductions in muscle mass and strength are accompanied by a reduction in MU number (Doherty et al., 1993) and histological changes which are suggestive of neuronal remodeling in elderly people (Brown & Hasser, 1996). Both motor unit recruitment and firing frequency are reduced in older adults (Narici et al., 2008). Age-related loss of muscle mass has been demonstrated to involve a greater loss of fast-fiber cross-sectional area (Marcell, 2003), which is accompanied by a reduced reinnervation capacity (Lexell et al., 1988; Marcell, 2003). The muscle appears to compensate for this reduction in MUs by hypertrophy of existing smaller and slower MUs that attempt to reinnervate faster fibers and transform them into slower myosin fiber types (Doherty et al., 1993), thus partially explaining why slower muscle is preserved in aging (Marcell, 2003).

5.2 Sarcopenia

Sarcopenia can be defined as the gradual loss in muscle tissue during aging, that result in diminished mass and strength (Marcell, 2003). The rate of muscle loss with age is approximately 1%–2% per year past the age of 50 (Marcell, 2003). 10% – 25% of persons under the age of 70 years are sarcopenic, whereas beyond the age of 80 greater than 30% of women and 50% of men are sarcopenic (Baumgartner et al., 1998)

The consequences of sarcopenia include decreased strength, metabolic rate, and maximal oxygen consumption (Marcell, 2003), which contribute to weakness and loss of independence. The loss of aerobic capacity with age is predominantly due to a loss of muscle mass (Fleg & Lakatta, 1988). This loss of fitness is also observable in highly active older adults, yet display rates of decline are similar to their sedentary peers (Marcell, 2003). The sequel of sarcopenia may contribute to frailty, decreased capacity for independent living, and subsequent increased health care costs (Marcell, 2003). The physiological factors that contribute to the process of sarcopenia are multifactorial, occurring over a prolonged time period, possibly with no identifiable single cause or mechanism. Various mechanisms have been suggested to explain the change in total muscle mass observed including: 1) a lack of regular physical activity, 2) a change in protein metabolism, 3) alterations in the endocrine milieu, 4) a loss of neuromuscular function, 5) altered gene expression, and 6) apoptosis; (Marcell, 2003).

5.3 Muscle alterations with age

At whole muscle level, the reduction in intrinsic force observed with ageing is probably the result of the combined effect of changes (Narici et al., 2008) in: 1) muscle architecture, 2) tendon mechanical properties, 3) neural drive, and 4) single fibre specific tension. A reduction in single fibre specific tension is one of the major factors contributing to the decline in intrinsic muscle force (Narici et al., 2008). The

evidence suggests that this is tightly associated with a decrease in the number of actomyosin cross-bridges rather than in the force exerted by each cross-bridge (D'Antona et al., 2003). A reduction in excitation-contraction coupling may also contribute to the decrease in specific tension in old age (Narici et al., 2008). Other contributors include a reduction in neural drive to the agonist muscles and an increase in neural drive to the antagonist muscles (Komi, 2003 p-409). An increased co-activation of antagonist muscles, probably necessary for joint stabilization, has been suggested as a possible mechanism for the loss of force with ageing (Narici et al., 2008).

5.3.1 Effects of ageing on muscle architecture

Narici and colleagues (2003), studied the effect of aging on human gastrocnemius medialis muscle architecture, comparing young and older subjects using computerized tomography and ultrasonography. They found that in the elderly, anatomic cross-sectional area and volume were, respectively, 19.1% and 25.4% smaller than in the young adults. Also, fascicle length and pennation angle were smaller in the elderly group by 10.2% and 13.2%, respectively (Figure 10). When the data for the young and elderly adults were pooled together, pennation angle significantly correlated with anatomic cross-sectional area. Because of the reduced volume and fascicle length in the elderly group, the resulting physiological cross-sectional area was found to be 15.2% smaller (Narici et al., 2003). Stenroth et al., (2012) found similar results, reporting that gastrocnemius medialis and soleus muscle thickness was decreased with ageing.

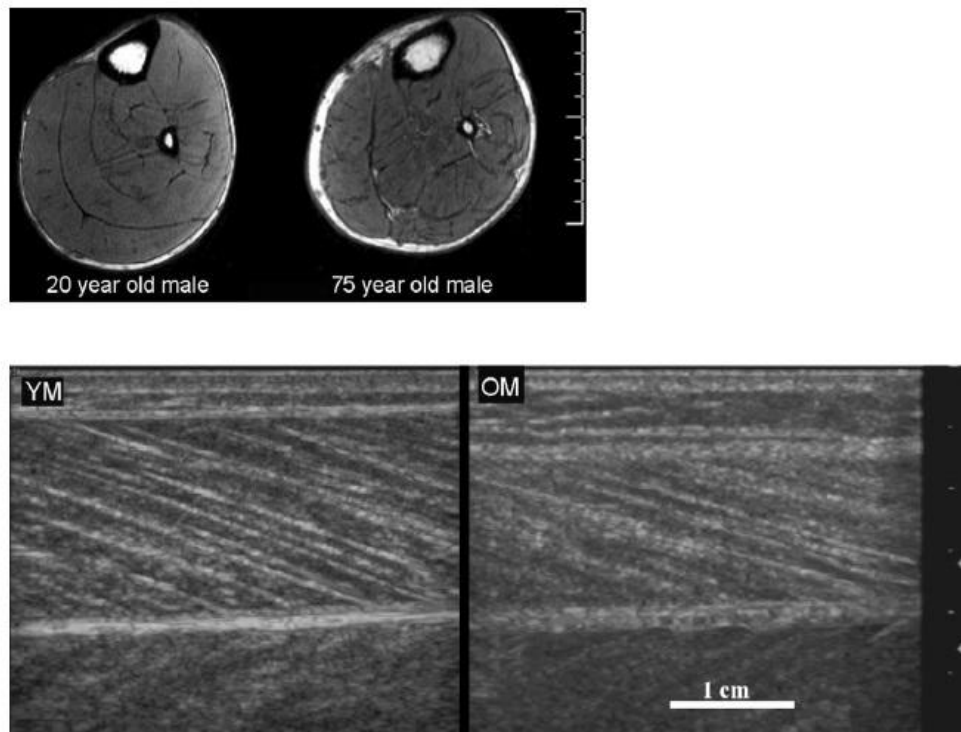


FIGURE 10. (Top) Axial-plane MRI scans of the calf muscles of a young male aged 20 years and an older male aged 75 years matched for anthropometric characteristics and physical activity level. (Bottom) Sagittal-plane sonographs of the gastrocnemius medialis muscle in the same subjects. In the older individual, muscle fibre fascicle length and pennation angle are visibly smaller than in the younger adult (from Narici et al., 2008).

The smaller pennation angles and fascicle lengths in older individuals suggest that, with ageing, sarcomeres in parallel and in series are lost. The mechanism responsible of this phenomenon could be a post-transcriptional protein synthesis processes (Russell et al., 2000). Differences in muscle architecture may account for about 50% of the loss in muscle function in the elderly. However, the actual functional outcome of these architectural alterations will also depend on tendon stiffness (Narici et al., 2008).

5.3.2 Effects of ageing on tendons

With ageing tendons undergo many biochemical, cellular, mechanical and pathological changes that bring about a general decline in the structure and function of the tendon. This decline is characterized by a reduced ability to adapt to environmental stress and loss of tissue homeostasis (Tuite et al., 1997).

At cellular level, there is a change in shape (longer, slimmer and more uniform) and a decrease in the number of tenoblasts per unit of surface area and per unit of volume (Tuite et al., 1997). The ability to synthesize proteins and amino acids is decreased as a response to the decrease in organelles such as rough endoplasmic reticulum. The changes in tendon matrix are accompanied by altered enzyme activity, extracellular water content and decreased mucopolysaccharide content. Total glycosaminoglycan and glycosaminoglycan fraction show mild decrease with ageing (Tuite et al., 1997). Several changes involve collagen molecules: total amount and volume density of collagen increases, collagen synthesis and degradation diminishes, collagen fiber diameter increases, and nonreducible cross linking increases. This causes changes in tendon mechanical properties that include: a decrease in ultimate strain, ultimate load, elastic modulus, tensile strength and an increase in stiffness (Tuite et al., 1997).

Stenroth and colleagues, (2012) examined the concurrent age-related differences in tendon properties, comparing young and old subjects. At tendon level, they found that older participants had 17% lower Achilles tendon stiffness and 32% lower Young's modulus than young participants. Tendon cross-sectional area was 16% larger in older participants. The comparison between old and young subjects with similar strengths did not reveal a difference in tendon stiffness. They suggest that regardless of age, Achilles tendon mechanical properties adapt to match the level of muscle performance. Old people may compensate for lower tendon material properties by increasing tendon cross-sectional area. Lower tendon stiffness in older subjects might be beneficial for movement economy in low-intensity locomotion and thus optimized for their daily activities (Stenroth et al., 2012).

5.4 Age-related changes in sensory systems for postural control

Age-related changes in the nervous system includes loss of brain weight (10% of its weight by the age of 90 years) (Sturnieks et al., 2008), reduced cerebral blood flow, reduced level of neurotransmitter synthesis and loss of neurons, with alterations in their morphological (myelin and density of dendritic connection) and biophysical (conduction velocity of action potentials) properties (Enoka, 2008).

With aging there is a progressive loss of functionality of the systems that contribute to the control of posture: visual, somatosensory and vestibular systems (Bronstein et al., 2004). In older individuals, somatosensory information (touch sensitivity and proprioception) is the most important contributor to postural stability, followed by visual and vestibular input (Lord, et al., 1991).

Aging results in reduced number of Pacinian and Meissner's receptors and morphological changes to the muscle spindle, with a corresponding decrease in vibration perception, touch thresholds and muscle length changes (Sturnieks et al., 2008). Studies have found significant age-related declines in position sense of the hip, knee and ankle joint (Sturnieks et al., 2008).

In general, vision becomes progressively worse after the age of 50 (Gittings & Fozard, 1986). The visual changes associated with aging include a decrease in visual acuity, visual field, and accommodation (Bronstein et al., 2004; Sturnieks et al., 2008). Visual disturbances result in an increase of the oscillations of the body in bipedal position up to 30 %, particularly in the anteroposterior direction (Lord & Menz, 2000).

Evidence suggests that there is a loss in vestibular function with normal ageing. Older people with vestibular hypofunction often have impairments in posture and gait, which is characterized by postural instability and a broad-based, staggering gait pattern with unsteady turns (Sturnieks et al., 2008). Anatomical studies on the peripheral labyrinths show attrition of neural and sensory cells as a function of age,

(Sturnieks et al., 2008). In addition to degraded input from the sensory channels with age, there is also evidence of changes in central processing mechanisms which may impair the ability to integrate sensory information and reduce the ability to compensate for unreliable or discordant sensory input (Sturnieks et al., 2008)

5.5 Age-related changes in gait patterns

Gait changes are common with increasing age. Older adults tend to walk with slower velocity, shorter step length, wider step width and a relatively increased proportion of time spent in the double-support phase (Bronstein et al., 2004; Prince et al., 1997; Sturnieks et al., 2008). It is not clear whether these changes are due to physical limitations or an adaptive strategy for improved safety (Sturnieks et al., 2008). Older adults are also less capable of incorporating the avoidance of an obstacle into their normal gait patterns (Sturnieks et al., 2008).

Kinematic and kinetic alterations in older people compared to young have been extensively reported (Winter et al., 1990). Kinematics modifications include: reduced hip motion (Kerrigan et al., 1998), reduced angular velocity of the lower trunk (Gill et al., 2001), increased anterior pelvic tilt (Kerrigan et al., 1998), and reduced ankle range of motion (Prince et al., 1997). Kinetic alterations include: increased hip extension moment during swing phase (Mills & Barrett, 2001), reduced ankle power generation (Kerrigan et al., 1998), and increased knee absorption during the transition between stance and swing (Prince et al., 1997). Increased mechanical energy demands of lower limb musculature have also been reported (McGibbon et al., 2001).

5.5.1 EMG alterations in gait

Neuromuscular adaptations are a response to age-related impairments and play a key role in causing gait changes in the elderly. These adaptations are direct or indirect responses to a primary impairment, and exist to fulfill a compensatory role in healthy elders and elders with known impairments (McGibbon, 2003). For instance, it has been demonstrated that older individuals with poor balance increase their muscle activity during dual-task performance (Fraser et al., 2007).

As previously mentioned, older adults exhibit decreased peak ankle plantar flexor power during push off, accompanied by either increased peak hip extensor power during early-stance, and/or increased peak hip flexor power generation during late-stance (McGibbon & Krebs, 2004). This “distal to proximal shift” in power production exists even among active-healthy older adults, and seems to be more pronounced at faster walking speeds (McGibbon, 2003; Schmitz et al., 2009; Silder, et al., 2008). Schmitz and colleagues (2009) investigated this shift, evaluating the effects of age and speed on the activation of lower extremity muscles during human walking. EMG from major lower extremity muscles were recorded as healthy young and older adults walked over ground at slow, preferred and fast speeds. Compared to the young adults, the old group exhibited greater activation of the tibialis anterior and soleus during mid-stance at all walking speeds. Also, old subjects showed greater activation of the vastus lateralis and medial hamstrings during loading and midstance at the fast walking speed, suggesting increased coactivation across the ankle and knee. In addition, older adults depend less on soleus muscle activation to push off at faster walking speeds (Schmitz et al., 2009) (Figure 11).

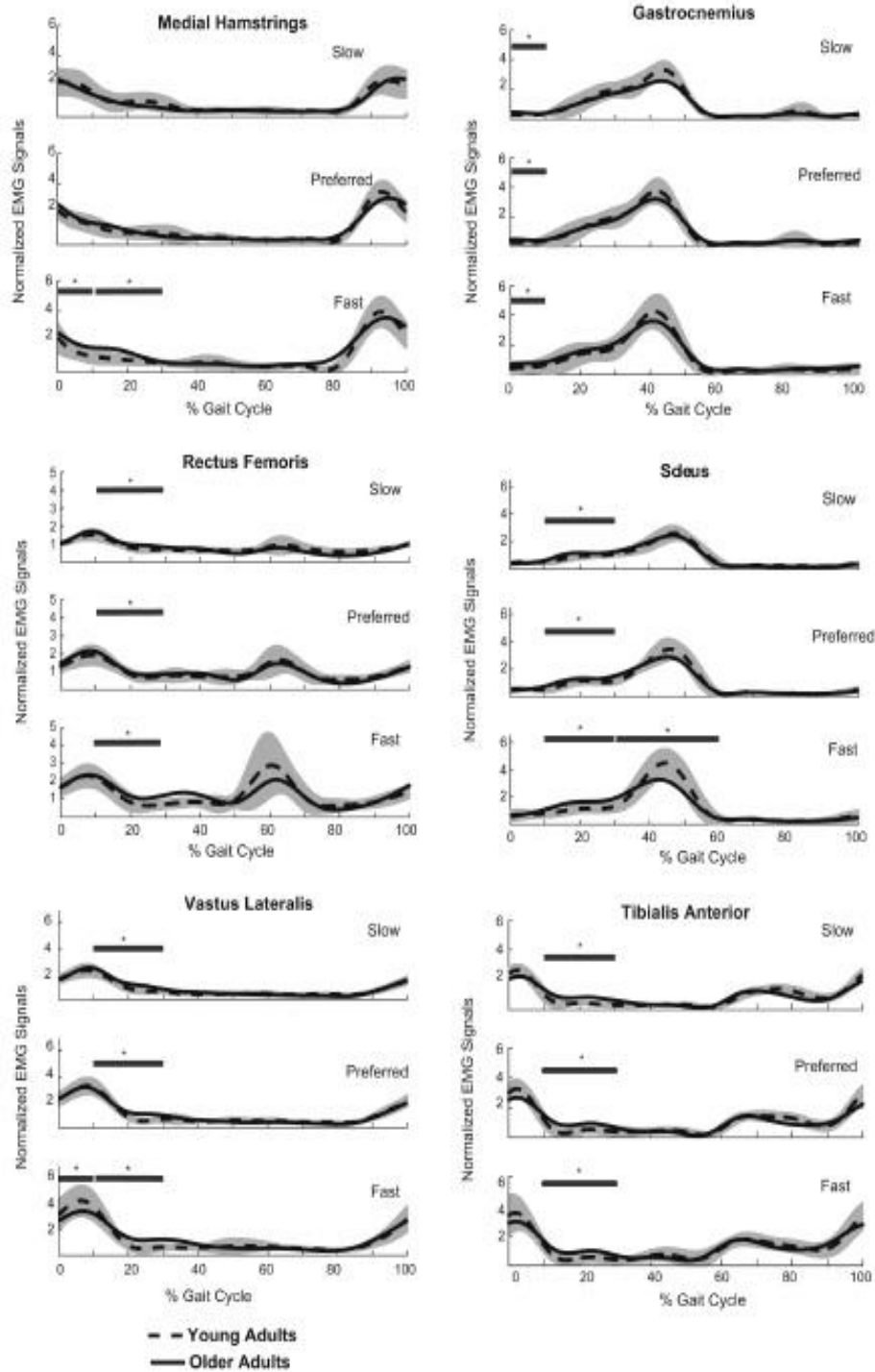


FIGURE 11. Ensemble averaged EMG activities for young and older adults at the, preferred and fast walking speeds. The shaded portion represents plus and minus one standard deviation of the young adult's data. The horizontal lines above the curves indicate phases of the gait cycle where the average normalized activities over a phase of the gait cycle differed significantly between the age groups (from Schmitz et al., 2009).

Complementary results during walking have shown that maximum walking speed is limited by impaired neuromuscular force and activation of the triceps surae muscle group in elderly (Clark et al., 2013) and a disproportionate EMG recruitment of hip muscles, particularly at steeper uphill walking (Franz & Kram, 2013). Moreover, Schmitz and colleagues group previously showed that the older adults analyzed in his study generated more peak hip extensor power and did significantly more positive work by both the hip extensors and flexors, when compared to younger subjects (Silder et al., 2008).

The results of these investigations suggest that age-related changes in neuromuscular activity reflect a strategy of stiffening the limb during single support and likely contribute to reduced push off power at fast walking speeds being compensated by hip extensor activity (Schmitz et al., 2009). These changes are most likely the result of age-related impairment in ankle-power generating capacity (McGibbon, 2003) and with the loss of elastic properties in calf muscles (Sawicki et al., 2009), which limits gait characteristics and may contribute to falls in the elderly (McGibbon, 2003). Neuromuscular adaptations at the hip function appears to compensate for reduced capacity of ankle plantarflexors, assisting in leg swing initiation via hip flexors (McGibbon, 2003). Increased levels of hamstring activity in the older adults present during loading and mid-stance at faster walking speeds, may contribute to the increased hip extensor power during early-stance (Schmitz et al., 2009)

Cocontraction has been observed as a task independent strategy that is used to stiffen the joint and enhance the stability. There is evidence for spinal circuits and cortical mechanism mediating this change in motor behavior (Hortobágyi & Devita, 2006). Older adults may employ greater coactivation of the ankle muscles during mid-stance to increase ankle stiffness and accommodate potential balance concerns (Schmitz et al., 2009). Further, individuals with a fear of falling increase muscular coactivation at the ankle joint during walking (Nagai et al., 2012).

Kang & Dingwell, (2009) compared lower extremity muscle activation dynamics in young and older adults during walking by defining a multivariate state space for muscle activity. When comparing continuous multivariate EMG dynamics, older adults demonstrated greater local and orbital instability of their EMG patterns. Muscle activation dynamics were strongly manifested in kinematics. These changes in EMG dynamics may be related to increased neuromotor noise associated with aging and may indicate subtle deterioration of gait function that could lead to future functional declines (Kang & Dingwell, 2009).

6. COST OF TRANSPORT IN ELDERLY

For an unknown reason, and despite the gait adaptations present in elderly population, the net metabolic COT increases with age (Hortobágyi et al., 2011; Malatesta et al., 2003; Martin et al., 1992; Mian et al., 2006; Ortega & Farley, 2007; Ortega et al., 2008). Thirty years ago Waters and colleagues presented normative data that summarize the energy requirements of level outdoor walking, revealing that the net oxygen cost per meter walked for senior subjects is significantly higher than the value for young adults (Waters et al., 1983). Moreover, this shift is not related with the physical activity status of the senior subjects (Martin et al., 1992). Although elderly adults consume more energy than young adults at all speeds, both consume the least metabolic energy to walk a given distance at intermediate speeds, consuming more energy when they use faster or slower speeds (Martin et al., 1992; Ortega & Farley, 2007). This observation suggests that similar biomechanical factors influence the metabolic cost of walking regardless of age (Ortega & Farley, 2007).

6.1 Biomechanical Factors related with COT

Ortega & Farley, (2007) tested the hypothesis that individual limb work explains the greater metabolic COT in elderly adults. The COT and individual limb work performed on the center of mass was determined during walking at a range of speeds in young and elderly adults. Their results demonstrated that the greater COT in elderly adults cannot be explained by a difference in individual limb work. The same group evaluated the effects of aging and arm swing on the metabolic cost of stability in human walking (Ortega et al., 2008). As humans age, their ability to actively control lateral stabilization during walking may decline due to progressive impairment of neuromuscular function, increasing the COT; although arm swing is not entirely passive, it may reduce the need for more metabolically expensive stabilization techniques like increasing trunk muscle force generation or adjusting step width (Ortega et al., 2008). To test these parameters, they provided external

lateral stabilization while young and elderly subjects walked at $1.3 \text{ m}\cdot\text{s}^{-1}$ on a motorized treadmill with and without arm swing. Their results showed that the greater metabolic cost of walking in elderly adults is not caused by a greater cost of lateral stabilization. Moreover, arm swing reduces the metabolic cost of walking in both young and elderly adults likely by contributing to stability (Ortega et al., 2008)

Malatesta and colleagues tested whether the lower economy of walking in healthy elderly subjects is due to greater gait instability, assessed by the fluctuation magnitude (e.g., the variance, the size of the fluctuation) and fluctuation dynamics of stride time (e.g. how one stride changes from the next, independently of the variance). They demonstrated increased gait instability and greater energy expenditure in healthy elderly subjects while walking. However, there was no significant correlation between gait instability with energy cost of walking at preferred walking speed (Malatesta et al., 2003) leading the authors to suggest that an increase in mechanical work may play a dominant role in the increased COT. This question was addressed by Mian and colleagues who investigated the mechanical work, efficiency, and antagonist muscle coactivation to better understand the cause of the elevated metabolic COT in older adults. Their results showed that healthy elders with no gait impairment have an elevated COT which is not explained by an elevation in whole body mechanical work (Mian et al., 2006). Coactivation was 31% higher in the old group for antagonist muscles of the thigh, being this moderately correlated with COT, suggesting that increased coactivation may offer partial explanation for the elevated COT (Mian et al., 2006).

6.2 Neuromuscular activity and COT

The lower extremity antagonist coactivation in elderly walking was evaluated by Peterson & Martin, (2010). They tested if older adults have higher levels of coactivation about the thigh and shank than young adults across a range of walking speeds, and if higher levels of coactivation are associated with higher COT in both groups. Coactivation about the thigh was higher in older adults, whereas coactivation about the shank was not different between age groups. Total coactivation (thigh coactivation plus shank coactivation) showed significant positive relationships to COT at all walking speeds (Peterson & Martin, 2010). These results imply that coactivation contributes to higher COT in older adults.

Although these studies reported associations between coactivation and COT, they did not examine the possibility that an age-related increase in muscle activity per se contributes to COT and whether increased COT is also present in other locomotor tasks (Hortobágyi et al., 2011). Hortobágyi et al., (2011) examined the association between COT, agonist muscle activity, and antagonist coactivity in young and old adults walking in a decline, level, and incline situation (Figure 12). The main findings of the study were that old versus young adults expended 18.4% more metabolic energy per unit mass and distance of walking, and this increased cost of gait was associated with the magnitude of agonist and antagonist muscle coactivation (Hortobágyi et al., 2011). Agonist muscle activity accounted for up to ~50% of the variation in COT in old adults and this group activated their leg muscles during ascent and level gaits substantially higher (Hortobágyi et al., 2011)

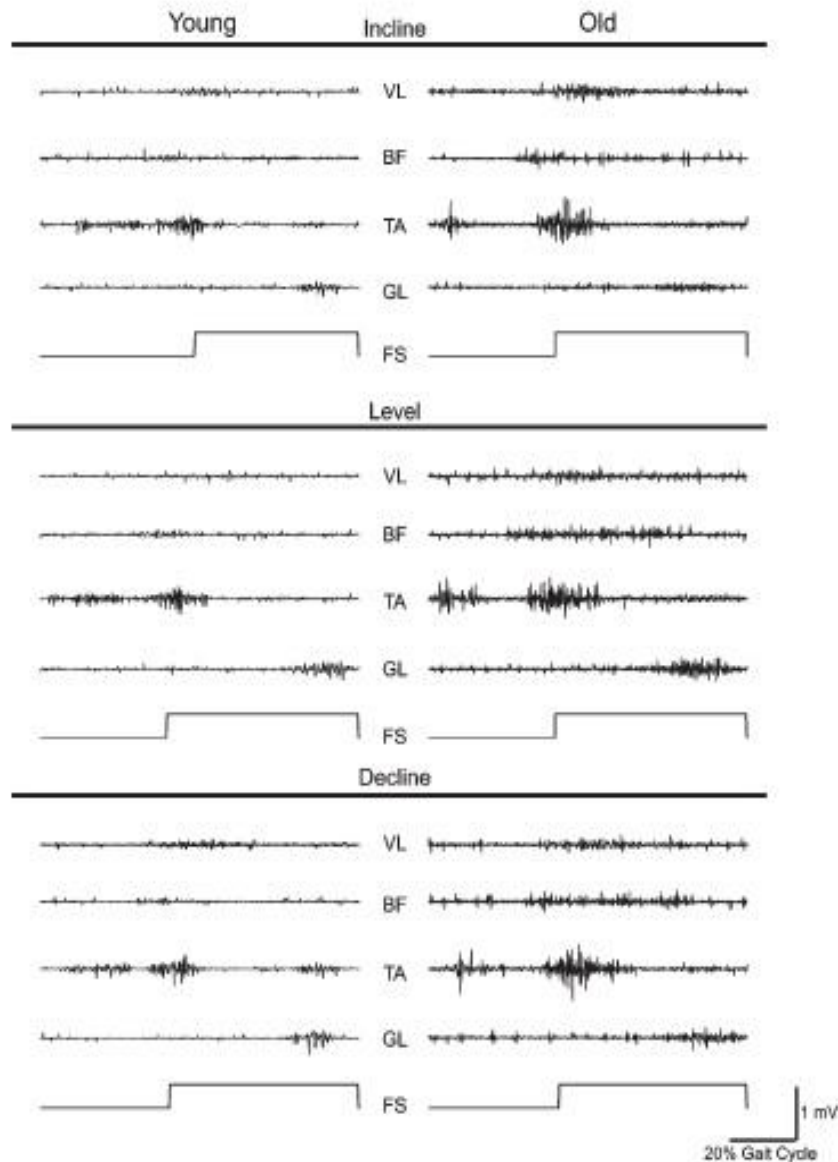


FIGURE 12. Typical surface EMG activity recorded during incline, level, and decline walking at $0.98 \text{ m}\cdot\text{s}^{-1}$ in a young (age 25 years, female participant, left column) and an old (age 83 years, male participant) participant. Within each panel, the top tracing is the activity of the vastus lateralis (VL), second tracing is biceps femoris (BF), third tracing is tibialis anterior (TA), and the fourth tracing is gastrocnemius lateralis (GL) of the right leg. The lowest tracing in each panel depicts the foot switch signal, and the upward deviation denotes heel strike. Note that the level of the gross EMG activity and coactivation of muscle pairs (VL–BF and TA–GL) is higher in the old compared with the young participant (from Hortobágyi et al., 2011)

In sum, because increased COT in old adults is not related with mechanical factors, neural mechanisms like an increase in agonist muscle activation and antagonist muscle coactivation during the gait cycle could mediate the age-related increase in COT (Hortobágyi et al., 2009, 2011). This could be explained by the increase of neural cost and relative effort needed to execute activities of daily living present in old subjects (Hortobágyi et al., 2003), and with the general reduction in the activity of motor cortical inhibitory circuits with age (Hortobágyi & Devita, 2006). There is also a down-regulation of spinal reciprocal inhibition during standing and walking in old compared with young adults (Kido et al., 2004).

Recently, the activity of individual lower limb muscles was studied in young adults, revealing that their metabolic activity is minimized at specific walking speeds, but the different muscles have dissimilar economy performance (Carrier et al., 2011). Accordingly, may be useful to reveal the muscle activity and metabolic behavior of individual muscles in elderly walking. This information could give new insights into the sources of the increased COT in elderly population.

7. STUDY AIMS AND HYPOTHESES

The COT in elderly subjects is increased in comparison to young adults, independently of the walking speed. Several investigations have revealed that this fact is not related to mechanical parameters (e.g. work generated), and that changes in the neuromuscular activity of the muscles of the lower extremities are more likely to explain this phenomenon. Altered coactivation and increased EMG activity have been found to be correlated with the increased COT in elderly subjects. Recent evidence in young subjects suggests that the activity of lower limb muscles is minimized at specific speeds, but all muscles are not tuned at the same speed. However, there is no research comparing individual muscle activity patterns between young and old subjects. The objective of this thesis was to qualitatively compare the muscle activity pattern of the lower extremities between healthy young and elderly subjects, over a range of walking speeds in order to infer the contributions of individual muscles to changes in COT in both age groups. To achieve this objective, we used the integrated muscle activity per distance traveled (CMAPD), an EMG tool that provides a correlative indication of muscle metabolism, and we related this to the COT. This information enables us to determine the contribution of individual muscles to total energetic cost, giving new insight into sources of movement inefficiency in elderly walking. In future, this information could also be useful when conducting training or rehabilitation programs to improve walking efficiency.

Research question: How can we explain the higher energy cost of walking in older compared to younger adults?

Hypothesis: Speed-dependent increases in oxygen cost in older adults will be related to higher CMAPD of some or all muscles across the range of speeds investigated.

8. METHODS

8.1 Participants

A convenience sample of 26 subjects (13 young and 13 old subjects) was recruited (Table 1), using the following inclusion criteria: adults in an age-range from 18-30 years old and older adults from 70-80 years old. Exclusion criteria for both groups were pain during walking or past musculoskeletal injuries that affected their walking ability. Based on an extensive health history questionnaire and a physical activity questionnaire (Voorrips et al., 1991) that were conducted by an experienced laboratory staff, old adults were healthy, functional and able to execute the walking tasks without complications or fatigue. Recruitment was done through email advertisements and telephone calls to university students and elderly clubs. All participants gave written informed consent before participating in the study. The local ethical committee approved all methods of the study, conformed to the standards set by the latest revision of the Declaration of Helsinki.

Table 1. Characteristics of Old and Young groups. (N=26)

	Young (n=13)	Old (n=13)
Age (Years)	24.4 (\pm 3.7)	73.53 (\pm 3.7)
Weight (Kg)	76.2 (\pm 6.5)	82.9 (\pm 8.9)
Height (cm)	1.8 (\pm 0.1)	1.8 (\pm 0.1)
Body Mass Index	23.8 (\pm 1.8)	27.1 (\pm 2.9)
Preferred Speed*	4.8 (\pm 0.6)*	4.0 (\pm 0.4)*
Physical Activity Level**	High	High

Values are mean (SD)

* Significantly different ($p=0.001$)

** Voorrips et al., 1991

8.2 Experimental Protocol

Participants reported to the laboratory for one 2-hour session and wore shorts and sneakers. For the experimental trials, data were collected as the subjects walked on a horizontal custom-built motorized treadmill (University of Jyväskylä, Finland). All the participants had an adequate habituation period to become familiar with the study, treadmill and the experimental situation. Before the walking trials, the subject stood calmly in the treadmill for 3 minutes, and EMG and metabolic data were collected. Afterwards, 7 walking trials of 4 minutes each were collected randomly: at the preferred speed (previously calculated, Table 1) and 15, 30, and 45 % higher/slower than the preferred speed. A foot switch under the right heel synchronized with the EMG recording was used to detect gait events. Both groups wore a harness hooked to the treadmill jail for safety purposes.

8.3 EMG and metabolic measurements

Surface EMG from 10 different muscles in the right lower limb was recorded. Bipolar electrodes (Ag–AgCl, 2 cm interelectrode distance) were placed over the vastus lateralis (VL), vastus medialis (VM), rectus femoris (RF), semitendinosus (ST), biceps femoris (BF), tibialis anterior (TA), lateral gastrocnemius (LG), medial gastrocnemius (MG) soleus (SOL), and flexor hallucis longus (FHL) muscles according to the recommendations of SENIAM (Hermens et al., 1999). Before placement, the skin was shaved, abraded with sand paper and cleaned with alcohol to ensure an interelectrode impedance value below 5 Ω . The EMG signals were transmitted and band-pass filtered (20-500 Hz) using a wireless recording system (Desktop DTS, Noraxon, Scottsdale, USA; sampling rate 1.5 kHz; signal amplification 1000). All the signals were recorded with a 16-bit AD-board (Power 1401, CED, Cambridge, UK; sampling frequency 1500 Hz) and using Spike2 Software (CED, Cambridge, UK).

For metabolic measurements, participants were equipped with a mask connected to a computerized metabolic system (Oxycon Pro; Viasys Healthcare, Hoechberg, Germany). Oxygen (VO_2) and carbon dioxide (VCO_2) expired gases were analyzed using a breath-by-breath analysis during the entire test. The flow, volume, and gas analyzer were calibrated before each test according to the manufacturer's instructions.

8.4 Data Analysis

EMG analysis was done on the data collected during the last minute of the recording in a stride-by-stride basis for each speed. The cumulative activity required from each muscle to traverse a kilometer (CMAPD) was calculated for each muscle, based on Carrier et al (2011) description. EMG signals were subtracted of any DC offset, high-pass filtered at 20 Hz, low-pass filtered at 300 Hz, and smoothed by a moving window of 15 ms. EMG stride curves were identified using the foot switch signals, with the help of a semiautomatic program including visual control. Strides that exceeds in +/- 20% the average value of stride duration were excluded from the analysis. Then, the root mean square (rms) was calculated for each stride. To calculate the CMAPD, rms amplitudes were normalized to a travel distance of 1 km, using the following equation:

$$CMAPD[\mu V \times s / km] = \frac{rms[\mu V]}{v[m / s]} \times 1000$$

Where the rms value is the average across one stride, and "v" is locomotor speed, multiplied by 1000 to get the distance of 1km.

Averaged CMAPD values were calculated using 25(SD= 5) strides, separately for every muscle, subject, and speed respectively. To identify curve characteristics of these CMAPD values versus locomotor speed, second-order polynomial functions were fitted to the data by using least-squares regression. To provide a graphical representation of the median values of CMAPD versus locomotor speed for each

muscle, CMAPD were normalized separately for every subject by relating all values of CMAPD to the value occurring at maximum speed.

The rationale of this method is in the fact that integration of the EMG recording, provides a reliable correlative indication of muscle metabolism within the recording field of the electrode (Blake & Wakeling, 2013; Carrier et al., 2011; Praagman et al., 2003; Winter, 2005 p-273). If the contractile state (e.g., concentric, isometric, or eccentric) of the muscle fibers remains constant in a normal situation (e.g. without fatigue), the metabolic cost of contraction occur at fixed values. Therefore, the ratio of the metabolic cost of contraction versus the metabolic cost of activation/deactivation remains constant, regardless of the number of steps taken to travel 1 km or the number of fibers recruited per step (Carrier et al., 2011).

Metabolic analysis of VO_2 and VCO_2 (milliliters/minute) was done with the averaged data over the final minute of each walking speed, when every participant reached aerobic metabolic steady state (respiratory exchange ratio less than 1.0). We estimated the rate of energy cost from the VO_2 and VCO_2 data normalized to body mass. To determine net metabolic rate, resting metabolic rate measured during standing was subtracted from gross metabolic rate for each trial. Cost of walking was computed by dividing net metabolic rate ($ml\ O_2/kg$) by walking speed (km/h), giving energy cost per unit distance traveled ($ml\ O_2/kg/km$). All analyses were performed by custom programs using MATLAB (MathWorks) environment.

8.5 Statistical Analyses

Optimal speeds among groups were compared using Student's t tests. To determine the effects of age and speed of walking on COT, a two-factor ANOVA was used. When ANOVA revealed significant interaction effects, t tests were used to make appropriate pairwise comparisons. To see if there was a relationship between COT and CMAPD across the range of speeds investigated, correlations were computed

between these variables for each muscle in both groups. The Pearson's correlation coefficients (r-values) were interpreted using Dancey and Reidy's categorization (Dancey & Reidy, 2007) and coefficients of determination (r^2) were calculated.

9. RESULTS

Statistical differences among groups were found in the preferred walking speeds ($p < 0.001$) (Table 1). Mean COT for both groups showed the characteristic U-shaped curve with lower values at intermediate walking speeds (Figure 13). The mean integrated muscle activity required to walk a kilometer (CMAPD) for all examined muscles presented the same trend when plotted vs. walking speed. The lowest values for COT and CMAPD were found around $4.0 \text{ km}\cdot\text{h}^{-1}$ for the old group, and at $4.8 \text{ km}\cdot\text{h}^{-1}$ in the young group (Figure 13). COT was higher in the old group ($p = 0.000$), and pairwise comparisons between speeds revealed differences in six of the seven speeds (Figure 13, Table 2). Qualitative analysis showed higher CMAPD values for the old group in comparison to the young group at all speeds (Figure 13).

Table 2. Pairwise comparison between old and young group COT values according to walking speed. COT values are expressed as $\text{ml O}_2/\text{kg}/\text{km}$.

Speed comparison	Group Mean		Difference	p value	95% Confidence Interval of difference
	Young	Old			
P-45%	168	222	54.8	0.004	-90.92 to -18.62
P-30%	170	215	45	0.02	-82.59 to -7.412
P-15%	167	210	43.7	0.01	-76.05 to -11.33
P*	159	204	44.7	0.006	-75.74 to -13.64
P+15%	175	212	36.9	0.01	-64.96 to -8.887
P+30%	184	215	30.2	0.04	-59.47 to -0.9927
P+45%	211	224	13.5	0.31	-40.41 to 13.48

*P: preferred walking speed. Percentages are from the P speed

CMAPD values per muscle as a function of speed are shown in Figure 14 for the young group and in Figure 15 for the old group. In the young group, most of the muscles presented lower values of CMAPD at intermediate speeds, and increases as speed increased above or decreased below this optimum (Figure 14). However, BF, TA and SOL muscles exhibited relatively constant values at the different speeds (flat curves). LG muscle showed slightly higher CMAPD at intermediate walking speeds,

although results for this muscle were inconsistent. In the old group, CMAPD values exhibited a curvilinear and, in most cases a U-shaped relationship with locomotor speed. However, soleus and MG muscle CMAPD were again relatively independent of speed (Figure 15).

Correlation analyses between CMAPD and COT showed weak associations for most of the muscles in both groups. In the young group (Figure 16), coefficients of determination (r^2) values for the correlation between CMAPD and COT ranged between 0.003 and 0.250 across all muscles. In VL, CMAPD accounted for 25% of the variance in COT. The old group (Figure 17) presented the same tendency of low correlations, with r^2 values between 0.048 to 0.16, the latter value being for VL, which accounted for 16% of COT (moderate correlation, $r=0.4$). In this group, the calf muscles exhibited a trend towards higher coefficients of determination for LG, MG, and FHL compared with the young group.

Group mean COT vs. Speed and group mean CMAPD from all muscles combined vs.
speed

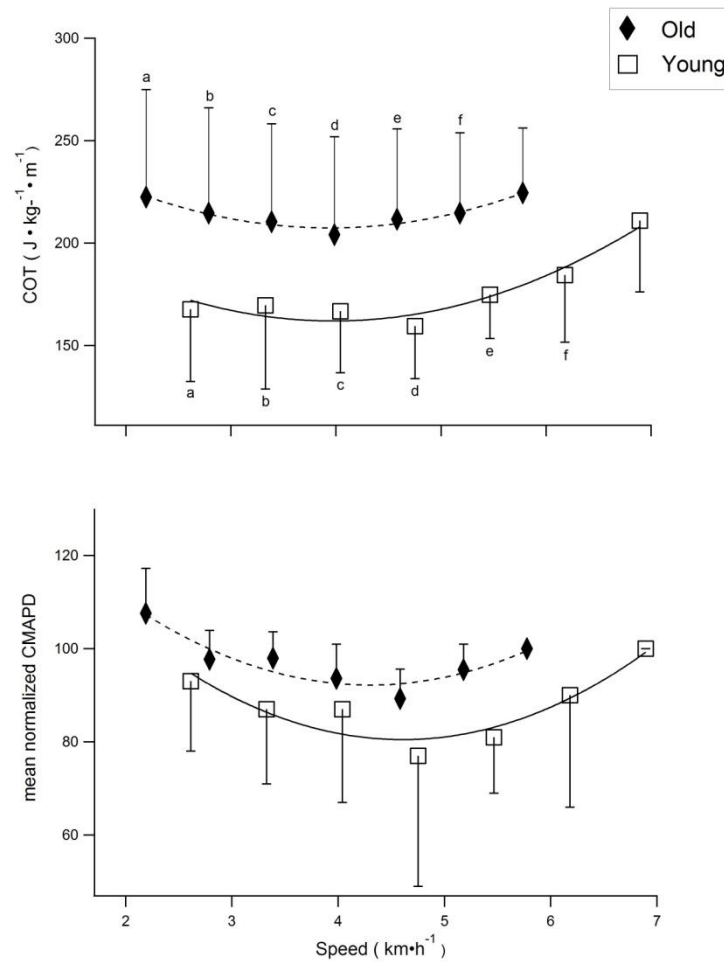


FIGURE 13. Mean cost of walking (COT) and the mean cumulative activity required by all examined muscles to traverse a kilometer (CMAPD) presented versus walking speed. Lines represent second-order polynomial functions fitted to the data by using least-squares regression. CMAPD is normalized relative to the value occurring at the fastest speed. ^{a,b,c,d,e,f} means significantly different.

CMAPD per muscle as a function of speed - Young group

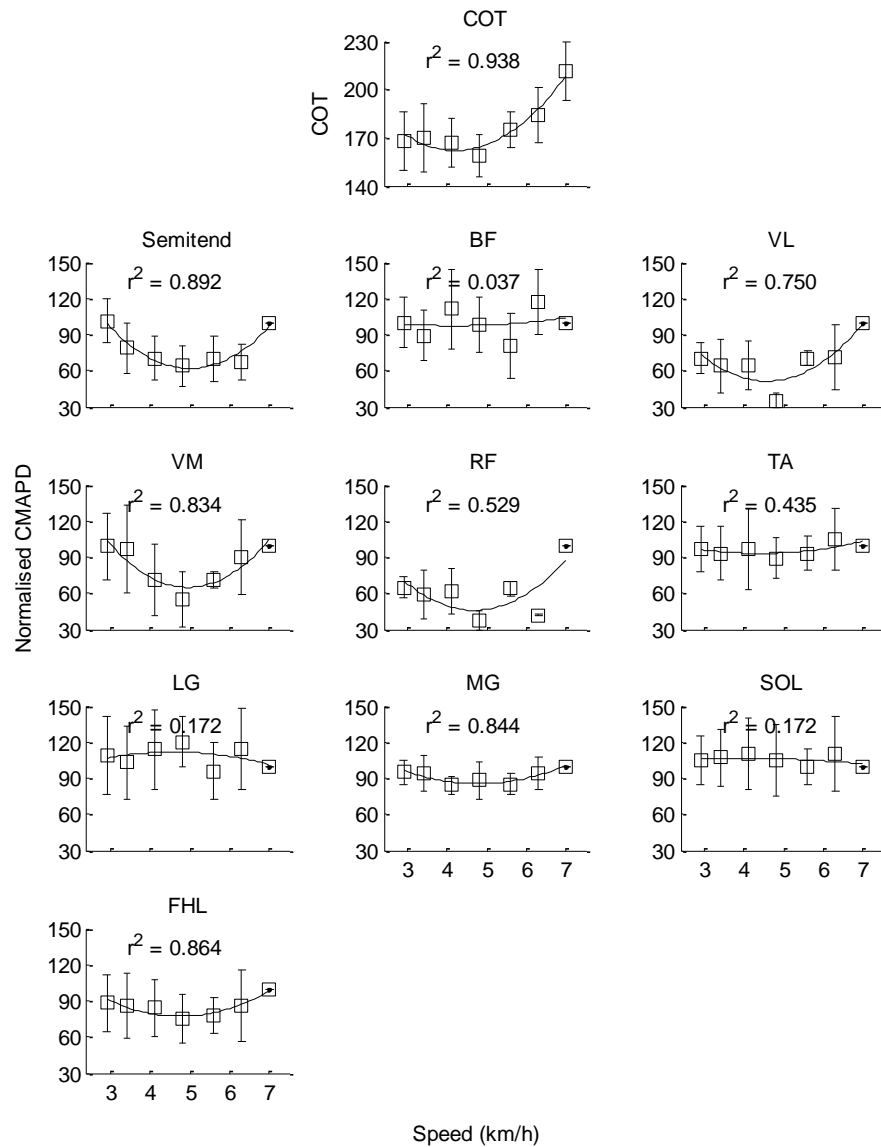


FIGURE 14. Cumulative activity required from each muscle to traverse a kilometer (CMAPD) presented versus walking speed for the young group. Lines represent second-order polynomial functions fitted to the data by using least-squares regression. CMAPD is normalized relative to the value occurring at the fastest speed. Error bars represent standard deviation. r^2 values represent coefficients of determination.

CMAPD per muscle as a function of speed- Old group

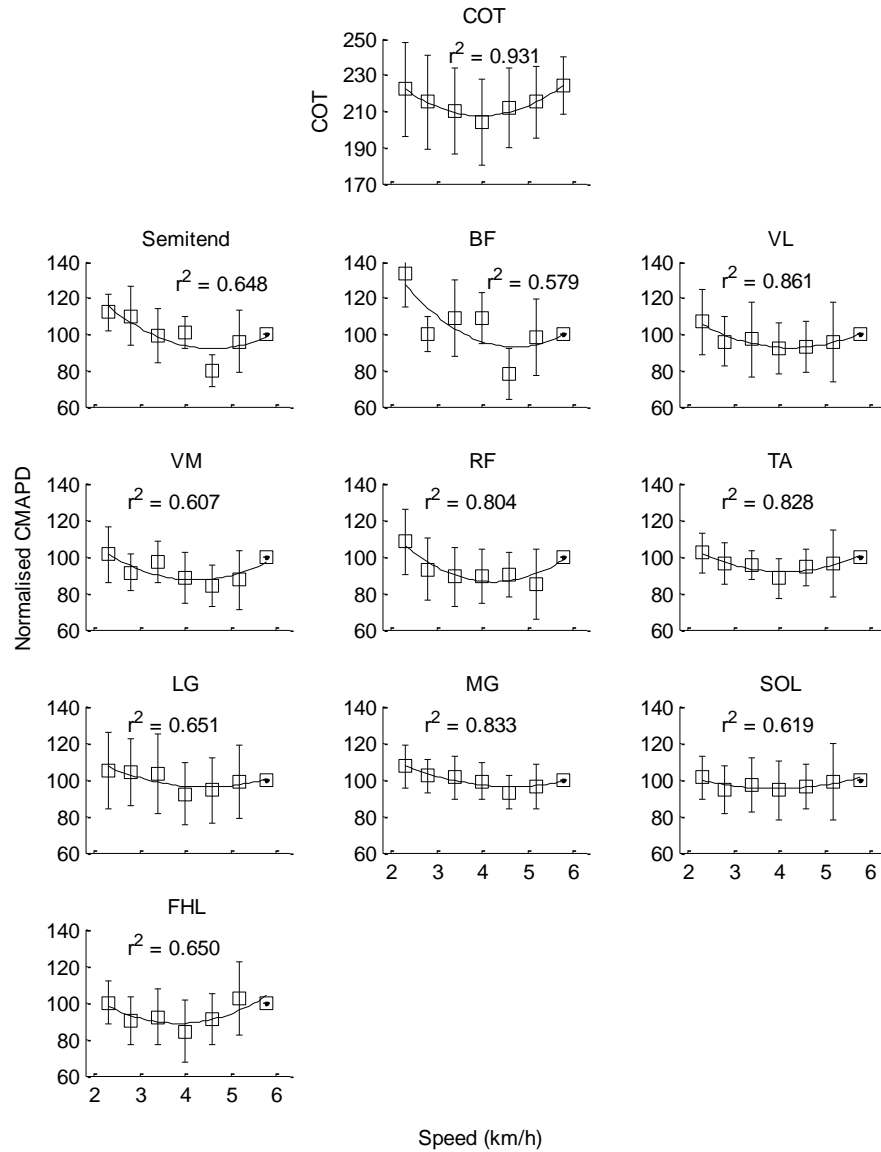


FIGURE 15. Cumulative activity required from each muscle to traverse a kilometer (CMAPD) presented versus walking speed for the old group. Lines represent second-order polynomial functions fitted to the data by using least-squares regression. CMAPD is normalized relative to the value occurring at the fastest speed. Error bars represent standard deviation. r^2 values represent coefficients of determination.

COT vs. CMAPD for each muscle - Young group

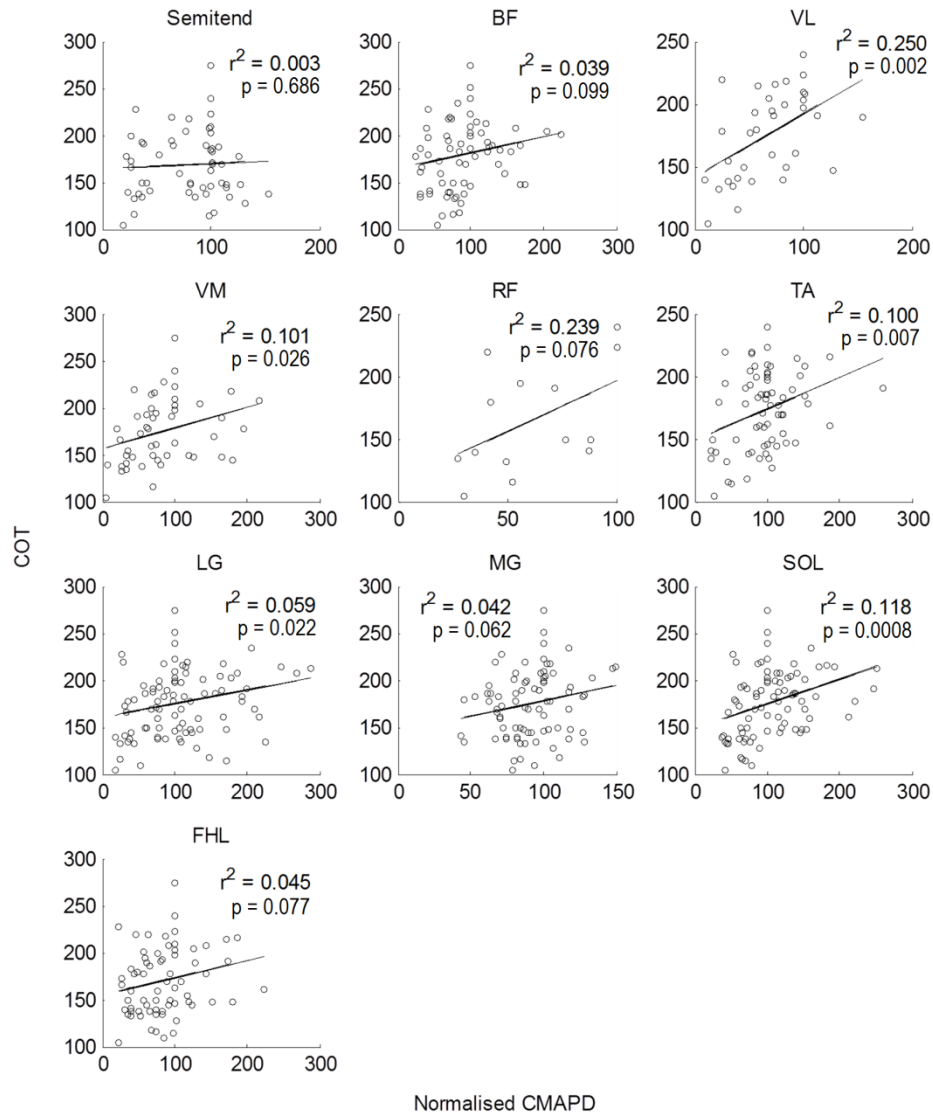


FIGURE 16. Correlations between cost of walking (COT) and cumulative activity required from each muscle to traverse a kilometer (CMAPD) in the young group. Lines represent regression for each muscle. r^2 values represent coefficients of determination. Note that very few values were obtained for RF in this group (see discussion for justification).

COT vs. CMAPD for each muscle- Old group

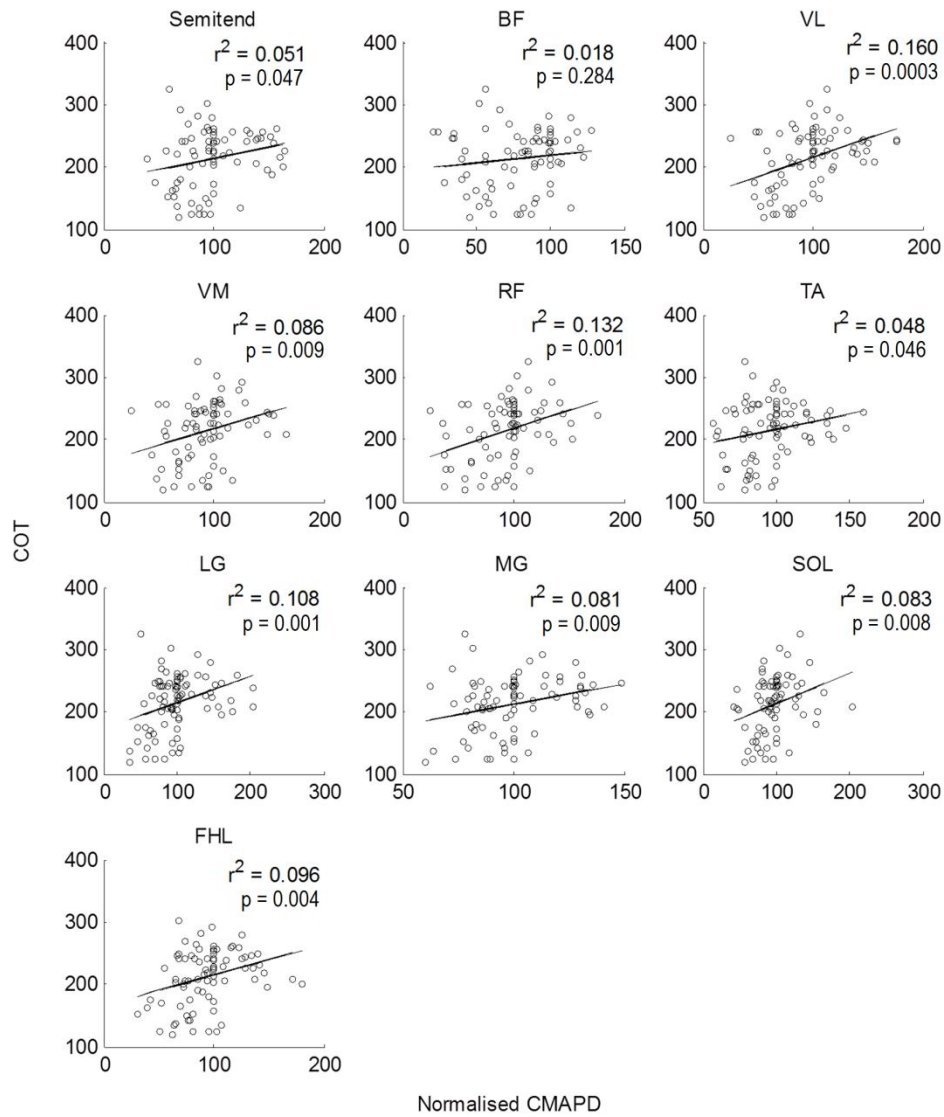


FIGURE 17. Correlations between cost of walking (COT) and cumulative activity required from each muscle to traverse a kilometer (CMAPD) in the old group. Lines represent regression for each muscle. r^2 values represent coefficients of determination.

10. DISCUSSION

The objective of this thesis was to qualitatively compare the muscle CMAPD values of the lower extremities between healthy young and elderly subjects, over a range of walking speeds in order to infer the contributions of individual muscles to changes in COT in both age groups. The results showed an increased mean COT in the old group, and imply that mean CMAPD values were also higher in this group across walking speeds. Our hypothesis that higher oxygen cost at walking speeds faster or slower than the energetically optimal speed is related to higher CMAPD in all or some muscles is accepted, due to the fact that in both groups some proximal muscles exhibited CMAPD values that were moderately correlated with COT. However, some other muscles, notably soleus, exhibited speed-independent CMAPD, suggesting that this muscle contributes minimally to changes in COT. In the old group, correlations between CMAPD and COT were modestly higher in the calf muscles, suggesting that these muscles may function less economically in old age, and may thus contribute relatively more to changes in COT in comparison with the young group.

10.1 Group mean CMAPD and COT

Our qualitative analyses indicate an increased mean CMAPD in the older group in comparison to the young group during all walking speeds. It could be speculated that this is mainly related with changes in neural activation patterns. Increased COT in old adults is not associated with mechanical factors (Malatesta et al., 2003; Mian et al., 2006; Ortega & Farley, 2007; Ortega et al., 2008), and it has been demonstrated that the magnitude of agonist activation (Hortobágyi et al., 2011) and antagonist muscle coactivation (Hortobágyi et al., 2009, 2011; Mian et al., 2006) could mediate the age-related increased cost of gait, so this is likely also true for CMAPD. Thus, muscle activation dynamics may be affected with aging (Kang & Dingwell, 2009) indicating subtle deterioration of gait function, as evidenced by decreased walking economy and increased CMAPD values.

Our results showed CMAPD and COT with minimal values at intermediate speeds. Minimization of COT at specific speeds may be due to muscle's capacity to perform work with highest energetic efficiency at intermediate shortening velocities and/or greatest pendular transfer of kinetic and potential energy at intermediate speeds (Carrier et al., 2011; Cavagna et al., 1977). Knee flexion in the stance phase is also minimal around optimal COT, which is related with decreased cost of muscle work (Winter, 1983).

The significance of the observation that muscle activity is minimized at specific speeds could be that changes in muscle activity during walking broadly reflect changes in the metabolism of the muscles studied (Carrier et al., 2011). EMG provides some information about the contractile state of a muscle, and may thus be a relative measure of muscle metabolism (Winter, 2005 p-273). At the level of individual muscles, greater force and work are produced by increased activity of motor units, and increased force and work production are associated with elevated muscle metabolism (Blake & Wakeling, 2013; Carrier et al., 2011; Praagman et al., 2003). Thus, muscle activity measured with CMAPD could be a good descriptor of mean muscle metabolism during walking at different speeds. Moreover, in both groups, COT and CMAPD presented parallel changes in the U shaped curves at different speeds, reflecting a good correspondence between these two parameters. Thus, our results support the notion that CMAPD can broadly indicate muscle metabolism, and that changes in COT can be attributed to changes in muscle CMAPD.

10.2 Individual muscle CMAPD

Our second finding was the CMAPD U-shaped curves for most of the muscles in both groups when plotted against speed. Interestingly, the curves in LG and TA muscles were largely flat in the young group, but slightly curved in the old group. MG and SOL curves were mainly flat in both groups. Flat CMAPD curves could represent a

strategy to enable relatively good economy when walking both slow and fast, presumably broadening the range of sustainable speeds. As mentioned above, Carrier et al (2011) showed that not all lower limb muscles are adapted to function most economically at the same walking or running speeds, so the economy of locomotion is not maximized. This pattern may be related to the selection of a broader range of sustainable speeds, and/or to improve performance in motor behaviors not related to locomotion (Carrier et al., 2011).

CMAPD curves for MG and SOL muscles seem to be not affected by aging. Ankle plantar–flexor muscles are a vital source of mechanical power for human locomotion (Farris & Sawicki, 2012a; Winter, 1983). Gastrocnemius is important in providing power for propulsion during walking, with MG showing relatively isometric behavior associated with considerable stretch and recoil of the elastic series element (Farris & Sawicki, 2012a; Ishikawa et al., 2005). Further, the MG is the main propeller for swing initiation (Neptune et al., 2001). Nevertheless, it is noteworthy soleus behavior, because of its importance as the primary force generator in the triceps surae group during walking (Cronin et al., 2013). In comparison to gastrocnemius muscles, soleus makes a larger contribution to ankle torque, makes greater use of elastic energy storage and reuse, and is metabolically more efficient in walking (Krishnaswamy et al., 2011). Soleus also has a larger cross-sectional area (Ward et al., 2009) and shorter fascicles than either gastrocnemius head (Maganaris et al., 1998), reducing the required activation volume for a given force. Moreover, soleus contains more slow fibers that are less fatigable (Gollnick et al., 1974). Cronin et al (2013) demonstrated that soleus exhibited consistent contractile behavior regardless of walking speed, concluding that soleus appears to play an important functional role, especially when walking for prolonged periods or at speeds above the most energetically efficient (Cronin et al., 2013). The present study offers further evidence for the versatility of soleus, and suggests that this is largely maintained in old age.

A possible explanation for the different CMAPD curves between groups could be the aging effect over neuromuscular function of calf muscles. Older adults present a

distal to proximal shift in power production during push off (McGibbon, 2003; McGibbon & Krebs, 2004; Winter et al., 1990), with a decreased peak ankle plantar flexor power (McGibbon, 2003) that seems to be more pronounced at faster walking speeds (Schmitz et al., 2009; Silder et al., 2008). This power loss could be related to a decreased strength capacity, selective death of type II fibers and decreased neural drive to agonist muscles (Komi, 2003 p-409). It seems that from all possible movement sequences, elderly tend to adopt a coordination and control solution that is relatively economical in terms of energy expenditure, to perform the task according to their neuromuscular limitations (Sparrow & Newell, 1998); this solution could be the selection of a most economical speed for some of the calf muscles. However, regardless of walking speed, older individuals exhibit higher COT and CMAPD values than their younger counterparts.

Slightly curved CMAPD values across speeds imply that these muscles function economically at their optimal speeds, but may be associated with slightly poorer economy when walking at speeds substantially slower or faster than their optimal speeds. Since aging affects neuromuscular function, muscles exhibiting this behavior could represent a strategy to rely more on muscles that are independent of speed and more economical, like soleus (Krishnaswamy et al., 2011). In fact, this hypothesis seems to be supported when comparing the coefficient of determination for the calf muscles between age groups: soleus muscle exhibited minimal change between speeds, whereas larger r^2 differences for LG and MG were found. SOL and gastrocnemius muscles perform distinct mechanical roles in force generation and power production in the various phases of stance (Neptune et al., 2001) and across different speeds (Farris & Sawicki, 2012a), thus they show independent metabolic performance. The different CMAPD behavior between groups and among muscles at different walking speeds, support the idea that aging affects the economy of individual muscles differently according to the functional role of the specific muscle.

Our CMAPD values for some of the lower leg muscles in the young group differ from the curves by Carrier et al., (2011), who presented U-shaped curves for almost all

muscles during walking. These differences could be primarily due to methodological issues: they used fixed walking speeds plus the preferred speed, whereas ours were all individualized relative to preferred speed. Further, individual differences may exist in terms of the function of different muscles.

10.3 Correlation between CMAPD and COT

In both age groups, the metabolic cost of contraction in proximal leg muscles such as the quadriceps seems to increase dramatically when walking at speeds faster or slower than the energetic optimum. This suggests that the proximal muscles make a relatively large contribution to speed-dependent changes in COT. The higher correlation found in the old group between CMAPD and COT for VL in comparison to the other lower leg muscles, could be functionally relevant given the previously proposed distal to proximal shift in power production pattern present in elderly population (McGibbon, 2003). However CMAPD-COT correlations for VL in the young group were also high, indicating that this muscle group may only be adapted to function economically at a very narrow range of speeds. Future studies should also examine CMAPD values for the hip muscles, which may also contribute to changes in COT.

If we compare the coefficient of determination in ankle muscles between groups, we see a trend in the old group towards moderately higher values (excluding soleus). This may mean that changes in COT in this group are more dependent on ankle CMAPD than in the young group. The mechanism behind this could be that calf muscles are energetically more expensive in the elderly.

In young adults, calf muscle fascicles act relatively isometrically during walking stance phase (Ishikawa et al., 2005). However, Achilles tendon shows substantial length changes (Lichtwark & Wilson, 2006), which correspond to an increase in the strain of the series elastic elements (Lichtwark et al., 2007). Storing and releasing

elastic energy in the Achilles tendon during each step greatly enhances the efficiency of ankle joint work (Sasaki & Neptune, 2006; Sawicki et al., 2009). Old people show lower tendon material properties, with decreased Achilles tendon stiffness (Stenroth et al., 2012). The reduction in tendon stiffness has an important functional implication: for a given number of serial sarcomeres in a fiber, an older tendon would stretch more on muscle contraction, thus causing its sarcomeres to shorten more than in a younger less extensible tendon (Narici et al., 2008). This may cause a reduction in contractile force, expected from a change in sarcomere working length to a new length corresponding to less optimal myofilament overlap (Narici et al., 2008). Thus to attain the same level of force output, muscles have to perform more work, increasing the energy expenditure. Lower tendon stiffness in older subjects may make lower speed walking relatively more economical, as suggested by the lower optimal walking speed in this group. This may represent optimization for their daily activities (Stenroth et al., 2012), but at the expense of higher muscle activation.

10.4 Limitations

The results of this study should be interpreted considering certain limitations. Body masses between groups presented significant differences. However, we normalized oxygen consumption to body mass, and in CMAPD curves, the values were normalized for every subject by relating all CMAPD values to the value at the fastest speed. Our objective wasn't to compare directly the actual CMAPD values between groups, thus we believe that our findings are valid. Moreover, we ran a separate analysis in which we excluded the subjects with outlier mass values, matching both groups (N=18). Since we didn't find relevant differences between both sample's results, we decided to keep the original subject sample.

Our qualitative results of CMAPD values higher in the old group could depend of the normalization process. In Figure 18, CMAPD values are presented for both groups pairing walking speeds. We can see that the trend of the fitting curve may depend

over the maximum speed, which is our value of normalization. Could be possible that if we normalize to the slowest speed instead the maximum speed, the trend can change. Moreover, could be a drawback the non normalization of EMG signals to a parameter that allows group comparison (e.g. maximum voluntary contraction, M-wave maximum value) prior to the calculation of CMAPD. However, in direct discussion with one of the authors of the cited method (Anders C), we concluded that EMG normalization prior to CMAPD it is not an important step that can affect the outcomes of the calculation.

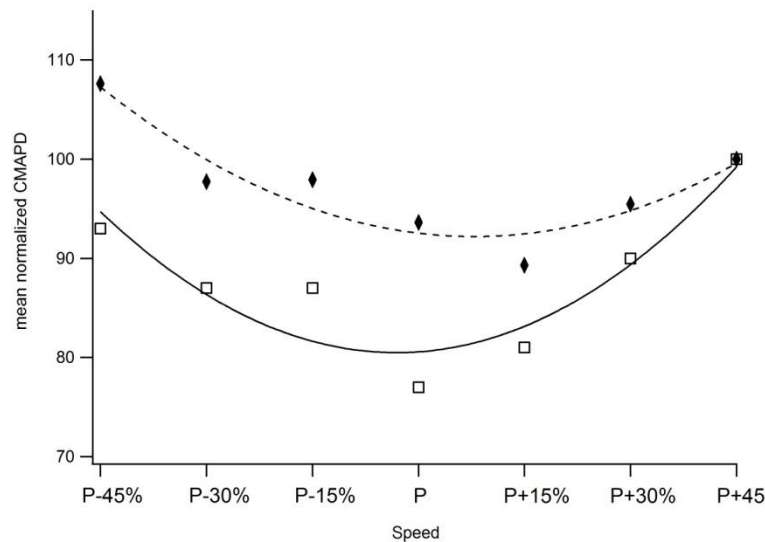


Figure 18 CMAPD values for Old (filled diamonds) and young group (open squares). P is the preferred walking speed, and percentages are from the P speed. See text for details.

Some of the studies comparing COT between different age groups used the same walking speeds between groups (Hortobágyi et al., 2011). We decided to not follow this trend, based on the fact that one of the primary characteristics of gait in older adults is a reduction in preferred walking speed (Himann et al., 1988; Panizzolo et al., 2013). This age-related reduction in walking speed reflects a reduced motor capacity that may be linked with a comparatively high metabolic rate in older adults for a given speed (Martin et al., 1992; Panizzolo et al., 2013). Further, MG operates less efficiently at speeds that do not correspond to optimal COT (Farris & Sawicki, 2012),

and this may also be true for other muscles. Thus, the use of a standardized speed does not allow valid comparisons between old and young groups, as evidenced by our finding that preferred speed was statistically slower in the older group.

One of the muscles had fewer cycles to analyze after the EMG data processing. RF in the young group presented almost no activity at slow walking speeds in some subjects, leading to fewer cycles to process and less reliable results for this muscle. Moreover, technical problems with the wireless EMG system resulted in greater data loss for this muscle than other muscles. Recent evidence supports the fact that RF is often mainly silent at slow walking speeds (Ivanenko et al., 2006), so CMAPD data from this muscle may give misleading results when comparing values across different speeds as we have done.

11. CONCLUSIONS

The cost of walking is an important feature of human transportation. It tells us how the control system is performing in controlling the transformation of chemical energy into mechanical energy. Thus gaining insight about this phenomenon could lead us to a better understanding of the physiological changes occurring in challenged populations. Increased cost of walking in elderly has been previously established; however the mechanisms behind this are still unknown. The focus of this investigation was on the individual lower leg muscle cost of walking in young and old populations, since there is a lack of published literature about muscle economy. We used a novel feature, the cumulative activity required from each muscle to traverse a kilometer (CMAPD), as a non-invasive technique to evaluate muscle metabolism. The results of this study indicate that at group level, speed-dependent changes in COT are reflected by muscle CMAPD values. At the muscle level, our findings suggest that calf muscles in particular (except soleus) present different trends in CMAPD behavior between young and old groups, being more dependent on speed of walking in older adults. However, soleus muscle presented constant CMAPD values regardless of speed in both groups. Due to soleus functional importance during gait, this may represent a relevant physiological modulation to maintain its metabolic function over a broad range of sustainable speeds. If different pathologies are able to change muscle metabolic behavior, soleus may be an important target muscle in interventions aiming to maintain economy. Furthermore, in both age groups, more proximal leg muscles generally showed large increases in CMAPD when altering walking speed away from the preferred speed. Thus, these muscles seem to make a relatively large contribution to changes in COT regardless of age.

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