

Optimization-Based Models of Muscle Coordination

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PRILUTSKY, B.I., and V.M. ZATSIORSKY. Optimization-based models of muscle coordination. *Exerc. Sport Sci. Rev.*, Vol. 30, No. 1, pp 32–38, 2002. *Optimization-based models may provide reasonably accurate estimates of activation and force patterns of individual muscles in selected well-learned tasks with submaximal efforts. Such optimization criteria as minimum energy expenditure, minimum muscle fatigue, and minimum sense of effort seem most promising.* **Keywords:** muscle activation patterns, motor skills, metabolic energy expenditure, fatigue, sense of effort

INTRODUCTION

The human motor system has many kinematic degrees of freedom (DoF) and it has more muscles than DoF—it is said to be *redundant*. Due to this redundancy, a motor task, for instance walking, can be performed in different ways and numerous combinations of muscle forces can generate the same joint torques. However, the muscle activation patterns (MAP) of different people performing the same well-learned task are very similar. This consistency seems to indicate that in the control of individual muscle forces, the central nervous system (CNS) uses specific principles that are the same in various people. The quest for these control principles is called the *force distribution problem*. It has been hypothesized that the MAP selected by the CNS are *optimal* with respect to some unknown criteria (*i.e.*, the minimum or maximum of a certain objective function, for example, energy expenditure). Optimization-based models have attracted interest from many researchers.

In this article, we first consider the musculoskeletal redundancy. Secondly, we review several optimization-based models applied to well-learned tasks with submaximum efforts. Thirdly, we compare the predicted and measured MAP. Finally, we discuss validation and interpretation of the optimization results.

MUSCULOSKELETAL REDUNDANCY

The human body has 244 kinematic DoF (9). This number greatly exceeds six DoF, which are required to position a body segment in a desired place with a desired orientation. Because of the redundant number of DoF, there are an infinite number of ways of performing a motor task. Despite this kinematic redundancy, apparently, the motor control system selects a limited number of them to accomplish the desired motor tasks.

A conservative estimate of the number of skeletal muscles in the human body is 630. Thus, on average, one DoF is controlled by 2.6 muscles ($=630/244$). Because at least two muscles are available to produce a joint moment about one given DoF, there are an infinite number of muscle force combinations to produce a required joint moment. For example, forces F_1 and F_2 of two antagonist muscles can be combined in various ways to contribute to a joint moment M : $M = d_1 \cdot F_1 - d_2 \cdot F_2$, where d_1 and d_2 are known moment arms of muscle forces F_1 and F_2 , respectively. This equation has an infinite number of solutions.

In addition, muscles (or their parts) typically produce moments about several DoF. In the human upper and lower extremities, each muscle or muscle part creates moments about four DoF on average (9). Commonly, when a muscle generates a moment with respect to a particular DoF (*primary moment*) it also creates additional undesirable moments about other DoF (*secondary moments*), which should be compensated by other muscles that in turn create undesirable moments about other DoF (*tertiary moments*) and so on. Despite these complexities, animals and people activate muscles in a coordinated manner.

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Accepted for publication: September 26, 2001.

OPTIMIZATION-BASED MODELS

Problem Formulation and Applications

The fact that the musculoskeletal system is redundant and that apparently only a limited number of MAP are used in skilled tasks has led to the development of optimization-based models for estimating activation and forces of individual muscles. The main assumption in these models is that the MAP are selected in such a way as to optimize a specific objective function or a combination of objective functions (7,14). There are two types of optimization-based models: static and dynamic.

In static models, it is assumed that the MAP at any movement instant are independent of those at other instants. In other words, the value of the objective function does not depend on time explicitly. In static optimization, muscle activation and/or forces are calculated for each time instant of a movement. For example, optimal forces of nine muscles in a two-dimensional, four-segment model of the leg (Fig. 1) can be found by solving the following static optimization problem for each time instant:

$$\text{minimize cost function } Z = f(F_1, F_2, \dots, F_9), \quad (1)$$

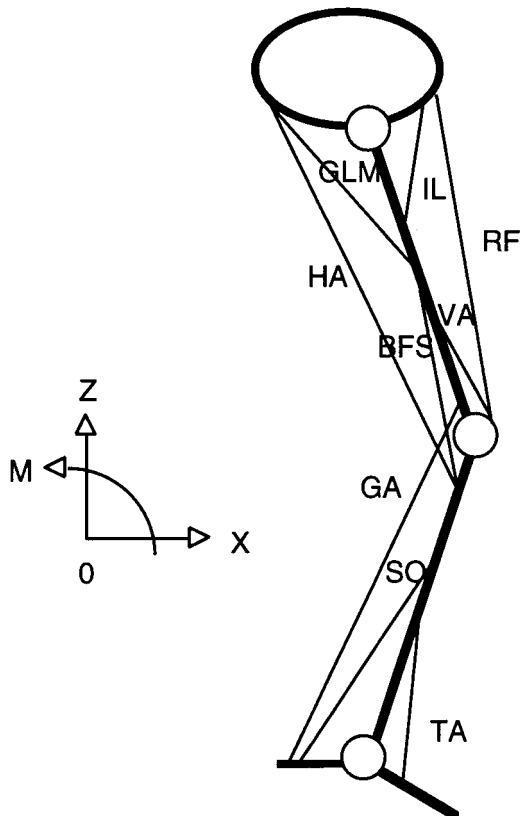


Figure 1. A two-dimensional model of the human leg. It has three DoF and is controlled by nine muscles. Therefore, the moments (M) at the joints can be produced by an infinite number of muscle force combinations. TA is tibialis anterior, SO is soleus, GA is gastrocnemius, VA is vastii, RF is rectus femoris, BFS is short head of biceps femoris, HA is two-joint hamstrings, GLM is gluteus maximus, and IL is iliacus. For review of model parameters (segment inertial parameters, muscle moment arms, $PCSA_i$, muscle composition, F_{max} , V_{max}) and their values (10).

subject to the equality constraints

$$M_1 = d_{11} \cdot F_1 - d_{12} \cdot F_2 - d_{13} \cdot F_3$$

$$M_2 = -d_{23} \cdot F_2 + d_{24} \cdot F_4 + d_{25} \cdot F_5 - d_{26} \cdot F_6 - d_{27} \cdot F_7$$

$$M_3 = -d_{37} \cdot F_7 + d_{38} \cdot F_8 - d_{39} \cdot F_9 \quad (2)$$

and the inequality constraints

$$F_1, F_2, \dots, F_9 \geq 0, \quad (3)$$

where M_1 , M_2 , and M_3 are the resultant moments at the ankle, knee, and hip joints, respectively, and d_{ji} are the moment arms of the i -th muscle with respect to the j -th joint (the moment arms are assumed to be known).

A variety of optimization criteria have been used in the literature to solve the above problem (for example (7,14)). Some of the criteria have been selected arbitrarily, whereas others have been based on various physiological reasons. Among the latter are versions of criteria of minimum muscle fatigue, minimum muscle stress, and minimum metabolic energy expenditure. Two most frequently used versions of minimum muscle fatigue criteria, Z_1 and Z_2 , are formulated as follows, first (5):

$$Z_1 = \max_i \{1/T_i\} \rightarrow \min, i = 1, \dots, 9 \quad (4)$$

where Z_1 is muscle fatigue function; $T_i = a_i \cdot (F_i/F_{i \max} \cdot 100)^{p_i}$ is endurance time of the i -th muscle; $a_i = \exp(3.48 + 0.169 \cdot S_i)$ and $p_i = -0.25 - 0.036 \cdot S_i$ are the functions of the percentage of slow-twitch fibers in the i -th muscle, S_i , derived from experiments on cat muscles (5); and $F_{i \max}$ is maximum isometric force of the i -th muscle. The maximum isometric force of each muscle can be estimated as $F_{i \max} = K \cdot PCSA_i$, where $K = 40 \text{ N/cm}^2$ on average.

The second formulation of fatigue criterion is (4):

$$Z_2 = \sum_{i=1}^9 (F_i/PCSA_i)^p \rightarrow \min, p = 2, 3, 4 \quad (5)$$

where Z_2 is a muscle fatigue function; $PCSA_i$ is the physiological cross-sectional area of the i -th muscle; and constant p was derived from the experimentally obtained relationship between muscle stress ($F/PCSA$) and endurance time (T) of human muscles ($p = 3$ on average) (for details see (4)). Mathematically, criterion Z_2 is equivalent to minimizing a norm $N = [\sum (F_i/PCSA_i)^p]^{1/p}$ of a vector $[F_1/PCSA_1, F_2/PCSA_2, \dots, F_9/PCSA_9]$. When the value of p approaches infinity, the above norm becomes the maximum norm, and its optimum solution approaches the equal distribution of stresses among the involved muscles in a one-DOF case (see, for example, (4)). This property of polynomial criterion Z_2 led to the development of the min/max optimization criterion, $\max\{F_i/PCSA_i\} \rightarrow \min$, which was first presented in a bound formulation (2):

$$Z_3 = \sigma \rightarrow \min \quad (6)$$

where $\sigma > F_i/PCSA_i$ ($i = 1, \dots, 9$) is the upper bound for stresses of all muscles. When the power p in criterion Z_2 approaches infinity, the solutions of these criteria converge

to the solution of criterion Z_3 (13). The formulations of the above criteria suggest that muscle stress and muscle fatigue criteria are related.

Criteria from another group minimize energy expenditure. Consider, for example, a minimum metabolic cost criterion suggested by Alexander (1) and examined in (10):

$$Z_4 = \sum_{i=1}^9 a_i^p \cdot F_{i \max} \cdot v_{i \max} \cdot \Phi[v_i/v_{i \max}] \rightarrow \min, p = 1, 2, \quad (7)$$

where Z_4 is the metabolic rate of the i -th muscle and function Φ determines the metabolic cost; $F_{i \max}$ and $v_{i \max}$ are known maximum force and maximum velocity of the i -th muscle, respectively; v_i is instantaneous velocity of the i -th muscle; and a_i ($0 \leq a_i \leq 1$) is the unknown normalized activation of the i -th muscle, sought by minimizing criterion Z_4 . Moment constraints (equation 2) for this criterion take into account the muscle force-velocity properties (for details, see (1) and (10)).

Static optimization models are especially well suited for estimating activation and forces of individual muscles in static tasks, e.g., exerting external forces in different directions. The major shortcomings of applying static optimization models to dynamic tasks include the following (3,7): (i) in many dynamic tasks, the dynamics of the skeleton and muscles at any time instant are likely to depend on the dynamics during other time instances (e.g., a stretch of the muscle-tendon unit in one movement phase can modify motor performance in the next phase) and (ii) static optimization models typically cannot predict kinematics and dynamics of movement when only initial and/or final states of the system are known.

Dynamic optimization-based models can overcome these limitations (3,7). Dynamic optimization problems are solved only once for the entire movement time by minimizing a functional, the value of which often depends on the time-dependent system state variables (e.g., joint angles and their time derivatives), the control variables (e.g., muscles activation), and values of the state variables and their time derivatives at the initial and/or final movement instants. The solution of the dynamic optimization problem, i.e., optimal MAP, must satisfy the differential constraints, which include the equations of skeletal motion and the equations describing muscle activation and muscle-tendon dynamics. When optimal activation patterns are found, muscle forces, joint moments, and the kinematics of the system can be obtained. Among limitations of dynamic optimization-based models, probably the most important is that these models require the knowledge of a large number of model parameters describing a substantially more sophisticated model of muscle contraction dynamics. The exact values of these parameters in humans are essentially unknown. In dynamic optimization, muscle stress, muscle fatigue, metabolic energy expenditure, movement performance (time, speed, height), or combinations of those can be optimized.

Because of the relative simplicity of static optimization models, they have been used more often than dynamic models to predict patterns of muscle activation and forces in

dynamic tasks (for review, see (10,14)). Therefore in this review, we consider mostly static optimization models.

In the above formulations of static and dynamic optimization problems it was assumed that muscles are controlled independently. In reality, this may not be the case. To explain this idea, let us compare the muscles with the hand fingers. When people are asked to generate force using one finger, other fingers also involuntarily produce force. This phenomenon is called *enslaving* (15). It is not known whether the enslaving exists at the level of muscle control. If it does, the enslaving may explain some nonoptimal patterns of muscle activity. Present optimization-based models do not consider possible enslaving.

COMPARING PREDICTIONS WITH MEASUREMENTS

At present, subject-specific values of muscle activation and forces cannot be predicted by optimization-based models because many of subject-specific model parameters are not known. The optimization-based models, however, can predict nominal patterns of muscles activation in a typical subject with typical model parameters in some motor tasks (3,7,10,14). Examples of reasonably good correspondence between the measured MAP and MAP predicted by criteria Z_2 , Z_3 , and Z_4 in human walking and cycling are shown in Figures 2 and 3. In these tasks, the Pearson correlation coefficients calculated between predicted and measured patterns are typically between 0.6 and 0.9 for the majority of muscles. However, force predictions and EMG for some muscles have dissimilar patterns (rectus femoris in walking, Fig. 2; soleus and gluteus maximus patterns predicted by criterion Z_4/p ($N = 1$) in cycling, Fig. 3).

Three main obstacles make the distribution problem difficult to solve: 1) incompleteness of the models, 2) insufficient accuracy of the model parameters, and 3) difficulty in validating the models.

1) Muscle forces creating moments about one DoF also induce mechanical effects about other DoF. Ideally, optimization models should be applied to the entire body in three-dimensional space. In reality, the majority of the developed models target either a single joint or a single extremity in two-dimensional space (for rare exceptions, see (7) and (14)). Hence, numerous secondary and tertiary moments are neglected. For instance, the trunk is not included in the model presented in Figure 1 and, hence, the effects of the hip joint moments on the upper part of the body are disregarded. The inclusion of additional DoF and body parts increases the model's complexity. Most importantly, including many DoF increases the number of assumptions that have to be made and, hence, may decrease rather than increase the accuracy of the prediction.

2) As seen from the formulation of optimization problem (1–7), there are many model parameters ($d_{j,i}$, $PCSA_i$, $F_{i \max}$, $v_{i \max}$) and input variables (M_j , v_i) that need to be estimated to calculate muscle forces or activation. A sensitivity analysis of the optimization-based models to errors in the model and input parameters suggests that values of muscle forces may be very sensitive to variation in muscle moment arms, physiological cross-sectional area, muscle fiber composition, and joint moments (for review, see (10)). Therefore, it is gener-

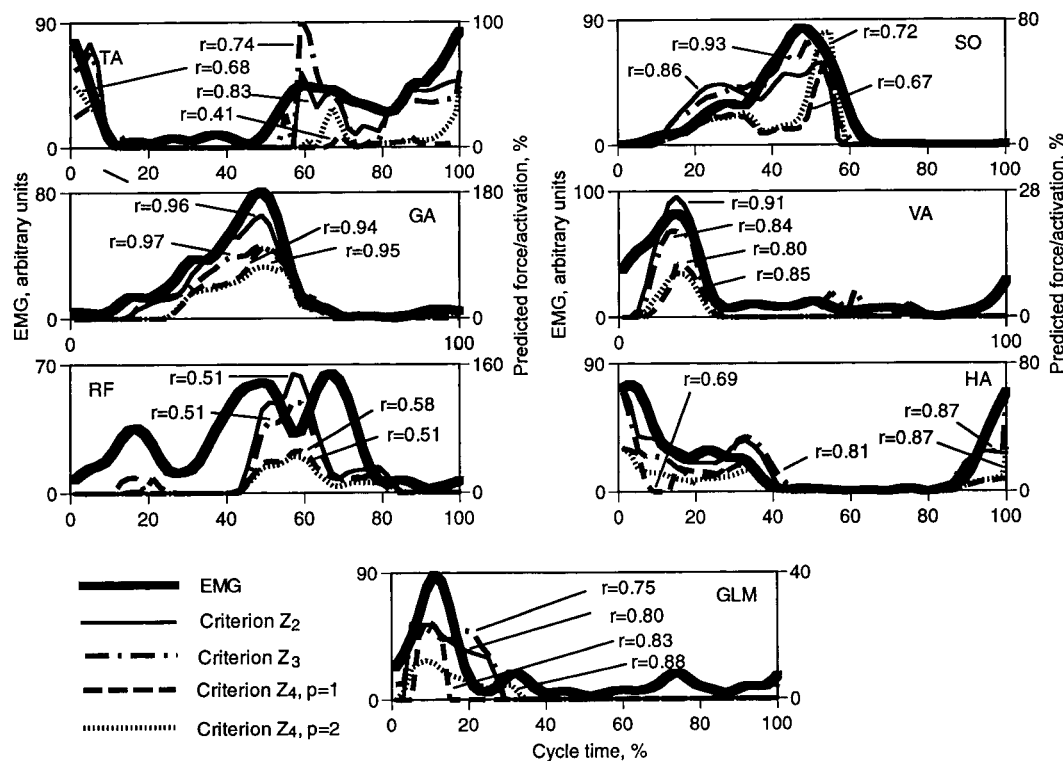


Figure 2. Recorded EMG linear envelopes (EMG) and muscle forces and activation predicted by optimizing minimum fatigue criterion Z_2 , min/max criterion Z_3 , and minimum metabolic cost criteria (Z_4 , $p = 1$ and $p = 2$) during cycle of walking. EMG was obtained from 10 subjects walking on a treadmill with a speed of $1.82 \text{ m} \cdot \text{s}^{-1}$, and muscle forces and activation were calculated from kinematics and ground reaction forces of one typical subject during over ground walking at a similar speed (10). The EMG linear envelopes were normalized to the EMG peak in the cycle and shifted in time by 40 ms to account for the delay between the EMG and the joint moments. The Pearson correlation coefficients (r) calculated between the EMG and predicted force/activation patterns are typically between 0.7 and 0.9 (exception: the RF muscle). The best performance is demonstrated by the minimum fatigue criterion Z_2 ; the linear version of the metabolic cost criterion (Z_4 , $p = 1$) has typically the worst performance. [Adapted from Prilutsky, B.I., "Coordination of two- and one-joint muscles: functional consequences and implications for motor control," *Motor Control* 4:18, 2000, and from Prilutsky, B.I., "Muscle coordination: the discussion continues," *Motor Control*, 4:103, 2000. Copyright © 2000 Human Kinetics Publishers, Inc. Used with permission.]

ally difficult to compare absolute values of predicted and measured muscle forces. However, published reports on sensitivity analyses suggest that, in contrast to force magnitudes, time patterns of predicted forces are less sensitive to errors in model parameters.

Another complication in the comparison of the predicted and measured muscle forces and activation is the influence of the muscle force-length-velocity properties on the actual muscle force output. The formulation of the static optimization problem presented above does not account for many of these properties (however they can be accounted for in static optimization to a certain extent; see, for example (3)). In some tasks, however, the force-length-velocity properties seem not to significantly affect predictions of the actual force output. For example, measured forces of the cat soleus, gastrocnemius, and plantaris during walking and trotting at different speeds were rather successfully predicted by static optimization and criterion Z_1 (Fig. 4; (12)) without accounting for the force-length-velocity properties of the muscles. In human walking, including the muscle force-length-velocity properties into the static optimization problem did not substantially change the obtained optimal solution (3).

3) In human studies it is difficult to measure forces in individual muscles. Therefore, predicted on/off timing or time histories of muscle forces are often compared against the

on/off timing or time histories of EMG linear envelopes. The comparison of time histories seems more revealing, because predicted forces and EMG can have similar on/off timing but different time histories. It should be noted that predicted forces and EMG patterns can be compared if the force-EMG relation is defined (e.g., linear). This seems to be the case in a number of isometric tasks and some dynamic tasks like load lifting, cycling, and walking in humans (3,10). Thus, these activities are convenient for the application and evaluation of static optimization methods.

Another experimental paradigm, which seems free of the above-mentioned limitations, is direct measurements of finger forces in multifinger tasks. The model of hand fingers has been used to study motor redundancy (15). Optimal finger forces were calculated by solving the following optimization problem:

Minimize

$$Z_5 = \left(\sum_i^n \left(\frac{F_i}{F_{mi}} \right)^p \right)^{1/p} \quad (8)$$

subject to constraint function:

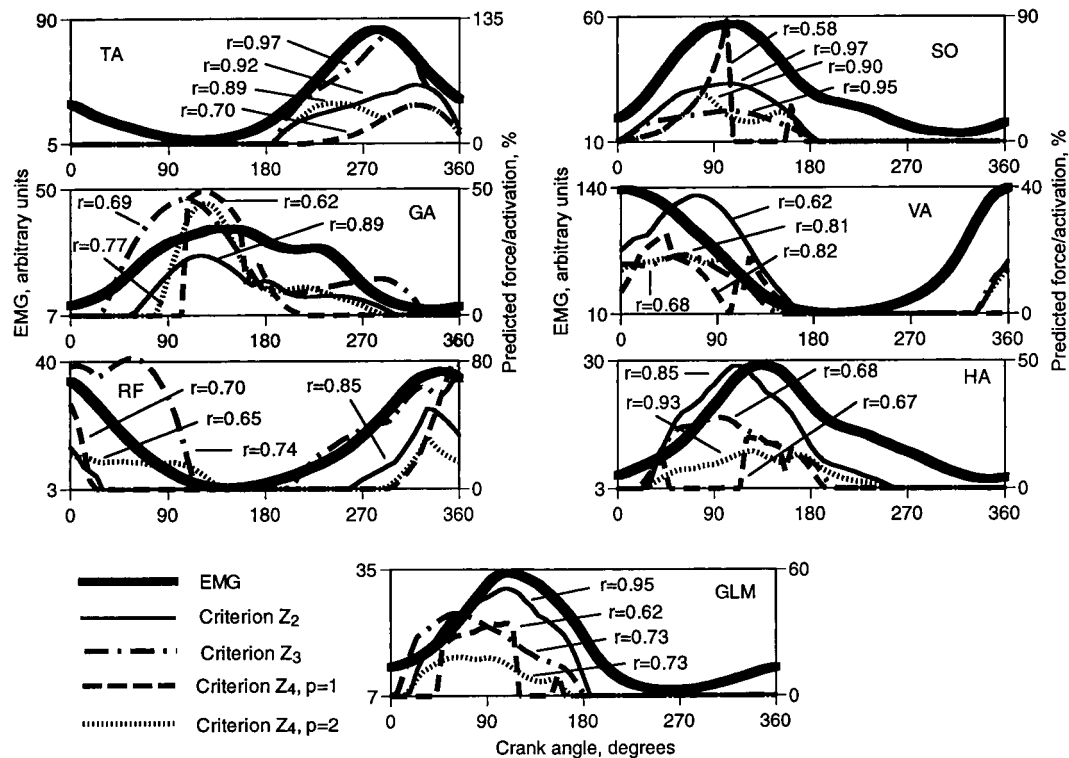


Figure 3. Recorded EMG linear envelopes (EMG) and muscle forces and activation predicted by optimizing minimum fatigue criterion Z_2 , min-max criterion Z_3 , and minimum metabolic cost criteria (Z_4 , $p = 1$ and $p = 2$) during cycle of pedaling at a cadence of 60 rpm and a power of 200 W. The EMG was recorded, and the muscle forces and activation were calculated from kinematics and pedal reaction forces of one typical subject (11). The EMG linear envelopes were normalized to the peak EMG values recorded in maximum isometric contractions. The EMG envelopes were shifted in time to account for the delay between the EMG and the joint moments. The time shift was found for each muscle by cross-correlating the EMG envelopes and the joint moments (11). The Pearson correlation coefficients (r) calculated between the EMG and predicted force/activation patterns are typically between 0.6 and 0.9. The best performance is demonstrated by the minimum fatigue criterion Z_2 ; the linear version of the metabolic cost criterion (Z_4 , $p = 1$) has typically the worst performance.

$$h = \sum_{i=1}^n F_i = F_{tot} \quad (9)$$

where i stands for a finger involved in a task, F_i are individual finger forces, p is value of power ($p > 1$), n is the number of fingers involved in the tasks ($n = 2, 3, 4$), and F_{tot} is the total force level achieved by all the involved fingers.

INTERPRETATION AND VALIDATION

Despite the fact that quantitative subject-specific predictions of MAP are very difficult to achieve at present, some important insights can be made based on qualitative comparisons of measured and predicted MAP. It seems remarkable that MAP of such dissimilar human movements as human walking (Fig. 2), cycling (Fig. 3), exerting isometric forces in different directions (10), and some other tasks have been qualitatively predicted by minimizing the same cost functions of muscle fatigue and metabolic cost (Z_2 and Z_4). These optimization criteria predict: (i) *reciprocal coactivation of one-joint antagonist muscles* (e.g., tibialis anterior vs soleus, Figs. 2 and 3); (ii) *coactivation of one-joint synergists with their two-joint antagonists* (e.g., VA vs HA, Figs. 2 and 3); (iii) *simultaneous activation of synergists crossing the same joints* (e.g.,

medial and lateral heads of gastrocnemius; three heads of vastii; (4); and (iv) *a strong relationship between force and activation of two-joint muscles and moments at the two joints* (a two-joint muscle has the greatest activation when acting as an agonist at the two joints and the smallest activation when acting as an antagonist at both joints (for review, see (10))). All these features of muscle coordination can be seen, to a certain extent, in the MAP of a number of skilled tasks performed with submaximal effort and in a stereotypic manner.

Which Criterion Is Better?

To select an optimization criterion for interpreting MAP among all tested criteria, one can rely on at least three factors: (i) quantitative measures of the criterion performance, i.e., errors of predicted forces (if measured forces are available (12,15)), or correlation coefficients (in the case of qualitative pattern comparisons; Figs. 2 and 3); (ii) a physiological meaning of the cost function; and (iii) availability of reasonable physiological mechanisms that could implement a given criterion.

In the case of cat locomotion, criterion Z_1 predicts muscle forces with smaller errors than criterion Z_2 (see Fig. 4; see also Table 1 in (12)), whereas criterion Z_2 demonstrates slightly higher correlation between predicted and measured MAP in

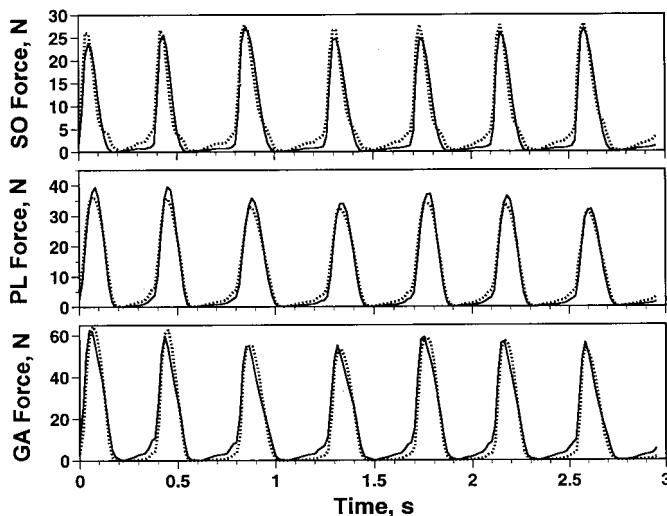


Figure 4. Measured forces (solid lines) and predicted forces (using criterion Z_7 ; dotted lines) of the cat soleus (SO), plantaris (PL), and gastrocnemius (GA) muscles during seven consecutive step cycles of trotting of the cat at a speed of $1.5 \text{ m} \cdot \text{s}^{-1}$. Because the percentage of slow-twitch fibers engaged in the force development during this trial was unknown, different physiologically reasonable values were examined (see Table 2 in (12)). The percentage of slow-twitch fibers in SO, GA, and PL used to calculate forces presented in this figure were 100%, 20%, and 35%, respectively. [Reproduced from Prilutsky, B.I., W. Herzog, and T.L. Allinger. Forces of individual cat ankle extensor muscles during locomotion predicted using static optimization. *J. Biomech.* 30:1029, 1997. Copyright © 1997 Elsevier Science Ltd. Used with permission.]

studied human tasks (10,11). Both of these criteria minimize muscle fatigue.

The analysis of muscle forces and activation in humans, as predicted by optimizing linear criteria (see, for example, seemingly logical minimum metabolic cost criterion Z_4 with $p = 1$ (equation 7; Figs. 2 and 3)), indicates that linear criteria do not adequately predict activation patterns of some synergist muscles (e.g., individual heads of gastrocnemius and vastii (4)). The same criterion Z_4 with $p = 2$ has a substantially better performance (Figs. 2 and 3). However, setting $p = 2$ has been done arbitrarily, merely to make the cost function nonlinear and to eliminate the deficiency of linear criteria that cannot predict more than three simultaneously active muscles for the given optimization problem (1–3). Of course, there are other formulations of the metabolic criteria (3), which can have a better performance.

Minimum fatigue criteria Z_1 and Z_2 , min/max criterion Z_3 , and minimum metabolic cost criterion Z_4 seem reasonable for tasks with submaximum efforts (walking, running, cycling, load lifting, contact force tasks, etc.), in which the time of sustaining a given performance (i.e., endurance time) may be critical and should be maximized. The minimum fatigue function $1/T = F/PCSA^3$ (see criterion Z_2 , equation 5) closely resembles the function that relates the perceived effort to the exerted muscle force (for details, see (10)). This leads to speculation that humans might solve some motor redundancy problems based on the sense of perceived effort. For example, there are indications that a preferred gait (walking or running) and preferred rate of pedaling in cycling are selected based on the sense of effort rather than on the metabolic cost (for references, see (10)).

The sense of effort is thought to originate primarily from motor commands but also from afferent signals from muscles and joints. Thus, minimizing the sense of effort may be interpreted, to some extent, as minimizing the central motor commands to motor neuron pools. These commands can be perceived through corollary discharges/efference copy of the motor commands from the motor to the sensory cortex. This minimization of central motor commands is analogous to the principle of “minimization of interaction” between different motor levels of control, which was thought to be a central mechanism of mastering expedient behavior by the nervous system (6) and which is consistent with the idea of lowering a level of control from higher to lower centers during acquisition of motor skills.

When finger forces, rather than muscle forces, were explored, minimal-norm criterion Z_5 (equation 8) was successful in predicting the individual finger forces during pressing tasks (15). However, this criterion did not predict finger forces correctly when the task was to exert a torque on a hand-held object. The reason for the poor performance was that the criterion neglects the enslaving effects that cause involuntary activation of the antagonist fingers. In manipulative tasks, the index and middle fingers and the ring and little fingers exert moments of normal force about a pivot point, created by the thumb, in opposite directions. The antagonist fingers generate moments of force opposite to the resultant moment produced by all fingers. For instance, if the resultant moment is in pronation, an antagonist finger generates a supination moment. Activation of the antagonist fingers in the torque production tasks was observed experimentally; however, criterion Z_5 neglects it.

How Well Do Optimization Approaches Work in General?

In the literature, reports about the application of optimization methods range from stories of success (12) to accounts of failure (8). Personal opinions also range from extremely pessimistic (“...there is no objective function that has been shown to predict individual muscle forces accurately” and the optimization “has repeatedly failed to give acceptable results”; (8), p. 187) to very optimistic (“During gait, the observed muscle activity (as determined by EMG) shows substantial agreement with that activity pattern predicted when endurance is used as the optimization criterion”; (4), p. 793). There are several reasons for such diverse opinions. First, there is no accepted standard on what to consider a successful prediction of activation patterns. The predicted and measured patterns presented in Figures 2–4 can be perceived by some readers as examples of a good correspondence, whereas other readers will evaluate the same results much more pessimistically. Second, the optimization may fail or succeed because of the incompleteness of the model and/or errors in parameter estimation. These deficiencies can be overcome in the future with the advent of new theoretical and experimental methods. Third, some cost functions may not work well for some motor tasks. Our bias is that the negative results obtained in some research projects do not undermine the applicability of the optimization methods in principle.

SUMMARY

The human body has 244 kinematic DoF. Therefore, there are an infinite number of ways to position a body segment in a desired place with a desired body orientation in three-dimensional space. The number of muscles in the human body exceeds the number of kinematic DoF at a ratio of approximately 2.6:1, *i.e.*, one DoF is served on average by 2.6 muscles. Each muscle, or its part, in the human upper and lower extremities creates moments, on average, about 4 DoF. Therefore, each muscle might create undesirable moments about DoF that are not directly involved with the task; these moments have to be counterbalanced. Due to muscle redundancy, a given joint moment combination can be produced by an infinite number of muscle force combinations. Despite abundant alternatives, in many skilled tasks, different people utilize similar movement kinematics, kinetics, and MAP. A common assumption is that the employed patterns are chosen because they are *better* than others, or, in other words, *optimal*. In mathematical language, one may say that the CNS selects a particular MAP (and, therefore, movement kinetics and kinematics) by optimizing a certain objective function. This presumption has led to the development of static and dynamic optimization-based models that allow for estimations of MAP. Although both types of models have their own advantages and limitations, dynamic models have more applications and potentially may give more accurate predictions of MAP. The comparison of predicted and measured MAP in a number of skilled tasks with submaximum efforts and relatively little demands on movement accuracy and speed (level walking in cats and humans, cycling, load lifting, and exerting isometric forces) suggests that MAP in these motor tasks might be selected based on some of the following three physiological cost functions: metabolic energy expenditure, muscle fatigue, and the sense of perceived effort.

Acknowledgments

We thank our colleagues Drs. R. J. Gregor, M. L. Latash, and Z.-M. Li for valuable discussions and suggestions on earlier drafts of the manuscript and for their contribution to the results discussed in the manuscript. We also thank two anonymous reviewers for their valuable suggestions.

The preparation of this manuscript was supported in part by the Center for Human Movement Studies of Georgia Institute of Technology, Atlanta, GA.

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