

RELATIONSHIP BETWEEN MECHANICAL COST FUNCTIONS AND MUSCLE OXYGEN CONSUMPTION

M. Praagman¹, H.E.J. Veeger^{1,2}, F.C.T. van der Helm², and E.K.J. Chadwick²

¹Faculty of Human Movement Sciences, Institute for Fundamental and Clinical Human Movement Sciences, Vrije Universiteit Amsterdam, Amsterdam, The Netherlands.

²Man-machine Systems Group, Department of Mechanical Engineering, Delft University of Technology, Delft, The Netherlands

INTRODUCTION

In biomechanical studies inverse-dynamic models are often used to predict muscle forces. The distribution of those forces among the muscles is often calculated by optimising a cost function, assuming that movements are controlled in an optimal manner. Unfortunately the quantity optimised in real life is unknown and only assumptions can be made. Many different cost functions have been proposed (see Tsirakos et al. 1997 for an overview). Although a few are based on physiological reasons, most cost functions are chosen rather arbitrarily. Non-linear cost functions provide physiologically more realistic results than linear cost functions, since linear cost functions predict sequential recruitment of muscles instead of load sharing. (Tsirakos et al. 1997).

It is often assumed that in real life movements are performed minimising energy consumption (Hardt, 1978; Van der Helm, 1991; Alexander, 1997) yet only a few cost functions predicting energy consumption have been proposed (Hatze and Buys, 1977; Hardt, 1978; Alexander, 1997). Equations such as those proposed by Hatze and Buys (1977) or Zahalak and Ma (1990) can be used to calculate energy consumption, but require parameters that are often unknown for human muscles. Instead most cost functions are mechanical cost functions based on muscle force (F), often weighted by physiological cross sectional area (PCSA) or maximal force (F_{max}) (Tsirakos et al., 1997). Although some of them are supposed to be related to physiological costs like energy consumption or fatigue, clear relationships have never been proven.

The aim of this study was to analyse the relationships of two mechanical cost functions (the well known minimum stress cost function and a newly-proposed energy-related cost function) with experimentally determined muscle oxygen consumption. The energy-related cost function represents both the cross-bridges in parallel and in series, whereas the stress cost function only accounts for the cross-bridges in parallel. Since the metabolic cost of a muscle is the summed cost of the sarcomeres it was expected that the energy-related cost function would be a better representation of energy consumption than the stress cost function

METHODS

The stress cost function is one of the most commonly used optimisation criteria and minimises squared muscle stress (Crowninshield and Brand, 1981):

$$\text{MIN} \sum_{i=1}^n \left(\frac{F_i}{PCSA_i} \right)^2 \quad (1)$$

of which Prilutsky (2000) stated that it is likely that this criterion leads to economy of metabolic energy expenditure.

The energy-related cost function proposed here, is based on the two major energy consuming processes in the muscle: the detachment of cross-bridges and the re-uptake of calcium. Under isometric conditions the number of attached cross-bridges is linearly related to muscle force. When the same muscle force is maintained with longer muscle fibres, more sarcomeres are in series and more cross-bridges are attached. Therefore the energy consumption rate for detachment must be scaled by muscle fibre length (l_f):

$$F \cdot l_f \quad (2)$$

The re-uptake of calcium can be described by the product of muscle volume and active state:

$$V \cdot \alpha \approx V \cdot (F / F_{max}) \quad (3)$$

A combination of Eq. 2 and 3 leads to the final cost function:

$$\text{MIN} \sum_{i=1}^n m_i \left(\frac{c_1 F_i}{PCSA_i} + c_2 \left(\frac{F_i}{F_{i,max}(l,v)} \right)^2 \right) \quad (4)$$

in which m is muscle mass and fibre length is represented by $m/PCSA$. c_1 and c_2 are constants.

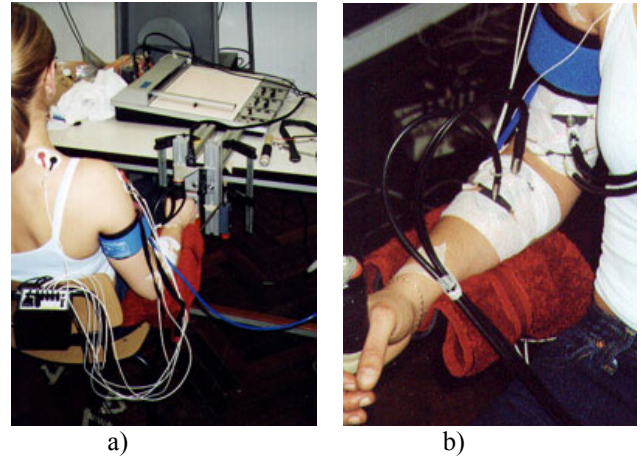


Figure 1: Experimental set-up. a) Moments were measured using a vertical handle, which was fixed to a six-degree-of-freedom force transducer and placed in front of the subject. b) NIRS data were measured with fibre optic cables that were attached to the skin above BB and BR. EMG electrodes were placed on the skin in between the cables.

To achieve an indication of energy consumption in vivo experiments were done in which muscle oxygen consumption ($\dot{V}O_2$) was measured with Near InfraRed Spectroscopy (NIRS). NIRS is a non-invasive method to determine tissue oxygenation, based on oxygen-dependent absorption changes of haemoglobin. Near Infrared light is

transmitted through the muscle tissue by two fibre optic cables, at three different wavelengths (905, 850 and 770 nm) and the absorption of the light is measured. The changes in absorption at the discrete wavelengths can be converted into changes in concentration of oxyhaemoglobin (O₂Hb) and deoxyhaemoglobin (HHb) using a modified Lambert-Beer law in which a path length factor (DPF) is incorporated to correct for scattering of photons in the tissue (Colier et al., 1992). When measurements are done during arterial occlusion and the DPF is known, it is possible to quantify muscle oxygen consumption. The blood supply to the muscle ceases due to the occlusion, therefore the decrease of [O₂Hb] reflects the oxygen consumption of the muscle. From the gradient of the [O₂Hb] decrease, the oxygen consumption per unit of time ($\dot{V}O_2$) can be calculated.

Subjects were seated in a chair with their right arm slightly abducted and flexed forward and their forearm in a neutral and horizontal position, holding a vertical handle with their right hand (Figure 1a). This handle was fixed to a six-degree-of-freedom force transducer (AMTI 500), which recorded the forces and moments the subject applied to the handle. The position of the subject was recorded by measuring the 3D co-ordinates of bony landmarks on the thorax, clavicle, scapula, humerus, ulna and radius, with a 3D digitiser (Pronk, 1991).

NIRS measurements were performed on four arm muscles, m. biceps caput breve (BB), m. biceps caput longum (BL), m. brachioradialis (BR) and the m. triceps caput laterale (TL). Two continuous-wave, near-infrared spectrophotometers (OXYMON, Artinis Medical Systems, Arnhem, The Netherlands.) (Van der Sluijs, 1998) were used (inter-optode distance of 4 cm and a DPF of 4.3), which made it possible to measure the haemoglobin concentrations of two muscles simultaneously (Figure 1b). Simultaneously surface EMG of the muscles was recorded (inter-electrode distance of 1.7 mm, 1000 Hz sample frequency, analog low-pass filter of 400 Hz).

Subjects were asked to perform isometric contractions exerting several moment combinations around the humero-ulnar and radio-ulnar joints: flexion (FL), flexion-supination (FS), flexion-pronation (FP), extension (EX), extension-supination (ES) and extension-pronation (EP). All contractions were performed at three force levels: 10%, 25% and 50% MVC. As soon as the required force level was achieved, an arterial occlusion was applied by inflating a thin cuff around the upper arm. The periods of occlusion and force production varied from 20 to 30 seconds depending on the force level and each period was followed by a period of rest to recover. The [O₂Hb] and [HHb] as well as the external forces and moments were recorded continuously. EMG was recorded during the periods of force production only.

For each subject the orientations of the skeletal elements were calculated from the measured 3D co-ordinates, following the protocol described in Van der Helm (1997a). The individual 3D orientation of the skeletal elements as well as the measured external forces and moments were input to an inverse-dynamic musculo-

skeletal model of the shoulder and elbow (Van der Helm, 1994; 1997b). Both cost functions were used for the optimisation. For each subject the model predicted muscle forces of 31 shoulder and elbow muscles and for the BB, BL, BR and TL the individual cost values were calculated.

The predicted cost values as well as $\dot{V}O_2$ and EMG values were normalised for each subject and muscle. Linear regression and correlation were performed to evaluate the relationship between $\dot{V}O_2$ and cost. T-tests for independent values were used to analyse whether there was a significant difference between muscle activation predicted by the model, measured by $\dot{V}O_2$ or registered by EMG.

RESULTS

Extension and flexion moments generated by the subjects varied between -19.4 Nm (\pm 3.6) and 16.2 Nm (\pm 3.4) and supination and pronation moments varied between -2.5 Nm (\pm 0.8) and 3.1 Nm (\pm 1.6). Both EMG and $\dot{V}O_2$ increased linearly with increasing load. T-tests showed no significant differences between normalised $\dot{V}O_2$ and normalised EMG values for any of the muscles.

Optimising stress led to a good correspondence between $\dot{V}O_2$ and cost for the TL (Table 1 and Figure 2). However for the three flexor muscles cost values were significantly lower than $\dot{V}O_2$ values (Figure 2). If the cost function is a measure of energy consumption it is expected that normalised $\dot{V}O_2$ values would be equal to normalised cost values. The conditions for which the difference between $\dot{V}O_2$ and cost was larger than 10% could be divided into four categories (Figure 3):

- cost differed from $\dot{V}O_2$ but not from EMG;
- the magnitudes differed but the activation patterns were in general comparable;
- the model predicted no muscle activity while $\dot{V}O_2$ did show activity;
- $\dot{V}O_2$ showed no activity while the model did predict activity.

While for the first category it is likely that the difference is caused by an error in the $\dot{V}O_2$ determination, the latter three categories are probably related to the model or cost function.

Table 1. Regression equation, correlation coefficient (R) and root mean square error (RMS) for the relationship between $\dot{V}O_2$ and cost (predicted with the stress cost function ($f1$) or the energy-related cost function ($f2$)) defined by $\dot{V}O_2 = a \cdot \text{cost} + b$

Muscle	f	a	b	R	RMS
BB	1	0.96	7.89	0.91	12.15
	2	0.92	3.83	0.94	9.91
BL	1	0.80	10.71	0.70	22.10
	2	0.88	7.39	0.86	15.67
BR	1	0.85	5.55	0.83	14.83
	2	0.92	1.12	0.95	8.67
TL	1	0.96	1.40	0.96	8.11
	2	0.82	0.96	0.93	11.30

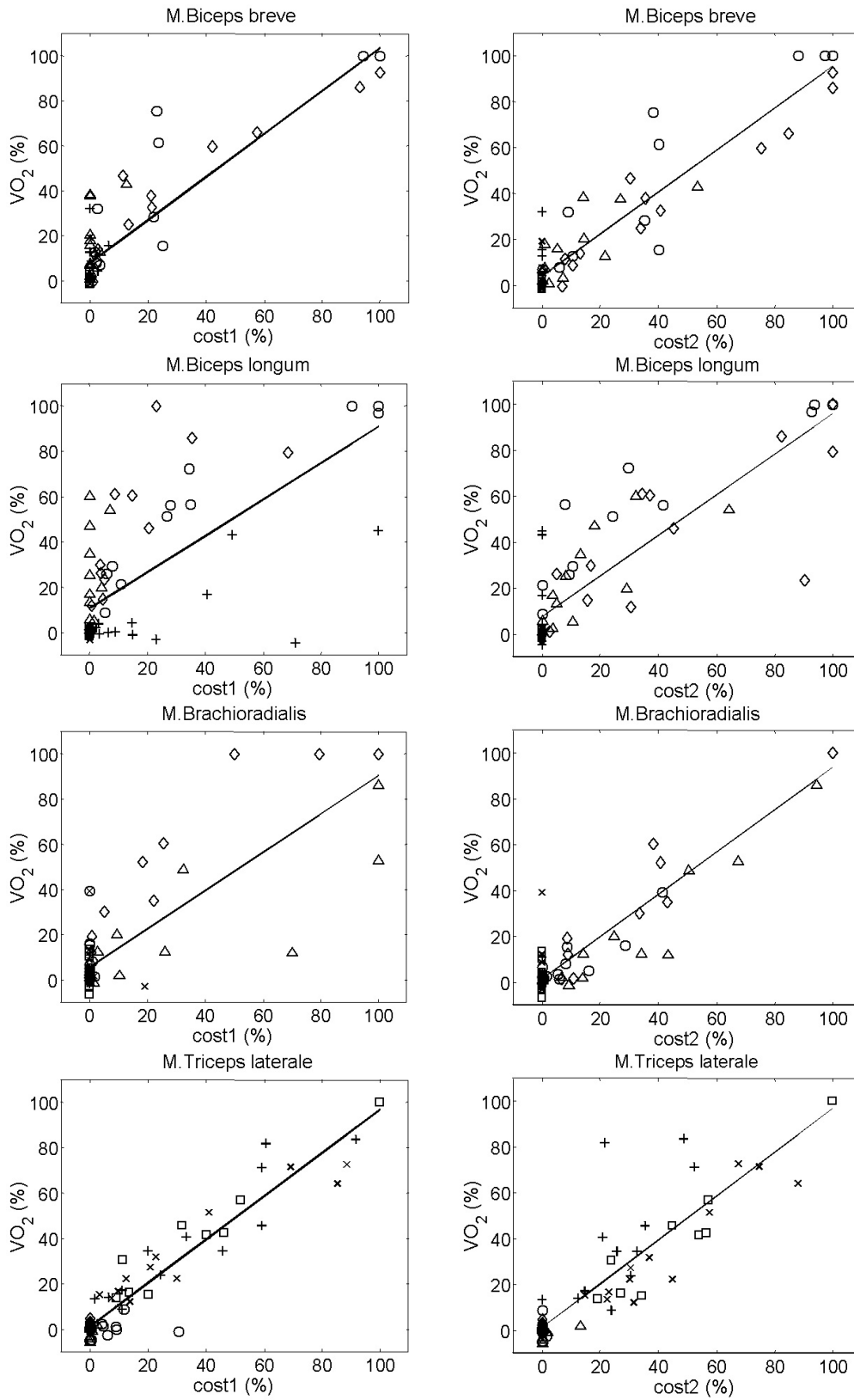


Figure 2. $\dot{V}O_2$ (n=4) plotted against cost predicted with the stress cost function (left) and the energy-related cost function (right). The different symbols represent the different contractions: \diamond :FL, O:FS, Δ :FP, \square :EX, +:ES, x:

Using the energy-related cost function instead of the stress cost function a far better correspondence between cost and $\dot{V}O_2$ was achieved for all three flexor muscles (Figure 2 and Table 1). T-tests did not show any significant differences between cost and $\dot{V}O_2$ for any of the muscles. The number of conditions in which the difference between $\dot{V}O_2$ and cost was above 10% was decreased and the remaining differences were mainly differences in magnitude and not in activation pattern. There were only a few cases in which the model predicted no muscle activity while $\dot{V}O_2$ did show activity or vice versa (Figure 3).

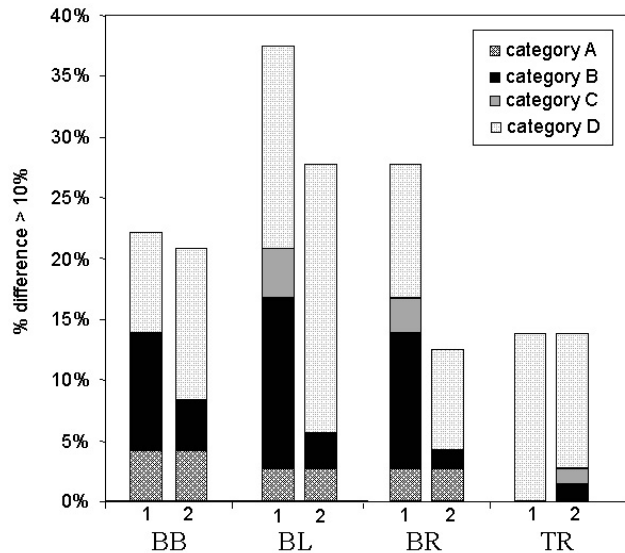


Figure 3: The amount of conditions (%) in which the difference between $\dot{V}O_2$ and cost exceeds 10% (see text) for the stress cost function (1) and the energy-related cost function (2), divided into four categories: (a) error in $\dot{V}O_2$ recording, (b) difference in magnitude but not in activation pattern, (c) model predicted no activity while $\dot{V}O_2$ did show activity, (d) $\dot{V}O_2$ showed no activity while the model did predict activity.

DISCUSSION

In the present study the correspondence to $\dot{V}O_2$ of two different cost functions was evaluated: the well-known stress cost function and the newly-proposed energy-related cost function. Both cost functions were based on mechanical properties related to muscle force and can be used by any inverse dynamic model. There are two main differences between the stress cost function and the new energy-related cost function: (1) the energy-related cost function consists of not only a quadratic term but also a linear term and (2) the energy-related cost function represents both the cross-bridges in parallel and in series by including not only PCSA but also muscle mass. The stress cost function accounts only for the cross-bridges in parallel. Since the metabolic cost of a muscle is the summed cost over the sarcomeres it was expected that the energy-related cost function would be a better representation of energy consumption than the stress cost function.

When the stress cost function is minimised, the predicted load sharing depends on the product of moment arm and squared PCSA (Dul et al., 1984). Using the energy-related cost function, it is not only muscles with large moment arms and large PCSA's that are preferred but also those with small masses and short fibre lengths. In addition the linear component will affect the load sharing since a linear term leads to sequential recruitment whereas quadratic terms lead to synergism.

In this study no significant differences between EMG and $\dot{V}O_2$ were found. This corresponded to an earlier study in which we found a linear relationship between EMG and $\dot{V}O_2$ during isometric contractions (Praagman et al., 2003). In the present study EMG was used to filter possible errors in the $\dot{V}O_2$ determination. The conditions in which $\dot{V}O_2$ differed from cost, where at the same time no difference between EMG and cost was found, were discarded.

Predicted cost values were compared to $\dot{V}O_2$ values measured during isometric contractions in which combinations of flexion-extension moments and pro- and supination moments were generated. Subjects were seated with the elbow flexed and the forearm in a neutral position. From a mechanical point of view flexion moments are supposed to be mainly generated by both heads of the m. biceps (BB and BL), the m. brachialis and the m. brachioradialis (BR). Extension moments will be mainly produced by all three heads of the m. triceps. Due to the neutral position of the forearm it was expected that the BR would not contribute to required pro/supination moments. Supination moments were expected to be produced by the BB, BL and the m. supinator, and pronation moments by the m. pronator quadratus and m. pronator teres. The BB and BL will directly be influenced by the external pro/supination moments due to their function as supinators. Changes in the activity of the BB and BL will alter the total load sharing and hence both BR and the lateral head of the triceps (TL), as well as other muscles, can be indirectly influenced by pro/supination moments as well.

It is unrealistic to expect complete agreement between $\dot{V}O_2$ and cost for two reasons: (1) the position of the subjects was not recorded continuously therefore it is possible that minor changes in position occurred during the experiment and (2) the model is based on one anthropometrical data set obtained in a cadaver study (Veeger et al., 1997) while subjects vary in morphology and anthropometrics. For this reason only differences above 10% have been analysed.

The stress cost function provides satisfactory results for the mono-articular TL but not for the bi- and even tri-articular flexor muscles. The cases in which the model predicted no muscle activity while $\dot{V}O_2$ did show activity or vice versa were further investigated. It seems that pro/supination moments have a disproportionately large effect on the optimisation, compared to flexion/extension moments. The BB and BL are not activated during FP due to their undesired supination moment. During FS the BR does not contribute to the required flexion moment since

the m. biceps is preferred due to its desired supination moment. Although this does not seem very surprising from a mechanical point of view, these findings were in contrast to the NIRS and EMG measurements, which did show activity of these muscles. The model also predicted activity of the BL during ES despite its undesired flexion moment. NIRS measurements showed this for only two of the four subjects.

With the energy-related cost function most of the above-mentioned problems were solved. By including a linear term and muscle mass in the criterion the load-sharing changes in several ways. The contribution of the relatively small pronator and supinator muscles increases. The BB for instance contributes to the flexion moment during FP since the undesired supination moment can be compensated for by the relatively 'low cost' m. pronator quadratus. This favouring of smaller muscles also leads to a decrease in force in the BB and BL, and an increase in force in the BR and the supinator muscle during FS, reflecting what was seen in the NIRS measurements. The increase in activity of the m. supinator also results in non-activity of the BL and BB during ES. This does not completely correspond to the experimental results in which, as mentioned above, activity of the BB and BL during ES was seen for two subjects. Since this effect was not recorded for all subjects it is likely that these differences are caused by individual differences in morphology. An EMG study of Buchanan et al. (1989) also showed variation in activity of the m. biceps during extension-supination among different subjects. Since the model is not individualised the model cannot reflect these individual differences.

Although muscle length remained constant in these experiments and force-length characteristics were not yet taken into account, it is found that including muscle mass and indirectly, fibre length, into the criterion has a major effect on the load sharing. When muscle length changes the effect of muscle mass may change and the linear term may become more important. Therefore in a future study muscle length will be varied.

The energy-related cost function consists of a linear as well as a quadratic term; the contribution of each term is defined by the constants c_1 and c_2 . Changing the constants and therefore the ratio between the two terms will influence the load sharing as well. In the current study these constants were chosen rather arbitrarily. It is expected that more improvement can be achieved by optimising these constants.

In conclusion it can be said that the newly proposed energy-related cost function appears to be a better measure for muscle energy consumption than the stress cost function and leads to more realistic predictions of muscle activation. Further research on the effect of muscle length and the ideal ratio between the linear and quadratic term is expected to lead to further refinement of this energy-related cost function.

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