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Modeling the neural control and biomechanics of locomotion

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A computer-assisted general neuro-mechanical model of limb movements is described. Different kinds of movements, for instance leg movements as walking and arm and hand movements as reaching an object are very important activities in everyday life. Neural control is responsible for the coordinated activities of muscular and skeletal structures. Here a simple neuro-mechanical model is presented to mimic experimentally measured limb movements by simulated motoneuron firing rates. The development of this kind of model applies methods originated from different fields as biology, mathematics and informatics.

1. Introduction

Limb movements are controlled by motor commands of the central nervous system (CNS). These commands descend to spinal motoneurons and these motoneurons stimulate muscles. Consequently the muscles exert forces and generate torques in the joints of a limb. The torques generated by muscle forces and the external forces may rotate the joints and move the limb and lead to motor behaviors like locomotion.

The proper execution of limb movements requires well coordinated interaction between neural, muscular and skeletal structures (Gielen et al. 1987, Zajac 1989, Zajac et al. 1990). Thus, models of such movements should incorporate factors from the molecular level to the control of entire limbs. Modeling techniques are needed to obtain a deeper understanding of how motoneuron activity drives muscle contraction, joint rotation, limb movement and locomotion. The different parts of the system are widely studied. Our work with Dr, Kerry Walton and Prof. Rodolfo Llinas at the New York University aimed to integrate the different levels and we raised the concept of an integrated model for limb movements control. The model generates muscle forces and joint rotations as a function of activation signals from motoneuron pools.

The multilevel control of limb movements and locomotion is known and has already been well studied ((Szekely 1989, Szekely 2001)). The spinal cord with its motoneuron pools is an important level which is capable of sending impulses to muscle fibers to innervate skeletal muscles. We aim to relate such motoneuron pool activities to limb movement patterns while considering the level of the activated muscles and the rotated limb segments.

There is a considerable international literature on the modeling of neuro-musculo-skeletal systems that integrate neural control of movements, muscle activities and joint rotations. The modeling approaches range from mathematical models of motor control in humans [Zang and Sejnowski 1999] and from the biomechanics of walking in humans [Alexander 1992], to the control of robot arms by neuronal signals [Chapin et.al. 1999] and to the construction of walking robots [Beer et al, 1998]. Models are also applied in research related to functional electrical stimulation of muscles and in developing neuroprostheses for paralised patients [Donoghue et.al 1998, Nathan and Tavi 1990, Riener 1999].

At the molecular level muscle activity has been studied by the famous Hungarian born nobel laurate biologist Abert Szentgyorgyi, he studied submolecular processes and suggested to descend from the level of molecules to those of electrones (Szentgyorgyi 1958). Recently the change of calcium concentration inside the muscle fiber as a response to variable neural stimulation frequencies [Otazu et. al. 2001] has been modeled. The dependence of movement performance on the stimulation pattern for different multi-joint limb positions has also been modeled [Van Soest et. al. 1994] and models for reflex mechanisms have been elaborated [Gielen et.al. 1987]. The behavior of single-joint systems has been modeled by applying optimisation criteria [Hogan 1984]. When these models are generalized to multi-joint movements [Flash and Hogan 1985,], the problem of redundancy or overcompleteness becomes an important factor. Redundancy in this context means that the number of muscles and joints participating in the movement are higher than necessary to execute an intended movement and there are many combinations of muscle activities and joint rotations to execute the given motor task.

At the level of the central nervous system, the role of the cerebellum in motor control is well known and has been widely modeled [Arbib, Erdi, Szentagothai 1998, Llinas and Wels 1993]. The activity of neurones in the motor cortex has been also studied. Planning and execution of voluntary

limb movements were represented by the activity of a set of neurones and muscles and as a result, by the orchestrated rotations of joints [Bizzi et.al.1991].

Besides physiological properties, the influence of the physical environment and external forces also play an important role in mammalian motor function.

2. Our modeling method

2.1 Direct model

Angular changes in the joints must be computed knowing the firing rates of the muscles' motoneuron pool. This is called a direct problem.

The model considers the initial geometry of an n-joint limb, the intersegmental joint angles, the sites of muscle attachments and the masses of the limb segments. A uniform distribution of mass is assumed in the limb segments. We assume that the limb moves on a plane and the limb segments are represented as lines connecting neighboring joints (Figure 1). A muscle is represented by its midline (action line) that connects its attachment sites in two segments via a given point near the spanned joint. In the case of monoarticular flexor muscles this "pulley point" is the closest point of the particular muscle-tendon system to the rotational center of the joint. The geometry of the muscles is provided as two lines that originate on the proximal and distal sites of attachment and are connected at the pulley point. (Figure 2.)

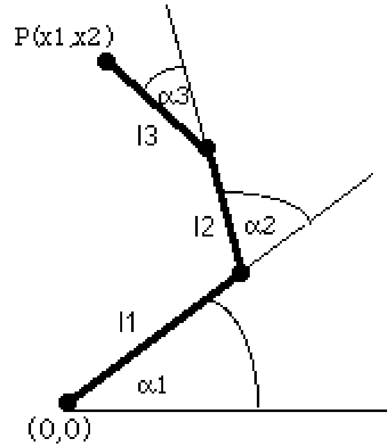

Figure 1. Three-joint limb in a plane. The joint angles (α_1, α_2, α_3) and limb segment lengths (l_1, l_2, l_3) determine the position of the endpoint of the limb: P(x1,x2).

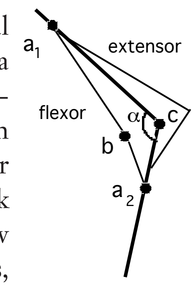

Figure 2. Graphical representation of a single-joint musculo-skeletal system with a flexor-extensor muscle pair. Thick and thin lines show bones and muscles, respectively. As presented for the flexor, each muscle has a proximal (a_1) and distal (a_2) insertion point and a pulley point (b) close to the rotational center of the joint (c).

The motor command for each muscle is described as a sequence of stimulation pulses originating from a motoneuron pool.

The output of the model is angular

motion in the joints. This output is referred to as the generated "movement pattern" and will be represented graphically showing the angular changes in the joints.

The frequency of the stimulation pulses (discharge rates of motoneuron pools) is the most important variable in the model. We investigated how the frequencies of the discharge rates of motorneuron pools of flexor and extensor muscles are associated with certain movement patterns. Changing this frequency, the movement can be artificially controlled.

Mechanical properties of the muscles are given by biomechanical characteristics. Such characteristics are the relationship between muscle force and muscle length (Fig. 2.) and the relationship between muscle force and neural stimulation frequency (Fig. 3.)

The force-length functions applied in this model represent how the total muscle force relates to the whole muscle-length (Enoka 1988). The shape of this function varies among muscles. We applied two hypothetical F-L relations in the model, using the following parabolic functions:

$F1(L)=$
$(-4*Fmax*((L-Lmin)(Lmax-Lmin)-1/2)^2+2)/2$
(a)

$F1(L)=-$
$4*Fmax*((L-Lmin)(Lmax-Lmin)-1/2)^2+1$
(b)

where *Lmin* is the shortest muscle length and *Lmax* is the maximum stretched length of the muscle, *Fmax* is the maximal force.

The first relationship (a) reaches its maximum value at resting length and is 50% of the maximal force at the minimal and maximal muscle length (Fig.3 solid line). In the second relationship (b) the force reaches its maximum about midway between the minimal and maximal muscle length but it decreases close to zero near the minimal and maximal lengths (Fig 3 broken line).

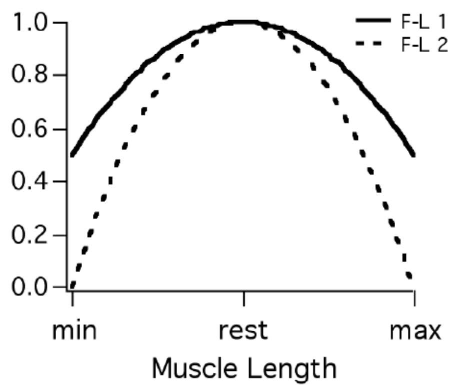

Figure 3. Force-length relationship: The active force a muscle can exert as a function of muscle length.

The force-frequency relationships of the muscles are approximated by monotone increasing functions with zero value at stimulation frequency of 0 Hz and maximal value *Fmax* at the frequency *sat* where the force saturates. The force-frequency relation applied in the model:

$F2(f) = \sin(\varpi\pi(f/sat-1/2))+1 \quad \text{if } 0<f<sat;$
(1)

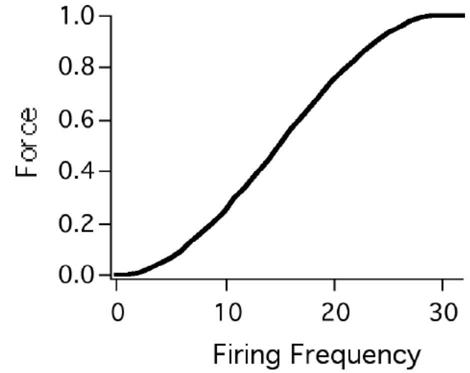

Figure 4. Force-frequency relation. The active force a muscle can exert as a function of muscle length.

The velocity of muscle shortening is given in the relationship that describes how the velocity of muscle contraction depends on muscle force.

A load parameter that simulates the effect of body weight on limb movements is also included in the model.

The motor command for each muscle is modeled as a sequence of stimulation pulses. In each time interval, the command for each muscle is a single element that is the firing rate of the muscle's motoneuron pool. Using this command, the model generates angular motions in the joints.

The total movement time is partitioned into intervals of Δt and the stimulation frequency *f* is given in each time interval. First, the active muscle force *Fa* is computed from the values of the force-frequency and force-length functions at the actual frequency *f* and muscle length *L*. The muscle length is assumed to be constant during the short time interval Δt. If we know the muscle maximal shortening velocity *vmax* and the actual shortening velocity *v*, then according to the Hill equation (Hill 1938) the muscle force may be computed as:

$Fa= F1(L)*F2(f)*a*(vmax-v)/(a*vmax+v);$

If the muscle length increases during the movement then the model generates a passive force. If the muscle length exceeds *Lp* then a force *Fp*, is generated that is approximated by the next quadratic function of muscle length *L*.

$Fp(L)=$
$4*(L\tilde{}Lp)2, \text{ if } Lp<L<Lmax \text{ and } Fs(L)=0 \text{ if } L\tilde{}\ Lp$

This function is shown at Fig 3B. Its value is 0 if the muscle length is smaller than the optimal length and it shows a quadratic increase if the length exceeds the optimal length. The total muscle force is the sum of the active and passive muscle forces:

$F = Fa + Fp$

This force generates torque on the joint. To relate forces to angular motions we must know the inertial properties of the rotated body parts. The body segments are modeled by straight lines assuming that their center of mass is located in the middle of the line. The moment of inertia of such a body segment is computed as $m*1/12(h^2+r^2)$ where *r* is the distance between the center of mass and the rotational center, *h* is the length, and *m* is the mass of the segment. The inertia of the body part that is rotated by a given joint is the inertia of all of the rotated body segments with respect to the given joint.

The angular acceleration *Am* caused by a muscle force is computed as the force *F* multiplied by the lever arm *R* divided by the moment of inertia *I*:

Am=F*R/ I

In addition to the muscle force a gravitational force causes torque in the joint. This latter torque *Tg* is the sum of the gravitational torques of the body segments that are rotated by the joint. The angular acceleration induced by the gravitational force is computed as:

Ag=Tg / I.

The total angular acceleration is the sum of the two accelerations:

A= Am+Ag = (F*R+Tg)/ I

Applying integral kinematics (Zatsiorsky 1998), the angular displacement caused by the muscle activities in a given gravitational environment is computed from the total angular acceleration by integrating it twice over time.

Thus the model computes the joint angle for a discrete point of time ($t + \Delta t$), then updates the configuration of the limb (muscle length, joint angles) and repeats this procedure for the next discrete points of time $t + 2^* \Delta t$, $t + 3^* \Delta t$. This computation provides the time course of the joint angle.

If multijoint systems are considered then the motor command for each joint rotation is computed separately by the algorithm summarized above.

2.2 Inverse model

Iterative application of the above model offers a tool to find a motor command to produce desired angular changes. Since this kind of iteration is time consuming and may lead to a solution by chance, we were looking for an efficient way to find an appropriate stimulation pattern. The problem is that an infinity number of different simulation patterns may produce the same angular changes. If a particular stimulation pattern has to be derived from a given desired kinematic movement pattern (angular changes), then we face an inverse problem. The issue is that there are many different muscle activity combinations that will produce the same angular motion. The present inverse model generates an angular motion in such a way that at any instant, one member of each muscle pair (either the flexor or the extensor) is passive while the other muscle may do work. This assumption leads to an angular movement that requires minimal total work from the muscles.

If the function $\alpha(t)$ that gives the time course of angular displacement in a joint is differentiated twice then the time course of angular acceleration $A(t)$ is provided. We apply numerical differentiation to approximate the angular acceleration for discrete time intervals (t, $t + \Delta t$). Applying the above given relationship of the force, lever arm, and inertia gives the total muscle force that generates the required rotation in the joint:

F= (A*I -Tg) / R

After this total muscle force is determined, the active muscle force is computed as follows:

F1 = (F - Fp) * (a * vmax + v) / (F2(L)*a*(vmax-v))

Where *Fp* is the passive force, *F2(L)* is the function of the force-length relation, *v* is the shortening velocity of the muscle, *vmax* is the maximal shortening velocity, *a* is constant (coefficient of shortening heat) and *F1* gives the normalized active force.

Finally, the needed stimulation frequency *f* is computed by applying the inverse of the function that gives the force-frequency relationship. The value of the inverse function at *F1* gives the stimulation frequency that produces the required angular change in the current time interval, Δt. For instance, using the function that gives the above written Force-frequency relationship, we obtain the following function to compute the stimulation frequency:

f(F1)= (arcsin(F1/Fmax-1)/π+1/2) *sat

where *Fmax* is the maximal muscle force and *sat* is the frequency at which the force saturates.

The model computes a sequence of frequency values that generates the required angular trajectory. First, it is determined for a given angular change in a time interval of Δt. Then, the configuration of the limb is updated and the new intersegmental joint angles are used to compute the motor command for the next time interval.

3. Result

Here we present an example for the application of the model. We applied the model for the simulation of walking in the rat. The joint angular changes required as input parameters for the inverse model were taken from experimental measurements. The masses of the limb segments were calculated as percentages of the whole body mass. To study the role of flexors and extensors in the knee and ankle joints we used one theoretically defined flexor and one extensor for each joint. For each muscle the maximal available force was 300N. The maximal shortening velocity was 0.1m/s.

The measured angular changes in the knee and ankle joints during one step and the corresponding flexor and extensor firing rates computed by the inverse model are shown in Fig. 5. The force-length relationship that is used to simulate this step is given by (b). During the stance phase the extensor muscles are activated to work against gravity because the weight of the animal is loaded on the leg. The extensor motoneuron firing rates show a slow increase followed by a decrease during this phase. At foot lift a sudden increase in flexor motoneuron firing rate ensures the required impulse for joint flexion then the flexor motoneuron firing rate slowly decreases as the joints are flexed. At the end of the swing phase the extensors are activated and the limb is extended with a small flexion before foot contact. These activity patterns ensures the use of minimal total work.

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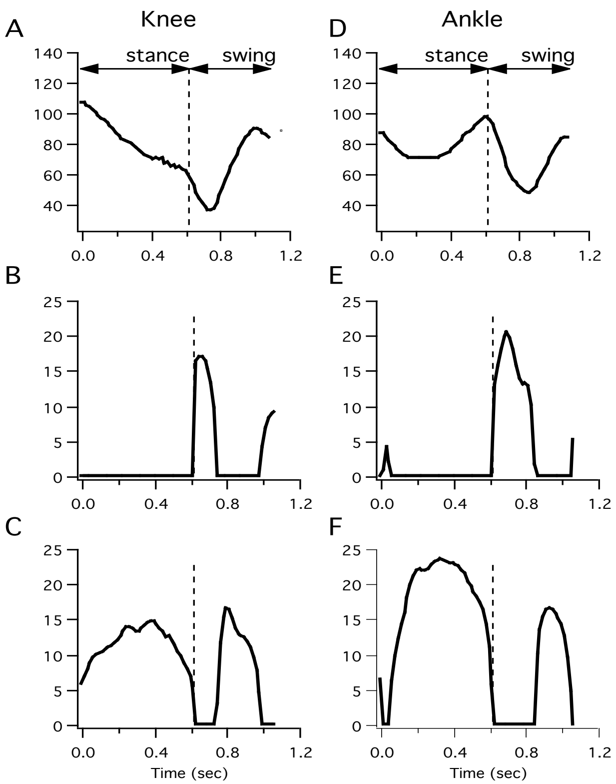

Figure 5. Measured knee joint angle (A) and predicted knee flexor (B) and knee extensor (**C**) motoneuron pool activity during the step. Measured ankle joint (D) and predicted ankle flexor (E) and ankle extensor (F) activities. Note that onset of flexor activity corresponds to the beginning of the swing phase.

As an example to determinate the sensitivity of the model to model parameters we present the effect of change on the force-length relation here. Knowing the experimentally measured time course of the joint angles, we computed firing frequencies assuming different force-length relationships. First we applied the F-L relation (a) to simulate individual steps of the walking rats (Fig. 6 solid lines). Then we simulated the same steps applying the F-L relation (b). (Fig. 6, broken lines). We found that using relation (*a*), the required discharge rates of the motoneuron pools were smaller than using (b). This is presented in Figure 6. for the flexor and extensor muscles for the knee and ankle joint.

Figure 6. Effect of force-length relationship on predicted motoneuron firing frequency. A: Two force-length relationships. Comparison of predicted knee flexor (**B**) and extensor (**C**) motoneuron pool activity for F-L relationship *a* (solid line) and *b* (broken line). D&E Same as B&C for the ankle. Higher frequency is predicted for the same joint movement when the force is zero at minimum and maximum muscle length. From Laczko J., Walton K., Llinas R.: A [54] neuro - mechanical transducer model for controlling joint rotations and limb movements. Clinical Neuroscience, In Press

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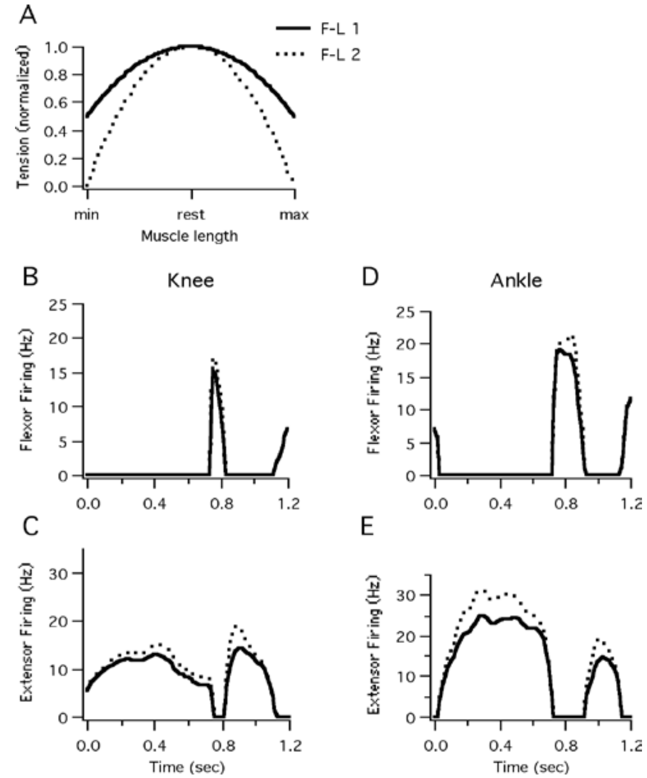

The application of the model to hindlimb movement of the rat during walking has previously been presented in abstract form (Laczko et al. 2003, Laczko et al. 2004) and in a detailed form in the Clinical Neuroscience (Neurologiai Szemle) in Press, in Budapest.

3. Conclusion and perspectives

We initiated a modeling technique for studying limb movement control.

Neural control of limb movements is much more sophisticated involving fine interaction of excitatory and inhibitory spinal neuronal activities and reflexes. The co-contarction of the participating muscles and the synergy of joint rotations must also be considered in the modeling methods. We extend our model taking into account these factors. Based on the presented model we plan common American-Hungarian research projects.

The model can generally be applied for mammalian locomotion and specifically for human locomotion and it provides a research tool that can be applied in medical rehabilitation. The output of the model can be compared to experimentally measured angular changes and torques in the joints. Thus the model may predict experimental outcomes in research and the effect of therapeutic techniques on medical application. This kind of research relates to the control of devices that help to replace movement abilities of people with motor dysfunction. One particular application is the functional electrical stimulation. This approach helps to develop control algorithms for neuro-prosthetic devices for spinal cord injured patients: surface electrodes are placed on the skin above the muscles of the paralised limb and these electrodes may stimulate motoneurons of the muscles by the computed stimulation pattern. Mathematical modeling and computer simulation helps to choose the required stimulation pattern for a desired limb movement. Before the stimulation pattern is applied in reality the effect of the stimulation may be studied using the computer model. The model helps to indentify movement parameters and biomechanical characteristics like the presented muscle force - muscle length relationship or other intrinsic properties that can not be measured experimentally.

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Researching Literature in Minnesota
How Updike's Fiction Meets Life in the Upper Midwest

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Abstract

My paper summarizes my experiences in the United States during my Fulbright grant from a double perspective. I first look at my professional achievements during the nine months spent at the University of Minnesota, delineating the framework of the project I am working on and assessing the progress I made by the end of the grant. Then I write about my personal and non-academic experiences: the way of life I became part of, the places and people I got to know and met, and the manifold ways in which I feel I benefited from this opportunity. My paper is illustrated by photos I took during the grant period.

1. Academic Achievements

I applied for the Fulbright Research Grant in the hope that a nine-month period spent at an American research university would help me progress considerably with my dissertation and give me the chance to gather material for finishing the paper later, possibly after the end of the grant period. As for my host university, I chose the University of Minnesota for two reasons. Firstly, it has a huge research library (with more than 5 million volumes in total) including an exhaustive collection in humanities and literature. Secondly, my would-be supervisor, Professor Kent Bales,