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Short communication

Does ankle joint power reflect type of muscle action of soleus and gastrocnemius during walking in cats and humans?

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ABSTRACT

The main objective of this paper is to highlight the difficulties of identifying shortening and lengthening contractions based on analysis of power produced by resultant joint moments. For that purpose, we present net ankle joint powers and muscle fascicle/muscle–tendon unit (MTU) velocities for medial gastrocnemius (MG) and soleus (SO) muscles during walking in species of different size (humans and cats). For the cat, patterns of ankle joint power and MTU velocity of MG and SO during stance were similar: negative power (ankle moment × angular velocity < 0), indicating absorption of mechanical energy, was associated with MTU lengthening, and positive power (generation of mechanical energy) was found during MTU shortening. This was also found for the general fascicle velocity pattern in SO. In contrast, substantial differences between ankle joint power and fascicle velocity patterns were observed for MG muscle. In humans, like cats, the patterns of ankle joint power and MTU velocity of SO and MG were similar. Unlike the cat, there were substantial differences between patterns of fascicle velocity and ankle joint power during stance in both muscles. These results indicate that during walking, only a small fraction of mechanical work of the ankle moment is either generated or absorbed by the muscle fascicles, thus confirming the contribution of in-series elastic structures and/or energy transfer via two-joint muscles. We conclude that ankle joint negative power does not necessarily indicate eccentric action of muscle fibers and that positive power cannot be exclusively attributed to muscle concentric action, especially in humans.

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1. Introduction

Although the two types of dynamic muscle action during natural movements (concentric/shortening and eccentric/lengthening) have been studied for over a century (Abbott et al., 1952; Asmussen, 1953; Chauveau, 1901; Duchateau and Enoka, 2008; Hill, 1938; Komi, 1973; Margaria, 1968), researchers still debate the semantics of the terms eccentric and concentric contraction (Cavanagh, 1988; Faulkner, 2003). It also remains unclear how these two types of muscle action can be identified in natural movements. The main objective of this paper is to highlight the difficulties of identifying contraction type based on analysis of power produced by resultant joint moments, which has become a standard procedure.

Based on early work by Herbert Elftman (Elftman, 1939a, 1939b) and James Morrison (Morrison, 1970), the recently deceased David Winter proposed some basic principles regarding identification of muscle action type during natural movements using net power produced by the resultant joint moment (Robertson and Winter, 1980; Winter, 1978). After experimental confirmation that the sum of powers of all resultant muscle moments and joint forces applied to a rigid body segment equaled the rate of change of segment total energy, it was postulated that if the resultant muscle moment at a joint is in the same direction as the joint angle changes (i.e. net joint power is positive), the muscles crossing the joint act concentrically. A negative net joint power indicates absorption of mechanical energy by lengthening contractions, which occur when the resultant muscle moment and joint angular velocity have opposite signs. The term 'muscle' refers here to all tissues surrounding the joint including the joint capsule, ligaments and muscle–tendon units (MTU). The latter includes all structures between the muscles' origin and insertion. In this interpretation of muscle contraction type, it is assumed that the resultant muscle moment at a joint, as computed by inverse dynamics, can be fully ascribed to agonistic skeletal muscles. In other words, the contribution of antagonistic muscles and 'passive' structures such as ligaments is neglected. In

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addition, joint power analysis does not refer to actual anatomically defined muscles, but to a single equivalent, one-joint muscle (Robertson and Winter, 1980; Winter, 1978) whose power (muscle force × MTU velocity) equals net joint power (resultant muscle moment × joint angular velocity), assuming workless joint constraints (e.g., Storace and Wolf, 1979).

The association between net joint power and contraction type of muscles crossing the joint has been debated extensively and it has been suggested that net joint power is not always indicative of muscle contraction type, i.e. shortening or lengthening of the MTU or muscle belly (Elftman, 1939a,1939b; Ishikawa et al., 2005a; Morrison, 1970; Prilutsky et al., 1996c; Sasaki et al., 2009; van Ingen Schenau, 1989; Zajac et al., 2002; Zatsiorsky, 2002). The main reasons for this incongruity are the following: (1) net joint power does not have to equal total power of all MTUs crossing the joint (even if antagonistic muscles do not generate power) due to the presence of two- or multi-joint muscles that can transfer mechanical energy to/from the segments forming the joint from/to other body segments (for reviews see van Ingen Schenau, 1989; Zatsiorsky and Prilutsky, 2012). It should be noted that the segments forming a joint can also transmit/receive mechanical energy to/from other body segments due to the action of joint forces that do not generate/absorb energy (e.g., Robertson and Winter, 1980; Zajac et al., 2002; Zatsiorsky, 2002). This energy transfer has the same influence on net joint power and total MTU power, and thus does not affect inferences about muscle contraction type from net joint power. (2) There may be a mismatch between net joint power (equivalent to total MTU power when energy transfer by bi-articular muscles is insignificant) and power generated by the muscle contractile tissue or fascicles (muscle force × muscle fascicle velocity) due to the presence of in-series elastic structures (Maas and Lichtwark, 2009; Windhorst, 2008; Zajac, 1989) and the effects of pennation angle (Roberts, 2002). Series compliance of tendinous connective tissue allows storage of energy and return of elastic energy that can decouple work done on or by the MTU from that of the muscle fascicles (Lichtwark and Wilson, 2006; Roberts et al., 1997).

Until recently, this debate has been based predominantly on human studies that combined the assessment of joint power with the estimation of MTU and muscle fascicle behavior using musculo-skeletal models (Bobbert et al., 1986; Prilutsky and Zatsiorsky, 1994; Sasaki et al., 2009) or animal studies on extensively dissected MTUs (Ettema et al., 1990; Zuurbier and Huijing, 1992). Due to the use of sonomicrometry in animals (Griffiths, 1989,1987) and ultrasonography in humans (Henriksson-Larsen et al., 1992; Kawakami et al., 1993; Rutherford and Jones, 1992), muscle fascicle length can now be examined in vivo. Using these methods, further support has been found for the argument that joint power does not necessarily reflect muscle fascicle contraction type (e.g., Biewener and Roberts, 2000; Ishikawa et al., 2005a; Spanjaard et al., 2008).

However, we have not encountered a study in which joint power is directly compared to muscle fascicle length changes. Estimating contraction type at the fascicle level during a particular phase of net joint power may be relevant for rehabilitation and sport science, for example to assess the risk of muscle damage, or whether the muscle is performing a therapeutically prescribed type of muscle action.

Here we present joint powers and muscle fascicle behavior for two functionally important ankle extensors during walking in humans and cats, whose in vivo maximum tendon stresses (Pollock and Shadwick, 1994), and thus discrepancy between MTU and muscle fascicle length changes, were expected to differ. Specifically, we compared the pattern of joint power during walking with instantaneous length changes at the MTU and muscle fascicle level of one-joint soleus (SO) and two-joint medial gastrocnemius (MG) muscles.

2. Joint power and muscle contraction type in the cat

In Fig. 1, data from one representative cat (mass: 4.1 Kg) walking on a level surface are presented. The cat walked at a freely chosen speed of 0.70 ± 0.06 m/s during which the stance phase occupied 65% of the total step cycle. All surgical and experimental procedures were in agreement with the "Principles of laboratory animal care" (NIH No.86-3, 1985) and approved by the institutional animal care and use committee of the Georgia Institute of Technology, where cat data were collected.

Group means (5–6 cats) for MG and SO fascicle lengths and velocities (Maas et al., 2009), and hindlimb joint powers have been presented previously (Prilutsky et al., 2011). SO muscle is active from approximately the last 15% of the swing phase to ~80% of the stance phase (see Gregor et al., 2006). For MG, the onset of EMG activity is similar to SO, but EMG offset occurs earlier (~65% of the stance phase). Thus, SO and MG are predominantly active during the stance phase of walking (which is also the case in humans, see Lay et al., 2007). Therefore, we have focused our comparisons on the stance phase.

Patterns of ankle joint power and MTU velocity of MG and SO during stance were qualitatively similar: negative power accompanied MTU lengthening and positive power accompanied MTU shortening. The transition from negative to positive power

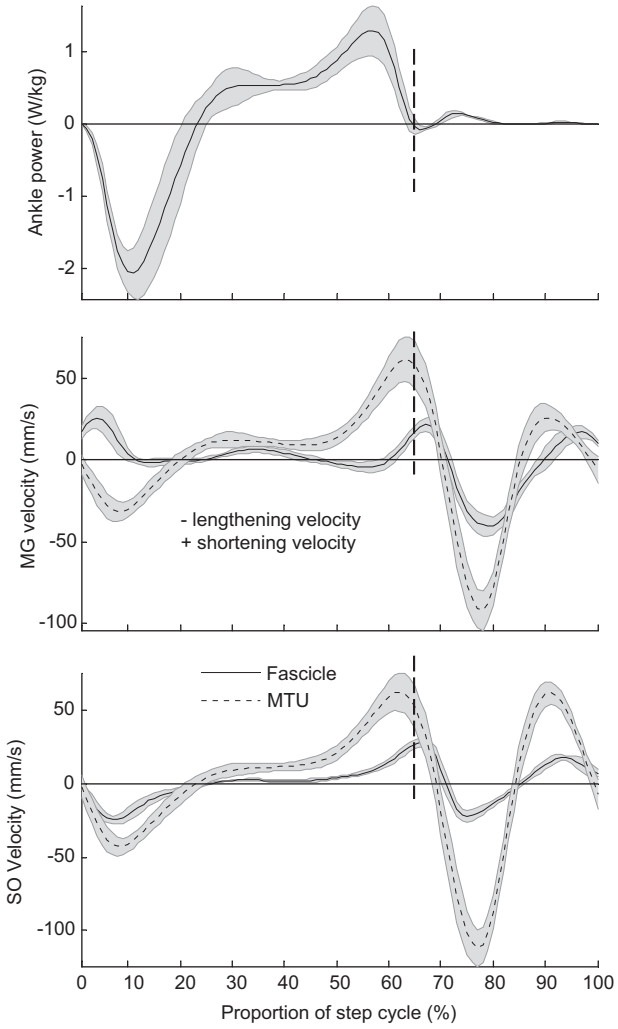


Fig. 1. Ankle joint power, MTU velocity and fascicle velocity of MG and SO muscles (mean ± SD, $n=9$ strides) during overground walking in the cat as a function of normalized step cycle time. The step cycle starts with paw contact and the vertical dashed lines indicate paw lift-off.

occurred simultaneously with the transition from MTU lengthening to shortening for SO. In MG, however, the change in sign of MTU velocity occurred prior to the change in sign of joint power.

As the pattern of SO fascicle velocity was qualitatively similar to that observed at the MTU level, the pattern of fascicle velocity was also similar to the ankle joint power pattern during stance. In contrast, substantial differences between ankle joint power and fascicle velocity patterns were observed for MG. At the beginning of the stance phase, when joint power was negative, the MG fascicles either shortened or operated almost isometrically. The second half of stance was characterized by positive ankle joint power, whilst MG fascicles initially shortened, but then lengthened.

3. Joint power and muscle contraction type in humans

In Fig. 2, data from a young, healthy male are presented (32 years, mass: 73 kg). The subject walked overground on a level surface at a self-selected speed of 1.32 ± 0.03 m/s during which the stance phase occupied 61% of the step cycle. Ethics approval was obtained from the Institutional Human Research Ethics Committee of the University of Queensland, Australia, where human data were collected, and all relevant ethics guidelines were followed.

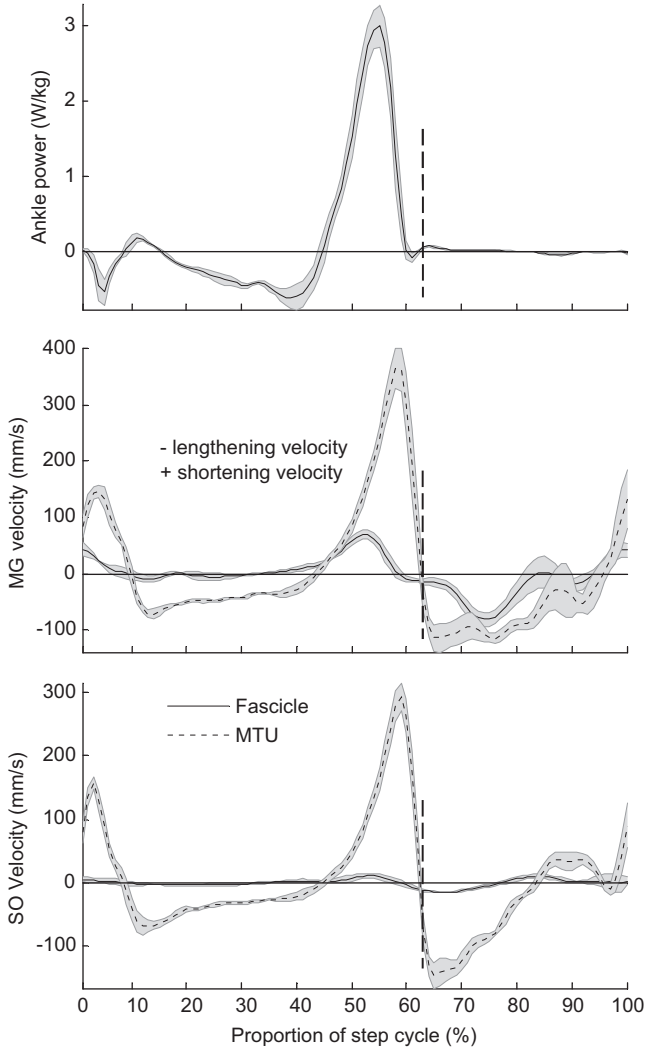


Fig. 2. Ankle joint power, MTU velocity and fascicle velocity of MG and SO muscles (mean $\pm$ SD, $n=5$ strides) during overground walking in humans as a function of normalized step cycle time. The step cycle starts with foot contact and the vertical dashed lines indicate foot lift-off. For both cat and human data, fascicle and MTU velocities were calculated by differentiating length changes with respect to time. Human fascicle data were analyzed using an automated tracking algorithm (Cronin et al., 2011).

Unlike in the cat, early stance of human walking was associated with MTU shortening. In this phase, negative power was generated by the active ankle dorsi-flexors, while the ankle plantar-flexors showed relatively low activity. For the remainder of stance, like in the cat, patterns of ankle joint power and MTU velocity were qualitatively similar.

In both muscles, there were substantial differences between patterns of fascicle velocity and ankle joint power during stance. In MG, mid-stance was characterized by fascicle lengthening or isometric behavior whilst ankle power was negative. During push-off, positive power occurred during fascicle shortening, although the latter occurred earlier. In SO, there was very little concordance between fascicle velocity and ankle power. The fascicles were almost isometric for most of the step cycle, exhibiting peak shortening and lengthening velocities of just 10.8 and 15.1 mm/s, respectively. Conversely, joint power varied substantially and exhibited several changes in polarity throughout the step cycle.

4. Conclusion

In both cats and humans, ankle joint power during the stance phase of level walking gives a reasonable estimate of periods when the MTU is lengthening or shortening, for both one-joint soleus and two-joint gastrocnemius, but is a poor predictor of muscle fascicle contraction type during walking. Our data suggest that only a small fraction of net ankle power was generated by the muscle fascicles, especially in humans, and thus recoil of in-series elastic structures must have contributed. It should be noted that at other joints that are crossed by MTUs with considerably shorter tendons, as well as in smaller animals, fascicle behavior may be more strongly coupled to joint power. The elastic contribution to energy generated by human SO MTU during walking is $\sim$91% (estimated from Fig. 4 in Ishikawa et al., 2005b), whereas tendons of cat SO and MG during walking only provide 21% and 31%, respectively (see Tables 2 and 3 in Prilutsky et al., 1996b). Our results and the above estimates are consistent with previous reports that the capacity of strain energy storage in ankle extensor tendons (Pollock and Shadwick, 1994) and efficiency of terrestrial locomotion (Taylor and Heglund, 1982) increase with animal mass. A small part of ankle power can be attributed to energy transfer between the knee and ankle joints, although the contribution of this mechanism in walking cats is relatively small (Prilutsky et al., 1996a). We conclude that at the ankle joint, identification of muscle contraction type based on analysis of joint power often gives incorrect results.

Conflict of interest statement

None of the authors have any conflict of interest to declare.

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References

Abbott, B.C., Bigland, B., Ritchie, J.M., 1952. The physiological cost of negative work. Journal of Physiology-London 117, 380–390.

Asmussen, E., 1953. Positive and Negative Muscular Work. Acta Physiologica Scandinavica 28, 364–382.

Biewener, A.A., Roberts, T.J., 2000. Muscle and tendon contributions to force, work, and elastic energy savings: a comparative perspective. Exercise and Sport Science Reviews 28, 99–107.

Bobbert, M.F., Huijing, P.A., van Ingen Schenau, G.J., 1986. A model of the human triceps surae muscle–tendon complex applied to jumping. Journal of Biomechanics 19, 887–898.

Cavanagh, P.R., 1988. On 'muscle action' vs 'muscle contraction'. Journal of Biomechanics 21, 69.

Chauveau, A., 1901. La depense énergétique qu entraînent respectivement le travail moteur et le travail résistant de l'homme qui s'élève ou descend sur la roue de Hirn. Évaluation d'après l'oxygène absorbé dans les échanges respiratoires. Comptes rendus hebdomadaires des séances de l'Académie des sciences 132, 194–201.

Cronin, N.J., Carty, C.P., Barrett, R.S., Lichtwark, G., 2011. Automatic tracking of medial gastrocnemius fascicle length during human locomotion. Journal of Applied Physiology 111, 1491–1496.

Duchateau, J., Enoka, R.M., 2008. Neural control of shortening and lengthening contractions: influence of task constraints. Journal of Physiology-London 586, 5853–5864.

Elftman, H., 1939a. Forces and energy changes in the leg during walking. American Journal of Physiology 125, 339–356.

Elftman, H., 1939b. The function of muscles in locomotion. American Journal of Physiology 125, 357–366.

Ettema, G.J.C., Vansoest, A.J., Huijing, P.A., 1990. The role of series elastic structures in prestretch-induced work enhancement during isotonic and isokinetic contractions. Journal of Experimental Biology 154, 121–136.

Faulkner, J.A., 2003. Terminology for contractions of muscles during shortening, while isometric, and during lengthening. Journal of Applied Physiology 95, 455–459.

Gregor, R.J., Smith, D.W., Prilutsky, B.I., 2006. Mechanics of slope walking in the cat: quantification of muscle load, length change and ankle extensor emg patterns. Journal of Neurophysiology 95, 1397–1409.

Griffiths, R.I., 1987. Ultrasound transit time gives direct measurement of muscle fibre length in vivo. Journal of Neuroscience Methods 21, 159–165.

Griffiths, R.I., 1989. The mechanics of the medial gastrocnemius-muscle in the freely hopping wallaby (Thylogale-billardierii). Journal of Experimental Biology 147, 439–456.

Henriksson-larsen, K., Wretling, M.L., Lorentzon, R., Oberg, L., 1992. Do muscle-fiber size and fiber angulation correlate in pennated human muscles? European Journal of Applied Physiology 64, 68–72.

Hill, A.V., 1938. The heat of shortening and the dynamic constants of muscle. Proceedings of the Royal Society of London B 126, 136–195.

van Ingen Schenau, G.J., 1989. From rotation to translation: Constraints on multi-joint movements and the unique action of bi-articular muscles. Human Movement Science 8, 301–337.

Ishikawa, M., Komi, P.V., Grey, M.J., Lepola, V., Bruggemann, G.P., 2005a. Muscle–tendon interaction and elastic energy usage in human walking. Journal of Applied Physiology 99, 603–608.

Ishikawa, M., Komi, P.V., Grey, M.J., Lepola, V., Bruggemann, G.P., 2005b. Muscle–tendon interaction and elastic energy usage in human walking. Journal of Applied Physiology 99, 603–608.

Kawakami, Y., Abe, T., Fukunaga, T., 1993. Muscle-fiber pennation angles are greater in hypertrophied than in normal muscles. Journal of Applied Physiology 74, 2740–2744.

Komi, P.V., 1973. Measurement of the force-velocity relationship in human muscle under concentric and eccentric contractions. In: Cerquiglini, S., Venerando, A., Wartenweiler, J. (Eds.), Medicine in Sport. Biomechanics III No. 8. Karger, Basel, pp. 224–229.

Lay, A.N., Hass, C.J., Nichols, T.R., Gregor, R.J., 2007. The effects of sloped surfaces on locomotion: An electromyo graphic analysis. Journal of Biomechanics 40, 1276–1285.

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, 4379–4388.

Maas, H., Lichtwark, G.A., 2009. Is muscle–tendon unit length a valid indicator for muscle spindle output? Journal of Physiology (London) 587, 13–14.

Maas, H., Gregor, R.J., Hodson-Tole, E.F., Farrell, B.J., Prilutsky, B.I., 2009. Distinct muscle fascicle length changes in feline medial gastrocnemius and soleus muscles during slope walking. Journal of Applied Physiology 106, 1169–1180.

Margaria, R., 1968. Positive and negative work performances and their efficiencies in human locomotion. Internationale Zeitschrift für Angewandte Physiologie 25, 339–351.

Morrison, J.B., 1970. The mechanics of muscle function in locomotion. Journal of Biomechanics 3, 431–451.

Pollock, C.M., Shadwick, R.E., 1994. Allometry of muscle, tendon, and elastic energy storage capacity in mammals. American Journal of Physiology 266, R1022–R1031.

Prilutsky, B.I., Zatsiorsky, V.M., 1994. Tendon action of two-joint muscles: transfer of mechanical energy between joints during jumping, landing, and running. Journal of Biomechanics 27, 25–34.

Prilutsky, B.I., Herzog, W., Leonard, T., 1996a. Transfer of mechanical energy between ankle and knee joints by gastrocnemius and plantaris muscles during cat locomotion. Journal of Biomechanics 29, 391–403.

Prilutsky, B.I., Herzog, W., Leonard, T.R., Allinger, T.L., 1996b. Role of the muscle belly and tendon of soleus, gastrocnemius, and plantaris in mechanical energy absorption and generation during cat locomotion. Journal of Biomechanics 29, 417–434.

Prilutsky, B.I., Petrova, L.N., Raitsin, L.M., 1996c. Comparison of mechanical energy expenditure of joint moments and muscle forces during human locomotion. Journal of Biomechanics 29, 405–415.

Prilutsky, B.I., Maas, H., Bulgakova, M., Hodson-Tole, E.F., Gregor, R.J., 2011. Short-term motor compensations to denervation of feline soleus and lateral gastrocnemius result in preservation of ankle mechanical output during locomotion. Cells Tissues Organs 193, 310–324.

Roberts, T.J., 2002. The integrated function of muscles and tendons during locomotion. Comparative Biochemistry and Physiology A 133, 1087–1099.

Roberts, T.J., Marsh, R.L., Weyand, P.G., Taylor, C.R., 1997. Muscular force in running turkeys: the economy of minimizing work. Science 275, 1113–1115.

Robertson, D.G.E., Winter, D.A., 1980. Mechanical energy generation, absorption and transfer amongst segments during walking. Journal of Biomechanics 13, 845–854.

Rutherford, O.M., Jones, D.A., 1992. Measurement of fiber pennation using ultrasound in the human quadriceps invivo. European Journal of Applied Physiology 65, 433–437.

Sasaki, K., Neptune, R.R., Kautz, S.A., 2009. The relationships between muscle, external, internal and joint mechanical work during normal walking. Journal of Experimental Biology 212, 738–744.

Spanjaard, M., Reeves, N.D., van Dieen, J.H., Baltzopoulos, V., Maganaris, C.N., 2008. Lower-limb biomechanics during stair descent: influence of step-height and body mass. Journal of Experimental Biology 211, 1368–1375.

Storace, A., Wolf, B., 1979. Functional analysis of the role of the finger tendons. Journal of Biomechanics 12, 575–578.

Taylor, C.R., Heglund, N.C., 1982. Energetics and mechanics of terrestrial locomotion. Annual Review of Physiology 44, 97–107.

Windhorst, U., 2008. Muscle spindles are multi-functional. Brain Research Bulletin 75, 507–508.

Winter, D.A., 1978. Calculation and interpretation of mechanical energy of movement. Exercise and Sport Sciences Reviews 6, 183–201.

Zajac, F.E., 1989. Muscle and tendon: properties, models, scaling, and application to biomechanics and motor control. Critical Reviews in Biomedical Engineering 17, 359–411.

Zajac, F.E., Neptune, R.R., Kautz, S.A., 2002. Biomechanics and muscle coordination of human walking. Part I: introduction to concepts, power transfer, dynamics and simulations. Gait Posture 16, 215–232.

Zatsiorsky, V.M., 2002. Kinetics of human motion. Human Kinetics, Champaign, IL.

Zatsiorsky, V.M., Prilutsky, B.I., 2012. Biomechanics of skeletal muscles. Human Kinetics, Champaign, IL.

Zuurbier, C.J., Huijing, P.A., 1992. Influence of muscle geometry on shortening speed of fiber, aponeurosis and muscle. Journal of Biomechanics 25, 1017–1026.