Simulation of the motor units control during a fast elbow flexion in the sagittal plane

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Abstract

The fact that muscles are composed of different Motor Units (MUs) is often neglected when investigating motor control by macro models of human musculo-skeletal-joint systems. Each muscle is associated with one control signal. This simplification leads to difficulties when mechanical and electrical manifestations of the muscle activity are juxtaposed. That is why a new approach for muscle modelling was recently proposed (Journal of Biomechanics 2002;35:1123–1135). It is based on MUs twitches and a Hierarchical Genetic Algorithm (HGA) is implemented for choosing the moments of activation of the individual MUs, thus simulating the control of the nervous system. Its basic benefit is obtaining the complete information about the mechanical and activation behaviour of all MUs, respectively muscles, during the whole motion. Its possibilities are demonstrated when simulating fast elbow flexion. Three flexor and two extensor muscles, each consisting of approximately real number of different types of MUs, are modelled. The task is highly indeterminate and the optimization is performed according to a fitness function that is an assessed combination of criteria (minimal deviation from the given joint moment, minimal total muscle force and minimal MUs activation). The influence of the weight of the first criterion (the one that reflects the importance of the movement accuracy on the predicted results), is investigated. Two variants concerning the muscle MUs structure are also compared: each muscle is composed of four distinct types MUs and the MUs twitch parameters are uniformly distributed.
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1. Introduction

The control of the human limb motions has been investigated by using macro-biomechanical models, paying attention to the muscle synergy and total individual muscle forces [31,32]. It is accepted that the muscles performing motions are single force generators (i.e. muscle is a functional unit) and it is supposed that the human nervous system controls each muscle by one control signal (neural input) [18,44]. Since the number of the unknown muscle forces exceeds the number of the moment equations, different optimization techniques are used (for review see [33]). Whatever design variables (i.e. muscle forces [34] or muscle activation signals [36]) have been used in various optimization tasks (under dynamic or static conditions), the fact that the muscles are composed of different motor units (MUs), which are actually subjects of control, has been neglected. The great number of MUs in the muscles (e.g. the biceps brachii has 774 MUs ([37], see also [2])) makes the usage of conventional optimization techniques very difficult. The macro-biomechanical models can not give an image of how the individual MUs work and how are they controlled. The nervous system controls the muscle force by including/excluding MUs and by changing their discharge pattern, i.e. through recruitment and rate coding [40]. The force developed by an MU due to a single impulse (twitch) is a non-linear, bell-shaped time function. The repetitive impulses cause an increase of the mechanical output of the MU reaching unfused or fused tetanus [5], and this force is a very complex time function. That is why it is impossible to reconstruct the forces of individual MUs from the total muscle force, predicted by optimization methods. On the other hand, the usage of processed surface electromyographic signal

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(EMGs) as a control signal [25] over the whole muscle is also questionable, since this signal is not linearly proportional to the percent of active MUs. In addition, a demarcation between different MUs types is hard to be made with EMGs, while their mechanical properties are very different. An experimental validation of the predicted muscle forces by static optimization is often performed through processed surface EMGs. Generally, such a validation is doomed to failure not only for well known problems [1,16,27,30,38,39,43] with suitable registration and processing of these signals and questionable relationship "muscle force—EMGs", but also because the summations of the twitches into the total muscle force and the summation of the action potentials into the surface EMGs are two very different processes. The result of the second process depends essentially on the position of the electrode, and hence on the disposition of the MUs within the muscle [6].

Experimental methods based on surface or intramuscular EMGs can give information for discharge patterns of individual MUs, however the simultaneous precise registration of the human MUs individual forces in vivo is difficult. The decomposition of surface EMGs [23] meets problems concerning the identification of individual MUs. The usage of intramuscular electrodes faces the problem of selectivity and gives information about a limited number of MUs. Using only electrical evidences for the MUs activity, it is difficult to separate the MUs into the three main types: slow, fast-twitch fatigue resistant and fast-twitch fatiguable MUs. Thus, the role of this differentiation during various motions can not be investigated. As to the force developed by an MU, much has been done by Celichowski [5], but only by performing animal experiments with artificial stimulation with constant frequencies. The "twitch interpolation" method [11] does not assure that an individual MU twitch is registered. As for the spike-triggered averaging method for twitch parameters registering in vivo, its restrictions are discussed in [8,20].

The approach, which was recently proposed by the authors [35] and implemented in MotCo software package (http://motco.dir.bg), combines the merits of the methods discussed above and can supply us with broad information about the functioning and control of MUs. Here, the muscle is not considered a single force generator, but a mixture of MUs with different peculiarities. The aim is to find such control of all MUs, so that a given motion is performed. Independently of the simulative nature of the approach, comparing the simulation results with experimental ones, the parameters of the model can be justified, so that the model approximates reality well enough. Simulations can give information unattainable by means of natural experiments. For example, the time moments of inervation and the respective mechanical responses of *all* MUs are software outputs, MUs can be classified as slow, intermediate and

fast, different muscle diseases can be modelled, and the movements with different purposes can be compared. Like other models, the results of simulations with MotCo software package can not be directly associated with particular physiological cases, especially bearing in mind the lack of information about MUs in living human muscles and the dependence of simulation results on many model parameters. It is, however, a useful tool for teaching, demonstration purposes and sensitivity analysis. The previously reported simulations [35] were made aiming to compare the new approach with static optimization and were performed with a small number of MUs composing the muscles. Increasing this number to a real one increases the computational cost greatly and this is the main disadvantage of the approach. Modelling the muscles with a real number of MUs, however, can give more correct images about MUs functioning and more suitable parameters for comparison with experimental data.

The aim of the paper is to show the possibilities of MotCo package for simulation of elbow flexion in the sagittal plane with a duration of 350 ms modelling all muscles participating in this motion by a real number of MUs. The motor task is represented by a fitness function, that is a weighted sum of three criteria: minimal deviation from the given joint moment, minimal total muscle force and minimal MUs activation. The weight coefficient at each criterion determines its importance and adjusts the measurement units. The differences between the predicted results for the following two cases are investigated: (1) each modelled muscle consists of 25% fast-fatiguable, fast-fatigue resistant, intermediate and slow MUs; (2) the parameters of the MUs twitches are continuously distributed. Also studied is the influence of different movement purposes by varying the weight coefficient at the joint moment goal, thus emphasising on the greater accuracy of the motion performance (increasing this weight coefficient) or on the smaller total muscle force and MU activation (decreasing this weight coefficient).

2. Methods

2.1. Elbow model

A fast elbow flexion in the sagittal plane is simulated. The model has one degree of freedom. The arm is fixed vertically. The forearm and hand are modelled as one rigid body [35] that performs a fast flexion from 0° (full extended forearm) to 150° (full flexed forearm) with a duration of 350 ms. A symmetrical sinusoidal law for the angle velocity and acceleration has been accepted in good agreement with data reported for ballistic motions (for details see [35]). It is supposed that three muscles take part in the elbow flexion—BIC (m.biceps brachii),

BRA (*m. brachialis*) and BRD (*m. brachioradialis*) and two muscles perform extension—TRI (m.triceps brachii) and ANC (*m. anconeus*). The lever arms of the muscles depend on the joint angle and are calculated using literature regression equations [24,28]. The moment equation with respect to the axis of flexio/extensio in the elbow has the form:

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

where F_i are the muscle forces; d_i are the moment arms of these forces; M_{ext} is the external joint moment; G and I_{zz} are the gravity force and the inertial moment of the hand and forearm; $\ddot{\varphi}$ is the angular acceleration; l_G is the distance from the axis of rotation in the joint to the application point of G. The used data for the present calculations are average values: $l_G = 0.18$ m, $I_{zz} = 0.01087$ [kg.m^2 and $G = 13.72$ N (http://motco.dir.bg/Data/index.html).

2.2. MUs modeling

It is supposed at first that all muscles consist of four basic types of MUs, namely: fast-twitch fatiguable (FF), fast-twitch fatigue resistant (FR), intermediate (IM) and slow-twitch (S). The total number of MUs of the modelled muscles has been chosen proportionally to the physiological cross-sectional areas (PCSA) (the basic value is 774 MUs for BIC [37]). Hence, the number of MUs of BRA is 804, of BRD is 193, of TRI is 685 and of ANC is 180. It is supposed that all muscles have a nearly equal percentage of MUs from all types. The basic parameters of the twitches of MUs (see Figs. 1 and 2) are given in Table 1. It is supposed then that the time parameters of the twitches of the MUs within a muscle are uniformly distributed from the minimal value (first row of Table 1) to the maximal value (last row of Table 1) with the increments given in Table 2. The increment of the maximal twitch amplitudes (ΔF_{MU}) is calculated in accordance with the maximal forces of the modelled muscles that are calculated by their PCSA.

2.3. Hierarchical genetic algorithm (HGA) for simulation of the MUs activity

The approach and the algorithm are presented elsewhere [35]. A brief, simplified description is given below. The MU twitch (the mechanical response of a MU to one neural impulse) has a specific bell-shaped form that depends on the MU type (Figs. 1 and 2). It has been approximated by an exponential function (see [35]). Repetitive neural stimuli with interpulse time interval greater than the absolute refractory period[1] (T_{ref})
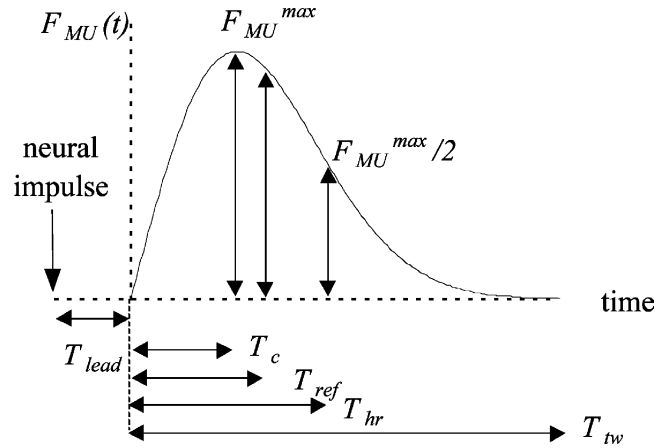
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[1] All temporal parameters in the text are connected with the mechanical manifestation of the MU, but not with the electrical one.

Fig. 1. 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 of the MU and the start of the mechanical activity; T_c—"contraction time": time interval between the start of the MU contraction and the time for which the MU force reaches its maximum; T_{ref}—"absolute refractory period": during this time the MU is unable to response to new neural impulses, for the present simulations $T_{ref} = T_c$; 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}. Note that in the literature this term is usually related to the time interval T_{hr}-T_c; T_{tw}—duration of the twitch.
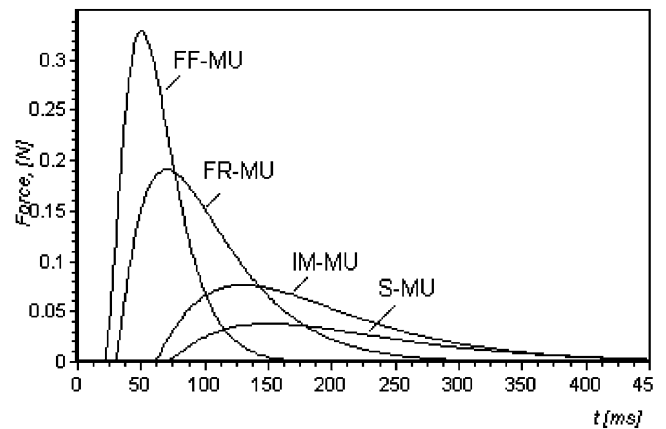

Fig. 2. The twitches of the MUs from the four distinct types: fast-twitch fatiguable (FF), fast-twitch fatigue resistant (FR), intermediate (IM), slow-twitch (S).

Table 1
Parameters of the four types MUs considered

MU type	Twitch parameters				
	T_{lead} [ms]	T_c [ms]	T_{hr} [ms]	T_{tw} [ms]	F_{MU}^{max} [N]
FF	20	30	60	120	0.3288
FR	30	40	100	240	0.191
IM	60	70	175	420	0.0764
S	70	80	200	480	0.0382

Table 2
Increments for calculation of the twitch parameters of the MUs when they are uniformly distributed. Each temporal characteristic of the *i*th MU of the respective muscle is calculated by the equation $T_{(*)}(i) = T_{(*)} + i.\Delta T_{(*)}$, where $T_{(*)}$ are the time parameters from the first row of the Table 1, $i = 0,1,2,...,$ Num-1 and Num is the number of the MUs of the respective muscle. The maximal amplitude of the *i*-th MU twitch is calculated in a similar way, but the increment ΔF_{MU} is computed so that the sum of the tetanus forces of all MUs of a muscle is equal to the maximal possible force of this muscle. The maximal forces of the modelled muscles are calculated by multiplying their PCSA by the value of 50 N/cm^2 and they are as follows: 268.5 N for BIC, 277.5 N for BRA, 66.5 N for BRD, 236.5 N for TRI and 62 N for ANC

Muscle	ΔT_{lead}	ΔT_c	ΔT_{hr}	ΔT_{tw}	ΔF_{MU}	number of MUs
BIC	0.0647	0.0647	0.181	0.466	−0.00028701	774
BRA	0.0623	0.0623	0.174	0.448	−0.00027489	804
BRD	0.260	0.260	0.729	1.875	−0.00114833	193
TRI	0.07299	0.07299	0.204	0.526	−0.00032188	685
ANC	0.279	0.2793	0.782	2.011	−0.00123138	180

cause superposition of the twitches up to unfused or fused tetanus [5,29]. The total muscle force can be determined from the time moments of neural activation of its MUs. That is why these moments have been chosen as design variables of the model. These variables are called "genes" of the "individual" in the terms of the genetic algorithm. They represent a potential solution of the optimization task. The HGA is inspired by the natural evolution where only the fittest individuals survive. The algorithm uses genetic operations (mutation and crossover) that modify and combine separate solutions (individuals). Then, a set of better solutions is chosen (i.e. fittest individuals survive) according to some fitness function, and genetic operations are applied again. The fitness function, *FitFun*, measures to what extent the current solution satisfies a set of criteria. In the present paper the used fitness function is an assessed combination of the following criteria: ΔJ—minimal total error between the desired (computed from eq. (1)) joint moment and the joint moment computed as sum of the muscle forces (obtained by the predicted mechanical activity of the MUs) multiplied by their lever arms; *Sum*—minimal sum of all predicted muscle forces; *Act*—minimal muscle activation, i.e. minimal total number of impulses. Hence:

$$FitFun = k_1\Delta J + k_2 Sum + k_3 Act, \qquad (2)$$

where k_1, k_2 and k_3 are constants.

3. Results

Three simulations were performed:

- flexion with duration 350 ms with the basic four types of MUs and coefficients in the fitness function $k_1 = 100$, $k_2 = 1$ and $k_3 = 1$;
- flexion with duration 350 ms with coefficients in the fitness function $k_1 = 100$, $k_2 = 1$ and $k_3 = 1$, but with uniformly distributed MUs;
- flexion with duration 350 ms with the basic four types

of MUs, but with different coefficients in the fitness function, namely $k_1 = 20$, $k_2 = 1$ and $k_3 = 1$; $k_1 = 30$, $k_2 = 1$ and $k_3 = 1$; $k_1 = 40$, $k_2 = 1$ and $k_3 = 1$; $k_1 = 50$, $k_2 = 1$ and $k_3 = 1$; $k_1 = 60$, $k_2 = 1$ and $k_3 = 1$.

Some results from the first simulation (performed with the four basic types MUs (see Fig. 2 and Table 1)) are shown in Figs. 3–6. The coefficient k_1 in the fitness function (eq. (2)) is a hundred times greater than the other two coefficients. As a result, the required elbow joint moment (bold line in Fig. 3a) is satisfied well within the time interval [0, 350 ms]. A preceding period of 80 ms and a subsequent period of 50 ms are also included in all figures, aiming to show the muscle behaviour before the start and after the end of the motion (see the discussion in [35]). The calculated joint moment (grey line in Fig. 3a) is the sum of the moments of all predicted muscle forces. These moments are obtained by multiplying the predicted forces of all modelled muscles (Fig. 3b) by their lever arms. The contribution of the four MUs groups in formation of the total force of m.BRA is shown in Fig. 3c. The force of each muscle is the sum of the mechanical responses of all its MUs (Fig. 4a) to the activation chosen by HGA (Fig. 4b). Samples of the mechanical responses of three MUs from each type are given in Fig. 4c–f. Having the time moments of impulsation of all MUs (Fig. 4b) different activation characteristics can be calculated. The so-called "simulated EMG activity" is presented in Fig. 5a–e. These graphics show the number of impulses received by all MUs of the respective muscle within a given time interval (in the present example this interval is one millisecond). In order to separate the participation of different groups of MUs, all characteristics can be obtained individually for each group (see Fig. 5f–i). Other MUs characteristic, often used in experiments in vivo, is the interpulse interval. In Fig. 6 the histograms of the interpulse intervals (the time intervals between two consecutive discharges of a MU) of all modelled muscles are presented.
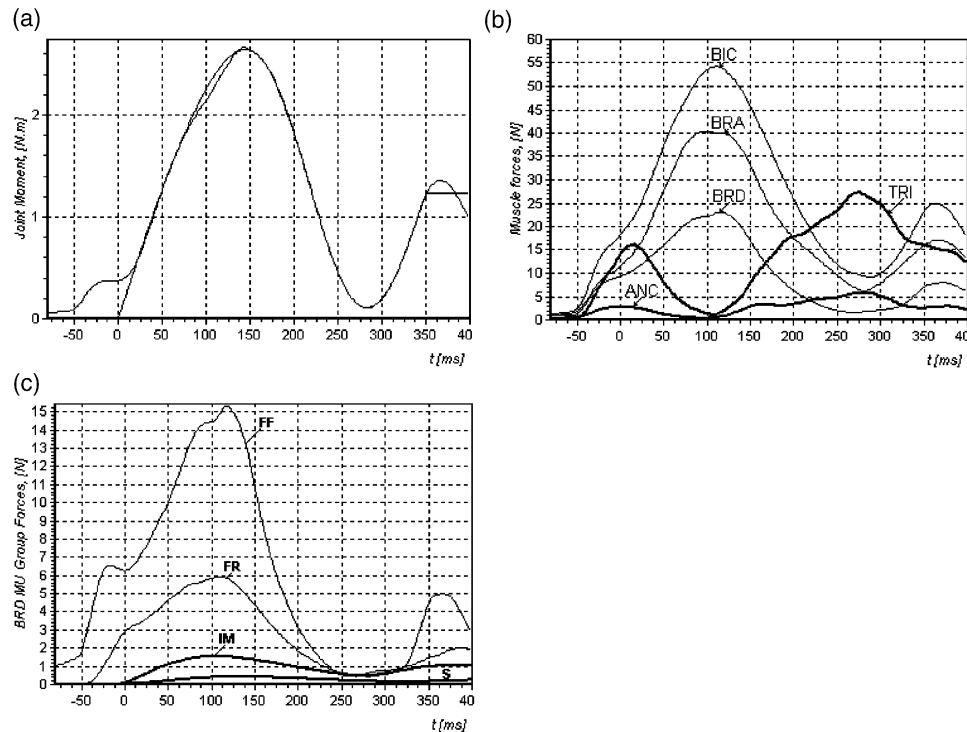
Most results from the second simulation, where the

Fig. 3. The results from the simulation, when four distinct types of MUs are considered and the weights in the fitness function are $k_1 = 100$, $k_2 = 1$ and $k_3 = 1$. a) required (bold line) and calculated (grey line) joint moment; b) calculated muscle forces; c) the contribution of the four MUs types to the formation of the total force of muscle BRD.

parameters of the MUs were uniformly distributed, were very similar to those obtained in the previous case. The main difference was found in the distribution of the interpulse intervals (Fig. 7). The predicted muscle forces were smoother (not shown by a figure), but not pronounced.

Changes in the weights of the fitness function considerably influence the predicted muscle forces' distribution (Fig. 8). When $k_1 = 20$ an antagonistic activity is not predicted, when $k_1 = 30$ a little force appears in m.TRI, when $k_1 = 100$ besides m.TRI an appreciable activity in m.ANC is predicted. We shall note that for $k_1 \leq 30$ the force of the m.BRD is greater than the force of m.BRA, while for $k_1 \geq 40$ this order changes. This fact can be explained by the greater moment arm of m.BRD compared with m.BRA during the whole range of elbow angle.

4. Discussion

The main purpose of the paper is to show the possibilities of the authors' approach to motor control study. The previously reported simulations [35] were performed with about ten times less MUs composing the muscles. Increasing this number to a realistic one, the computational cost increases greatly but, the benefit is a more realistic image about functioning of the MUs and the whole muscles. Knowing the motor task (i.e. defining it by the required joint moment (Fig. 3a)) and the aim of the motion (represented by the fitness function) the total forces of all modelled muscles are predicted (Fig. 3b). So, the force-sharing problem is solved. Since the mechanical responses of all MUs are known (Fig. 4a), the contribution of the different MUs groups in forming the total muscle force can be distinguished (Fig. 3c). Since the exact time moments of firing of each MU are known (predicted by HGA—Fig. 4b), different activation characteristics can be derived. The number of impulses applied over all muscle MUs during a given time interval (Fig. 5a–e) shows its total activity during the motion. When the number of MUs is a realistic one (for a comparison see Fig. 6 in [35] where this number was about ten times less), these graphics are more suitable for comparison with experimentally measured EMGs than the predicted muscle forces (Fig. 3b), since they are closer in nature to the electrical manifestation of the muscle activity. Actually, the "simulated EMG activity" is proportional to the number of neural impulses, it does not depend on the mechanical properties of the MUs and it is not delayed time as in the mechanical activity does. The histograms of the interpulse intervals (Figs. 6 and 7) give information about the average and the temporal frequencies of MUs discharging. They can be separately derived for different MUs types, which implies the existence of a possibility
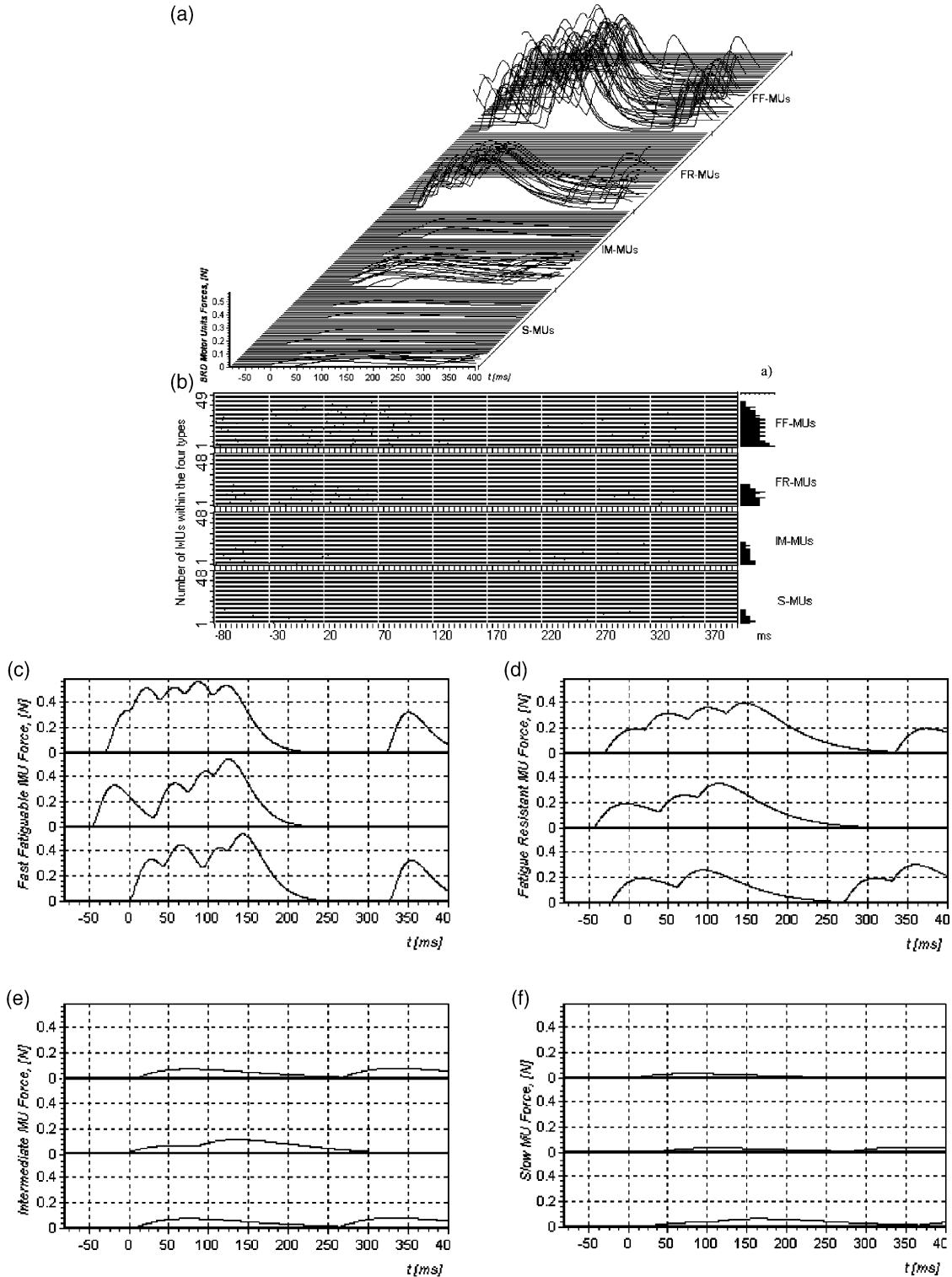
Fig. 4.   Mechanical responses of MUs of muscle brachioradialis during the whole motion and the corresponding time moments at which each MU receives its impulses. a). mechanical responses of all MUs which are arranged in the following order: slow (S), intermediate (IM), fast-twitch fatigue resistant (FR) and fast-twitch fatiguable (FF); b). time moments at which each MU is activated. Two MUs are presented within each row (a little up and a little down). Each point corresponds to one neural impulse. The bars in the right correspond to the total number of impulses of the respective MU; c–d). mechanical responses of some FF, FR, IM and S MUs of the same muscle.
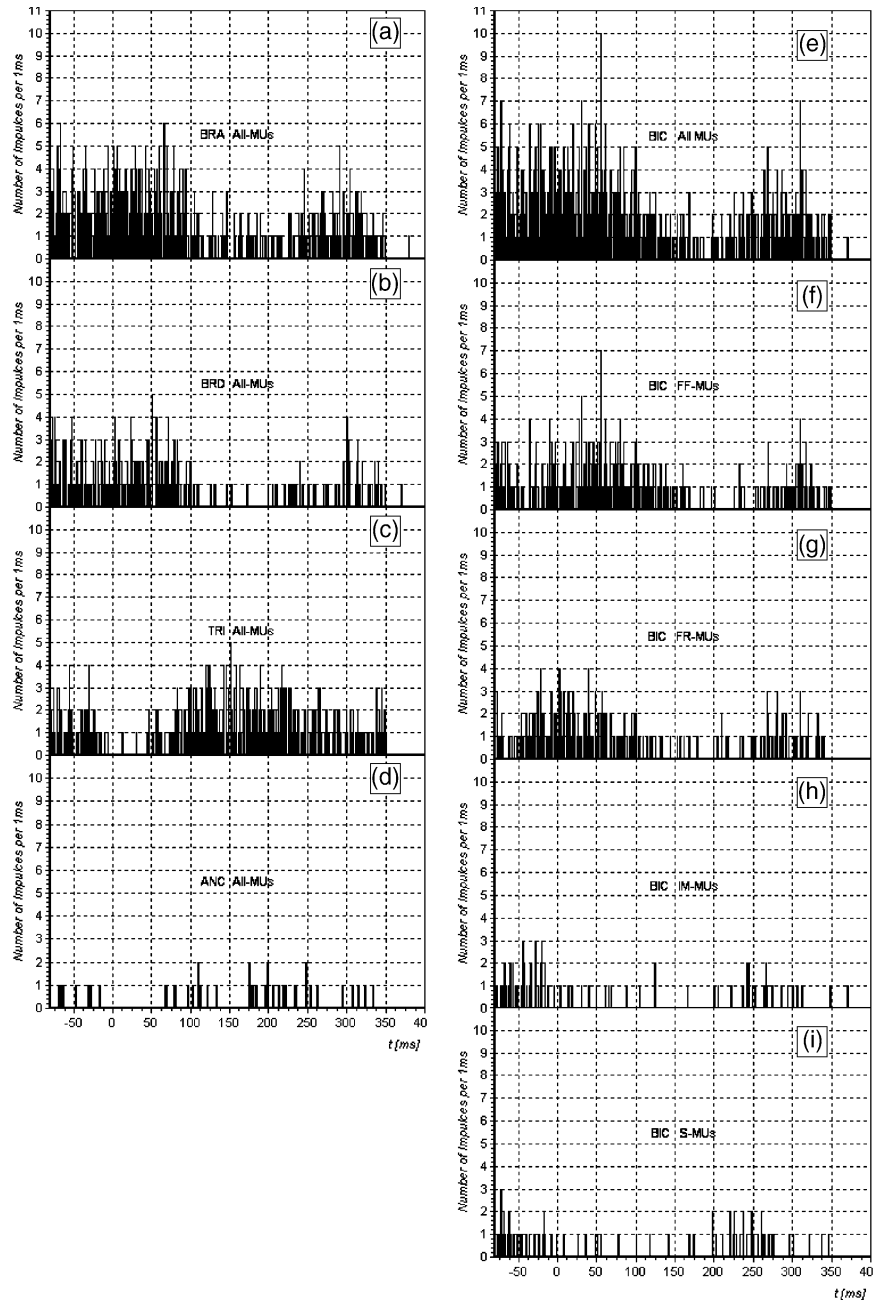
Fig. 5. "Simulated EMG activity". (a)–(e) the number of the neural impulses received by the MUs of the respective muscles within each time interval of one millisecond; (f)–(i) the number of neural impulses received separately by the four distinct types of MUs composing the muscle BIC.

for investigating the differences in their control during various motions.

The main question is to what extent do the simulation results resemble reality. It is difficult to give an answer to this question because of insufficient data from real experiments and because of many model parameters which can vary. The total mechanical effect of all muscles acting in the elbow joint can register, yet not the individual muscle forces (and this hampers the suitable choice of the weight coefficients in the fitness function—Fig. 8). Moreover this refers to the MUs twitches and

the choice of their suitable number and parameters. As discussed in the Introduction, there are problems with the usage of experimentally measured surface or intramuscular EMGs for validation of the predicted muscle forces and for assessment of the activity of separate MUs. Surface EMGs depend on the distance between the electrode and the signal source, and signals coming from neighbouring muscles can not be precisely separated, i.e. the cross-talk effect exists. Intramuscular electrodes can not register all muscle MUs during the motion. However, independently of the simulative nature
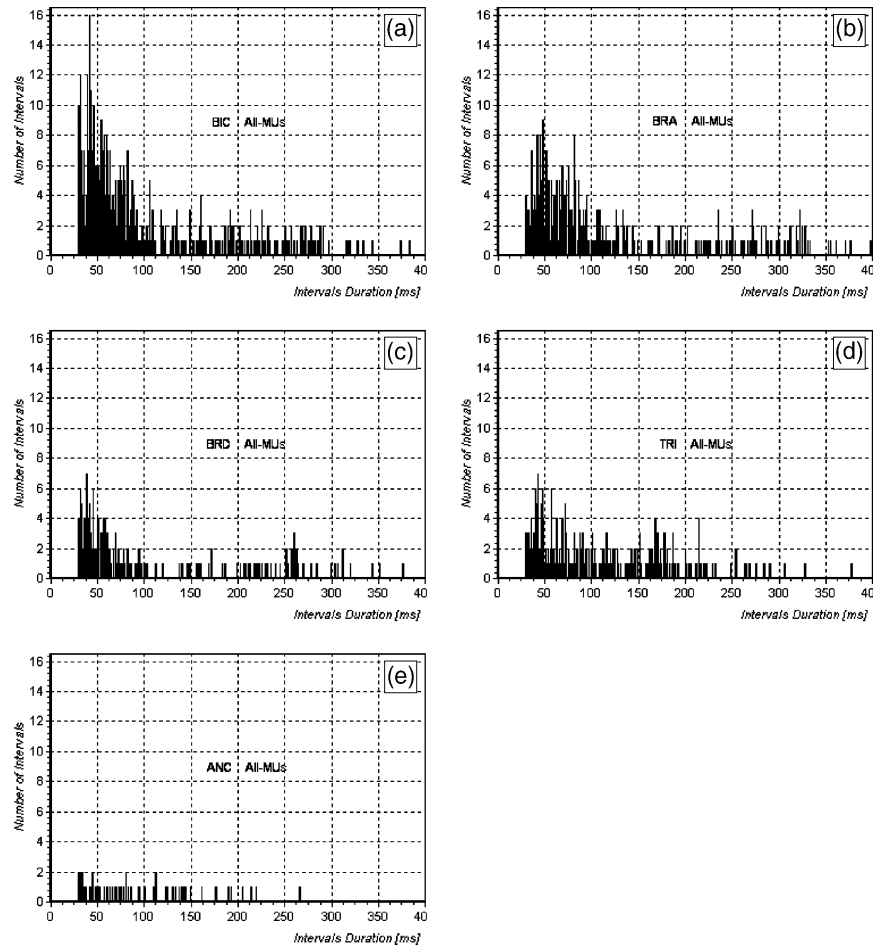
Fig. 6. Distribution of the interpulse intervals for all five modelled muscles during the whole movement when muscles consist of four types of MUs. Each bar represents the number of interpulse intervals with the corespondent duration (for example the last bar in the right for m.ANC means that only one interpulse interval between 270 ms and 280 ms is found among the activation of all MUs of this muscle).

of our approach, the predicted results suggest some general conclusions. The given joint moment is well described with the predicted by HGA MUs activation for all numerical experiments, except a small time interval around the start of the motion, and another one after the end of the motion. We shall mention that the implemented HGA produces highly consistent results during multiple runs and it is able to provide solutions independently of the model parameter changes. The reasons for the differences between the desired and calculated joint moment between 0 and 20 ms (note that the optimization has been performed only within the time interval 0–350 ms) is probably the unrealistically modelled abrupt start of the motion (see also discussion in [35]). The predicted total muscle forces show a behaviour that is typical for ballistic motion [12]—first apparent burst of the flexors, increasing extensors' activity during the deceleration phase of the motion and final flexors' activity (Fig. 3b, see for comparison [10]). There exists a significant overlapping of the forces of the muscles from the antagonistic groups and apparent synergistic actions (note that the behaviour of the extensors

is different when the aim of the motion is changed, see Fig. 8 and discussion below). The observed initial apparent burst of m.TRI in Fig. 8b–f can be due to the analytical model of the considered joint moment, again. The rather steep increase of the joint moment can not be obtained only by summing the fast MUs twitches of the flexor muscles. Such an initial burst of all muscle forces (see Fig. 8f) can also be due to the preparation for the motion.

As expected, the contribution of the fast MUs is predominant (Fig. 3c), since the simulated motion is rather fast. As for the MUs mechanical responses, a force similar to unfused tetanus is observed for some fast MUs (Fig. 4c and d). The duration of the simulated motion is too short for making more conclusions about any tetanic behaviour and fatigue investigation. The same refers to the "size principle". The modelled joint moment is nonlinear, with steep acceleration and deceleration phases. This necessitates the participation of all fast MUs independently of their maximal forces. The most frequently observed interspike intervals have been about 50 ms (Figs. 6 and 7) for all muscles, which means an average
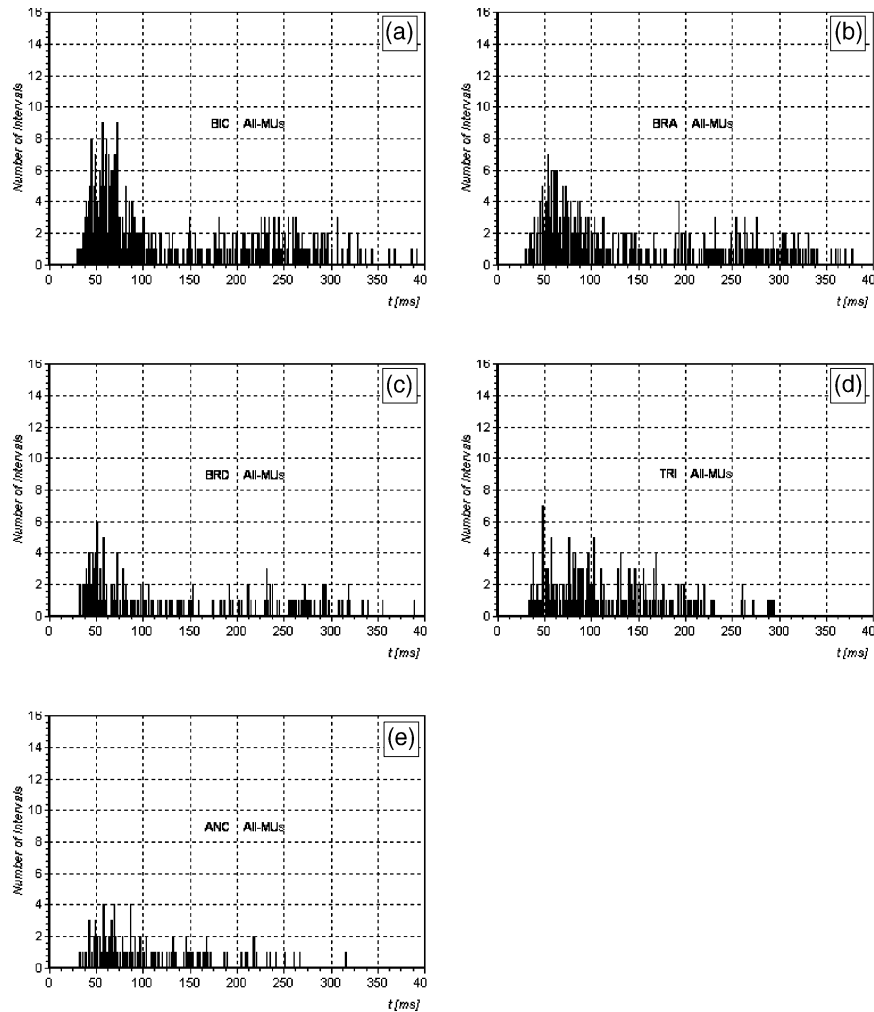
Fig. 7.   Distribution of the interpulse intervals for all five modelled muscles during the whole movement in case when the parameters of the MUs are uniformly distributed.

frequency of 20 Hz. Milner-Brown et al. [26] report that normal interpulse intervals for a human finger muscle is between 140 and 50 ms and the normal physiological range of frequency is 8–20 imp/s. Carpentier et al. [4], investigating voluntary contractions of a small muscle in a human finger report maximal firing rate of 30 Hz. Gydikov et al. [15], investigating maximal voluntary contraction at elbow joint report a value of 22 imp/s for *m. biceps* brachii. The maximal firing rates of MUs of *m. brachialis* during rapid cyclic elbow movements reported in [41] are around 30 Hz. Some authors report shorter inter-spike intervals [13,14,20], even less than 20 ms. We did not predict inter-spike intervals less than 30 ms because of the accepted values of the twitch parameters, namely $T_{ref} = T_c \geq 30$ ms (see Table 1). These parameters can be easily changed through the program interface if the actual ones are known. The distribution of the inter-spike intervals (respectively the average firing frequencies) does not differ essentially among the muscles from a synergistic group (Figs. 6 and 7). This finding differs from the observations of van Groeningen

et al. [42], who found differences in MUs activation of m. BIC and m. BRD. Le Bozec and Maton [22] also reported essential differences between the firing rates of m. TRI and m. ANC. These differences can be due to various proportions between fast and slow MUs in these muscles, while in the present simulations they were chosen equally. According to Le Bozec and Maton [22] m. ANC has about 62.9% slow fibres and m. TRI about 36.2%. Muscle BRA also seems to be faster than m. BIC [17]. However, we shall emphasize that these data concern the muscle fibres, but not the MUs. That is why in this paper we proposed that the MUs composition of all muscles was the same. Further simulations will consider cases with different muscle compositions. Lacking information about both the composition of the *living* human muscles from different MUs [3] and about the characteristics of their twitches in vivo, we only tested the hypothesis of some authors [19] that the twitch parameters of different MUs are distributed continuously. The contraction times and half-relaxation times reported for some human hand muscles [4,7,9,21] are widely dis-
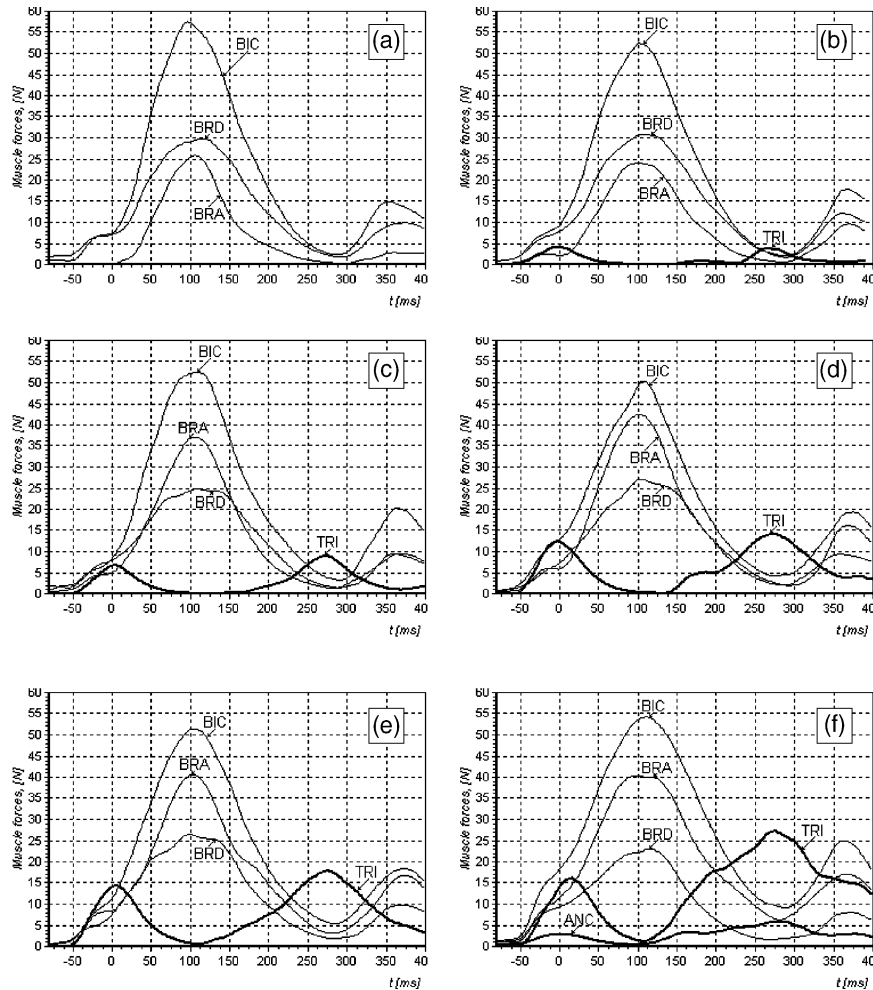
Fig. 8. Predicted muscle forces for different weights in the fitness function when muscles consist of four types of MUs. a) $k_1 = 20$, $k_2 = 1$ and $k_3 = 1$; b) $k_1 = 30$, $k_2 = 1$ and $k_3 = 1$; c) $k_1 = 40$, $k_2 = 1$ and $k_3 = 1$; d) $k_1 = 50$, $k_2 = 1$ and $k_3 = 1$; e) $k_1 = 60$, $k_2 = 1$ and $k_3 = 1$; f) $k_1 = 100$, $k_2 = 1$ and $k_3 = 1$ (this figure is the same as Fig. 3b, but is plotted for comparison).

tributed among average values. Our parameters (Table 1) fitted well with these average values. In order to investigate whether the MUs twitch parameters have a significant influence on the predicted results, numerical experiment was held, supposing that the muscle MUs are not strictly distributed among four distinct MUs groups, but are uniformly distributed. The results were very similar to those obtained with the four distinct types of MUs, with the sole difference of the smoother distribution of the interpulse intervals (Fig. 7) and smoother predicted muscle forces. The great number of the MUs in a real muscle and the relatively small influence of an individual MU force over the behaviour of the whole muscle provide an adequate explanation of this result. The greater smoothness can be due to the wider diversity of the MUs twitch forms, which prevents local bulges that can be obtained by the superposition of twitches with identical parameters.

The basic control mechanism in the simulations is the fitness function (see eq. (2) and Fig. 8). It is a combi-

nation of different criteria with clear physiological meaning. The relative importance of each criterion can be tuned up changing the weight coefficient k_i of the respective criterion. In the present paper it has been investigated how the predicted muscle forces change when the accuracy demands of the movement vary. The results show that the motion may be performed without antagonistic co-contraction (Fig. 8a), with little participation of m. TRI (Fig. 8b), or with participation of both extensors, m. TRI and the small m. ANC (Fig. 8f). The greater is coefficient k_1, the more precisely is the motion performed and the greater co-contraction is observed (see also [35] for interpretation). These coefficients can be justified according to the instructions given to the subjects and comparing temporarily the EMGs of the main muscles involved in the motion. The flexion movement in the sagittal plane with a duration of 350 ms was chosen intentionally. With chosen mass-inertial parameters, the external moment (Fig. 2a) is always positive, but about 280 ms comes near zero. So, the action of the

extensor muscles is not obligatory (Fig. 8a). Depending on the requirements for preciseness of the motion, our approach can predict antagonistic co-contraction in various extents. Should the same motion be performed in the horizontal plane, however, the joint moment will have both positive and negative phases (because of the absence of the moment of the gravitational force) and nonzero forces of TRI and ANC will be strictly necessary.

5. Conclusions

The proposed approach and the implemented software are capable of supplying us with extensive information about the individual muscle forces and the mechanical responses of their motor units, as well as about the neural control during a motor act, which is unattainable by experimental methods. Thus it is a useful tool for teaching, simulation and demonstration purposes. Independently, on the simulative nature of the approach the obtained results are in accordance with the data available in literature. Since the parameters of the MUs twitches are inputs in the software, they can be adjusted to the experimental measured ones, so that the results are closer to the reality. These parameters change during fatigue, ageing, and different muscle diseases, and hence these processes can also be investigated. Further simulations with more degrees of freedom models are also forthcoming.

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