Recruitment by size and principle of least action

W. Senn, K. Wyler, H.P. Clamann, J. Kleinle, M. Larkum,
H.-R. Lüscher, L. Müller, J. Streit, K. Vogt, T. Wannier

*Institut für Informatik und angewandte Mathematik, Universität
Bern, Neubrückstrasse 10, CH-3012 Bern, Switzerland
and
Physiologisches Institut, Universität Bern, Bühlplatz 5, CH-3012
Bern, Switzerland*

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The size principle implies that the motoneurons of a muscle pool are activated in ascending order of their sizes when that pool of motoneurons receives a common, increasing input. We suggest a simple discrete Lagrangian for an isometrically contracting skeletal muscle. Minimizing the time integral of this Lagrangian leads to recruitment of motor units according to increasing size.

1 Introduction

A skeletal muscle consists of several hundred motor units of different sizes. Due to the large number and the different properties of these units, their order of recruitment has to be specified in an suitable way. This task is autonomously performed by the motoneuron pool in the spinal cord. The pool as a whole receives input from the central nervous system or from some receptors and spreads it to its motoneurons. The recruitment order of the motoneurons as a function of the input to the pool is well known as **size principle**, see e.g. (Henneman et al., 1965):

> The recruitment of a motor unit is directly related to its size i.e. to its force-generating properties.

Thus, smaller units producing less tension are recruited at a lower level of input into the pool, larger units are recruited gradually at a higher level.

There are several physiological reasons why such a recruitment by increasing size should be good for. One of the explanation is Weber's law according to which the force of the additionally recruited motor unit should be proportional to the total muscle force at the moment of recruitment. In (Hatze, 1979) Weber's law is deduced from the point of view of minimizing the influence of noise in a biological receptor. In our previous work (Senn et al., 1995) we proposed an information theoretical approach which explains the same recruitment order. We showed that minimizing the expected error in force generation is equivalent to the maximization of information extraction from an input signal. For a layout of further physiological reasons we refer to the overview (Henneman, 1990).

In the present technical report we propose a discrete Lagrangian of a very simple muscle model neglecting heat production. We show that the principle of least action minimizing the time integral of the Lagrangian implies recruitment according to increasing size. This is an appealing approach since it makes a link to the very successful principle of least action in theoretical physics.

Our approach conceptually is similar to the minimum energy approach in (Hatze and Buys, 1977). Therein the authors consider a total energy E of the actual muscular contraction including all relevant phenomenological effects. The energy functional is of the form ' $E =$ effective work + activation heat + maintenance heat + shortening heat + dissipation heat '. There are 3 types of motor units with increasing size: slow-twitch, intermediate and fast-twitch. Each type contributes differently to the total energy E. Numerical calculations show that E is minimized during recruitment if first slow-twitch, then intermediate and last fast-twitch muscle fibers are recruited. Indeed, this ordering agrees with recruitment by size.

An apparent difference to our approach is Hatze's rich muscle model considering all possible types of energy. On one hand, of course, such a model is closer to the biology. On the other hand, the same richness prevents an analytical treatment of the model and prevents an explanation of the size principle within this model. This lack is overcome in our present work.

2   Lagrangian of a simple muscle model

We consider a slow isometric contraction of a skeletal muscle leading from the totally relaxed state to the maximally contracted state of the muscle fibers. During such an isometric contraction, heat production is neglected and the muscle energies we are considering are potential energy V and kinetic energy T of the moving filaments. Thus, we consider a conservative system with constant energy $T + V$.

Let us define the Lagrangian L of the form 'kinetic energy minus potential energy', $L = T - V$. Instead of the total muscle force $F(I)$ as function of the input I, we consider the total contraction length $C(t)$ as a function of time t. The effective muscle force F at time t is assumed to be proportional to the contraction length $C(t)$. The contraction length $C(t)$ is identified by the total number of active cross-bridges within the muscle at time t. We again assume N motor units which each contribute to this number when they are recruited (cf. Figure 1, left). The **number of active cross-bridges** of the i-th motor unit is characterized by $c_i(t - \tau_i)$, where τ_i is the time of recruitment and $c_i(\tilde{t})$, $\tilde{t} = t - \tau_i$,

$$c_i(\tilde{t}) = \begin{cases} 0 & ; \quad \tilde{t} < 0 \\ c_i = \text{const} & ; \quad \tilde{t} \geq 0 , \quad i = 1, \dots, N . \end{cases} \tag{1}$$

The motor units contribute to the **total contraction length** according to

$$C(t) \equiv C_{\tau_1, \dots, \tau_N}(t) \doteq \sum_{i=1}^{N} c_i(t - \tau_i) . \tag{2}$$

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For simplicity, let us restrict to discrete possible recruitment times τ_i of the motor units. We therefore require $\tau_i \in \{\triangle t, 2\triangle t, \ldots, N\triangle t\}$.

Now, the **potential energy** V of the muscle is assumed to be proportional to the remaining contraction length, i.e. to the total number of cross-bridges which may be activated additionally. Setting $C_{tot} \doteq \sum_{i=1}^{N} c_i$, we define

$$V \doteq k_V \cdot (C_{tot} - C)$$

with some constant $k_V > 0$. The **kinetic energy** T of the muscle is defined by

$$T \doteq \frac{k_T}{2} \cdot \left(\frac{\triangle C}{\triangle t}\right)^2 ,$$

where $k_T > 0$ is some constant and $\frac{\triangle C(t)}{\triangle t} = \frac{C(t) - C(t - \triangle t)}{\triangle t}$ is the velocity of contraction. For the **Lagrangian** $L \doteq T - V$ we get

$$L = \frac{k_T}{2} \cdot \left(\frac{\triangle C}{\triangle t}\right)^2 - k_V \cdot (C_{tot} - C) .$$

3 The principle of least action and its consequence

Given the contraction length $C(t) \equiv C_{\tau_1, \ldots, \tau_N}(t)$ as a function of $t \in (\triangle t, N\triangle t)$ we define the **action** $A(C)$ by

$$A(C_{\tau_1, \ldots, \tau_N}) \doteq \int_0^{N\triangle t} L(t)\, dt = \sum_{\tau=1}^{N} \left(\frac{k_T}{2} \left(\frac{\triangle C(\tau \triangle t)}{\triangle t}\right)^2 - k_V (C_{tot} - C(\tau \triangle t)) \right) \triangle t .$$

According to the principle of least action, the time evolution of the muscle during recruitment is determined by the minimum of the action $A(C) = \int L(C)\, dt$. The motor units are recruited in order to minimize this action $A(C_{\tau_1, \ldots, \tau_N})$ with respect to all discrete recruitment times $\tau_1, \ldots, \tau_N$ with $\tau_i \in \{\triangle t, \ldots, N\triangle t\}$.

Theorem 1 Let the motor units satisfy (1) with the constraint that $c_i \geq \frac{k_V}{k_T} N (\triangle t)^2$ and let them be enumerated such that $c_1 \leq \ldots \leq c_N$. Let $C_{\tau_1, \ldots, \tau_N}(t)$ denote the total contraction length (2) depending on possible recruitment times $\tau_i \in \{\triangle t, \ldots, N\triangle t\}$ of the motor units. *Then, the action $A(C_{\tau_1, \ldots, \tau_N})$ is minimal if and only if the motor units are recruited according to their size, i.e. if $\tau_i = i \cdot \triangle t$, $i = 1, \ldots, N$.*

The proof essentially works as follows (cf. Figure 1, right): In order to minimize the part $\int T\, dt$ in $A = \int (T - V)\, dt$, the recruitment times $\tau_i \in \{\triangle t, 2\triangle t, \ldots, N\triangle t\}$ all have to be different. If, in contrast, one had e.g. $\tau_k = \tau_{k+1}$, the contribution to $\int T\, dt$ would be $\frac{k_T}{2\triangle t}(c_k + c_{k+1})^2$. If, however, $\tau_k < \tau_{k+1}$, the contribution would only be $\frac{k_T}{2\triangle t}(c_k^2 + c_{k+1}^2)$, where the cross-term $\frac{k_T}{\triangle t} c_k c_{k+1}$ does not arise anymore. We conclude that at every time $i \cdot \triangle t$ exactly one of the motor units has to be recruited.
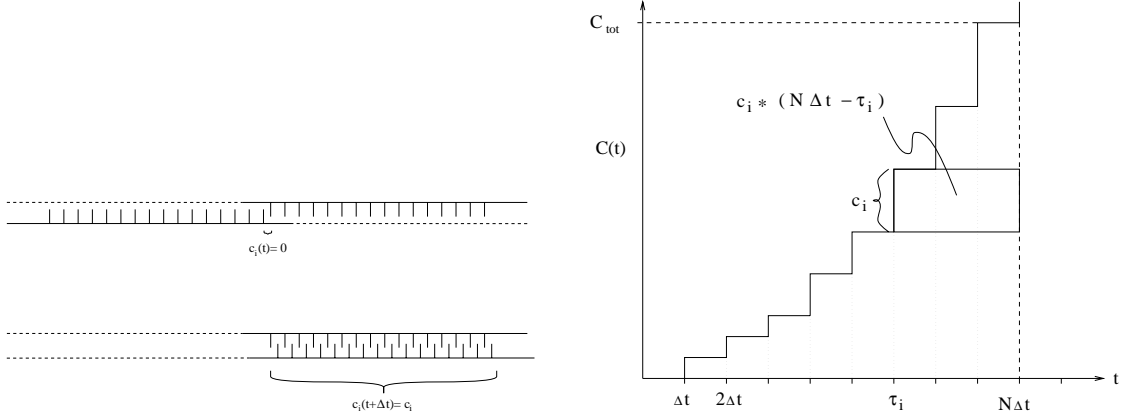
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Figure 1: Left: The contraction length c_i of motor unit i is proportional to the number of cross-bridges it may activate. Right: The total contraction length $C(t)$ as a function of t and the recruitment times τ_i. The area below the curve is corresponds to $\int(-V)\,dt$. The squares of the jump-heights are, after summation, equal to $\int T\,dt$.

Under this condition, the minimization of the part $\int(-V)\,dt$ in $A = \int(T - V)\,dt$ requires that small motor units are recruited first. Indeed, $\int(-V)\,dt = \text{const} + k_V \triangle t \sum_{i=1}^{N} c_i \cdot (N \triangle t - \tau_i)$ and this is smallest if both, $(c_1, \ldots, c_N)$ and $(\tau_1, \ldots, \tau_N)$, are ordered by size. Note that the sum in the last equation corresponds to the area below the curve in Figure 1, right. A more detailed consideration shows that the minimization of $\int T\,dt$ and $\int(-V)dt$ indeed may be treated independently (cf. Appendix).

Finally, let us assert that the this 'least action'-approach could be generalized to motor units with rate modulation as well to a continuous spectrum of possible recruitment times. However, the value of the proposed model is seen to be rather a conceptual one: Why is it the principle of least action which, apparently in physiology too, may explain existing structures? While from the mathematical point of view the answer is given, the question is, once more, raised from a philosophical point of view.

Appendix

Proof of theorem 1 We first show that the mapping $\tau : \{1, \ldots, N\} \longrightarrow \{\triangle t, \ldots, N \triangle t\}$, $i \to \tau_i$, is injective. Suppose that this would not be the case and that $\tau_i = \tau_j$ for some $i \neq j$. Now, the action $A = \int(T - V)\,dt$ could be decreased by assigning j some new value $\tilde{\tau}_j$ not lying in the image of τ. By doing this, the part $\int T\,dt$ decreases at least by $k_T \cdot \frac{c_i c_j}{\triangle t}$. On the other hand, since $|\tilde{\tau}_j - \tau_j| \leq (N-1) \cdot \triangle t$, the integral $\int V\,dt$ will increase less than $k_V \cdot N \triangle t \cdot c_j$. To cancel this defect we require

$$k_T \cdot \frac{c_i c_j}{\triangle t} \geq k_V \cdot N \triangle t \cdot c_j, \quad \text{or}, \quad c_i \geq \frac{k_V}{k_T} \cdot N(\triangle t)^2 .$$

Knowing the injectivity of τ, one is allowed to minimize $\int(-V)\,dt$ separately. This is possible since $\int T\,dt$ has the same minimal value for any injective mapping τ (namely $\min \int T\,dt = \frac{k_T}{2\triangle t}\sum_{i=1}^{N} c_i^2$). But

$$\int_0^{N\triangle t}(-V)\,dt = -k_V C_{tot} N\triangle t + k_V \triangle t \sum_{i=1}^{N} c_i \cdot (N\triangle t - \tau_i) = \text{const} - k_V \triangle t \sum_{i=1}^{N} c_i \tau_i \ ,$$

and $\sum_{i=1}^{N} c_i \tau_i$ with $c_1 \leq \ldots \leq c_N$ takes the maximal value when the mapping τ is chosen to be $\tau_i = i \cdot \triangle t$. $\qquad \square$

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