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TECHNICAL REPORT TR-05-2023

A HILL-TYPE CONTINUUM MODEL OF A MUSCLE FIBRE

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LAST UPDATED: October 26, 2023	**LAST REVISION:**	**DATE APPROVED:**

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1. Executive Summary

TBD

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Consider the mass-enhanced muscle model from Ross & Wakeling 2016 [1] driven by an external force F_{ext} applied on the last mass. Mathematically, it can be described as a system of N ODEs as follows:

$$\begin{cases} m_1 \dfrac{d^2 x_1}{dt^2} = F_2(\lambda_2, \epsilon_2) - F_1(\lambda_1, \epsilon_1), \\ m_2 \dfrac{d^2 x_2}{dt^2} = F_3(\lambda_3, \epsilon_3) - F_2(\lambda_2, \epsilon_2), \\ \qquad\qquad \vdots \\ m_N \dfrac{d^2 x_N}{dt^2} = F_{ext} - F_N(\lambda_3, \epsilon_3). \end{cases} \tag{2.1}$$

Denoting by x_i the position of the i-th mass, the stretch (normalized length) and strain rate (normalized velocity) can be written as

$$\lambda_i = \frac{x_i - x_{i-1}}{L/N}, \quad \epsilon_i = \frac{\dot{\lambda}_i}{\epsilon_0} = \frac{\dot{x}_i - \dot{x}_{i-1}}{\epsilon_0 L/N}, \quad i = 1, \ldots, N \tag{2.2}$$

where L denotes the length of the muscle (which could be taken as the optimal length) and ϵ_0 is the maximum strain rate of the muscle fibre. In addition, $x_0 = 0$. Typically, the spacing between masses is considered constant. Call it Δx. We have therefore $\Delta x = L/N$. Moreover, writing these quantities in terms of displacements u_i, where $x_i = x_i^0 + u_i$ and x_i^0 is the initial position of the i-th mass, we have the following:

$$\lambda_i = \frac{x_i - x_{i-1}}{\Delta x} = \frac{u_i + x_i^0 - u_{i-1} - x_{i-1}^0}{\Delta x} = 1 + \frac{u_i - u_{i-1}}{\Delta x}, \tag{2.3}$$

the latter because $x_i^0 - x_{i-1}^0 = \Delta x$. Moreover,

$$\epsilon_i = \frac{\dot{x}_i - \dot{x}_{i-1}}{\epsilon_0 \Delta x} = \frac{1}{\epsilon_0} \frac{d}{dt} \left(\frac{u_i - u_{i-1}}{\Delta x} \right) = \frac{1}{\epsilon_0} \frac{d}{dt} \left(1 + \frac{u_i - u_{i-1}}{\Delta x} \right). \tag{2.4}$$

We are interested in studying the behaviour of the system as $N \to \infty$, or equivalently, as $\Delta x \to 0$. This is the **continuum limit**. It turns out that, as $\Delta x \to 0$, the previous two equations define the following quantities:

$$\lambda := \lim_{\Delta x \to 0} \lambda_i = 1 + \frac{\partial u}{\partial x}, \quad \epsilon := \lim_{\Delta x \to 0} \epsilon_i = \frac{1}{\epsilon_0} \frac{\partial \lambda}{\partial t}. \tag{2.5}$$

That is, we have recovered the one-dimensional version of the stretch and strain rate variables that are commonly considered in solid mechanics.

Going back to the system (2.1), it is customary to consider $m_i = m/N$, where m is the mass of the whole muscle. This means that, $m_i = m \Delta x / L$. Also, because $F_i = F(\lambda_i, \epsilon_i)$ where F is Hill's force, we may rewrite (2.1) as

$$\begin{cases} \frac{m}{L}\frac{d^2x_1}{dt^2} = \frac{F(\lambda_2,\epsilon_2)-F(\lambda_1,\epsilon_1)}{\Delta x}, \\ \frac{m}{L}\frac{d^2x_2}{dt^2} = \frac{F(\lambda_3,\epsilon_3)-F(\lambda_2,\epsilon_2)}{\Delta x}, \\ \qquad\vdots \\ \frac{m}{L}\frac{d^2x_N}{dt^2} = \frac{F_{ext}-F(\lambda_N,\epsilon_N)}{\Delta x}. \end{cases} \tag{2.6}$$

Claim 2.1. *The system of ODEs* (2.1) *corresponds to a first-order method of lines discretization of the partial differential equation*

$$\rho_0 \frac{\partial^2 u(x,t)}{\partial t^2} = \frac{\partial F(\lambda,\epsilon)}{\partial x}, \quad (x,t) \in (0,L)\times(0,\infty), \tag{2.7}$$

subject to mixed boundary conditions

$$u(0,t) = 0, \quad F(\lambda,\epsilon)\big|_{x=L} = F_{ext}, \tag{2.8}$$

and initial conditions

$$u(x,0) = \frac{\partial u(x,0)}{\partial t} = 0. \tag{2.9}$$

*Here, ρ_0 would be the **linear density** of muscle tissue, which can be computed from the volumetric muscle density ρ_0^V as $\rho_0 = \rho_0^V \cdot CSA$.*

Note that the Neumann condition in (2.8) corresponds to a nonlinear type of boundary condition depending on $\frac{\partial u}{\partial x}$. Thus, the problem is at least well-defined (whether it is *well-posed* is a different story). A more common Neumann boundary condition for this problem (but perhaps not applicable to muscle, see footnote) is to prescribe a strain at the end, that is,

$$\frac{\partial u}{\partial x}\Big|_{x=L} = \frac{\sigma_{ext}}{E}.$$

where σ_{ext} is an external stress and E is the Young's modulus of the material[1].

Proof. Indeed, consider a discretization $\{x_0, x_1, \dots, x_N\}$ of the interval $[0,L]$ where $x_0 = 0$ and $x_N = L$. Then, define $u_i = u(x_i,t)$, and consider a *backwards* first-order formula to discretize (in space) the stretch and strain rates, that is,

$$\lambda_i = \lambda(x_i,t) = 1 + \frac{u_i - u_{i-1}}{\Delta x}, \quad \epsilon_i = \epsilon(x_i,t) = \frac{1}{\epsilon_0}\frac{d\lambda_i}{dt}.$$

These are precisely the equations in (2.2). Now, to discretize the gradient on the right-hand side of (2.7), consider a *forwards* first-order difference:

$$\frac{m}{L}\frac{d^2u_i}{dt^2} = \frac{F(\lambda_{i+1},\epsilon_{i+1}) - F(\lambda_i,\epsilon_{i+1})}{\Delta x}, \quad i = 1,\dots,N.$$

[1] Ogneva et al. [2] reports values of $E \approx 30$ kPa for a muscle fibre in a relaxed state and $E \approx 66$ kPa in a fully-active state for rat soleus muscle. These measurements were performed at the M bands, which differ from measurements at Z bands.

Given that there is not an x_{N+1} mass, the force required at this "ghost" node can be taken precisely as F_{ext}, i.e. $F(\lambda_{N+1}, \epsilon_{N+1}) = F_{ext}$. In addition, we have taken $\rho_0 = m/L$. Thus, the previous expression is just (2.6). □

Remark 2.2. *Mathematically speaking, F only needs to be a "nice" (i.e. at least continuous) function, not necessarily Hill's force. However, if F is indeed Hill's force, then I conjecture that the equation* (2.7) *corresponds to the deformation of a muscle fibre in which every point inside is subjected to Hill's force.*

Remark 2.3. *The continuum limit may seem excessive at first, but we have to keep in mind that N, the number of masses in the ODE system, will never reach the number of sarcomeres in a muscle fibre. For instance, we may well have between 20,000 to 25,000 sarcomeres per 10 cm of muscle fibre. For a muscle that is 30 cm long, we are currently taking $N = 16$ masses.*

One advantage of the PDE (2.7) is that it is easy to add, say a Neo-Hookean contribution:

$$\rho_0 \frac{\partial^2 u}{\partial t^2} = \frac{\partial}{\partial x} F(\lambda, \epsilon) + \frac{\partial}{\partial x}\left(c_1 \lambda + \frac{c_1 \log(\lambda) + c_2}{\lambda} \right),$$

where $c_1, c_2 > 0$ are the Lamé coefficients of the material (these are typically denoted by λ and μ, but we have not used this notation here for obvious reasons).

It remains to propose a method to evaluate the descending limb instability in the model (2.7), if it is present at all.

Bibliography

[1] S. A. Ross & J. M. Wakeling. Muscle shortening velocity depends on tissue inertia and level of activation during submaximal contractions. Biol. Lett. 12 (2016), 20151041.

[2] I. V. Ogneva, D. V. Lebedev & B. S. Shenkman. Transversal stiffness and Young's modulus of single fibers from rat soleus muscle probed by atomic force microscopy. Biophysical Journal 98 (2010), 418–424.