

**This is an electronic reprint of the original article.
This reprint *may differ* from the original in pagination and typographic detail.**

Author(s): Finni Juutinen, Taija; Cronin, Neil

Title: Muscle-tendon mechanics and energetics during walking, running and jumping.

Year: 2012

Version:

Please cite the original version:

Finni Juutinen, T., & Cronin, N. (2012). Muscle-tendon mechanics and energetics during walking, running and jumping.. In E. Bradshaw, A. Burnett, & P. A. Hume (Eds.), eProceedings of the 30th Conference of the International Society of Biomechanics in Sports (pp. 23-29). Australian Catholic University, Melbourne, 115 Victoria. ISBS - Conference Proceedings Archive. <https://ojs.ub.uni-konstanz.de/cpa/article/view/5150>

All material supplied via JYX is protected by copyright and other intellectual property rights, and duplication or sale of all or part of any of the repository collections is not permitted, except that material may be duplicated by you for your research use or educational purposes in electronic or print form. You must obtain permission for any other use. Electronic or print copies may not be offered, whether for sale or otherwise to anyone who is not an authorised user.

Keynote speakers

Tuesday 8:30-9:30 am Professor Taija Juutinen Finni, University of Jyväskylä, Jyväskylä, Finland. Muscle-tendon mechanics and energetics during walking, running and jumping (KS)

Muscle-tendon mechanics and energetics during walking, running and jumping

Taija Finni and Neil Cronin

**Neuromuscular Research Center, Department of Biology of Physical Activity,
University of Jyväskylä, Finland**

In the human lower limb, muscles and tendon tend to interact in an efficient manner during common movements like walking, running and jumping. This pattern of interaction exploits the ability of muscles to produce forces efficiently at low shortening velocities, whilst tendons act as springs that help to store elastic energy during the contact phase, and return a large proportion of the energy in the pushoff phase. This pattern of muscle-tendon interaction can be disrupted in novel tasks or as a consequence of ageing or disease, resulting in a decrease in movement efficiency.

KEYWORDS: Muscle-tendon unit, walking, running, jumping.

Introduction

Muscle-tendon units are clever machinery that are well adapted to the tasks that they perform. Whether the muscle is short, thick, pinnate, fast or slow, it can function together with its tendon in a range of conditions. When we consider common human movements such as walking, running and jumping, it is clear that there is a fundamental difference in the nature of these tasks with regard to parameters like kinetics or kinematics. In spite of this, a wealth of recent data has suggested that there is an overriding principle in the interaction of locomotor muscles and tendons: there is a tendency to maximise the amount of muscle-tendon unit (MTU) stretch that is taken up by the relatively compliant tendon, whilst muscles tend to perform minimal work and shorten at low velocities relative to their maximal shortening velocity (Finni, Komi, & Lepola, 2000; Lichtwark & Wilson, 2006).

This pattern of interaction is energetically beneficial for at least two reasons. Firstly, tendons are well adapted to act as springs because they have low energy dissipation, returning in an elastic recoil approximately 93% of the work previously done stretching them, and dissipating only 7% as heat (Ker, 1981). Secondly, ATP consumption is lowest at low shortening velocities (Ryschon, Fowler, Wyson, Anthony, & Balaban, 1997). These two factors combined minimise the amount of muscular energy needed to power a movement and also minimise the amount of energy dissipated from the system during the movement, helping us to achieve a given distance, height or speed efficiently. Thus, the integration of muscle and tendon into a single functional unit (the MTU) enables greater mechanical abilities than the capabilities of muscle contractile elements alone.

Muscle-tendon unit structure and function

It is not cross-sectional area or volume, but muscle architecture that is the main determinant of its function. A combination of different muscle lengths and pennation angles allow a continuum of functional demands to be met, ranging between high speed and high force generation. Synergistic muscles often have complimentary characteristics. For example, soleus muscle is the strongest single muscle with high endurance, while gastrocnemius enables high speeds of ankle extension but fatigues much faster (Lieber & Ward, 2011). If a muscle such as soleus contracts slowly and around optimal length, it can produce more force and thus have a smaller physiological cross-sectional area, which in turn allows it to be smaller and lighter, reducing metabolic cost and inertia at the distal leg. Functionally, the level of neural input has a major impact on the mechanical outcome in the muscle-tendon unit, although inherent mechanical factors such as joint configuration, moment arms, surrounding connective tissues and their stiffnesses also modify the force output (Lieber & Ward, 2011).

Indeed, while muscle also contains elastic properties, spring-like tendons have a far greater impact on the efficiency of locomotion. Besides tendon, other connective tissues also act as modulators of force output. Aponeuroses surrounding and sometimes protruding into the muscle also show elastic behavior that seems to be different between active and passive conditions (Azizi & Roberts, 2009; Finni, Hodgson, Lai, Edgerton, & Sinha, 2003; Lieber, Leonard, & Brown-Maupin, 2000). Recently, free Achilles tendon stiffness has also been shown to vary between different levels of contraction (Sugisaki, Kawakami, Kanehisa, & Fukunaga, 2011). These results highlight the complexity of the connective tissue structures, which should not be considered independent, but bound in three-dimensional space where forces can be transmitted through various pathways (Bojsen-Moller, Schwartz, Kalliokoski, Finni, & Magnusson, 2010; Huijing, 2009; Maas & Sandercock, 2010).

Muscle-tendon interaction and efficiency

It is now well recognized that tendon elasticity plays a major role in the efficient function of the human MTU, particularly in those of the calf region, which help to propel the body forwards in locomotion. Tendon elasticity is important for a number of reasons. Compliant tendons allow muscles to generate force at reduced speeds of contraction which consumes less energy in each fiber (Ryschon, Fowler, Wysong, Anthony, & Balaban, 1997). An additional consequence of lower shortening velocity is that the same force can be achieved with less recruited muscle fibers, which also reduces energy consumption. This effect has been demonstrated in turkey ankle extensors, in which the volume of muscle recruited to generate a unit force, as estimated from electromyography, was directly proportional to shortening velocity (Gabaldon, Nelson, & Roberts, 2008). Therefore, when the muscle is able to operate near isometrically, as is often the case in lower limb MTUs in locomotion, fewer muscle fibres need be activated to produce a given force, resulting in smaller energy consumption (Roberts, 2002).

Whilst the evolutionary advantage of reducing muscle energy costs is abundantly clear, there are a number of more subtle adaptations that appear to act to fine-tune the process of muscle-tendon interaction in movement. For example, to vary the amount of energy absorbed, the timing and duration of muscle activation is important. Very brief stimulations do not fully activate muscle fibers, which in turn allow less energy to be absorbed. Stimulations with long duration allow high forces to be generated but also cost more energy. In essence, it seems that our muscles require fine-tuning in their activation-deactivation timing in order for the benefits of an elastic tendon to be fully realized (Wilson & Lichtwark, 2011).

Within the concept of tendon elasticity, two elastic mechanisms that promote efficiency can be distinguished. The first is the tendon storage and reuse of elastic energy during locomotion and the other is a 'catapult' mechanism that increases power. The catapult mechanism has been recently demonstrated in frogs (Astley & Roberts, 2011). When frogs (or cats) prepare to jump, muscle fibers shorten and tendons are stretched. In the subsequent period of initial joint movement with high joint angular acceleration, muscle fascicle length change is minimal and the tendon produces the initial high power in the jump. This catapult mechanism of tendon seems to be a very different mechanism to that which occurs during cyclic locomotion. However, direct observations of this mechanism are rare and thus our understanding of it is in its infancy (Astley & Roberts, 2011).

In the following sections, typical locomotion characteristics with insights into associations between MTU mechanics and energetics are discussed. Its importance is also highlighted in conditions where the natural pattern is disrupted, usually resulting in a decrease in efficiency. Affecting variables such as intensity, aging, slopes etc. are also considered with the focus primarily on the lower leg MTUs that have a major importance in locomotion.

Walking

While the use of elastic potential of tendons is most often associated with running and jumping, it is also important for the energetics of walking. Longer Achilles tendon length has been suggested to explain the greater walking economy of African American (AA) women compared to European American women (McCarthy et al., 2006), suggesting that AA women are able to store and reuse more elastic energy from their longer tendons, walk with less muscle contractile activity and thus use less energy while walking (Hunter et al., 2011b).

Coupled to the use of tendons to store elastic energy, muscles have been shown to act essentially isometrically during the early to mid stance phase of walking (Fukunaga et al., 2001), and shorten at low velocities relative to their maximal capability during the pushoff phase (Lichtwark & Wilson, 2006). Therefore, in vivo observations support the notion that calf MTUs function in a way that exploits the properties of muscles and tendons during walking. However, this 'natural' pattern of muscle-tendon interaction is disrupted in certain conditions, as discussed in the following sections.

Slope. Walking downhill at a slight gradient is most efficient, whereas the steeper the uphill gradient, the higher the energy demand (Margaria, Cerretelli, Aghemo, & Sassi, 1963). Muscle fascicle measurements have shown that the MTU length increase that occurs in uphill walking is mostly taken up by the tendon, since fascicle behaviour remains quite constant across slopes, at least in medial gastrocnemius muscle (Lichtwark & Wilson, 2006). On the other hand, using an exoskeleton, Sawicki and Ferris (2009) reported that walking uphill increases the contribution of actively shortening plantar flexor muscles and reduces the use of elastic energy. They suggested that in uphill walking knee and hip joint muscle contributions to mechanical power increase. It should be noted that grade walking in most populations is less common than level walking, and may thus constitute a 'novel' task that disturbs the optimal pattern of muscle-tendon interaction, thereby decreasing efficiency.

High heels. One rather common way of walking that disturbs the natural pattern of muscle-tendon interaction is the use of high-heels. In women who wear over 5 cm high heels regularly, the gastrocnemius muscle fascicles are shorter than in controls subjects. During walking the heel wearers walk less efficiently with or without heels. In high-heel wearers the Achilles tendon is stiffer (Csapo, Maganaris, Seynnes, & Narici, 2010) and the muscle experiences higher strains and higher strain rates (Cronin, Barrett, & Carty, 2012).

Diabetes. Similarly to high-heel wearers, diabetic patients seem to have stiffer Achilles tendons. During walking the Achilles tendon does not lengthen and shorten as much as in age-matched non-diabetics. This in turn results in a larger proportion of MTU stretch being taken up by the muscle fibres. Both of these factors likely decrease walking efficiency (Cronin et al., 2010).

Prolonged exercise. When we walk for a period of 1h, the gastrocnemius muscle fascicles get shorter due to an increase in compliance of the tendinous tissues. Interestingly, this effect is not observed in soleus when walking on level ground, suggesting that the change occurs somewhere in the aponeuroses, since these muscles share a common distal tendon (Cronin, Peltonen, Sinkjaer, & Avela, 2011). The result of an increase in compliance is that more of the MTU stretch is transferred to the tendon, which would theoretically increase the storage of elastic energy in MG. However, we also noted an apparent decrease in neural activity of MG, which may have been compensated by an increase in soleus activation. Therefore, any positive change in MG stretch distribution may have been outweighed by changes in neural activation patterns. These data highlight the fact that MG and soleus can behave differently due to differences in architecture and properties, despite being synergistic muscles.

Aging. In elderly people, Achilles tendon compliance increases, which has been shown to decrease the amplitude of MG fascicle stretch during the contact phase of walking (Mian, Thom, Ardigo, Minetti, & Narici, 2007). As noted above, this could potentially increase elastic energy storage in this tendon. However, the net cost of walking may be as much as 30% higher in the elderly than in younger people (Mian, Thom, Ardigo, Narici, & Minetti, 2006), thus probably outweighing any advantages in tendon elastic energy use. Despite being beneficial for overall functional capacity, physical conditioning programs do not seem to change the cost of walking in older people (Martin, Rothstein, & Larish, 1992; Mian et al., 2007).

Training. Contrary to data obtained in older individuals, resistance training-induced increases in strength are associated with improved walking economy in pre-menopausal women aged approximately 35 (Hunter et al., 2008).

Running

Tendon elasticity has long been known to be a significant factor in running economy (Cavagna & Kaneko, 1977), whereby MTU lengthening during the stance phase is largely

absorbed by the tendon, allowing it to stretch and store elastic energy, most of which is then returned during tendon recoil in the pushoff phase (Alexander & Bennet-Clark, 1977). This is reflected in the anatomy of certain athletes. For example, in long distance runners a greater compliance of the quadriceps tendon is related to improved running economy at different speeds, whereas sprinters exhibit stiffer Achilles tendons, a necessity for rapid transfer of force to the skeleton (Arampatzis et al., 2006).

With a given tendon thickness, compliance increases with increasing tendon length. Indeed, the length of tendons seems to be an important factor for economical locomotion. Hunter et al. (2011a; 2011b) have shown that particularly Achilles tendon length but also quadriceps and patellar tendon lengths have a role in running economy. In fact, the tendon and aponeurosis of the triceps surae and quadriceps are estimated to store 75% of the energy stored in all the tendons active in running (Neptune & Sasaki, 2005). However, the relationship between quadriceps/patella tendon length and running economy is weaker than the relationship between Achilles tendon length and running economy. This is likely due to two main factors. First, plantar flexor pennation angles are greater than those of the quadriceps ($\sim 8\text{-}25^\circ$ for plantar flexors, $\sim 5^\circ$ for quadriceps) (Wickiewicz, Roy, Powell, & Edgerton, 1983). More highly pennate muscles with shorter fascicles favor greater compliance and improved economy (Biewener & Roberts, 2000; Roberts, 2002). Second, the almost 85% longer Achilles tendon length compared with the quadriceps/patella tendon length (Hunter et al., 2011a) should favor greater potential for storing elastic energy.

As well as tendon, muscle exhibits adaptations suited to running economy. For example, the MG fascicles shorten at a velocity concomitant with maximum power (one third of maximum shortening velocity) whereas the MTU shortens three times faster (Lichtwark & Wilson, 2006). Furthermore, when switching from walking to running at 2 m/s, the MG fascicles shift to lower operating velocities, which enables increases in peak muscle force and MG power output, both of which are required in running (Farris & Sawicki, 2012). Such adaptations are important because muscles around the ankle and knee joints contribute more than 70% of the total mechanical work during running (Abe, Fukashiro, Harada, & Kawamoto, 2001; Kumagai et al., 2000).

The apparent tuning of both muscle and tendon for running has functional consequences. Humans are able to run for long periods (at least 10 km) with relatively constant O₂ consumption and running kinematics (Finni, Kyrolainen, Avela, & Komi, 2003), and as in walking, the stride frequency that is freely chosen in running is the least metabolically expensive (Kaneko, 1990; Zarrugh, Todd, & Ralston, 1974). In addition, Achilles tendon stiffness is unaltered during a single bout of running lasting 30 minutes (Farris, Trewartha, & McGuigan, 2011).

Jumping

Wallabies and kangaroos serve as role models for bilateral hopping. Cavagna et al. (1977) obtained very high apparent efficiencies for kangaroos, which gave clear evidence for energy saving by elastic mechanisms. Tendon elasticity has long been considered to be much more important than muscle elasticity both in kangaroos and humans (Alexander & Bennet-Clark, 1977). In human hopping, tendon is responsible for about 90% of gastrocnemius MTU length change (Lichtwark & Wilson, 2005).

When different types of jumps are compared, the muscle-tendon mechanics are quite distinct. The relative importance of hip, knee and ankle extensor muscles depends on the movement amplitude. Hopping and drop jump performances with small knee joint angle changes emphasize the importance of calf muscles while in the squat jump (SJ) and counter movement jump (CMJ) the knee extensors dominate (Finni, Komi, & Lepola, 2000; Finni, Ikegawa, & Komi, 2001).

Human hopping experiments have demonstrated a dramatic increase in muscle activity for a given force output when hopping on extremely soft surfaces that do not allow effective use of elastic energy (Moritz & Farley, 2005). Conversely, when hopping height is increased on a hard surface, increases in EMG activity appear primarily in the eccentric phase (Finni, Komi, & Lepola, 2001; Ishikawa & Komi, 2004). This reduces the muscle stretch allowing the tendon to do more work. Thus, variations in neural input can maintain efficient patterns of muscle-tendon interaction in a variety of conditions. This has been clearly demonstrated in

animal experiments, where muscles switch on and off at appropriate phases of a movement cycle to maximise the effectiveness of elasticity (e.g. Ettema, 1996).

High tendon stiffness is important in powerful performances. In long jump, for example, a better outcome may be associated with higher tendomuscular stiffness in the calf muscles (Kyrolainen, Finni, Avela, & Komi, 2003). While long term exercise or training may affect tendon stiffness (Couppe et al., 2008), a single bout of hopping does not affect the stiffness of the Achilles tendon (Peltonen, Cronin, Avela, & Finni, 2010), as is the case in running (Farris, Trewartha, & McGuigan, 2011).

Aging reduces tendon stiffness that has consequences for jumping mechanics. In the elderly, an increase in tendon compliance has been shown to decrease muscle fascicle length changes during the contact phase of drop jumps (Hoffren, Ishikawa, & Komi, 2007). The elderly also had lower ankle joint stiffness, which was associated with a lower jumping height compared to younger subjects. Lower MG activity in the braking phase but higher muscle activity in the push off phase may be indicative of less efficient use of elastic mechanisms in the elderly. Interestingly, this activation pattern of the elderly subjects resembles that of young individuals after exhaustive cyclic exercise (Kuitunen, Kyrolainen, Avela, & Komi, 2007).

CONCLUSIONS: In the human lower limb, muscles and tendon tend to interact in an efficient manner during common movements like walking, running and jumping. This pattern of interaction exploits the ability of muscles to produce forces efficiently at low shortening velocities, whilst tendons act as springs that help to store elastic energy during the contact phase, and return a large proportion of the energy in the pushoff phase. This pattern of muscle-tendon interaction can be disrupted in novel tasks or as a consequence of ageing or disease, resulting in a decrease in movement efficiency.

REFERENCES:

- Abe, T., Fukashiro, S., Harada, Y., & Kawamoto, K. (2001). Relationship between sprint performance and muscle fascicle length in female sprinters. *Journal of physiological anthropology and applied human science*, 20(2), 141-147.
- Alexander, R. M., & Bennet-Clark, H. C. (1977). Storage of elastic strain energy in muscle and other tissues. *Nature*, 265(5590), 114-117.
- Arampatzis, A., De Monte, G., Karamanidis, K., Morey-Klapsing, G., Stafilidis, S., & Bruggemann, G. P. (2006). Influence of the muscle-tendon unit's mechanical and morphological properties on running economy. *The Journal of experimental biology*, 209(Pt 17), 3345-3357.
- Astley, H. C., & Roberts, T. J. (2011). Evidence for a vertebrate catapult: elastic energy storage in the plantaris tendon during frog jumping. *Biology letters*, .
- Azizi, E., & Roberts, T. J. (2009). Biaxial strain and variable stiffness in aponeuroses. *The Journal of physiology*, 587(Pt 17), 4309-4318.
- Biewener, A. A., & Roberts, T. J. (2000). Muscle and tendon contributions to force, work, and elastic energy savings: a comparative perspective. *Exercise and sport sciences reviews*, 28(3), 99-107.
- Bojsen-Moller, J., Schwartz, S., Kalliokoski, K. K., Finni, T., & Magnusson, S. P. (2010). Intermuscular force transmission between human plantarflexor muscles in vivo. *J Appl Physiol*, .
- Cavagna, G. A., Heglund, N. C., & Taylor, C. R. (1977). Mechanical work in terrestrial locomotion: two basic mechanisms for minimizing energy expenditure. *Am J Physiol*, 233(5), R243-61.
- Cavagna, G. A., & Kaneko, M. (1977). Mechanical work and efficiency in level walking and running. *The Journal of physiology*, 268(2), 467--81.
- Couppe, C., Kongsgaard, M., Aagaard, P., Hansen, P., Bojsen-Moller, J., Kjaer, M. et al. (2008). Habitual loading results in tendon hypertrophy and increased stiffness of the human patellar tendon. *Journal of applied physiology (Bethesda, Md.: 1985)*, 105(3), 805-810.
- Cronin, N. J., Barrett, R. S., & Carty, C. P. (2012). Long-term use of high heeled shoes alters the neuromechanics of human walking. *Journal of applied physiology (Bethesda, Md.: 1985)*, .
- Cronin, N. J., Peltonen, J., Ishikawa, M., Komi, P. V., Avela, J., Sinkjaer, T. et al. (2010). Achilles tendon length changes during walking in long-term diabetes patients. *Clinical biomechanics (Bristol, Avon)*, 25(5), 476-482.
- Cronin, N. J., Peltonen, J., Sinkjaer, T., & Avela, J. (2011). Neural compensation within the human triceps surae during prolonged walking. *Journal of neurophysiology*, 105(2), 548-553.
- Csapo, R., Maganaris, C. N., Seynnes, O. R., & Narici, M. V. (2010). On muscle, tendon and high heels. *The Journal of experimental biology*, 213(Pt 15), 2582-2588.

Ettema, G. J. (1996). Mechanical efficiency and efficiency of storage and release of series elastic energy in skeletal muscle during stretch-shorten cycles. *The Journal of experimental biology*, 199(Pt 9), 1983-1997.

Farris, D. J., & Sawicki, G. S. (2012). Human medial gastrocnemius force-velocity behavior shifts with locomotion speed and gait. *Proceedings of the National Academy of Sciences of the United States of America*, 109(3), 977-982.

Farris, D. J., Trewartha, G., & McGuigan, M. P. (2011). The effects of a 30-min run on the mechanics of the human Achilles tendon. *European journal of applied physiology*, .

Finni, T., Hodgson, J. A., Lai, A. M., Edgerton, V. R., & Sinha, S. (2003). Nonuniform strain of human soleus aponeurosis-tendon complex during submaximal voluntary contractions in vivo. *Journal of applied physiology (Bethesda, Md.: 1985)*, 95(2), 829-837.

Finni, T., Ikegawa, S., & Komi, P. V. (2001). Concentric force enhancement during human movement. *Acta Physiol Scand*, 173(4), 369-77.

Finni, T., Komi, P. V., & Lepola, V. (2000). In vivo human triceps surae and quadriceps femoris muscle function in a squat jump and counter movement jump. *Eur J Appl Physiol*, 83(4 -5), 416-26.

Finni, T., Komi, P. V., & Lepola, V. (2001). In vivo muscle mechanics during locomotion depend on movement amplitude and contraction intensity. *Eur J Appl Physiol*, 85(1-2), 170-6.

Finni, T., Kyrolainen, H., Avela, J., & Komi, P. V. (2003). Maximal but not submaximal performance is reduced by constant-speed 10-km run. *J Sports Med Phys Fitness*, 43(4), 411-7.

Fukunaga, T., Kubo, K., Kawakami, Y., Fukashiro, S., Kanehisa, H., & Maganaris, C. N. (2001). In vivo behaviour of human muscle tendon during walking. *Proceedings.Biological sciences / The Royal Society*, 268(1464), 229-233.

Gabaldon, A. M., Nelson, F. E., & Roberts, T. J. (2008). Relative shortening velocity in locomotor muscles: turkey ankle extensors operate at low V/V(max). *American journal of physiology.Regulatory, integrative and comparative physiology*, 294(1), R200-10.

Hoffren, M., Ishikawa, M., & Komi, P. V. (2007). Age-related neuromuscular function during drop jumps. *Journal of applied physiology (Bethesda, Md.: 1985)*, 103(4), 1276-1283.

Huijing, P. A. (2009). Epimuscular myofascial force transmission: a historical review and implications for new research. International Society of Biomechanics Muybridge Award Lecture, Taipei, 2007. *Journal of Biomechanics*, 42(1), 9-21.

Hunter, G. R., Katsoulis, K., McCarthy, J. P., Ogard, W. K., Bamman, M. M., Wood, D. S. et al. (2011a). Tendon length and joint flexibility are related to running economy. *Medicine and science in sports and exercise*, 43(8), 1492-1499.

Hunter, G. R., McCarthy, J. P., Bamman, M. M., Larson-Meyer, D. E., Fisher, G., & Newcomer, B. R. (2011b). Exercise economy in African American and European American women. *European journal of applied physiology*, 111(8), 1863-1869.

Hunter, G. R., McCarthy, J. P., Bryan, D. R., Zuckerman, P. A., Bamman, M. M., & Byrne, N. M. (2008). Increased strength and decreased flexibility are related to reduced oxygen cost of walking. *European journal of applied physiology*, 104(5), 895-901.

Ishikawa, M., & Komi, P. V. (2004). Effects of different dropping intensities on fascicle and tendinous tissue behavior during stretch-shortening cycle exercise. *Journal of applied physiology (Bethesda, Md.: 1985)*, 96(3), 848-852.

Kaneko, M. (1990). Mechanics and energetics in running with special reference to efficiency. *Journal of Biomechanics*, 23 Suppl 1, 57-63.

Ker, R. F. (1981). Dynamic tensile properties of the plantaris tendon of sheep (*Ovis aries*). *The Journal of experimental biology*, 93, 283-302.

Kuitunen, S., Kyrolainen, H., Avela, J., & Komi, P. V. (2007). Leg stiffness modulation during exhaustive stretch-shortening cycle exercise. *Scandinavian Journal of Medicine & Science in Sports*, 17(1), 67-75.

Kumagai, K., Abe, T., Brechue, W. F., Ryushi, T., Takano, S., & Mizuno, M. (2000). Sprint performance is related to muscle fascicle length in male 100-m sprinters. *Journal of applied physiology (Bethesda, Md.: 1985)*, 88(3), 811-816.

Kyrolainen, H., Finni, T., Avela, J., & Komi, P. V. (2003). Neuromuscular behaviour of the triceps surae muscle-tendon complex during running and jumping. *International Journal of Sports Medicine*, 24(3), 153-155.

Lichtwark, G. A., & Wilson, A. M. (2005). In vivo mechanical properties of the human Achilles tendon during one-legged hopping. *The Journal of experimental biology*, 208(Pt 24), 4715-4725.

Lichtwark, G. A., & Wilson, A. M. (2006). Interactions between the human gastrocnemius muscle and the Achilles tendon during incline, level and decline locomotion. *The Journal of experimental biology*, 209(Pt 21), 4379-4388.

Lieber, R. L., Leonard, M. E., & Brown-Maupin, C. G. (2000). Effects of muscle contraction on the load-strain properties of frog aponeurosis and tendon. *Cells, tissues, organs*, 166(1), 48-54.

- Lieber, R. L., & Ward, S. R. (2011). Skeletal muscle design to meet functional demands. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences*, 366(1570), 1466-1476.
- Maas, H., & Sandercock, T. G. (2010). Force transmission between synergistic skeletal muscles through connective tissue linkages. *J Biomed Biotechnol*, 2010, 575672.
- Margaria, R., Cerretelli, P., Aghemo, P., & Sassi, G. (1963). Energy cost of running. *Journal of applied physiology*, 18, 367-370.
- Martin, P. E., Rothstein, D. E., & Larish, D. D. (1992). Effects of age and physical activity status on the speed-aerobic demand relationship of walking. *Journal of applied physiology (Bethesda, Md.: 1985)*, 73(1), 200-206.
- McCarthy, J. P., Hunter, G. R., Larson-Meyer, D. E., Bamman, M. M., Landers, K. A., & Newcomer, B. R. (2006). Ethnic differences in triceps surae muscle-tendon complex and walking economy. *Journal of strength and conditioning research / National Strength & Conditioning Association*, 20(3), 511-518.
- Mian, O. S., Thom, J. M., Ardigo, L. P., Minetti, A. E., & Narici, M. V. (2007). Gastrocnemius muscle-tendon behaviour during walking in young and older adults. *Acta physiologica (Oxford, England)*, 189(1), 57-65.
- Mian, O. S., Thom, J. M., Ardigo, L. P., Morse, C. I., Narici, M. V., & Minetti, A. E. (2007). Effect of a 12-month physical conditioning programme on the metabolic cost of walking in healthy older adults. *European journal of applied physiology*, 100(5), 499-505.
- Mian, O. S., Thom, J. M., Ardigo, L. P., Narici, M. V., & Minetti, A. E. (2006). Metabolic cost, mechanical work, and efficiency during walking in young and older men. *Acta physiologica (Oxford, England)*, 186(2), 127-139.
- Moritz, C. T., & Farley, C. T. (2005). Human hopping on very soft elastic surfaces: implications for muscle pre-stretch and elastic energy storage in locomotion. *The Journal of experimental biology*, 208(Pt 5), 939-949.
- Neptune, R. R., & Sasaki, K. (2005). Ankle plantar flexor force production is an important determinant of the preferred walk-to-run transition speed. *The Journal of experimental biology*, 208(Pt 5), 799-808.
- Peltonen, J., Cronin, N. J., Avela, J., & Finni, T. (2010). In vivo mechanical response of human Achilles tendon to a single bout of hopping exercise. *The Journal of experimental biology*, 213(Pt 8), 1259-1265.
- Roberts, T. J. (2002). The integrated function of muscles and tendons during locomotion. *Comparative biochemistry and physiology. Part A, Molecular & integrative physiology*, 133(4), 1087-1099.
- Ryschon, T. W., Fowler, M. D., Wysong, R. E., Anthony, A., & Balaban, R. S. (1997). Efficiency of human skeletal muscle in vivo: comparison of isometric, concentric, and eccentric muscle action. *Journal of applied physiology (Bethesda, Md.: 1985)*, 83(3), 867-874.
- Sawicki, G. S., & Ferris, D. P. (2009). Mechanics and energetics of incline walking with robotic ankle exoskeletons. *The Journal of experimental biology*, 212(Pt 1), 32-41.
- Sugisaki, N., Kawakami, Y., Kanehisa, H., & Fukunaga, T. (2011). Effect of muscle contraction levels on the force-length relationship of the human Achilles tendon during lengthening of the triceps surae muscle-tendon unit. *Journal of Biomechanics*, 44(11), 2168-2171.
- Wickiewicz, T. L., Roy, R. R., Powell, P. L., & Edgerton, V. R. (1983). Muscle architecture of the human lower limb. *Clinical orthopaedics and related research*, (179)(179), 275-283.
- Wilson, A., & Lichtwark, G. (2011). The anatomical arrangement of muscle and tendon enhances limb versatility and locomotor performance. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences*, 366(1570), 1540-1553.
- Zarrugh, M. Y., Todd, F. N., & Ralston, H. J. (1974). Optimization of energy expenditure during level walking. *European journal of applied physiology and occupational physiology*, 33(4), 293-306.