Published in final edited form as:

J Biomech. 2012 June 1; 45(9): 1728–1732. doi:10.1016/j.jbiomech.2012.03.017.

Passive Elastic Properties of the Rat Ankle

Mengnan (Mary) Wu^a, Dinesh. K. Pai^b, Matthew. C. Tresch^{a,c,d}, and Thomas G. Sandercock^a

^aDepartment of Physiology, Northwestern University, Chicago, Illinois, USA

^bDepartment of Computer Science, University of British Columbia, Vancouver, British Columbia, Canada

^cDepartment of Biomedical Engineering

^dDepartment of Physical Medicine and Rehabilitation

Abstract

Passive properties of muscles and tendons, including their elasticity, have been suggested to influence motor control. We examine here the potential role of passive elastic muscle properties at the rat ankle joint, focusing on their potential to specify an equilibrium position of the ankle. We measured the position-dependent passive torques at the rat ankle before and after sequential cuts of flexor (a.k.a. dorsiflexor) and extensor (a.k.a. plantarflexor) ankle muscles. We found that there was a passive equilibrium position of the ankle that shifted systematically with the cuts, demonstrating that the passive torques produced by ankle flexor and extensor muscles work in opposition in order to maintain a stable equilibrium. The mean equilibrium position of the intact rat ankle ranged from 9.3–15.7 degrees in extension, depending on the torque metric. The mean shift in equilibrium position due to severing extensors ranged from 4.4–7.7 degrees, and the mean shift due to severing flexors was smaller, ranging from 0.9–2.5 degrees. The restoring torques generated by passive elasticity are large enough (approximately 1.5–5mNm for displacements of 18 degrees from equilibrium) to affect ankle movement during the swing phase of locomotion, and the asymmetry of larger extension vs. flexion torques is consistent with weight support, demonstrating the importance of accounting for passive muscle properties when considering the neural control of movement.

Keywords

passive properties; elastic properties; equilibrium position; muscle; rat; ankle joint; stiffness

Introduction

Studies on the contributions of musculoskeletal systems to motor control often focus on the properties of active force generation by muscle, since these properties play a direct role in the neural control of movement. However, the passive properties of the limb can also make

© 2012 Elsevier Ltd. All rights reserved.

Address for correspondence: Mengnan (Mary) Wu, Northwestern University, Feinberg School of Medicine, Ward 5-281, Physiology Dept., 303 E. Chicago Ave, Chicago, IL 60611, Phone: 312-503-1791, mengnanwu2012@u.northwestern.edu.

Publisher's Disclaimer: This is a PDF file of an unedited manuscript that has been accepted for publication. As a service to our customers we are providing this early version of the manuscript. The manuscript will undergo copyediting, typesetting, and review of the resulting proof before it is published in its final citable form. Please note that during the production process errors may be discovered which could affect the content, and all legal disclaimers that apply to the journal pertain.

Conflict of Interest Statement

All authors confirm they have no financial or other conflicts of interest relevant to this study.

important contributions to musculoskeletal function, dictating the inertial and passive viscoelastic properties of the limb in the absence of neural input and shaping the consequences of neural control [1, 4, 9, 23]. Passive properties have been demonstrated to increase energy efficiency in locomotion for animals [19, 20] and significantly contribute to phases of gait [13, 14] and lower extremity kinetics [24] in humans. Characterizing passive properties is therefore critical in understanding the control of movement.

In particular, the elasticity of muscles, tendons, ligaments, or other connective tissue within the limb can potentially make significant contributions to motor control. Recent research has demonstrated that passive elasticity of muscles is strong enough to define an equilibrium configuration of the insect limb and influence neural control [8, 26]. Passive elastic properties have been shown to define an equilibrium position in the human ankle [21], but the relative contributions of different elastic structures have not been clearly distinguished. In the present experiments, we more directly evaluate the potential role of passive elastic structures in mammals by showing that passive muscle properties contribute significantly to establishing the equilibrium position of the rat ankle, and separate out the contributions of different muscle groups by performing tendon cuts.

Methods

After approval by the Animal Care and Use Committee of Northwestern University, six female Sprague-Dawley rats were anesthetized, and their ankle muscles denervated by severing the sciatic and femoral nerves. The hindlimb was mechanically isolated at the lateral femur with the knee angle maintained at 90 degrees, and the animal was laid on its side with the left foot fixed rigidly to the experimental apparatus (Figure 1). Ankle torques were sampled from a reaction torque sensor (Interface Force MRT) at 10 kHz with a resolution of 9.96×10^{-2} mNm, and ankle positions were controlled by a brushless servo motor (Galil Motion Control BLM-N23-50-1000-B) and sampled at 512 Hz with a resolution of 1.57×10^{-3} radians. The axis of the motor and torque sensor was aligned carefully to the rat ankle's center of rotation to reduce potential errors in torque measurements [7].

Ankle positions were measured relative to the “zero” position of the ankle, where the foot was orthogonal to the tibia (Figure 1). Flexion (a.k.a. dorsiflexion) positions and torques were designated as positive in sign, and extension (a.k.a. plantarflexion) positions and torques as negative (Figure 1). We examined a range of joint angles (18 degrees of flexion to 36 degrees of extension or 72–126 degrees between the tibia and foot) similar to the range of motion exhibited in rat gait [22]. Torques were generally larger for ankle flexion positions than extension positions (Figure 2a–c), so the flexion position range was smaller to avoid high torques.

Passive torques were measured for three tendon conditions: 1) intact tendons, 2) severed primary extensors (triceps surae and plantaris), and 3) severed primary flexors (extensor digitorum longus and tibialis anterior) plus severed primary extensors. For each tendon condition, the ankle was first rotated through small consecutive displacements and then moved and held at constant position for stress relaxation to obtain a measure of torque without hysteresis effects [5]. Movements between ankle positions occurred at a slow constant velocity of 23 deg/s. For the movement with stress relaxation paradigm, each ankle position was held constant for two minutes to allow ankle torques to stabilize, and the last 30s of torque data was averaged for the “post-stress-relaxation” torque metric (Figure 2a) in accordance with procedures in previous rat hindlimb studies [6, 17, 18]. Torque during the last 10ms of movement before stress relaxation was averaged for a “dynamic” torque metric (Figure 2b). For the consecutive displacements paradigm, torque during the one-second

static period at a constant ankle position was averaged to obtain the “sequential-movement” torque metric (Figure 2c). We quantified these three torque metrics for each tendon condition.

The equilibrium position, at which zero torque should be produced, was calculated for each tendon condition and movement paradigm using linear interpolation [2] of torque vs. position data between adjacent data points. Repeated measures ANOVAs were performed for each torque metric with “tendon condition” as the single factor and equilibrium position as the dependent variable. Significance was set at 0.05 and post-hoc comparisons between tendon conditions were performed when justified, using a Bonferroni correction (α adjusted to 0.017).

Results

Torque vs. ankle position is plotted for one animal in Figure 2a–c (each subplot for a different torque metric), showing all tendon conditions (intact, extensors cut, flexors cut also). The three torque metrics show intact equilibrium positions in extension relative to zero position. For example, the post-stress-relaxation torque shows an equilibrium posture of 26 degrees in extension for the intact tendons condition. Ankle displacements away from this posture resulted in restoring torques driving the ankle back to this posture. The mean (over all animals) equilibrium positions for the intact ankle and all torque metrics are shown in Table 1. To evaluate whether the posture of the intact ankle was truly in equilibrium, we cut the primary extensors and re-measured the torques. As shown in Figure 2a–c, the equilibrium position of the ankle shifted towards flexion following this cut. When flexors were then cut, the equilibrium position shifted again, this time slightly towards extension. These results demonstrate that passive elastic properties of muscles specify an equilibrium posture of the rat ankle. Note that even after the primary flexor and extensor muscles were cut, there was still residual elasticity due to the remaining ligaments and muscles, although this elasticity was reduced.

Figure 2d–f shows the shifts in the equilibrium position for all animals and torque metrics, demonstrating the consistency of the results. For each animal, severing extensors shifted the position towards flexion (positive angle change) while severing flexors caused the position to shift towards extension (negative angle change). The mean (over animals) shifts in equilibrium position are shown in Table 1.

Repeated Measures ANOVAs showed a main effect of tendon condition on equilibrium position ($p < 0.05$) for all torque metrics. Post-hoc comparisons for the post-stress-relaxation and dynamic torque metrics showed that equilibrium positions were significantly different between intact and cut-extensors conditions as well as between cut-extensors and cut-flexors conditions. Post-hoc comparisons for the sequential- movement torque metric were not significant, presumably because of the reduced power after Bonferroni corrections and the increased variability of measurements due to history-dependent properties of passive tissues. Taken together, the results of Figure 2 show that passive elasticity of muscles contributes considerably to the equilibrium posture of the rat ankle.

We also noticed an asymmetry in ankle elasticity. As can be seen in Figures 2a–c, flexion displacements consistently resulted in larger restoring torques than equivalent extension displacements. To quantify this asymmetry, the torque at 10 degrees in flexion and extension relative to the equilibrium position was estimated using linear interpolation for each animal in the stress relaxation condition with all tendons intact. A t-test showed that the restoring torque was larger for flexion displacements than extension displacements ($p < 0.05$), confirming the asymmetry in ankle elasticity.

Discussion

These results demonstrate that opposing passive elastic forces of flexor and extensor muscles in the rat hindlimb contribute significantly to the equilibrium position at the ankle. Passive elastic properties specify a stable equilibrium ankle posture, like those observed for insect limbs and human ankles, suggesting that this role of passive properties should be observed in any low-inertial system and establishes the importance of these properties to vertebrate motor control.

The restoring torque magnitudes were approximately 1.5–5mNm for displacements of 18 degrees (Figure 2). Given a foot mass of approximately 1–2g, the passive elasticity measured here can significantly influence the position and movement of the ankle when not in ground contact, such as during the swing phase of locomotion, which spans 34.5 to –11.5 degrees (converted from [22]). At the flexion extreme of swing phase, the ankle torques will probably be even larger than the largest passive torque magnitudes measured in this study, which only measured up to 18 degrees (in flexion). It is important to note that there was a clear asymmetry in the contributions of flexor and extensor muscles in defining this equilibrium posture: extensors made a much larger contribution than flexors. A similar asymmetry has been observed at the human ankle [11], and the larger stiffness in flexion is potentially consistent with some role for these properties in weight support. The residual elasticity observed after cutting the main flexors and extensors (Figure 2) also illustrates that other muscles with primary actions outside of flexion/extension, along with joint ligaments, contribute to the observed equilibrium. Further work is required to better understand the relative roles of each of these structures in defining the passive properties at a joint. Although it is not clear whether this passive elasticity is a feature for the CNS to exploit or is a problem to overcome [8], our results demonstrate that passive elasticity in the rat is strong enough to affect normal hindlimb movements and must be accounted for by neural control. Further, passive elasticity might change following injury or disease [e.g. 15, 16], and these changes might significantly alter motor capabilities or control strategies.

The role of passive elastic properties is also clearly important to consider when creating musculoskeletal models. Passive joint torque is necessary to simulate normal finger movements and contributes to force transmission [10, 12]. In general, passive limb properties are not well-characterized in computational models, and capturing the passive behavior of musculoskeletal systems is often difficult. For instance, in many muscle models, passive elastic forces are assumed to begin at the muscle optimal fiber length and increase exponentially, such that the muscle would be slack at all shorter lengths [3, 25]. This relationship, however, is not strictly observed in real muscles; figure 3 shows that the shifts in equilibrium position due to tendon cuts are inconsistent with this assumption of muscle slack. Given the potential importance of passive elastic properties demonstrated here and elsewhere [13, 14, 19, 20, 24], it is likely that characterizing passive elastic properties of muscles will be critical in establishing accurate musculoskeletal models and in understanding the relationship between musculoskeletal properties and neural control.

Acknowledgments

This research was supported by NIH NIAMS R01AR053608 and NIH NINDS R21NS061208 to Matthew C. Tresch, National Defense Science and Engineering Graduate Fellowship to Mengnan (Mary) Wu, and by the Canada Research Chairs Program, NSERC, and Peter Wall Institute for Advanced Studies to Dinesh K. Pai. Special thanks to Prof. H. David Smith of Northwestern University for advice on statistical analysis.

References

1. Axelson HW, Hagbarth K-E. Human motor control consequences of thixotropic changes in muscular short-range stiffness. *Journal of Physiology*. 2001; 535(1):279–288. [PubMed: 11507177]
2. Brueckner S. Crossing. Matlab Central File Exchange. <http://www.mathworks.com/matlabcentral/fileexchange/2432>.
3. Chadwick EK, Blana D, van den Bogert AJ, Kirsch RF. A real-time, 3-D musculoskeletal model for dynamic simulation of arm movements. *IEEE Transactions on Biomedical Engineering*. 2009; 56(4):941–948. [PubMed: 19272926]
4. Collins S, Ruina A, Tedrake R, Wisse M. Efficient bipedal robots based on passive dynamic walkers. *Science Magazine*. 2005; 307:1082–1085.
5. Fung, YC. *Biomechanics: Mechanical Properties of Living Tissues*. Second Edition. New York: Springer; 1993. p. 41–43.
6. Gillette PD, Fell RD. Passive tension in rat hindlimb during suspension unloading and recovery: muscle/joint contributions. *Journal of Applied Physiology*. 1996; 81:724–730. [PubMed: 8872639]
7. Gosselink M, Drost MR, de Louw J, Willems PJB, Hesselink MKC, Dekkers ECA, Rosielle N, van der Vusse GJ, et al. In situ assessment of shortening and lengthening contractile properties of hind limb ankle flexors in intact mice. *Pflügers Archiv European Journal of Physiology*. 2001; 442:304–311. [PubMed: 11417229]
8. Hooper SL, Guschlbauer C, Blumel M, Rosenbaum P, Gruhn M, Akay T, Buschges A. Neural control of unloaded leg posture and of leg swing in stick insect, cockroach, and mouse differs from that in larger animals. *Journal of Neuroscience*. 2009; 29:4109–4119. [PubMed: 19339606]
9. Johanson ME, Murray WM. The unoperated hand: the role of passive forces in hand function after tetraplegia. *Hand Clinics*. 2002; 18:391–398. [PubMed: 12474591]
10. Kamper DG, Hornby TG, Rymer WZ. Extrinsic flexor muscles generate concurrent flexion of all three finger joints. *Journal of Biomechanics*. 2002; 21:361–369.
11. Kearney RE, Hunter IW. System identification of human joint dynamics. *Critical Reviews in Biomedical Engineering*. 1991; 18:55–87. [PubMed: 2204515]
12. Lee S, Kamper DG. Modeling of multi-articular muscles: importance of inclusion of tendon-pulley interactions in the finger. *IEEE Transactions on Biomedical Engineering*. 2009; 56(9):2253–2262. [PubMed: 19362899]
13. Mansour JM, Audu ML. The passive elastic moment at the knee and its influence on human gait. *Journal of Biomechanics*. 1986; 19:369–373. [PubMed: 3733762]
14. McFaul SR, Lamontagne M. In vivo measurement of the passive viscoelastic properties of the human knee joint. *Human Movement Science*. 1998; 17:139–165.
15. Mirbagheri MM, Alibiglou L, Thajchayapong M, Rymer WZ. Muscle and reflex changes with varying joint angle in hemiparetic stroke. *J Neuroeng. Rehabil*. 2008; 27:5–6.
16. Mirbagheri MM, Barbeau H, Ladouceur M, Kearney RE. Intrinsic and reflex stiffness in normal and spastic, spinal cord injured subjects. *Exp. Brain Res*. 2001; 141(4):446–459. [PubMed: 11810139]
17. Ochi E, Nakazato K, Ishii N. Effects of acute eccentric contractions on rat ankle joint stiffness. *Journal of Sports Science and Medicine*. 2007; 6:543–548.
18. Ochi E, Nakazato K, Ishii N. Effects of eccentric exercise on joint stiffness and muscle connectin (titin) isoform in the rat hindlimb. *Journal of Physiological Sciences*. 2007; 57:1–6. [PubMed: 17081353]
19. Proske U. Energy conservation by elastic storage in kangaroos. *Endeavour*. 1980; 4:148–153.
20. Roberts TJ, Marsh RL, Weyand PG, Taylor CR. Muscular force in running turkeys: the economy of minimizing work. *Science Magazine*. 1997; 275:1113–1115.
21. Souza TR, Fonseca ST, Goncalves GG, Ocarino JM, Mancini MC. Prestress revealed by passive co-tension at the ankle joint. *Journal of biomechanics*. 2009; 42:2374–2380. [PubMed: 19647832]
22. Thota AK, Watson SC, Knapp E, Thompson B, Jung R. Neuromechanical control of locomotion in the rat. *Journal of Neurotrauma*. 2005; 22(4):442–465.

23. Valero-Cuevas FJ, Yi J-W, Brown D, McNamara RV III, Paul C, Lipson H. The tendon network of the fingers performs anatomical computation at a macroscopic scale. *IEEE Transactions on Biomedical Engineering*. 2007; 54:1161–1166. [PubMed: 17549909]
24. Whittington B, Silder A, Heiderscheit B, Thelen DG. The contribution of passive-elastic mechanisms to lower extremity joint kinetics during human walking. *Gait and Posture*. 2008; 27(4):628–634. [PubMed: 17928228]
25. Zajac FE. Muscle and tendon: properties, models scaling, and application to biomechanics and motor control. *Critical Reviews in Biomedical Engineering*. 1989; 17(4):359–411. [PubMed: 2676342]
26. Zakotnik J, Matheson T, Durr V. Co-contraction and passive forces facilitate load compensation of aimed limb movements. *Journal of Neuroscience*. 2006; 26:4995–5007. [PubMed: 16687491]

Figure 1.

Photograph of rat foot attached to experimental setup with ankle at “zero” position, defined as the position at which the foot is orthogonal to the tibia. Flexion angles are designated as positive and extension angles as negative. The center of the ankle was aligned to the center of the torque sensor and motor. The knee angle was maintained at 90 degrees. The animal was laid on its right side so that ankle torques were not affected by gravity.

Figure 2.

a–c) All three torque metrics across all three tendon conditions for one sample animal. Blue = tendons intact, green = cut Achilles tendon (severing extensors TS and Pla), red = cut flexors EDL and TA in addition to cut extensors. Dots = data points. Solid colored vertical lines represent interpolated neutral (zero-torque) positions. Dashed horizontal and vertical black lines at zero torque and zero position are displayed for reference. Positive positions denote flexion, and positive torques denote flexion torque. In general, comparing before (blue) and after (green) cutting the primary extensors, most of the torque curve shifted toward greater flexion torque and the neutral position shifted towards flexion. Comparing before (green) and after (red) cutting the primary flexors, the torque curve shifted slightly

toward greater extension torque for extension positions, and the equilibrium position shifted towards extension. The red curve shows non-zero torques due to remaining muscles and joint ligaments. d–f) Change in neutral position after a tendon cut for all three torque metrics: d) corresponds to post-stress-relaxation torque, e) corresponds to dynamic torque, and f) corresponds to sequential-movement torque) and all six animals (grey x's) with mean and one standard deviation (solid black lines). Dashed horizontal black line at zero is displayed for reference. For each animal, severing extensors caused the position to shift towards flexion (positive change of angle) while severing flexors caused the position to shift towards extension (negative change of angle).

Figure 3.

Representation of the effect of severing muscle groups on neutral or zero-torque position for the hypotheses: a) flexors and extensors overlap to create the neutral position and b) slack in flexors and extensors create the neutral position. Orange curve = extensor contributions to passive torque, violet curve = flexor contributions. Horizontal axis shows joint angle with “f” for flexion and “e” for extension, and the vertical axis shows passive torque with T_f = flexion torque and T_e = extension torque. a) The neutral position with tendons intact is shown by the short vertical blue line and occurs where flexion and extension torques balance. After severing extensors, the neutral position shifts to the green line. b) The neutral position remains the same before and after removing extensors and is shown by the short vertical green line.

Table 1

Equilibrium positions for intact ankle and shifts in equilibrium position after each tendon cut.

Torque metric	Eqbm. pos. (degrees)	Conditions compared	Shift in eqbm. pos. (deg)
Post-stress-relaxation	-15.7 (6.3)	cut extensors vs. intact	7.7 [1.7] *
		cut flexors vs. cut extensors	-2.5 [0.6] *
Dynamic	-10.2 (2.7)	cut extensors vs. intact	4.4 [0.7] *
		cut flexors vs. cut extensors	-0.9 [0.2] *
Sequential-movement	-9.3 (5.0)	cut extensors vs. intact	5.2 [1.7]
		cut flexors vs. cut extensors	-1.3 [0.4]

Mean (SD)

Mean [SE]

* Significant difference ($p < 0.017$)

Flexion positions are positive, extension positions are negative. The position where the foot is orthogonal to the tibia is defined as the zero position.