The Influence of the Way the Muscle Force is Modeled on the Predicted Results Obtained by Solving Indeterminate Problems for a Fast Elbow Flexion

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A critical point in models of the human limbs when the aim is to investigate the motor control is the muscle model. More often the mechanical output of a muscle is considered as one musculotendon force that is a design variable in optimization tasks solved predominantly by static optimization. For dynamic conditions, the relationship between the developed force, the length and the contraction velocity of a muscle becomes important and rheological muscle models can be incorporated in the optimization tasks. Here the muscle activation can be a design variable as well. Recently a new muscle model was proposed [22]. A muscle is considered as a mixture of motor units (MUs) with different peculiarities and the muscle force is calculated as a sum of the MUs twitches. The aim of the paper is to compare these three ways for presenting the muscle force. Fast elbow flexion is investigated using a planar model with five muscles. It is concluded that the rheological models are suitable for calculation of the current maximal muscle forces that can be used as weight factors in the objective functions. The model based on MUs has many advantages for precise investigations of motor control. Such muscle presentation can explain the muscle co-contraction and the role of the fast and the slow MUs. The relationship between the MUs activation and the mechanical output is more clear and closer to the reality.

Keywords: Motor control; Indeterminate problem; Optimization; Motor unit; Elbow; Muscle force

INTRODUCTION

Several approaches could be applied for investigation of motor control strategies used by humans. The so called "static optimization" solves numerically or analytically differently formulated, constrained optimization tasks. Mathematically, these tasks are composed of a set of equations derived from the force and moment equilibrium along with inequality constraints setting upper and lower limits on the design variables. These design variables are usually the total mechanical output of the musculotendon units. Commonly the equations form an indeterminate system that imposes the use of optimization methods that are based on a relevant objective function. There are two possible ways for dealing with this objective function. The first one is construction of its analytical form according to some physiological considerations based on total muscle force, muscle stresses, endurance time, mechanical energy, saturation, etc. ([1–6]; for review see Refs. [7,8]). It is questionable, however, whether a simple

analytical mathematical function is adequate to represent the control of such highly complex and nonlinear systems. The second possibility is to form a complicated function of design variables allowing a good description of different biomechanical models and motor tasks without considering its physiological interpretation [9]. Similar to artificial neural networks, this function could be considered as an approximation of unknown interrelations between the variables of interest. Static optimization has its upholders [10] as well as its opponents [11]. A debatable point is its appropriateness for dynamic conditions. The main reasons for doubts are: the objective functions are usually time-independent; the contractile properties of the muscles, i.e. the well-known relationships of force with length and velocity, are not taken into consideration; the previous state of the muscles is not considered since the optimization is performed for a current time moment. Recent publications have shown that static optimization could be used with same success for dynamic conditions [12–14]. What is omitted when

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the muscle is considered as a simple force generator? The control signals in a muscle, coming from the motor axons to the muscle fibers, cause "contractions" of separate motor units (MUs), hence of a muscle part. These contractions always result in a force production, but not necessarily, always a change of the muscle length occurs. Hence, it could be considered that the force of a MU is controlled by neural impulses and thus the length and contraction velocity of a muscle are controlled indirectly. A feedback is needed for tracing the results from the action of the control system. Among other sensor information, afferent signals provide feedback for the current state of the length, contraction velocity and tension of the muscle from muscle spindles and Goldgy tendons. This is why Hill-type muscle models (they are also called phenomenological or rheological muscle models [15]) seem more adequate [16,17]. They consider a muscle as a specific visco-elastic material and the corresponding model represents the whole muscle as a combination of contractile and elastic elements. Besides the problems with the determination of specific constants for every muscle, the question about controlling neural signals arises when attempting to calculate directly the developed muscle force for a given length and contraction velocity. These signals can also be subjected to optimization, i.e. design variables, or processed electromyographic signals (EMGs) can be used as input. The surface EMGs reflect the overall neural activity of muscles and the problems with their proper registration, processing and relationship with developed muscle force are well known. Actually, the general effect of neural activity of MUs that compose the muscle is registered. Since there are different types of MUs with respect to the force capacity (cross-section area and respective maximal force) and to the contraction velocity (i.e. fast, slow and intermediate MUs), an exact relationship between developed muscle force and processed surface EMGs could not be established in the general case. In addition, the linear summation of the mechanical outputs of different MUs for forming the force output of the whole muscle seems reasonable, while such summation of electrical potentials does not [18]. The use of intramuscular electrodes allows to observe for the activity of selected MUs, but what portion of MUs in the muscle is currently activated can not be established.

For most of the used muscle models the mechanical output of a musculotendon unit is one force. Actually this force is a sum of the forces developed from individual MUs. The mechanical response of a MU to a neural pulse, the so called "twitch", has a well-known bell-shaped form. The parameters that describe this form are different for different MUs type. They depend on the current length of the muscle [19], presence of fatigue, age, sex and level of training [20,21]. To have as general output a smooth enough muscle force, the time sequence of activation of different MUs is very important. The authors are of the opinion, that models considering a muscle as a mixture of different MUs and the muscle mechanical output as a summation of MUs twitches, are more realistic and could

provide more realistic means for detailed investigation of motor control. That is why a new approach and computer algorithm based on MUs peculiarities was developed [22,23]. A hierarchical genetic algorithm (HGA) was implemented for predicting the time moments of neural activation of MUs of the modeled muscles. The software realization, MotCo package, can be inspected on the web site http://motco.dir.bg.

The aim of the present paper is to apply the above approaches: (1) static optimization, where the mechanical output of a muscle is considered as one musculotendon force; (2) optimization based on Hill-type muscle model where this force is dependent on the current muscle length and contraction velocity; and (3) the method based on MU twitches, i.e. implementation of HGA using the MotCo software, for investigation of a fast elbow flexion and to compare the results.

METHODS

A one-degree of freedom (DOF) model of the elbow in the sagittal plane is considered (for details see Ref. [22]). Five muscles are modeled—three flexors: m.biceps brachii (BIC), m.brachialis (BRA), m.brachioradialis (BRD) and two extensors: m.triceps brachii (TRI) and m.anconeus (ANC). Only fast elbow flexion from 0° to 150°, that is from fully extended to fully flexed forearm, for 0.25 [s] is considered. The following function is chosen for modeling the change of the elbow angle during motion:

$$\varphi(t) = -\frac{\varphi_{\text{ran}}}{2\pi}\sin\left(\frac{2\pi t}{T}\right) + \frac{\varphi_{\text{ran}}}{T}t, \qquad (1)$$

where $T = 0.25\,[s]$ is the duration of the flexion and $\varphi_{\text{ran}} = 5\pi/6\,[\text{rad}]$ is the range of the movement. In this way a symmetrical sinusoidal law for angle velocity and acceleration is modeled (see Fig. A1 in Appendix), that is in good agreement with reported data for ballistic motions [24,25]. The moment equation with respect to the axis of flexio/extensio in the elbow has the form:

$$\sum_{i=1}^{5} d_i F_i = M_{\text{ext}} \quad \text{where } M_{\text{ext}} = I_{zz}\ddot{\varphi} + Gl_G\sin(\varphi), \quad (2)$$

where $i = 1$–5 represents the muscles BIC, BRA, BRD, TRI and ANC, respectively and F_i are the respective muscle forces, d_i are the moment arms of the muscle forces, M_{ext} is the external joint moment due to the action of the inertial and the gravity forces, G and I_{zz} are the gravity force and the inertial moment of the hand and forearm, $\ddot{\varphi}$ is the angular acceleration and l_G is the distance from the axis of rotation in the joint to the application point of G. The muscle moment arms are dependent on the elbow angle and are calculated from the regression equations given in Refs. [26,27] (note that $d_i > 0$ for BIC, BRA and BRD, but $d_i < 0$ for TRI and ANC). The graphics $d_i(t)$ are shown in Fig. A2 in Appendix.

The used data for the present calculations are: $l_G = 0.18$ [m], $I_{zz} = 0.01087$ [kg m^2] and $G = 13.72$ [N].

Three cases with respect to the way of modeling the muscle forces and the respective optimization tasks will be considered.

One Force Independent of Muscle Length and Type of the Muscle MUs

It is supposed that the muscle force is independent of the current or previous state of the muscle, muscle contractile properties, etc. i.e. it is a simple design variable in the following optimization task:

OT1

$$\min \sum_{i=1}^{5} c_i F_i^n$$

at the equality constraint $\sum_{i=1}^{5} d_i F_i = M_{ext}$, where c_i ($i = 1, 2, \ldots, 5$) are weight coefficients that may have both positive and negative values [7,28].

The analytical solution of the optimization task obtained using Lagrange multipliers method is:

$$F_i = \sqrt[n-1]{\frac{M_{ext}^{n-1} d_i}{n S^{n-1} c_i}}, \quad \text{where} \quad S = \sum_{j=1}^{5} d_j \left(\sqrt[n-1]{\frac{d_j}{n c_j}} \right). \quad (3)$$

Apart from using this analytical solution, the same optimization task was also solved numerically by using the function *constr* of the optimization toolbox of MATLAB (MatWorks Inc.), but imposing additional inequality constraints $0 \leq F_i \leq F_i^{max}$, where F_i^{max} is the maximal possible force of the i-th muscle calculated by multiplying the physiologic cross-sectional area of the i-th muscle (PCSA$_i$) by 50 N/cm^2 [16]. The following values were used for PCSA: BIC-5.37 [cm^2]; BRA-5.55 [cm^2]; BRD-1.33 [cm^2]; TRI-4.37 [cm^2] and ANC-1.24 [cm^2]. Hence, the respective maximal forces are: $F_1^{max} = 268.5$ [N], $F_2^{max} = 277.5$ [N], $F_3^{max} = 66.5$ [N], $F_4^{max} = 236.5$ [N] and $F_5^{max} = 62$ [N].

Rheological Muscle Model Accounting for the Type of the Muscle MUs

The muscle is represented as a contractile element acting in parallel with a passive elastic element [29,30]. A series-elastic element is not considered since it corresponds to the tendon and aponeurosis at the muscle ends, so it is not an active muscle component. According to Brown *et al.* [30], the force of a muscle can be expressed relative to its current length ℓ, contraction velocity $\dot{\ell}$ and degree of activation α by the following equation:

$$F(\ell, \dot{\ell}, \alpha) = \alpha F^{max}[F(\ell)F(\ell, \dot{\ell}) + F_{PE2}(\ell)]$$

$$+ F^{max} F_{PE1}(\ell, \dot{\ell}), \quad (4)$$

where $F(\ell)$ represents the force–length relationship, $F(\ell, \dot{\ell})$ represents the force–velocity relationship, $F_{PE1}(\ell, \dot{\ell})$ and $F_{PE2}(\ell)$ represent passive elastic elements and F^{max} is the maximal isometric force and $0 \leq \alpha \leq 1$. ℓ is normalized to the optimal muscle length at which the muscle develops maximal isometric force.

Usually the human muscles are a mixture of different MUs [20]. Although an exact classification of MUs type is not established, three main types are usually differentiated—fast, slow and intermediate [31]. Brown *et al.* [30] distinguish fast-twitch and slow-twitch muscles using different constants for force–length–velocity relationships. For the current investigation, the equations and constants given in Ref. [29] (see Table I, page 123 in Cheng *et al.* [29]) are used. Supposing that the i-th muscle consists of $100 \cdot k_i$ percents fast-twitch fibers, where $0 \leq k_i \leq 1$, the Eq. (4) can be rewritten for the i-th muscle as follows:

$$F_i(\ell_i, \dot{\ell}_i, \alpha_i, k_i) = \alpha_i F_i^{max} \big[k_i F_i^f(\ell_i) F_i^f(\ell_i, \dot{\ell}_i)$$

$$+ (1 - k_i) F_i^s(\ell_i) F_i^s(\ell_i, \dot{\ell}_i) \quad (5)$$

$$+ F_{i PE2}(\ell_i) \big] + F_i^{max} F_{i PE1}(\ell_i, \dot{\ell}_i)$$

where $F_i^f(\ell_i)$, $F_i^f(\ell_i, \dot{\ell}_i)$, $F_i^s(\ell_i)$ and $F_i^s(\ell_i, \dot{\ell}_i)$ represent the force–length and the force–velocity relationships for fast and slow parts of the i-th muscle, respectively. According to Cheng *et al.* [29], the force in the parallel elastic element does not depend on the fiber types.

The length and the contraction velocity of each modeled muscle for the investigated fast elbow flexion are calculated by the regression equations for the length dependencies on the elbow joint angle given in Refs. [26,27]. Hence, given the elbow angle $\phi(t)$ from Eq. (1), the dependencies $\ell_i(\varphi)$ and $\dot{\ell}_i(\varphi)$ are known for each muscle (they are shown in Figs. A3 and A4 in Appendix). Therefore, the muscle forces are expressed by Eq. (5) as functions of time, degree of activation and the interrelation between the fast and the slow parts constituting the muscles. The optimization task can be formulated and solved differently. The first way is to assume that the muscle activations α_i are design variables, but not the muscle forces. Then two optimization tasks (OT2 and OT3) can be composed:

OT2

$$\min \sum_{i=1}^{5} \alpha_i$$

TABLE I Parameters of the considered two types of MUs (fast, slow) (see Fig. 1) given in [ms]

MU type	T_{lead}	T_c	T_{ref}	T_{hr}	T_{tw}
Fast	20	30	30	60	120
Slow	70	80	80	200	480

at the equality constraint: $\sum_{i=1}^{5} d_i F_i(\ell_i, \dot{\ell}_i, \alpha_i, k_i) = M_{ext}$ and the inequality constraints: $0 \le \alpha_i \le 1$ and $0 \le F_i(\ell_i, \dot{\ell}_i, \alpha_i, k_i) \le F_i^{max}(\ell_i, \dot{\ell}_i, k_i)$, for $i = 1, 2, \ldots, 5$;

OT3

$$\min \sum_{i=1}^{5} \left(\frac{F_i(\ell_i, \dot{\ell}_i, \alpha_i, k_i)}{PCSA_i} \right)^n$$

at the equality constraint: $\sum_{i=1}^{5} d_i F_i(\ell_i, \dot{\ell}_i, \alpha_i, k_i) = M_{ext}$ and the inequality constraints: $0 \le \alpha_i \le 1$ and $0 \le F_i(\ell_i, \dot{\ell}_i, \alpha_i, k_i) \le F_i^{max}(\ell_i, \dot{\ell}_i, k_i)$, for $i = 1, 2, \ldots, 5$; (note that here $F_i^{max}(\ell_i, \dot{\ell}_i, k_i)$ is the maximal force of the i-th muscle calculated for the current length and contraction velocity by substitution $\alpha_i = 1$ in the Eq. (5), i.e. when the muscle is fully activated).

The second way for formulation of the optimization task is to use the force–length–velocity relationship as a boundary condition only, hence as an upper limit of the possible maximal muscle force for current length and contraction velocity. This limit is used as weight factor in the objective function instead of PCSA [2]. Then the muscle forces F_i are design variables in the following optimization task:

OT4

$$\min \sum_{i=1}^{5} \left(\frac{F_i}{F_i^{max}(\ell_i, \dot{\ell}_i, k_i)} \right)^n$$

at the equality constraint: $\sum_{i=1}^{5} d_i F_i = M_{ext}$ and the inequality constraints: $0 \le F_i \le F_i^{max}(\ell_i, \dot{\ell}_i, k_i)$ for $i = 1, 2, \ldots, 5$, where the maximal muscle forces are calculated for current length and contraction velocity during the motion substituting $\alpha_i = 1$ in Eq. (5).

The OT2, OT3 and OT4 were solved numerically using the function *constr* of the optimization toolbox of MATLAB.

Muscle Model based on Motor Unit Twitches

The main difference here is that the mechanical output of a muscle is not one musculotendon force, but it is obtained by the summation of the mechanical responses of MUs that compose the whole muscle. The design variables are the time moments of neural activation of MUs. A HGA is implemented for this task (see, for details, Refs. [22,23]). A brief, simplified description of the algorithm is presented below. The MU twitch (the mechanical response of a MU of a single neural impulse) has a specific bell-shaped form (see Fig. 1a) that is dependent on the MU type (slow, fast) and was described analytically elsewhere [22]. Repetitive neural impulses with inter-pulses time period greater than the absolute refractory period (T_{ref}) cause a superimposition of the twitches (Fig. 1b) up to unfused and fused tetanus. Both maximal firing rate and maximal force of a MU depend on the chosen value of T_{ref}.
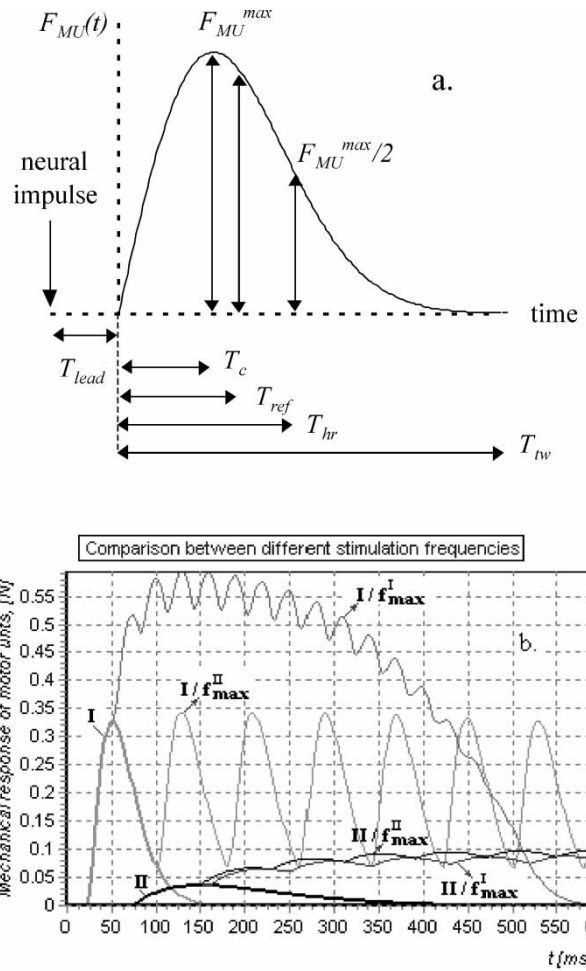

FIGURE 1 (a) MU twitch shape and parameters. F_{MU}^{max}-maximal force of the MU caused by one neural impulse; T_{lead}- "lead time": the time between the neural activation and the start of the force development; T_c-"contraction time": time from the start of the MU mechanical contraction, to the time where MU force reaches its maximum; T_{ref}-"absolute refractory period": during this time the MU is unable to respond to new neural activation; T_{hr}-"half-relaxation time": time from the start of the MU mechanical response to the time when the MU force becomes twice lower than F_{MU}^{max}; T_{tw}-duration of the twitch. (b) Forces developed by two types MUs, fast (I) and slow (II), stimulated with their maximal frequencies f_{max}^I and f_{max}^{II}. These depend on the absolute refractory period. Lines I / f_{max}^I and I / f_{max}^{II} are responses of fast MU stimulated with f_{max}^I and f_{max}^{II}, respectively; lines II / f_{max}^I and II / f_{max}^{II} are responses of slow MU stimulated with f_{max}^I and f_{max}^{II}, respectively.

The total muscle force is the sum of the developed forces of all MUs of this muscle. The time moments of neural activation of all MUs of a muscle are coded in a "string of genes" and overall activity of all modeled muscles is presented by an "individual" obtained by a concatenation of these strings. On each step of the algorithm, these "individuals" are modified by different genetic operations (mutation, crossover) that change in some way the moments of neural activation. The obtained solutions, old and new, are estimated by a fitness function and the better ones "survive". The genetic operations are applied again over these and this process continues until some end condition is fulfilled. In the present paper, the used

fitness function *FitFun* is a weighted combination of the following criteria: minimal total error (ΔM) between the desired (computed from Eq. (2)) joint moment and the joint moment obtained by summing the forces of all MUs and multiplying the calculated muscle forces by their lever arms; minimal muscle activation (MUAct), i.e. minimum of the total number of neural impulpes; minimal total muscle force (Sum). The optimization task is formulated as follows:

OT5

to find $t_{i,j}^k$ that minimize the function: FitFun = $w_{\text{mom}}\Delta M + w_{\text{act}}\text{MUAct} + w_{\text{for}}\text{Sum}$ at the inequality constraints: $t^{p+1}i,j - t^p i,j \geq T_{\text{ref}_{i,j}}$, $p = 1, 2, \ldots$, StimNum$_{i,j}$, and at given twitch form $F_{\text{MU}}(t, T_{\text{lead}}, T_c, T_{\text{ref}}, T_{\text{hr}}, T_{\text{tw}}, F_{\text{MU}}^{\text{max}})$ (see Fig. 1a) and percent of fast and slow MUs for the muscles,

where: $t_{i,j}^k$ is the k-th time moment of neural activation of the j-th MU of the i-th muscle; $T_{\text{ref}i,j}$ is the absolute refractory period of the j-th MU of the i-th muscle (see Fig. 1a and Table I); StimNum$_{i,j}$ is the number of impulses of the j-th MU of the i-th muscle for the whole duration of the movement; w_{mom}, w_{act} and w_{for} are weight factors at the following quantities:

$$\Delta M = \frac{1}{N_{\text{int}}}\sum_{j=1}^{N_{\text{int}}}\left(M_{\text{ext}}(t_0 + j{\cdot}\Delta t) - \frac{1}{N}\sum_{i=1}^{N}d_i F_i(t_0 + j{\cdot}\Delta t)\right),$$

i.e. total error between the desired and current joint moment;

$$\text{MUAct} = \sum_{i=1}^{N}\sum_{j=1}^{\text{Num}_i}\frac{\text{StimNum}_{i,j}}{\text{MaxStNum}_{i,j}(\text{duration})},$$

i.e. muscles' activation;

$$\text{Sum} = \frac{1}{N{\cdot}N_{\text{int}}}\sum_{i=1}^{N}\sum_{j=1}^{N_{\text{int}}}F_i(t_0 + j{\cdot}\Delta t),$$

i.e. the sum of the currently calculated forces of all muscles, where

$$N_{\text{int}} = \frac{\text{duration}}{\Delta t}.$$

Here N is the number of the modeled muscles ($N = 5$ for the current study), Num$_i$ is the number of the MUs of the i-th muscle; $F_i(t) = \sum_{j=1}^{\text{Num}_i}\sum_{k=1}^{\text{StimNum}_{i,j}}F_{i,j}^{\text{tw}}(t_{i,j}^1, t_{i,j}^2, \ldots, t_{i,j}^k, t)$, $(t_{i,j}^k \leq t)$ is the force of the i-th muscle as function of time t obtained by summing the force outputs, $F^{\text{tw}}(t_{i,j}^1, t_{i,j}^2, \ldots, t_{i,j}^k, t)$, of this muscle MUs caused by neural impulses applied at the times $t_{i,j}^k$; MaxStNum$_{i,j}$ is the maximal possible number of impulses for a given time

"duration" for which the j-th MU of the i-th muscle is able to respond (this number depends on the absolute refractory period for a MU); N_{int} is the number of the time intervals Δt for which the muscle forces are estimated, beginning from an initial time t_0. The inequality constraints reflect the fact that a MU does not respond with a rise in its force output if the time between two successive impulses is less than an absolute refractory period $T_{\text{ref}i,j}$.

There is a lack of information about the number and type of MUs for most of the muscles. The current simulations are performed with a nearly real number MUs, supposing that this number is proportional to PCSA of the muscle. As a basis, the value given in Ref. [32] for m.BIC, namely 774 MUs, is used. So, the numbers of the MUs for other muscles are: m.BRA-804; m.BRD-194; m.TRI-686; m.ANC-180. Different types of MUs can be modeled in the software setting different parameters of their twitches (Fig. 1a). Only two types are considered in this paper, fast and slow, and their parameters are given in Table I. It is assumed first that all muscles consist of 50% fast and 50% slow MUs. Then $F_{\text{MU}}^{\text{max}} = 0.3288$ [N] for fast and $F_{\text{MU}}^{\text{max}} = 0.0382$ [N] for slow MUs for all muscles. For the second numerical experiment, it is supposed that the muscles BRA, BRD and ANC consist only of fast MUs. Then their maximal forces are changed as follows: m.BRA-$F_{\text{MU}}^{\text{max}} = 0.19095$ [N]; m.BRD-$F_{\text{MU}}^{\text{max}} = 0.1905$ [N]; and m.ANC-$F_{\text{MU}}^{\text{max}} = 0.190425$ [N]. These maximal forces are calculated so that the sum of tetanic forces of all MUs of a muscle is equal to the maximal possible force of this muscle calculated by its PCSA.

RESULTS

Three-phasic behavior of muscles, typical for ballistic motions, can be predicted using static optimization even if the dynamic properties of the muscles are not accounted (Fig. 2a,b). The flexors are active when the external joint moment is positive, i.e. for $t \in (0, 0.16\,\text{s}) \cup (0.235\,\text{s}, 0.25\,\text{s})$. Extensor activities are predicted if $M_{\text{ext}} < 0$. The differences between the predicted muscle forces for $n = 2$ and 3 are not significant (Fig. 2a vs. 2b; see also Ref. [33]). The forces shown in Fig. 2a,b are obtained using the analytical solution of OT1 given by Eq. (3). The inequality constraints $0 \leq F_i \leq F_i^{\text{max}}$ are not imposed directly, but are satisfied because of used weight coefficients. According to previous investigations [34], when the absolute value of a weight coefficient is very big (here $|c_i| = 1500$ for extensors when $M > 0$ and for flexors when $M < 0$), the predicted force of the respective muscle is near zero. That is why antagonistic co-contraction is not predicted here. Because of the used weight coefficients the obtained solutions (Fig. 2a,b) coincide with these obtained by subroutine *constr* of MATLAB with the often used objective function $\sum_{i=1}^{5}(F_i/\text{PCSA}_i)^n$ for $n = 2, 3$ respectively and the inequality constraints $0 \leq F_i \leq F_i^{\text{max}}$. The analytical solution, however, is more precise and smooth.
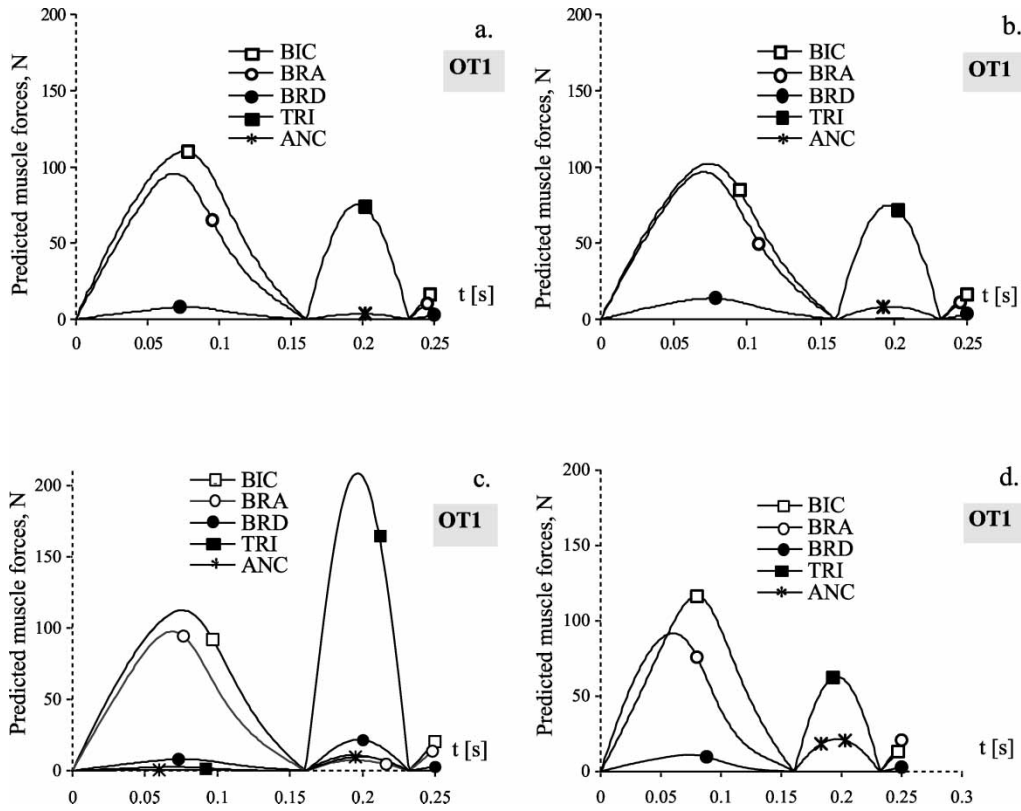
FIGURE 2 Predicted muscle forces using static optimization and the objective function $\min \sum_{i=1}^{5} c_i F_i^n$, i.e. solving the optimization task OT1. (a) $n = 2$, $c_i = (1/PCSA_i)^n$ for $i = 1, 2, 3$, $c_i = -1500$ for $i = 4, 5$ if $M_{ext} > 0$ and $c_i = 1500$ for $i = 1, 2, 3$, $c_i = -(1/PCSA_i)^n$ for $i = 4, 5$ if $M_{ext} < 0$. (b) $n = 3$, $c_i = -(1/PCSA_i)^n$ for $i = 1, 2, 3$, $c_i = -1500$ for $i = 4, 5$ if $M_{ext} > 0$ and $c_i = 1500$ for $i = 1, 2, 3$, $c_i = -(1/PCSA_i)^n$ for $i = 4, 5$ if $M_{ext} < 0$. (c) $n = 2$, $c_i = (1/PCSA_i)^n$ for $i = 1, 2, 3$, $c_i = -2$ for $i = 4, 5$ if $M_{ext} > 0$ and $c_i = 2$ for $i = 1, 2, 3$, $c_i = -(1/PCSA_i)^n$ for $i = 4, 5$ if $M_{ext} < 0$. (d) c_i has the analytical form from the Eq. (6). The following constants are used: $n = 2$, $n_1 = 2$, $n_2 = 0$, $\beta_1 = 84$, $\beta_2 = 85$, $\beta_3 = 85$, $\beta_4 = 90$ and $\beta_5 = 92$.

The minimization based on muscle stresses leads to an interrelation between the predicted muscle forces in a synergistic group proportional to their PCSA, namely

$$\frac{F_i}{F_j} = \sqrt[n-1]{\frac{|d_i|}{|d_j|} \frac{PCSA_i}{PCSA_j}} \ \text{(see Eq. (3))}.$$

Besides c_i, the muscle lever arms also influence the predicted muscle forces. The PCSAs of m.BIC and m.BRA have similar values and their predicted forces are near, but m.BIC force is larger since its lever arm is longer everywhere (see Fig. 2 in Appendix). If other c_i are used (see Fig. 2c), it is possible to predict antagonistic co-contraction.

Aiming to show how a new objective function could be constructed, the following time dependent analytical form of the weight coefficients can be used:

$$c_i = \text{sign}(d_i)$$

$$\times \frac{1}{(F_i^{max}(\ell_i, \dot{\ell}_i, k_i))^{n1}} \frac{1}{(PCSA_i)^{n2}} e^{\beta_i \cdot \text{sign}(-M_{ext}/d_i)}, \quad (6)$$

where $n_1 + n_2 = n$ and β_i is a parameter reflecting in percent the current capability of the muscle to develop force. For example, if a muscle has an optimal length, it is not fatigued, not damaged, etc. then $\beta_i = 100$, else $0 < \beta_i < 100$. If $\beta_i = 100$ and $n_1 = 2$, $n_2 = 0$, the results of using the optimization criterion $\min \sum_{i=1}^{5} c_i F_i^2$ with c_i having the form from Eq. (6) will coincide with those obtained by the criterion $\min \sum_{i=1}^{5} (F_i/F_i^{max})^2$. If $n_1 = 0$ and $n_2 = 2$, the results will coincide with those obtained by the criterion $\min \sum_{i=1}^{5} (F_i/PCSA_i)^2$. The advantage of this form of c_i is that it allows a simple derivation of an analytical solution of the optimization task. The direction of the muscle moment defines the sign of the weight coefficient, that is why the c_i for antagonistic muscles are with opposite sign. The interrelation between the direction of the muscle moment and the direction of the external moment defines when a muscle has to be preferably active. Like in the rheological muscle models, the current length, the contraction velocity and the percent of fast and slow MU could be accounted for in β_i. For example, if $\beta_i = 100 \times (1 - (|\Delta \ell_i|)/(L_{oi}))$, where $\Delta \ell_i$ is the deviation of the current muscle length from the optimal muscle length L_{0i}, the reduced capabilities of the muscle for force producing when its length is different from the optimal one, will be accounted for. The muscle forces calculated using Eq. (3) and c_i from Eq. (6) with $n = 2$, $n_1 = 2$, $n_2 = 0$, $\beta_1 = 84$, $\beta_2 = 85$, $\beta_3 = 85$, $\beta_4 = 90$, $\beta_5 = 92$ are shown in Fig. 2c. The maximal forces were computed using Eq. (5) and $\alpha_i = 1$ for all i supposing that all
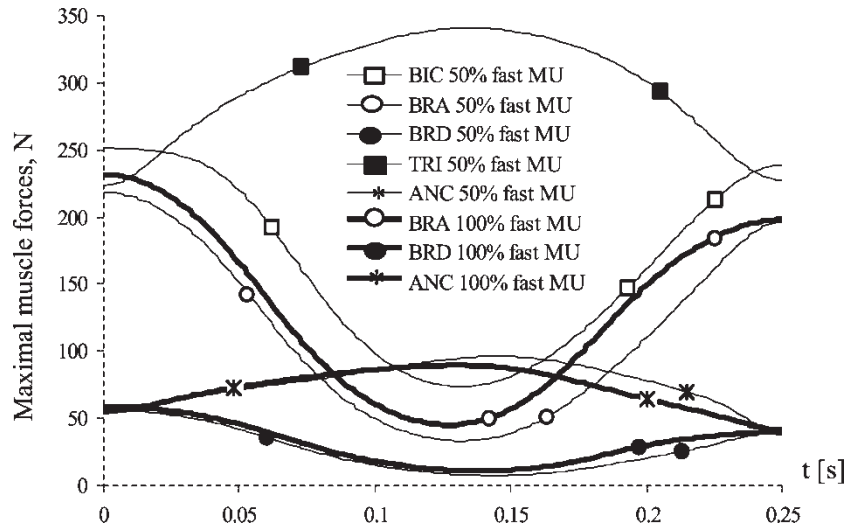
FIGURE 3   Maximal forces of the muscles during the motion when all muscles consist of 50% fast and 50% slow parts and when the muscles BRA, BRD and ANC consist of only fast MUs.

muscles consist of 50% fast and 50% slow MUs. They are changed considerably during the motion—see Fig. 3.

Using muscle activations as design variables, i.e. solving OT2 and OT3, besides the predicted individual muscle forces (Fig. 4a–d), a general information about the control of these muscles is obtained (Fig. 4e–h). Since the optimization criterion for OT2 is linear, the predicted results (Fig. 4a, b) show the typical behavior for such criteria, namely, inadequate muscle synergism. The muscle BIC is activated dominantly. When its force becomes insufficient for satisfying the external joint moment, i.e. it exceeds the maximal value, m.BRA is also included and after that, m.BRD, which has little non-zero force for a short time period. This is more clearly seen in Fig. 4e. When α_1 reaches its limit, α_2 becomes non-zero, when α_2 reaches 1, α_3 becomes non-zero. The force of the m.ANC is near zero. When the structure of the muscles BRA, BRD and ANC were changed, i.e. when they were composed of only fast fibers, the predicted muscle forces do not change practically (Fig. 4a vs. 4b), but the activation changes (Fig. 4e vs. 4f). In Fig. 4f, m.BRA does not reach its force upper limit, since its maximal force is bigger when it consists of only fast MUs (see Fig. 3). The results from solving OT3 (Fig. 4c,d,g,h) are very interesting. Here the aim was to find such α_i so that the moment equation is fulfilled, the minimum of the sum of the squared muscle stresses to be reached and the inequality constraints to be fulfilled. Hence, the difference from OT1 is that the design variables are muscle activation α_i, but not the muscle forces since they are expressed using Hill-type model by $\ell_i, \dot{\ell}_i, \alpha_i$ and k_i (see Eq. (5)). Figure 4d looks just like Fig. 2a where the results from solving OT1 with $n = 2$ were shown. This is due to the fact that the weight factor in the objective functions used for both OT1 and OT3 is the PCSA and the force limits for all muscle forces are not reached. Figure 4c slightly differs from Fig. 4d just because of reaching upper limits. When all muscles consist of 50% fast and 50% slow

parts, the maximal forces of the muscles BRA and BRD are lower (see Fig. 3) and this is why m.BRA reaches its limit in Fig. 4c (see also Fig. 4g), but when m.BRA consists of only fast MUs this does not happen. It is interesting that the interrelation between the forces of m.BIC and m.BRA is inverse to the interrelation between their α_i (Fig. 4c vs. 4g; Fig. 4d vs. 4h). The m.BIC develops bigger force, but the degree of the activity of m.BRA is higher.

The interrelation between the predicted forces in the muscles from a synergistic group changes when instead of PCSAs, the maximal muscle forces as functions of time, namely $F_i^{\max}(\ell_i, \dot{\ell}_i, k_i)$, are used as weight factors in the objective function, hence solving OT4 (Fig. 5a). The predicted force of m.BRA becomes significantly lower (see for comparison Fig. 5a vs. 4d) since the maximal force of m.BRA is lower than that of m.BIC for the whole movement duration (see Fig. 3). When the muscles BRA, BRD and ANC have only fast MUs, the results are nearly the same as those shown in Fig. 5a (not shown by a figure). They differ essentially, however, if the inequality constraints $F_i \leq F_i^{\max}(\ell_i, \dot{\ell}_i, k_i)$, are not included in the optimization task (Fig. 5b). The non smoothness of the curves in Fig. 5a between 0.075 [s] and 0.105 [s] is caused from reaching the upper limit for the m.BIC force.

The results from using the HGA with the muscle model based on MU unit twitches (Figs. 6a and 7a) show significant muscle co-contraction, especially essential in the time interval $t \in (0.1\,\text{s}, 0.15\,\text{s})$. In contrast to the previous models, the predicted force of m.BRA is bigger than that of m.BIC and this is more expressive when m.BRA consists of only fast MUs (Fig. 7a). Here the influence of the bigger lever arm of the m.BIC disappears because of the considered very fast motion. To perform such fast flexion, all fast MUs of all flexors must be activated initially. The number of the fast MUs of m.BRA is with 15 more than this of m.BIC for Fig. 6a and with 417 for Fig. 7a. That is why the m.BRA force is longer.
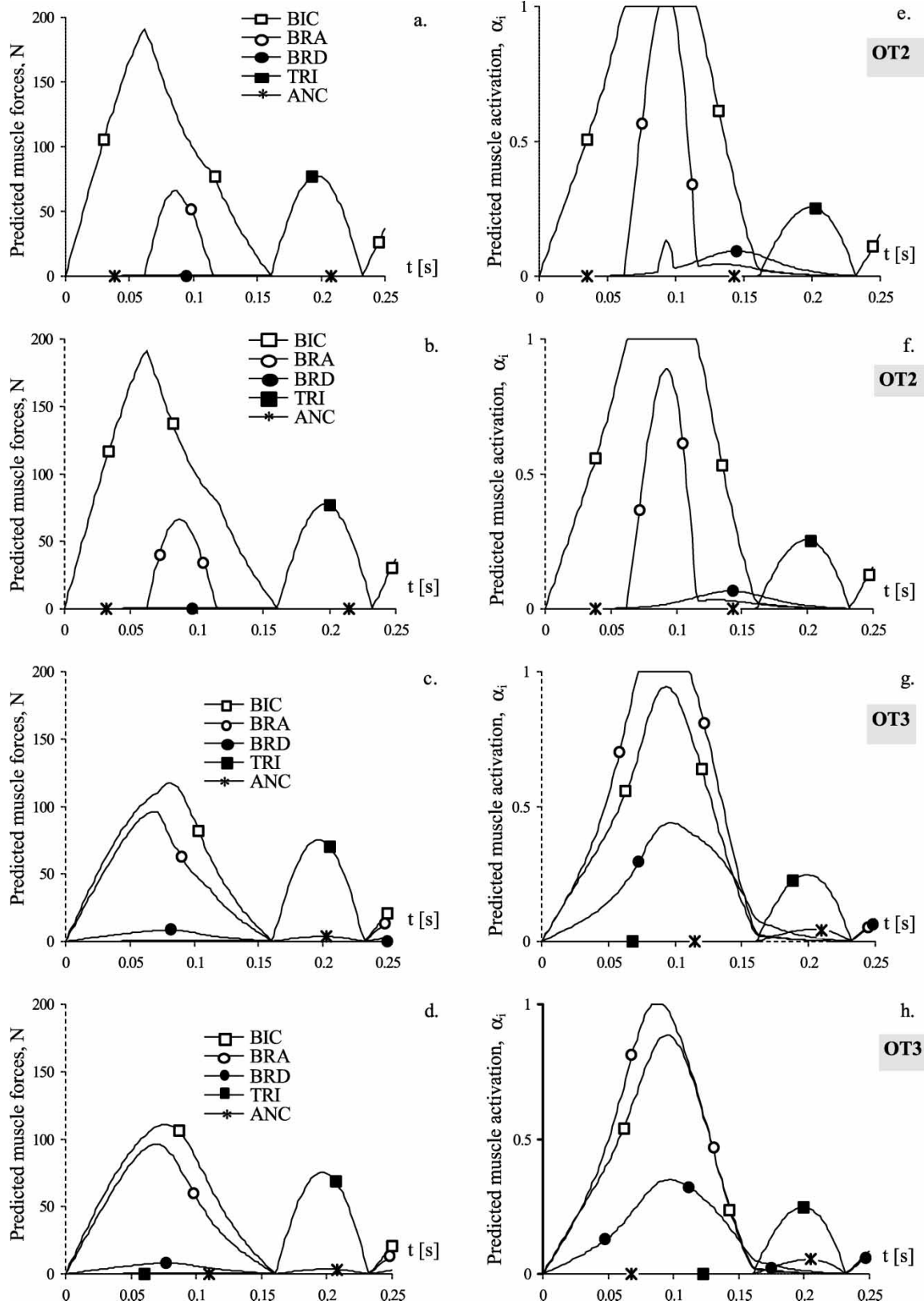
FIGURE 4   Muscle forces (first vertical panel) and muscle activation α_i (second vertical panel) predicted by solving the optimization tasks OT2 and OT3. First horizontal panel: OT2, all muscles consist of 50% fast and 50% slow MUs, i.e. $k_i = 0.5$ for all i. Second horizontal panel: OT2, the muscles BRA, BRD and ANC consist of only fast MUs, i.e. $k_1 = 0.5, k_2 = 1, k_3 = 1, k_4 = 0.5, k_5 = 1$. Third horizontal panel: OT3, $n = 2$, all muscles consist of 50% fast and 50% slow MUs, i.e. $k_i = 0.5$ for all i. Fourth horizontal panel: OT3, $n = 2$, the muscles BRA, BRD and ANC consist of only fast MUs, i.e. $k_1 = 0.5, k_2 = 1, k_3 = 1, k_4 = 0.5, k_5 = 1$.
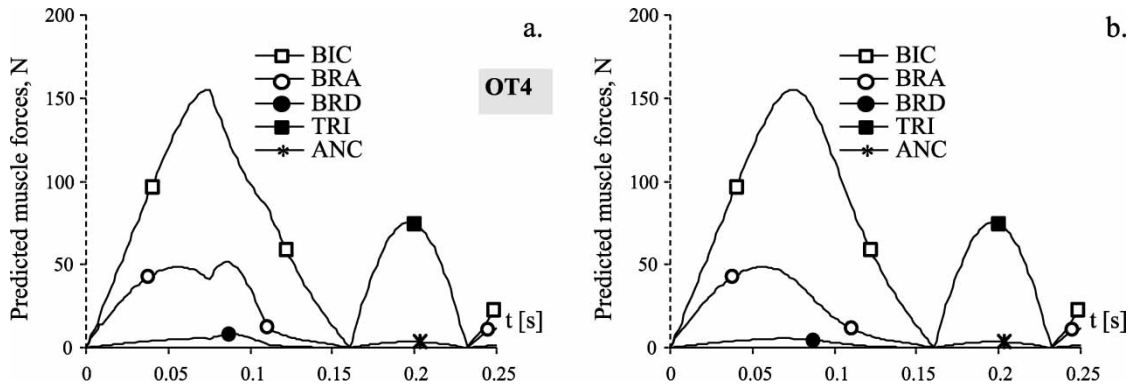
FIGURE 5   Muscle forces predicted by solving OT4 with $n = 2$. (a) All muscles consist of 50% fast and 50% slow MUs, i.e. $k_i = 0.5$ for all i. Upper limits for all muscles are taken into consideration. (b) All muscles consist of 50% fast and 50% slow MUs, i.e. $k_i = 0.5$ for all i. Upper limits, i.e. the inequality constraints: $0 \leq F_i \leq F_i^{max}(\ell_i, \dot{\ell}_i, k_i)$ are not imposed.

The longer m.ANC predicted force in comparison with other optimization tasks is again due to the necessity for activation of all fast MUs of the extensors, so that the deceleration phase of the movement is being performed. The change of the proportion between fast and slow parts in the muscles BRA, BRD and ANC influences their activation much more (Fig. 6c vs. 7c; Fig. 6d vs. 7d; Fig. 6e vs. 7e) in comparison with the optimization tasks in which the rheological muscle model was used. When the muscles become faster, their participation in the motion becomes more significant. The total activities of the faster muscles BRA, BRD and ANC increase considerably while they remain the same for m.BIC and m.TRI. This is clearly seen from the number of neural impulses applied on the MUs per each 1 ms time interval, i.e. the so-called "simulated EMG" by the authors (Figs. 6b–f and 7b–f). This number is not equivalent to the number of active MUs of a muscle, since one MUs may receive more than one impulse for the motion time and typical for fast motions doublets [35,36] are encountered.

DISCUSSION

The aim of the paper is to apply three different ways for muscle force modeling and to compare the results obtained by solving different optimization tasks based on these models. It is suitable to investigate a simple one DOF model for these purposes. The predicted muscle forces will be, of course, different if models with more DOF are used, but the main conclusions about the advantages or the disadvantages of some of the muscle models will be similar. Very fast elbow flexion is considered aiming to study the influence of the dynamic muscle properties and of interrelation between the fast and slow parts constituting a muscle. The phenomenological muscle model presented by Brown, Cheng and Loeb in Refs. [29,30] is used since it allows to separate the properties of slow and fast MUs and the constants in the force–length–velocity relationships for both MUs type, precisely obtained by natural experiments, are available.

Many scientists use such models relating muscle force proportionally to muscle activation, maximal isometric force, force–length and force–velocity relationships [37,38]. Hence, muscle activation is a parameter reflecting whole muscle control. Our interest was not to discuss the physiological meaning of this parameter and its relation with firing frequencies of the MUs or natural EMG signals.

There is no essential advantage with respect to the predicted muscle forces obtained by solving optimization tasks in which these forces are presented by a phenomenological muscle model, particularly regarding the antagonistic muscle co-contractions. The functions $\alpha_i(t)$ are supplements that give an additional information about the total muscle activity. A logical objective function when α_i are design variables is the linear sum of α_i, but the results from solving OT2 are not satisfactory (Fig. 4a,b). Rehbinder and Martin [37] proposed to use the sum of the squared muscle activation, i.e. $\min\sum_{i=1}^{5}\alpha_i^2$ in OT2. Notwithstanding that the arguments for doing this are not clear, we examined this criterion as well. Surprisingly, the results were very close to those obtained by solving OT4. The muscle forces' distribution was similar to the one shown in Fig. 5a. This similarity is due to the fact that the muscle force in the Eq. (5) is a linear function of α_i and the force of the passive elastic element PE1 is nearly negligible with respect to the other components of this equation. Actually, according to Eq. (5), the muscle force is a sum of two time-dependent functions, i.e. $F_i(t) = \alpha_i f_i^{(1)}(t) + f_i^{(2)}(t)$. The values of the function $f_i^{(1)}(t)$ are about thousand times greater that those of $f_i^{(2)}(t)$ for the whole movement duration for all muscles, hence $F_i(t) \approx \alpha_i f_i^{(1)}(t)$. Since $f_i^{(1)}(t) \approx F_i^{max}(t)$ (because the maximal muscle force is obtained for $\alpha_i = 1$), using the criterion $\min\sum_{i=1}^{5}\alpha_i^2$ is similar to using the criterion $\min\sum_{i=1}^{5}(F_i(t)/(F_i^{max}(t))^2$ if the optimization task is solved for every discrete t. According to Eq. (3), the relation between the predicted forces in the muscles from a synergistic group for the last criterion is $F_i/F_j = d_i(F_i^{max})^2/d_j(F_j^{max})^2$. There is a similar relation when the criterion is $\min\sum_{i=1}^{5}\alpha_i^2$. The similarity of Figs. 2a and 4d
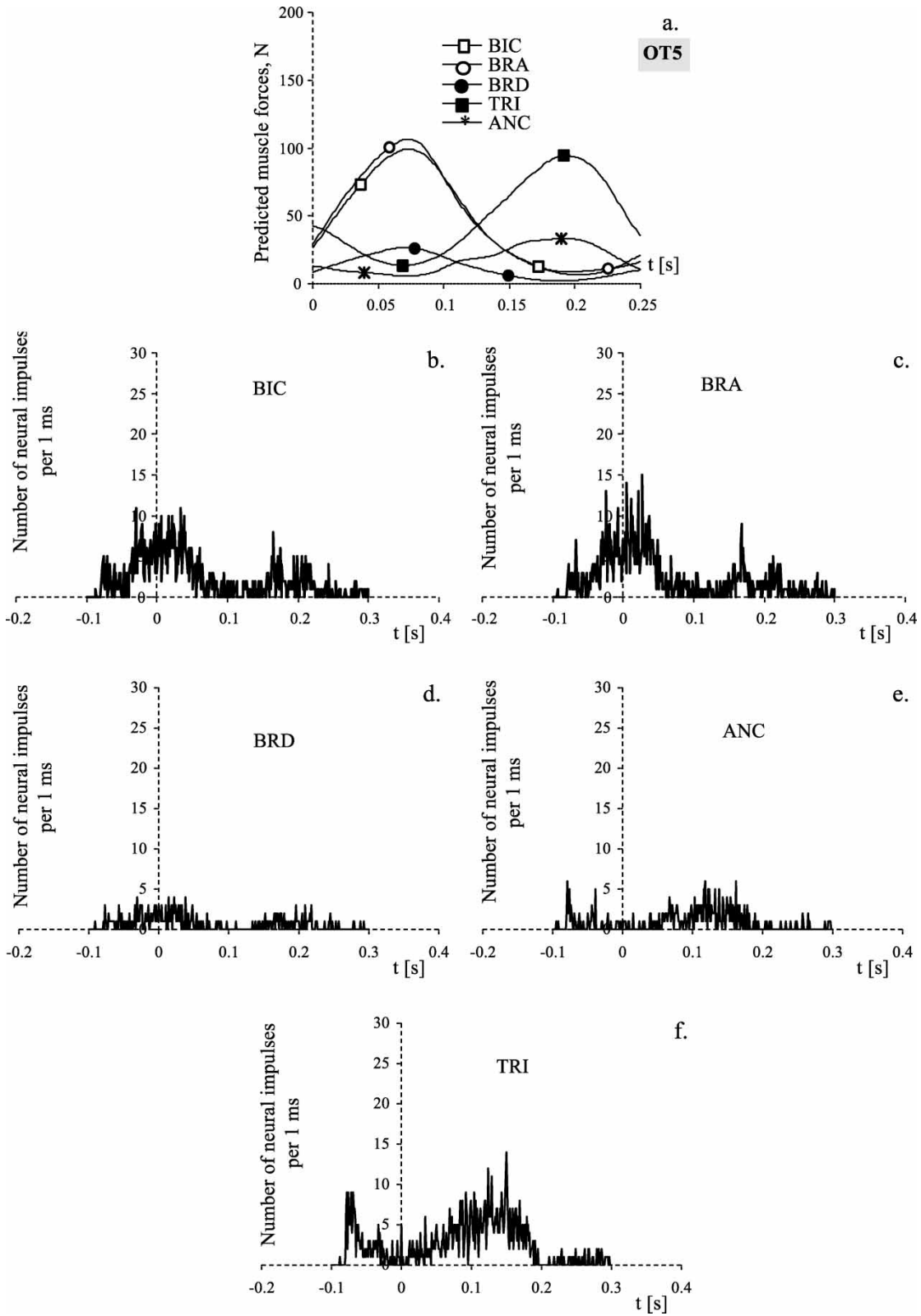
FIGURE 6   Muscle forces and activation predicted by MotCo software when all muscles consist of 50% fast and 50% slow MUs. The fitness function is: $1000 \times \Delta M + 1 \times \text{MUAct} + 1 \times \text{Sum}$. Figure (b)–(f) represents the number of neural impulses applied to the MUs of the respective muscle for every millisecond, i.e. the so-called "simulated EMG" by the authors (note that the time scale for these plots is longer than the ones for the other figures, because of the lead time influence).
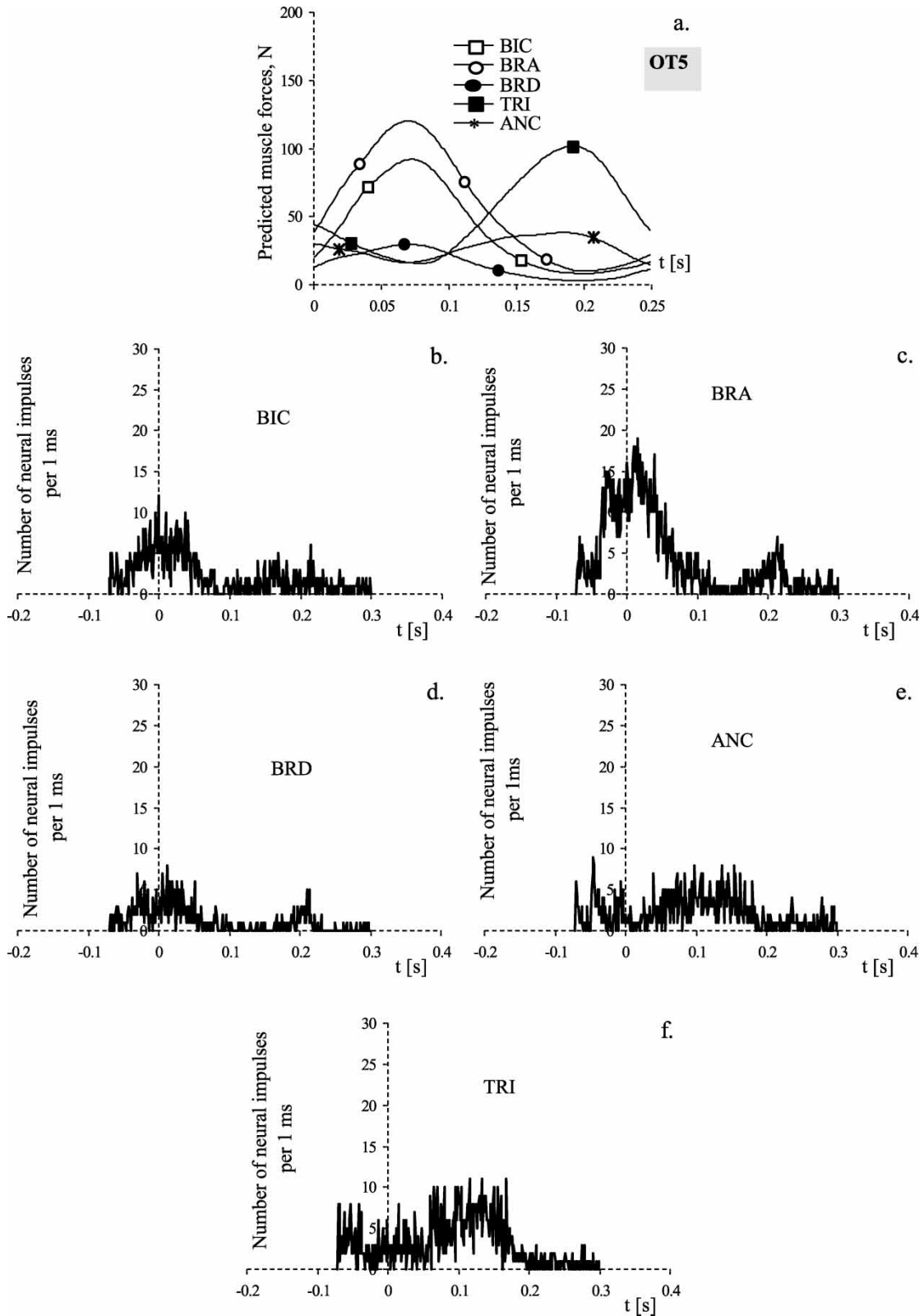
FIGURE 7   Muscle forces and activation predicted by MotCo software when the muscles BIC and TRI consist of 50% fast and 50% slow MUs, but the muscles BRA, BRD and ANC consist of 100% fast MUs. The fitness function is: $1000 \times \Delta M + 1 \times \text{MUAct} + 1 \times \text{Sum}$. Figure (b)–(f) represents the number of neural impulses applied to the MUs of the respective muscle for every millisecond (note that the time scale for these plots is longer than the ones for the other figures because of the lead time influence).

can be explained by such relations ignoring upper limits' constraints. Apart from the fact that the muscle forces are design variables for OT1 (Fig. 2a), but for OT3 (Fig. 4d) they are the muscle activations, the interrelation between the forces of the muscles from a synergistic group for both tasks, when $n = 2$, is $F_i/F_j = d_i(\text{PCSA}_i)^2/d_j(\text{PCSA}_j)^2$. In general, it could be proved that if the i-th muscle force is represented as a function of the muscle activation α_i, i.e. $F_i = f_i(\alpha_i)$, α_i are design variables and the optimization criterion is $\sum c_i f_i(\alpha_i)^n$, the muscle forces distribution will be the same as this obtained from applying static optimization with design variables F_i and the optimization criterion $\sum c_i F_i^n$. Hence, regarding the muscle forces' distribution, using such phenomenological models in optimization procedures does not lead to new solutions of the indeterminate problem. It seems more suitable to use such models for calculation of the maximal possible muscle forces for a given motion (Fig. 3) and to include these values in an objective function as this is proposed in Ref. [2], i.e. solving OT4 (see also Refs. [39,40]). These values strongly depend on contraction velocity and can change considerably the muscle force distribution (Fig. 5b vs. 2a) if the interrelation between the maximal forces of the muscles from one synergistic group changes during the motion. These maximal forces are subject to errors, however, since Eq. (5) includes many parameters specific for a muscle, they are very sensitive to the evaluation of the optimal muscle length, to the dependence of the muscle length from the joint angle and to the constants in the force–length–velocity relationship. Static optimization with design variables, simple muscle forces and quadratic objective function with PCSAs as weight coefficients can be used for dynamic conditions when objects of interest are general tendencies in motor control. Such an objective function as that from Eq. (6) with both positive and negative weight coefficients allows a derivation of a simple analytical solution even for models with more DOF [41].

It is questionable whether upper limit constraints $F_i \leq F_i^{\max}$ or $F_i \leq F_i^{\max}(\ell_i, \dot{\ell}_i, k_i)$ are necessary for formulating an optimization task, or they have to be included for choosing a suitable objective function. For the considered fast elbow flexion some maximal forces were reached when the contraction velocities of the muscles were very high (Figs. 4a–c and 5a). Note that the considered motion is an extreme case. The upper bound constrains cause somehow artificial and non-smooth inclusion in the movement of muscles that have not still reached their maximal forces (Fig. 5a vs. 5b). For computations with HGA, i.e. OT5, upper limits on the muscle forces were not imposed explicitly. Independent of this, the muscles can not exceed their physiological limits because of the maximal twitch force $F_{\text{MU}}^{\max}$. Comparing, however, the muscle forces presented in Figs. 6a and 7a with the maximal forces shown in Fig. 3, it can be seen that the predicted muscle forces of BRA and BRD are bigger than their $F_i^{\max}(\ell_i, \dot{\ell}_i, k_i)$ for $t \in (0.068\,\text{s}, 0.140\,\text{s})$. The MUs composing the modeled muscles, however, are able to

satisfy the required external joint moment with greater accuracy for the whole movement. This discrepancy can be due to non precise data for muscle lengths or to the constants used in the force–velocity relationship. Force–length–velocity relationships are obtained by an artificial, usually fixed and repetitive, muscle or nerve stimulation. Maybe, bigger muscle efforts can be developed during a natural, probably non-synchronized activation. The frequencies at which MUs reach their maximal forces are very different. They depend on their absolute refractory period (Fig. 1b). Obviously applying one and the same frequency for different MUs maximal activation of all MUs can not be provoked. Using the muscle model based on MUs artificial upper limit constraints are not needed. They are fulfilled indirectly, by setting the parameters of the twitches. If the forces, the type and the number of MUs are insufficient for performing a given motion, then this motion will not be performed and the required joint moment will not be satisfied.

The differences between the predicted muscle activation (Fig. 4e–h) and the predicted muscle forces (Fig. 4a–d) provokes a question concerning the use of EMG signals as means for verification of the modeled results. If α_i is considered as a global reflection of the control signals over a muscle (according to van Bolhuis and Gielen [38] α_i is "a measure for the amount of muscle activation"), an antagonistic co-contraction can be seen with respect to the muscle activations, but not with respect to the muscle forces (see Fig. 4g vs. 4c and Fig. 4e vs. 4a). For example, all α_i are different from zero for $t \in (0.16\,\text{s}, 0.23\,\text{s})$, but only m.TRI and m.ANC have nonzero predicted forces. The so called "simulated EMG" by the authors (Figs. 6b–f and 7b–f) that presents the number of neural impulses applied over the muscles for a given time period seems much closer to the surface EMGs than the predicted muscle forces. Hence, it seems more suitable to use this kind of available output of the MotCo software for comparison of the predicted results with some experimental ones than the muscle forces (see for comparison Fig. 3, pp.362 in Ref. [24] and Fig. 6b–f). Moreover, electromechanical delay is accounted for properly.

There is only limited data about the type and the number of MUs in the human limb muscles. In this paper, we considered only two hypothetical variants. For the first one all muscles consist of 50% fast and 50% slow parts. For the second numerical experiments we changed this proportion for the muscles BRA, BRD and ANC and they had only fast MUs aiming to see how the predicted results will change, but not because of evidence that muscles BRA, BRD and ANC are faster that m.TRI and m.BIC. Comparing these two variants for the optimization tasks where the rheological muscle model is used (Fig. 4a vs. 4b; Fig. 4c vs. 4d), the conclusion is that the interrelation between the fast and the slow parts of the muscles does not change the muscle force distribution apparently. The differences in the predicted muscle activation are bigger (Fig. 4e vs. 4f; Fig. 4g vs. 4h), but they are primarily due to

the fact that some of α_i reach their upper limits. The latter is connected with the change of the maximal muscle forces (Fig. 3). Maybe, the results will be different if the activation parameter is considered separately for slow and fast parts of the muscles, since the neural control of different MUs and their firing rates differ (Fig. 1b). This case, however, is not considered in the present paper, since the design variables will be twice greater than the simple muscle forces and the optimization tasks OT2 and OT3 will look different from OT1 and OT4. The differences between the predicted muscle forces by HGA when the muscles consist of different portion of fast MUs (Fig. 6a vs. 7a) are bigger than when the rheological muscle model is used. The change of the activities of the muscles BRA, BRD and ANC is too obvious (Fig. 6c vs. 7c; Fig. 6d vs. 7d; Fig. 6e vs. 7e). When all muscles consist of 50% fast MUs, the muscles BIC and BRA have nearly equally predicted forces since the number of their fast MUs is nearly the same. When m.BRA consists of only fast MUs, the HGA prefers its MUs and the predicted force of m.BRA increases in comparison with the force of m.BIC. The bigger difference between Fig. 6a and 7a is also due to the fact that the fast and the slow MUs differ not only in their maximal forces, but also in the time constants of their twitch form (see Table I). Even when all muscles consist of equal slow and fast parts, the contribution of the fast MUs to the total muscle force is incomparably bigger than the contribution of the slow MUs (Fig. 8). The HGA chooses what MU is suitable to be activated accounting for all parameters of the MUs twitches and probably this is the natural mechanism. Since the number of the neural impulses received from a muscle can be logically related

to registered EMG signals, it could be concluded that the latter depend significantly on the type of MUs that constitute the muscle. The observation that the activities of MUs, and hence the forces of the muscles, depend on the MUs type and the required motions, can help us to explain why for some motions small muscles such as m.ANC have a considerable activity. One of the reasons could be that caput longum of m.TRI is a biarticular muscle unit and during fast elbow motions it takes part in stabilization of the shoulder. So, probably using of its fast MUs is not so effective as using of the fast MUs of the monoarticular m.ANC. Another reason could be a deficiency of fast MUs in m.TRI, i.e. all fast MUs of all extensor muscles must be activated for performing the very fast elbow extension.

Considering a muscle as a mixture of different MUs significant antagonistic muscle co-contraction was predicted (Figs. 6a and 7a) and it was very different from this one shown in Fig. 2c (it has to be noted that solving OT1, it is impossible to predict non-zero muscle forces when the joint moment is zero). This muscle model can provide a physiologically based explanation of this experimentally observed phenomenon. Such co-contraction will be predicted by HGA even when the motions are slow and changes in the direction of the external joint moment do not exist. This is explained in detail elsewhere [22]. The main reason is the form of the MU twitch (Fig. 1a). The curve of the required joint moment is rather smooth. It is difficult to describe it by bell-shaped MU twitches. The twitches of the antagonistic muscle MUs produce moments with opposite direction and their superimposition make the movements more graceful. Another reason
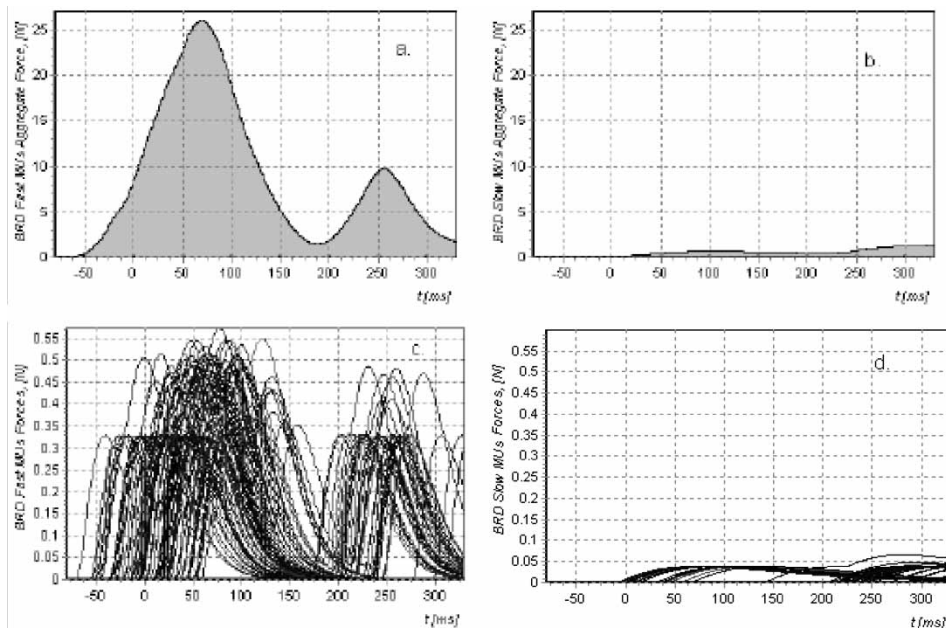

FIGURE 8 Contribution of the fast and slow MUs in the formation of the force of the whole muscle BRD from MUs twitches in the case when the muscle consists of 50% fast and 50% slow MUs. (a) The sum of the forces of all fast MUs. (b) The sum of the forces of all slow MUs. (c) The individual forces of all fast MUs. (d) The individual forces of all slow MUs.

for antagonistic co-contraction is the fixed time $(T_{tw} - T_c)$ that is necessary for the decrease of the force of an already activated MU to zero. When the joint moment changes very steeply, the antagonistic activity is necessary for compensation of the force of the previously activated MUs.

The difference between the muscle model, based on MUs and their twitches, and other ones is the highly nonlinear dependence between the activation (neural impulse) and the developed force (see Fig. 1). Rheological muscle models are not able to predict the twitch form [15]. It is possible to present each MU with separate constitutive equations as it is described in Cheng *et al.* [29], where a "Virtual Muscle" modeling package is presented, but we are not aware of reported investigations where this possibility is realized. Besides the problems with the necessary constants and activation signals for each MU, the problem with twitch prediction remains. The model considering a muscle as a mixture of MUs and calculating the whole muscle force on the base of the twitches of the individual MUs is closer to reality. The application of the developed MotCo software can provide a detailed insight into the motor control and can explain many physiological phenomena. It allows to investigate how motor synergies are achieved, to solve "indeterminate problems" avoiding the questions about the physiological interpretation of objective functions. There are many other advantages of employed approaches not considered in the present paper. A possibility for accounting for muscle fatigue is provided. Among the currently used criteria in the fitness function, many other time-dependent and time-independent ones can be added, thus motor tasks with other aims (for example, big accuracy of the end-point trajectory, posture support with minimum fatigue and so on) can be studied. The HGA presents a modeling means that is significantly closer to the natural way humans control their motor system. It mimics a trial and error method for training where the successful solutions are stored and further modified.

CONCLUSIONS

The main conclusions of the present paper are:

- modeling the muscle force output using Hill-type models does not help much when indeterminate problems are solved and does not give more realistic results; such presentation could be used for estimation of the current maximal muscle forces, which, for dynamic conditions depend much on the current muscle length and contraction velocity;
- since phenomenological muscle models are sensitive to many constants specific for each muscle and because of difference between the predicted muscle force and muscle activation, their application for direct calculation of the muscle forces using as input processed EMG signals is questionable;

- static optimization considering the musculotendon forces as design variables and using quadratic or cubic objective functions with weight coefficients related to the muscle PCSAs or maximal muscle forces could be used both for static and dynamic conditions (see also Ref. [42]) when one is interested in a global estimation of the muscle forces, joint moments and reactions;
- the muscle model based on MUs is more suitable for detailed investigation of the distribution problem and the control of the muscle activity, it is physiologically based and more realistic; the developed HGA based approach for finding the time moments of neural activation of all MUs allows to test many different optimization criteria and to trace how the muscle activity is changed during training.

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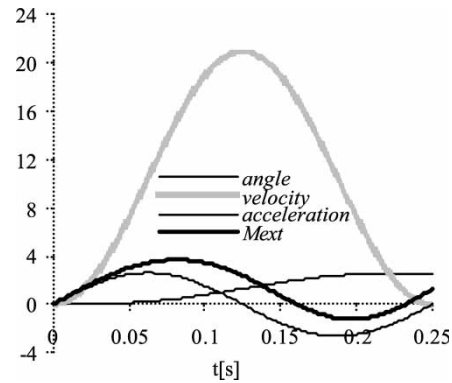
APPENDIX

FIGURE A1 Elbow angle, angle velocity, angle acceleration and external moment in the joint during the considered motion (a flexio from 0° to 150° for 0.25 [s]). The angle is given in radians, the velocity, in rad/s, the acceleration, in rad/s^2 (for better illustration, the true acceleration is divided by factor of 100), M_{ext} in [Nm].
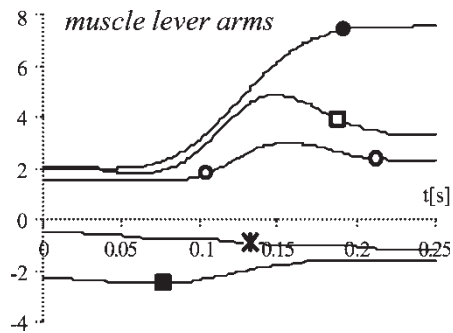

FIGURE A2 The muscle lever arms are calculated from the regression equations reported in Pigeon *et al.* [27] and Lemay and Crago [26]. They are given in centimeters. SYMBOLS: □ - BIC; ○ - BRA; ● - BRD; ■ - TRI; * - ANC.
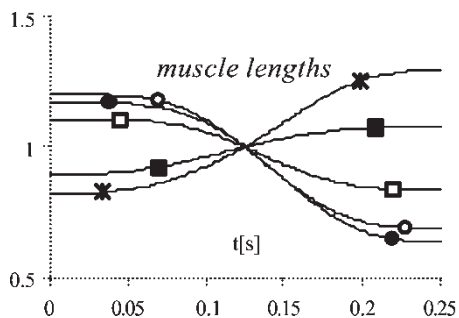
FIGURE A3   The muscle lengths are calculated from the regression equations given in Pigeon *et al.* [27] and Lemay and Crago [26]. They are normalized to the "optimal muscle lengths" L_{0i}. It is supposed that L_{0i} is the length of the *i*-th muscle at 75° flexed forearm, i.e. nearly to the middle of the anatomically admissible range of motions. The minimal shortening is 0.6384 of the optimal length and the maximal lengthening is 1.2918 of the optimal length. The symbols are the same as in Fig. A2.
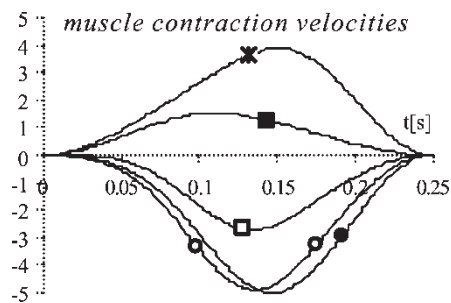

FIGURE A4   The contraction velocities of the muscles during the motions are calculated from the same regression equations and are again normalized to L_{0i}. Since the flexor muscles shorten during the whole motion, their velocities are negative, the opposite is true for the extensor muscles. The symbols are the same as in Fig. A2.