



How to model a muscle's active force–length relation: A comparative study

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Abstract

The active isometric force–length relation (FLR) of mammalian skeletal muscle is one of the most investigated characteristics throughout biomechanics. Numerous experiments have been conducted that reveal insights on the mechanisms of muscle contraction. However, the entity of molecular processes is yet not fully understood. Modelers thus rely on a rather descriptive characterization of experimental findings. Starting with the well-known, piece-wise linear formulation by A. Gordon, A. Huxley and F. Julian in 1966, a variety of structurally distinguishable FLR models have been developed. Five decades later, the original idea was taken up to derive the first purely physiological FLR formulation, based on sliding filament and cross-bridge theory. This derivation offers us the opportunity to contrast a broad variety of 19 distinct FLR models. By comparing their ability to fit experimental data, we deduce qualitative as well as quantitative acceptance criteria such as symmetry, normalization, complexity, and physiological interpretability. Resultant, different models comprise different advantages. The new piece-wise linear model is the overall most favorable, a further piece-wise exponential model is mathematically more robust, a polynomial model of fourth order has the best optimization properties, and a certain purely exponential model is the computationally cheapest. This work gives a detailed overview, as well as a mathematical/physiological assessment of existing FLR models, and serves as a guideline for modelers to choose a proper formulation based on individual requirements.

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1. Introduction

The active isometric force–length relation (FLR) of skeletal muscles constitutes a core element in biomechanical research and modeling. It describes the force that a single sarcomere, fiber or muscle is able to exert at a given

Abbreviations: CE, contractile element; cf., confer (compare); DOF, degree(s) of freedom; FLR, (isometric) force–length relation; GHJ, Gordon, Huxley and Julian; i.e., id est (that is); LSE, least-squares error; MTU, muscle–tendon unit; SLSE, scaled least-squares error; w.r.t., with respect to.

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length, relative to its maximum force. First quantitative measurements, conducted on frog gastrocnemius [1], go back to the end of the 19th century. Since then, the FLR is one of the experimentally most investigated muscle characteristics, see for example [2–29]. These experiments cover sarcomere experiments as well as measurements on fibers and whole muscles from various animals, mostly cat, frog, mouse, (stick) insect, rabbit and rat. First qualitative descriptions postulated the interaction of internal molecules: actin and myosin were assumed to act as sliding filaments [30,31], which are connected by cross-bridges [32,33], to produce a force in response to an electrical stimulation. From these theoretical considerations, A. Gordon, A. Huxley and F. Julian (short: GHJ) derived a FLR model, based on muscle structure [34], and compared it to their own measurements on frog sarcomeres [35]. The latter paper, as a first conflation of theory and experiments, became a standard reference for modelers as well as for experimenters.

Additional to the suggested piece-wise linear FLR from [35], modelers since have developed a variety of structurally different descriptions, see Section 2. However, almost all of those models contain a descriptive (best-fitting) rather than a functional basis. The sliding filament theory was indeed used to calculate the grid points for the piece-wise linear FLR [13], but the force occurring at the knee-point of the ascending limb remained a free parameter, cf. [36]. Recently, exactly five decades later, [37] presented the (to our knowledge) first purely physiologically-based model approach, where the complete FLR was parameterized using only the geometry of internal muscle structures. Orienting on the original approach by GHJ, they derived the equations for a complete piece-wise linear FLR from the lengths of the molecules actin and myosin as well as the myosin bare zone. In particular, this simple and straightforward model was used to explain frog [20] and rat fiber data, where a smaller second force peak at very short lengths occurred.

The FLR represents a part of a more complex muscle–tendon-unit (MTU) model, including further sub-models, such as parallel or serial elastic components, and therefore more parameters. A restatement of Occam’s razor in this context may stress that among all possible models, the one with the fewest assumptions or parameters should be used. On the one hand, more parameters or degrees of freedom (DOF) result in a lower residuum and therefore allow a better fit to the data. On the other hand, in algorithmic optimization, the effort for finding an optimal solution increases drastically with the number of parameters [38, “Too many parameters is not good”].

There are concerns that a simply scaled sarcomere FLR may not be appropriate to describe the FLR of a whole muscle, see for example [39,40], based on the following considerations. First, in a parallel and serial composition, the distribution of single sarcomeres may be influenced by stochastic effects [41]. As a consequence of an assumed normal distribution, the FLR should contain (parts of) a Gaussian function. Second, implications resulting from the three-dimensionality of muscles may occur: architectural particularities [42–44], pennation [45] or volumetric effects [46,27]. Third, experimental data suggest that not all sarcomeres lengthen simultaneously and equally. The so-called *sarcomere non-uniformity theory* [47,48] also serves for explaining history dependent effects [49]. Fourth, a species-specific design of different muscles may influence the operating mode and range [50]. Despite the mentioned arguments, there are, however, votes in favor of a scalability from sarcomere to whole muscle [51,52], especially when passive forces are accounted for appropriately in the determination of active force from total muscle force, cf. [53] and [54, Fig. 5]. For example, experimental data for rabbit hindlimb muscles [55] or rat medial gastrocnemius [56] have been successfully modeled using a scaled sarcomere FLR.

In a recent study [57], an attempt was made to compare different FLR models with respect to their ability to fit simulated and measured data. However, the study contained several drawbacks. Their findings were insignificant in terms of statistical characteristics, since no qualitative difference between model formulations, could be discovered. The reason for this insignificance, was the usage of utterly noisy simulated and experimental data [57, Figs. 4–5], such that every model function was shrouded by data clouds. Additionally, the existence of asymmetric exponential FLR models in literature was disregarded. Lastly, the study constituted a pure fitting exercise, neglecting the biomechanical quality of the results, such as physiological meaning of model parameters or consequences in application for theoreticians and experimenters.

In contrast, the aims of this article are to compare an exhaustive variety of FLR models by testing their ability to reproduce well-established muscle data from [35] and to work out quantitative as well as qualitative criteria for physiological FLR modeling. In Section 2, we introduce and group FLR models that appear in literature and summarize the least-squares fitting method. In Section 3, we make the models comparable by introducing a relative residuum, dependent on the number of inherent parameters and conduct a fit to the data. The results are then discussed in Section 4.

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