MUSCLE SERIES ELASTICITY: THEORETICAL AND EXPERIMENTAL CONSIDERATIONS

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Muscle series elasticity is easy to measure, but hard to associate with specific structures. It affects the length and rate of change in length of the contractile elements, provides possibilities for storage of elastic energy, and has been associated with energy saving mechanisms during movement. External tendons are clearly in series with the contractile machinery of the muscle, while aponeuroses are not. Aponeuroses have been implicitly or explicitly modeled as, or associated with, series elastic elements of the muscle's contractile machinery. However, theoretical models that enforce iso-volumetricity clearly reveal that aponeuroses cannot be considered in series with muscles or tendons. Experimental results confirm the theoretical conclusions and show that assuming aponeuroses to be part of the series elasticity of muscles over-estimates energy storage and metabolic cost savings.

KEY WORDS: muscle, series elasticity, aponeuroses.

INTRODUCTION: Although there is an abundance of literature talking about series elasticity in skeletal muscles, there are few manuscripts where the origin of this series elasticity is identified. In his classic work, Hill (1950) calls the series elasticity "tendon" but immediately added that this does by no means imply that series elasticity exists in the tendon alone and not in other "undamped" structures of the muscle fibres. It is one of the ironies of science that it is fairly easy to measure and describe series elasticity experimentally, while it is terribly difficult to say where this series elasticity resides and which structural components contribute to it in significant ways.

DISCUSSION: A good example of this conundrum is the role played by muscle aponeuroses (sometimes also referred to as internal tendons). Some define the aponeurosis as part of what they consider series elasticity (e.g. Lichtwark, Bougoulias & Wilson, 2007) others imply it indirectly, for example by defining that series elasticity can be obtained by subtracting fibre lengths from the total muscle tendon unit length (van Ingen Schenau, Bobbert & de Haan, 1997 – Figure 1). For many practical applications, the detailed structures making up series elasticity are of little importance. However, when studying energy storage in muscles or the *in vivo* mechanical properties of aponeuroses, treating series elasticity correctly becomes of primary interest as mis-interpretation can lead to grave errors in the conceptual thinking about these issues.

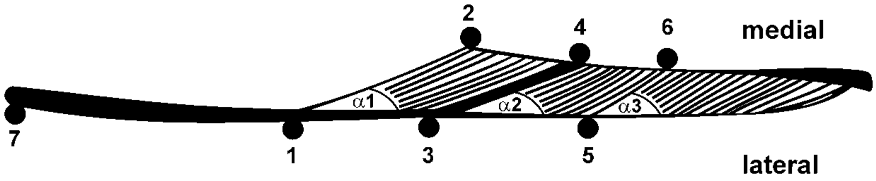

Figure 1: Schematic illustration of a uni-pennate muscle resembling a cat medial gastrocnemius. Markers 7-1 indicate the external tendon, markers 3 and 5 are attached to the lateral, and markers 2, 4, and 6 to the medial aponeurosis.

The concept of elements being arranged "in series" and "in parallel" is intended to describe ideal situations in structural mechanics, and they are well defined. The tendon in a muscle describes such an ideal situation: the tendon, independent of its material properties, has the same force as the muscle along its entire length, thus the notion of series elasticity is well justified. However, this is the kind of reasoning that has also led to quantifying the force in a tendon while recording the elongation (strain) in the corresponding aponeurosis and assuming that there is a relationship between these two measures that is governed solely by the constitutive equation of the aponeurosis (e.g. Magnusson, Aagaard, Dyhre-Poulsen & Kjaer, 2001; Muramatsu, Muraoka, Takeshita, Kawakami, Hirano & Fukunaga, 2001), an incorrect assumption as we will show below.

Subtracting fibre lengths from the total muscle tendon unit length to obtain series elasticity (van Ingen Schenau et al., 1997) assumes that length changes in muscle tendon units only occur in muscle fibres and elements arranged in series with the fibres. This thinking has led to vast overestimations of the contribution of series elasticity to work production in muscles (e.g., Roberts, Marsh, Weyand & Taylor, 1997), and has been shown to lead to "work-loops" with a net gain of work during stride cycles in the medial gastrocnemius of the cat, where muscle length, fibre length, and force in the tendon were measured directly and simultaneously during free locomotion at a variety of speeds (Figure 2). Needless to say that an elastic element under no circumstances can produce net work, therefore the assumption that series elasticity can be obtained by subtraction of fibre lengths form total muscle lengths is not correct.

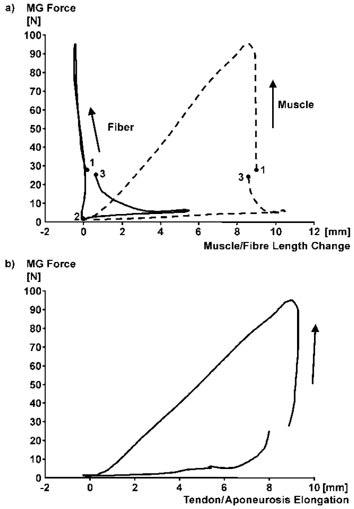

Figure 2: Medial gastrocnemius (MG) force vs. muscle (dashed line) and fibre length (solid line) changes (a), and vs. Tendon/aponeuroses elongation (b) for a representative step cycle of a cat running uphill at 4.0 m/s on a motor driven treadmill. During the stance phase (MG forces greater than about 25N; labels 1 to 2) fibre lengths remain virtually constant while muscle lengths decrease by almost 10mm. When calculating length changes (while accounting for changes in the angle of pennation; (Roberts et al., 1997), the resulting force-elongation curve (b) runs counter-clockwise. Again, one must be careful to not interpret figure (b) as a work loop, otherwise one would predict that the tendon/aponeurosis produces net work, an impossibility for a viscoelastic material. The "error" lies in the assumption that MG force (measured on the tendon using a buckle-type force transducer; (Herzog & Leonard, 1991; Walmsley, Hodgson & Burke, 1978)) is related through an "in series" arrangement to aponeurosis elongation. Note, fibre and muscle elongations were arbitrarily assumed to be zero at the lowest MG force. 1 to 2 indicates the stance phase; 2 to 3 the swing phase of the step cycle.

So why can't we just assume that aponeuroses are in series with muscle fascicles and tendons as suggested, for example, by Ettema and Huijing (1990) in their schematic of the structure of a uni-pennate muscle (Figure 3). There are a variety of possible explanations dealing with the molecular structure of fibre insertions into the aponeuroses, but even for the case where we pretend no structural cross-connections between muscle fibres, aponeuroses and other structural and contractile elements, aponeuroses would still not be “in series” with tendons for the simple fact that the muscle belly is essentially incompressible and has a shear modulus. For completeness, it must be pointed out that incompressibility and shear modulus contribute to changes in aponeuroses force, and tend to make it smaller than the force in the tendon, independently, and either one of these properties would cause a non-intuitive change in aponeuroses force transmission that cannot be obtained through a constitutive law of the aponeuroses or tendons in intact muscle (Epstein, Wong & Herzog, 2006).

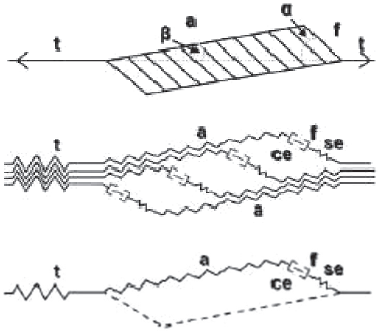

Figure 3: Schematic illustration of a uni-pennate muscle suggesting an in series arrangement of the aponeurosis (a) with the muscle fibres (f) and tendon (t).

For illustration, let’s imagine a uni-pennate muscle as shown in Figure (4) with an elastic tendon (T) elastic aponeuroses (A), contractile fibres (F) and an incompressible muscle belly (C). Stretching the muscle passively (Figure 5; arrow 1), then activating the muscle isometrically (arrow 2), shortening the muscles actively (arrow 3) and relaxing the muscle (arrow 4), the aponeurosis force-elongation curve produced shows net positive work (which is impossible as we gave the aponeurosis elastic properties), thereby illustrating that tendon (muscle) force cannot be related to aponeurosis elongation in a model of skeletal muscle that assumes incompressibility of muscles during contraction. The “steepness” of the force-elongation curve depends on the elastic properties given to aponeurosis and tendon, while the area covered by the curve depends on the shear modulus of the muscle. It should be pointed out that although the hysteresis produced by the muscle can be theoretically eliminated (by setting the shear modulus to zero), the tendon and aponeuroses forces will still differ, and thus tendon force cannot be related in an “obvious” way to aponeurosis elongations (Epstein et al., 2006).

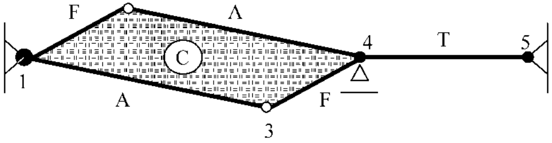

Figure 4: Mechanical system with elements *A, C, F,* and *T*. *A, C,* and *F* are not connected in a simplistic way to each other, while *T* is arranged in series with the complex ACF. *C* is assumed elastic and incompressible with a shear modulus, *μ*. *C* plays a sophisticated role in the mechanism of force transmission from *F* to *A* to *T*.

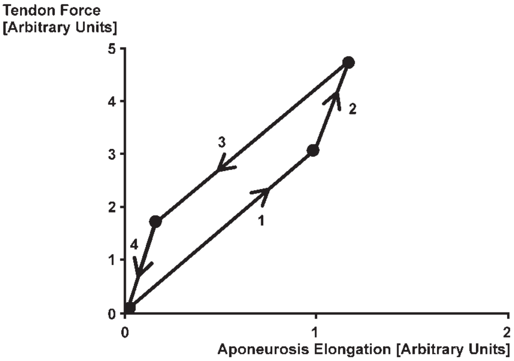

Figure 5: Tendon force vs. aponeurosis elongation obtained using the model shown in Figure (4). In phase 1, the muscle is passively stretched, in phase 2 it is activated, then it is actively shortened to its initial length in phase 3, and deactivated in phase 4. The fibre elements were endowed with contractility, the aponeurosis and tendon were assumed purely elastic, and the muscle tissue was assumed incompressible with a given elastic and corresponding shear modulus. The resulting force-elongation curve runs counter-clockwise, indicating once more that assuming the aponeurosis to be in series with the tendon would produce net mechanical work production for the depicted work loop cycle, an impossible result since the aponeurosis was assumed purely elastic.

CONCLUSION: In conclusion, tendon, aponeurosis and fibre forces are related in a complex and highly non-intuitive manner. Any modeling not accounting for the kinetic constraints imposed by incompressibility and shear, any interpretation of aponeurosis strain in relation to tendon force, or any consideration of elastic force recovery in aponeurosis considered "in series" with the tendon, will produce erroneous results, and has led to over estimating the role of series elasticity in the energetics of locomotion.

REFERENCES:

Epstein, M., Wong, M., Herzog, W. (2006). Should tendon and aponeurosis be considered in series? *Journal of Biomechanics,* 39, 2020-2025.

Ettema, G.J.C., Huijing, P.A. (1990). Architecture and elastic properties of the series elastic element of muscle-tendon complex. *Winters, J. M. and Woo, S. L. Y., Multiple Muscle Systems*. Springer Verlag, New York, pp. 57-68.

Herzog, W., Leonard, T.R. (1991). Validation of optimization models that estimate the forces exerted by synergistic muscles. *Journal of Biomechanics*, 24S, 31-39.

Hill, A.V. (1950). The series elastic component of muscle. *Proc R Soc Lond B Biol Sci*, 137, 273-280.

Lichtwark, G.A., Bougoulias,K., Wilson, A.M. (2007). Muscle fascicle and series elastic element length changes along the length of the human gastrocnemius during walking and running. *Journal of Biomechanics*, 40, 157-164.

Magnusson, S.P., Aagaard, P., Dyhre-Poulsen, P.; Kjaer, M. (2001). Load-displacement properties of the human triceps surae aponeurosis in vivo. *Journal of Physiology (Lond)*, 531, 277-288.

Muramatsu, T., Muraoka, T., Takeshita, D., Kawakami, Y., Hirano, Y., Fukunaga, T. (2001). Mechanical properties of tendon and aponeurosis of human gastrocnemius muscle in vivo. *Journal of Applied Physiology,* 90, 1671-1678.

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.

van Ingen Schenau, G.J., Bobbert, M.F., de Haan, A. (1997). Mechanics and energetics of the stretch-shortening cycle: a stimulating discussion. *Journal of Applied Biomechanics*, 13, 484-496.

Walmsley, B., Hodgson, J.A., Burke, R.E. (1978). Forces produced by medial gastrocnemius and soleus muscles during locomotion in freely moving cats. *Journal of Neurophysiology*, 41, 1203-1215.