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Extracting low-velocity concentric and eccentric dynamic muscle properties from isometric contraction experiments

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ABSTRACT

Determining dynamic properties of mammalian muscles, such as activation characteristics or the force–velocity relation, challenges the experimentalist. Tracking system, apparatus stiffness, load oscillation, force transducer, other sensors, and additional measuring devices may be incorporated, integrated and evaluated in an experimental set-up. In contrast, isometric contraction experiments (ICEs) are less challenging, but are generally not considered to reveal dynamic muscle properties. Yet, a sensitivity analysis of our muscle model discloses the influence of concentric, eccentric and activation parameters on isometric force development. Accordingly, we used solely experimental ICE data to identify muscle model parameters that generally describe concentric as well as eccentric muscle performance. In addition, we compared two different activation dynamics in regards to their physiological relevance to improve model-fits to ICE data. To this end, we optimized different combinations of such dynamic parameter subsets with respect to their influence on contraction solutions. Depending on muscle length in our optimized model, the contractile element reached shortening peaks during activation in the range 9–39% of its maximum contraction velocity, and about 8–25% during lengthening when deactivated. As a first result, we suggest one formulation of activation dynamics to be superior. Second, the step in slope of the force-velocity relation at isometric force was found to be the least influential among all dynamic parameters. Third, we suggest a specially designed isometric experimental set-up to estimate this transition parameter. Fourth, because of an inconsistency in literature, we developed a simple method to determine switching times of the neural stimulation and thus electro-mechanical delay (EMD) values from measuring muscle force in ICEs only.

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1. Introduction

Describing complex systems, models usually consist of several sub–models (or parts), delineating structurally or functionally distinct contributions to system dynamics. In biological systems, the parts interact mostly non-linearly. An essential scientific task is to validate such models by sorting out sub-models of low validity and to improve or exchange them if needed.

Muscular contraction can be examined by using macroscopic Hill-type muscle models [42]. These are often combined with model descriptions of electro-chemical processes that lead to muscle force production in response to neural stimulation, the so-called activation dynamics, see for example [31,61,93,100,102,103,105–107]. Some properties of coupled contraction–activation dynamics are well-established, for instance the force-length relation of muscle fibers [4,5,11,21,35,36,45,79,84,98] or the visco-elastic characteristics of tendon material [34,49,50,73,75,76,80,107]. A near-static condition, such as an isometric contraction, is appropriate for determining static properties, i.e. force-length relations, and implies minimized experimental complexity and methodical effort. It seems natural that determining dynamic properties, such as a fiber's force-velocity relation or activation dynamics, requires performing dynamic contraction modes. For this purpose, the experimentalist has to develop more elaborated and sophisticated experimental methods. However, in such dynamic contraction modes, the activity development and the muscle length change superpose each other on the contribution to form the actual fiber force, see [44].

Abbreviations: CC, concentric contraction; CE, contractile element; DAE, differential algebraic equation (system); EC, eccentric contraction; EMD, electro–mechanical delay; ICE, isometric contraction experiment; MTC, muscle tendon complex; ODE, ordinary differential equation; PEE, parallel elastic element; SDE, serial damping element; SEE, serial elastic element; w.r.t., with respect to.

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The concentric branch of the force-velocity relation is the most investigated dynamic muscle property. Experimental approaches are traceable to the nineteenth century and first quantitative results are dating back to the 1920s [20,41,58,60], culminating in the 1930s [19,42]. Attention has been paid to muscle activation dynamics in the late 1970s [31–33], late 1980s [61,102,105–107] and again during the last two decades [7,9,51,82,98]. Dynamic, dissipative properties of tendon and aponeurosis material [26] as well as activity-dependent, potentially visco-elastic properties of titin molecules [83] have recently been considered in muscle modeling as well.

Determining eccentric muscle properties challenges an experimentalist and requires extra-delicate set-ups. The muscle can be easily damaged [66,96,104], which obstructs both data quality and repeatability. Compared to the concentric case, experimental data on eccentric contractions are scarce [29,46–48,55,59,63,91,92,96]. Parameter values describing eccentric contractions differ considerably and ought to be treated with caution.

It is assumed that there is passive visco-elastic material (serial elastic and damping elements: SEE and SDE) in series to the contractile material (contractile element: CE) in a real muscle-tendon complex (MTC), see Fig. A.6. Be it in situ or in vitro, any isometric contraction experiment (ICE) on an MTC should then also be a source of information about the dynamic components, i.e. concentric and eccentric CE properties as well as activation. With the MTC held isometrically, a change in muscle stimulation from zero to maximum or vice versa will induce the CE to contract concentrically or eccentrically, respectively, against the SEE and SDE. There has not been brought attention to this fact, although ICEs are less challenging in terms of apparatus design and experimental execution, compared to eccentric contractions of the entire MTC. Furthermore, ICEs naturally provide a physiologically tolerable eccentric loading condition for the muscle material.

The first aim of our study was to assess the validity of several parts of a Hill-type muscle model for coupled contraction–activation dynamics. For this purpose, we compared two different model descriptions of both the eccentric branch of the CE force-velocity relation and the activation dynamics. We compared model simulations containing a complete set of Hill-type model parameters to literature data of a piglet muscle experiment [26]. Our aim was to identify the model part combination that shows a minimal least-square deviation from the experimental force–time curves, measured during isometric contractions of this muscle at various MTC lengths. In these experiments, the muscle was clamped unstimulated at a particular length. After a period of rest, it was fully stimulated at a certain switch-on time. One second later, at switch-off time, the stimulation was set to zero again. During the experiment, the MTC force output was measured. The best-fitting model was subjected to an optimization procedure that minimized the deviation from the measured data. As a consequence of checking and optimizing model validity, we determined dynamic muscle parameters of the Hill-type muscle model for concentric and eccentric contractions, together with parameters of the coupled model for contraction–activation dynamics. It is noteworthy here that the passive elastic properties of the SEE and parallel elastic element (PEE) were taken from literature [26] as is and the tendon-to-fiber length ratio is 3 in this MTC. The latter fact is a rather unusual choice in experiments determining CE properties and gives occasion to discussing the structural properties implied to be incorporated into current models of a Hill-type CE (see Section 4).

Our second aim was the optimization of experimental set-ups by purposefully limiting the information about muscle dynamics to force–time curves during isometric contractions. This self-limitation demonstrates that dynamic contraction parameters may be determined solely from this near-static contraction mode, which is easier to perform as compared to experiments in which the MTC length changes. Based on [57,82,97], a sensitivity analysis of the model dynamics revealed the influence of dynamic muscle parameters on the time evolution of the isometric force. Among all dynamic parameters, the ratio between the derivatives of the concentric and eccentric branch within the force–velocity relation at the isometric point (denoted by S_e) was least sensitive. Using sensitivity analysis, we can now suggest an isometric contraction experiment, optimized for solely determining the eccentric parameter S_e.

An interesting side effect arises from the necessity of knowing when exactly the finite changes in stimulation occur. The activation and dynamic contraction parameters sensitively influence the electro-mechanical delay (EMD), which is the time interval between a measurable change in stimulation input and the subsequently measurable change in force output. We realized, that the specification of the switch-off times in the experiments were unreliable. This challenge led to a method of extracting the EMD solely from experimental data of isometric contractions.

2. Model and methods

2.1. Model description

The used Hill-type muscle model was initiated by Günther et al. [26] and further developed by Haeufle et al. [27]. For a detailed description see Appendix A or [81]. The force-generating model structure is composed of four force-bearing elements: the serial elastic (SEE) and damping element (SDE) in series to the contractile (CE) and parallel elastic element (PEE), see Fig. A.6. The basic serial arrangement CE–SEE has first been advanced by Hill and Wilkie [38,40,101] based on two earlier papers [42,58]. It seems expedient to annotate that since then the picture is blurred as to what properties exactly account for the SEE. Until today, in particular, filament and cross-bridge compliances are not explicitly factored in to model formulations of the Hill-type, typically hyperbolic, CE force–velocity relation of active fiber material. The common experimental set-ups, like those early ones used by Hill [40,42], for determining this relation employ muscle or fiber preparations with minimized tendon and aponeurosis proportions, whereas Hill-type muscle models in computer models [24,30,71,72,99] usually attribute tendon/aponeurosis properties to the SEE. This is also the case within this study. We will pick up this point again in Section 4. The physiological properties of these elements, as assumed in our model, are illustrated in Figs. A.7 and A.9. The contraction dynamics of the force-bearing elements and coupled activation dynamics of the CE constitute the muscle model dynamics, see Eq. (3a) and (3b).

Let ℓ_{MTC}, ℓ_{SEE}, ℓ_{SDE}, ℓ_{CE} and ℓ_{PEE} denote the lengths of the four constituting elements composing the whole muscle-tendon complex (MTC).

$$\ell_{SEE} = \ell_{SDE}, \quad \ell_{CE} = \ell_{PEE} \quad \text{and} \quad \ell_{MTC} = \ell_{CE} + \ell_{SEE}, \tag{1}$$

and the one-dimensional force equilibrium

$$F_{MTC} = F_{CE} + F_{PEE} = F_{SEE} + F_{SDE} \tag{2}$$

apply, in which ℓ_i denotes the length of element i and F_i its generated force. Let σ represent the electrical stimulation at the surface of the muscle fiber material, which drives the MTC dynamics as an input control parameter. Furthermore, q_X denotes the muscle activity, which represents the MTC's second state variable alongside with ℓ_{CE}. Note that our use of q_X is completely consistent to the "active state" introduced by Hill [39]: it represents the ratio of attached cross-bridges in relation to all available ones which directly scales the current, potential isometric force. The force production of the MTC within an isometric contraction can then be described

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