Mathematical Biosciences 217 (2009) 64–76

Contents lists available at ScienceDirect

Mathematical Biosciences

journal homepage: www.elsevier.com/locate/mbs

Mathematical analysis of a muscle architecture model

Javier Navallas [a,*], Armando Malanda [a], Luis Gila [b], Javier Rodríguez [a], Ignacio Rodríguez [a]

[a] *Department of Electrical and Electronics Engineering, Public University of Navarra, Campus de Arrosadía s/n, 31006 Pamplona, Navarra, Spain*
[b] *Department of Clinical Neurophysiology, Hospital Virgen del Camino, C/Irunlarrea 4, 31008 Pamplona, Navarra, Spain*

ARTICLE INFO

Article history:
Received 20 November 2007
Received in revised form 14 May 2008
Accepted 2 October 2008
Available online 14 October 2008

Keywords:
Muscle model
Muscle architecture
Motor unit
EMG simulation

ABSTRACT

Modeling of muscle architecture, which aims to recreate mathematically the physiological structure of the muscle fibers and motor units, is a powerful tool for understanding and modeling the mechanical and electrical behavior of the muscle. Most of the published models are presented in the form of algorithms, without mathematical analysis of mechanisms or outcomes of the model. Through the study of the muscle architecture model proposed by Stashuk, we present the analytical tools needed to better understand these models. We provide a statistical description for the spatial relations between motor units and muscle fibers. We are particularly concerned with two physiological quantities: the motor unit fiber number, which we expect to be proportional to the motor unit territory area; and the motor unit fiber density, which we expect to be constant for all motor units. Our results indicate that the Stashuk model is in good agreement with the physiological evidence in terms of the expectations outlined above. However, the resulting variance is very high. In addition, a considerable 'edge effect' is present in the outer zone of the muscle cross-section, making the properties of the motor units dependent on their location. This effect is relevant when motor unit territories and muscle cross-section are of similar size.

1. Introduction

Muscle architecture modeling is central in the understanding of muscle function under different conditions and states. Both the mechanical behavior (exerted power and force, stiffness, fatigue resilience, etc.) and the electrical activity originated in muscle contraction, i.e., electromyographic (EMG) signals, are related to muscle architecture [1,2]. Realistic modeling allows to reach a deeper understanding of the mechanisms by which neural and muscle properties give rise to electromyograms and force [3].

Skeletal muscle is composed by a bundle of muscle fibers (MFs), which are elongated cells disposed in parallel and attached by its endings to the tendons. Each MF is innervated by a single motoneuron, from which it receives the electrical stimuli associated with contraction orders. Each motoneuron innervates a group of MFs, and the whole muscle is innervated by a number of motoneurons. Motor units (MUs) are functional units of muscle architecture, formed by a motoneuron and a set of MFs which are innervated by it. The set of MFs of a single MU, termed motor unit fibers (MUFs) [4,5] (also known as muscle unit [6]), appear to be restricted to a particular extent of the muscle, termed motor unit territory (MUT). MUTs of different MUs overlap in the muscle cross-section (MCS), hence MUFs of different MUs are intermingled. Three quantities of special interest for our analysis, allow to characterize the MU architecture: the number of MFs innervated by each MU, i.e., the motor unit fiber number (MUFN) (also known as MU size [7,8] or innervation ratio [9,10]); the area of the MUT when measured in the MCS, i.e., the motor unit territory area (MUTA); and the number of innervated MFs per unit of area inside the MUT, i.e., the motor unit fiber density (MUFD), which is simply the ratio of MUFN to MUTA.

Several steps must be undertaken to build a complete muscle architecture model. First, the muscle is usually modeled by a cylinder with given length and cross-section. Within the circular MCS, a grid of MFs is created. After this, the size and location of the MUTs, usually modeled as circles in the MCS, must be determined (Fig. 1(a)). Finally, the innervation process is recreated, selecting only one innervating MU for each of the existing MFs in the MCS. Usually, one of the MUs whose MUTs overlap at the position of the MF is selected (Fig. 1(b)). As a result of the innervation process, each MU has a number of innervated MUFs scattered within its territory (Fig. 1(c)). Following the approximations used by most of the published models, two desirable properties should hold in a muscle architecture model: the MUFN should follow Fuglevand exponential law [5,11]; and the MUFD should be fairly constant for all the MUs in the muscle [12,13].

Several muscle architecture models have been proposed for EMG modeling [11,14–17]. However, all of the published muscle models are presented in an algorithmic fashion: without any analytical study of the algorithms used or any statistical study of the resulting architecture. The aim of the work reported here is to

* Corresponding author. Tel.: +34 948169726; fax: +34 948169720.
E-mail address: javier.navallas@unavarra.es (J. Navallas).

0025-5564/$ - see front matter © 2008 Elsevier Inc. All rights reserved.
doi:10.1016/j.mbs.2008.10.004

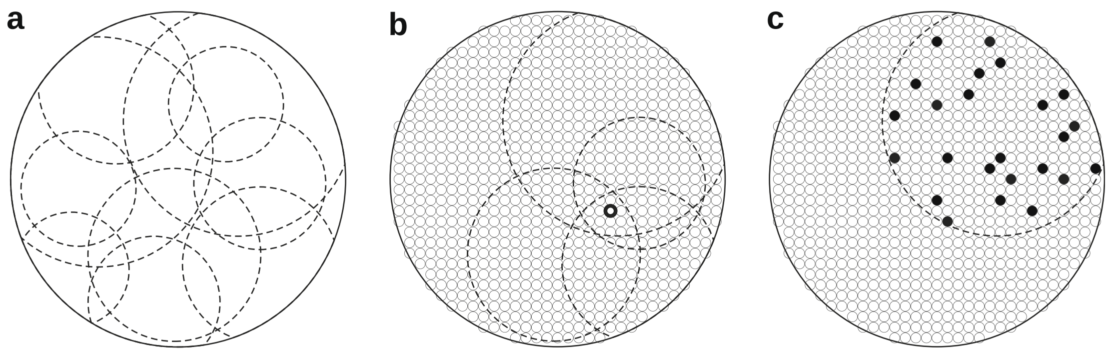

Fig. 1. Schematic representation of the steps involved in muscle model simulation: (a) MUTs (dashed circles) after being placed within the MCS (solid circle); (b) Grid of MFs (small circles) within the MCS, with one MF highlighted (thickened border). Only the MUs which MUTs cover the highlighted MF are represented. One of this MUs will be selected to innervate the MF; (c) One MU and its MUFs after the innervation process is completed. Note that all the MUFs lie inside the MUT (the relative size of the MFs has been enlarged for the sake of clarity).

develop analytical tools with which to obtain a deeper understanding of the different muscle models, particularly of the Stashuk model which is one of the most widely employed, and to test the degree to which the above mentioned postulates regarding the MUFN and the MUFD hold. Special emphasis is given to identifying the sources of randomness within the Stashuk model and to studying the impact of this randomness on the MUFN and MUFD distributions. Identification of the statistical mechanisms underlying muscle models should help in the construction of new muscle architecture models in better agreement with physiological observations.

The paper begins with a formal analysis of the Stashuk model. Using the definition of the algorithm as a point of departure, we proceed to obtain the statistical distributions of the resulting MUFN and MUFD. Our analytical solutions will be compared with the results obtained from simulations, and with the results expected from an ideal muscle model which satisfies the two target properties. The advantages and disadvantages of the Stashuk model, as well as its physiological plausibility, will be discussed. Finally, we will present some conclusions regarding the statistical properties of the MUFN and MUFD of the Stashuk model.

2. Analysis of Stashuk model

Simulation of muscle architecture, MUs, and MFs must be grounded on experimental findings. The distribution of the twitch force of the MUs in a muscle is not uniform, since there are more weak MUs than strong ones [18,19]. According to Fuglevand et al. [5] the distribution of twitch forces can be approximated by an exponential law. MUFN is related to the twitch force of the MU, as the MUFN appears to be the main factor affecting the MU twitch-force [12,20–22]. Assuming a linear relationship between these two quantities, MUFN can also be approximated by an exponential law. This leads to the first desired property for a muscle architecture model, that MUFN follow an exponential law. Experimental results show that MUT size increase is related with MUFN increase, there being a strong positive correlation between the two quantities [12,13,23]. This suggests that MUT area also follows an exponential law. In addition, experimental results show very low correlation between MUFN and MUFD, supporting the hypothesis that MUT size varies as a function of MUFN, thereby keeping the MUFD relatively constant across MUs [13]. This leads to the second desired property, that MUFD remains constant for all the MUs. However, there is also evidence that suggests that MUFD distribution can depend on the MU type [23]. Hence, we can consider the assumption of a constant MUFD as an approximation of the real properties of the entire MU pool, which are incompletely understood at the moment.

Based on these assumptions, Stashuk proposed a muscle architecture model which is built up in the following steps [11]:

- Creation of the muscle cross-section (MCS): a circle centered on $(0,0)$ with radius R.
- Calculation of the radii of the N motor units, according to an exponential law, with values from R_{min} to R_{max}.
- Placement of motor unit territory centers such that they are uniformly and independently distributed inside the MCS.
- Calculation of the M muscle fiber centers, evenly placed forming a rectangular grid inside the MCS.
- For each muscle fiber, selection of the innervating motor unit. Each innervating MU is randomly taken from the set of covering motor units, i.e., those which include the fiber in their territory.

In our analysis, we will proceed in a sequential fashion, from the principles of Stashuk model to the resulting MUFN and MUFD statistical distributions: the relationships between the involved quantities are depicted in Fig. 2. In the Stashuk model we can distinguish two independent sources of randomness: the placement of the MUTs, and the recreation of the innervation. To characterize the placement of the MUTs, we will obtain the probability that a MF is covered by a certain MU (Section 2.1) taking into account that the placement of the MUs in the Stashuk model is random. We will also calculate the probability that a pair of MFs are covered by a certain pair of MUs (Section 2.2). From the random placement of all the MUTs, we will calculate the total number of MUs covering a certain MF: the overlapping (Section 2.3), which is a random variable depending on the coverage probabilities.

After the MUTs are placed, we need to characterize the innervation process. The overlapping MUs covering a certain MF are candidates for innervating the MF, and one of them is selected at random. For each MF the number of overlapping MUs may be different (Section 2.4) and so is the probability that a given MU innervates them (Section 2.5). From the point of view of the MU, the innervation is a set of Bernoulli trials, each with its own innervation probability calculated at every MF position within the MUT. We will see how the expectation and variance of the innervation process can be calculated in terms of the sample mean of both the overlapping (Section 2.6) and the innervation probability (Section 2.7), when the sampling points are the MF positions inside the MUT. Finally, this will allow us to obtain the number of MFs innervated by a MU (Section 2.8) and the density of innervated fibers per unit of area (Section 2.9).