original scientific article
received: 2010-09-07

UDC: 616.74-073

TWITCH PARAMETERS IN TRANSVERSAL AND LONGITUDINAL BICEPS BRACHII RESPONSE

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ABSTRACT

Assessment of the contractile properties of skeletal muscles is continuing to be an important issue and a difficult task methodologically. Longitudinal direction of skeletal muscle contraction blurs intrinsic muscle belly contractile properties with many factors. This study evaluates and explains contractile properties such as: delay time (Td), contraction time (Tc), half relaxation time (Tr) and maximal amplitude (Dm) extracted from twitch transversal response and compare them with torque response. In fifteen healthy males (age 23.7 ± 3.4 years) isometric twitch transversal and torque responses were simultaneously recorded during graded electrically elicited contractions in the biceps brachii muscle. The amplitude of electrical stimulation was increased in 5 mA steps from a threshold up to a maximal response. The muscles' belly transversal response was measured by a high precision mechanical displacement sensor while elbow joint torque was calculated from force readings. Results indicate a parabolic relation between the transversal displacement and the torque Dm. A significantly shorter Tc was found in transversal response without being correlated to torque Tc ($r = -0.12$; $p > 0.05$). A significant correlation was found between torque Tc and the time occurrence of the second peak in the transversal response ($r = 0.83$; $p < 0.001$). Electrical stimulation amplitude dependant variation of the Tc was notably different in transversal than in torque response. Td was similar at submaximal and maximal responses but larger in transversal at just above threshold contractions. Tr has a similar linear *trend in both responses, however, the magnitude and the slope are much larger in the transversal response. We could conclude that different mechanisms affect longitudinal and transversal twitch skeletal muscle deformations. Contractile properties extracted from the transversal response enable alternative insights into skeletal muscle contraction mechanics.*

Keywords: skeletal muscle, contraction time, tensiomyography, torque

NAVOR IN ODEBELITEV TREBUHA MIŠICE BICEPS BRACHII NA ELEKTRIČNI DRAŽLJAJ

IZVLEČEK

Merjenje kontraktilnih lastnosti skeletne mišice je pomembno a metodološko zelo zahtevno področje. Običajen zajem informacije v vzdolžni smeri mišične akcije zamegli intrinzične kontraktilne lastnosti mišičnega trebuha. Študija obravnava kontraktilne lastnosti skeletne mišice, kot so: čas zakasnitve (Td), čas krčenja (Tc), polovični čas sproščanja (Tr) in največjo doseženo amplitudo (Dm), izračunane iz odziva mišice na en električni dražljaj - 'twitch' dražljaj. V študiji je sodelovalo petnajst zdravih moških preiskovancev (povprečna starost 23.7 ± 3.4 let). Mehanski odzivi mišice dvo-glave upogibalke komolca so bili zajeti iz odzivov sile (navora) in prečne odebelitve trebuha mišice tekom povečevanja amplitude električne stimulacije od praga krčenja, po 5 mA do največjega doseženega odziva. Prečna odebelitev trebuha mišice je bila merjena z linearnim senzorjem odmika, medtem, ko je bil navor v komolcu izračunan iz odziva sile v vzdolžni smeri. Rezultati pričajo o parabolni odvisnosti med Dm prečne odebelitve in vzdolžne sile mišice. Pomembno krajši je bil Tc prečne odebelitve, a ni bil povezan z Tc vzdolžnega navora ($r = -0.12$; $p > 0.05$). Medtem, ko smo ugotovili pomembno povezavo med Tc vzdolžnega navora in trenutkom pojava drugega vrha prečnega odziva ($r = 0.83$; $p < 0.001$). Variacija Tc, glede na amplitudo stimulacije, je bila drugačna kot pri vzdolžnem navoru. Ugotovili smo da je imel Td obeh metod podobne vrednosti pri submaksimalni in maksimalni električni stimulaciji, vendar je bil Td prečnega odziva pomembno višji pri nadpražni električni stimulaciji. Ugotovili smo, da je bil parameter Tr, izračunan iz obeh metod, linearno odvisen od amplitude stimulacije, vendar je bil naklon pri prečnem odzivu 2-krat višji. Zaključimo lahko, da različni mehanizmi vplivajo na deformacijo mišičnih struktur v vzdolžni in prečni smeri. Kontraktilne lastnosti izmerjene iz prečnega odziva nam nudijo nove vpoglede v mehaniko mišičnega krčenja.

Ključne besede: skeletna mišica, čas krčenja, tenziomiografija, navor

INTRODUCTION

Skeletal muscle contractile properties are studied in order to make conclusions about muscle composition (McComas & Thomas, 1968; Dahmane, Valenčič, Knez & Eržen, 2000), exercise velocity (Maffiuletti & Martin, 2001), muscle resistance to fatigue (Lindström, Magnusson & Petersén, 1970; Burke, Levine, Tsairis & Engel, 1971; Merletti, LoConte & Orizio, 1991), motor unit spatial distribution (Dahmane, Djordjević, Šimunič & Valenčič, 2005) and firing rate (Botterman, Iwamoto & Gonyea, 1986; Bernardi, Solomonow, Nguyen & Baratto, 1996). Most exact results would be obtained by in vitro experiments using invasive techniques. However, several difficulties and obstacles surrounding the regular use of invasive techniques result in the continuing search for alternative – non-invasive techniques that would improve our understanding of the contractile properties of muscles.

Distally detected muscle force/torque response invoked by an electrical twitch is frequently used to analyse muscle contractile properties (Hill, 1953; Close, 1972; Bülow, Norregaard, Danneskoild & Mehlsen, 1993; Hamada, Sale, MacDougall & Tarnopolsky, 2000). Allen, Lee & Westerblad (1989) suggest that such an approach should be considered with caution as single twitch stimulation does not release sufficient intracellular Ca^{2+} to uncover enough actin-myosin binding sites for development and transmission of maximum twitch force. Hoyle (1983) and Kawakami & Lieber (2000) further demonstrated that twitch force exerted by a contracted muscle belly has to transmit through connective tissue to be measured by an external force transducer. Usually there is already a slack of exerted muscle force present before the connective tissue is completely stretched and therefore representative muscle belly twitch force could not be measured unless longer tetanic stimulation is applied. Beside the elastic component of the connective tissue the damping component of the passive surrounding tissue also affects longitudinal twitch response making interpretation of the results toward extraction of intrinsic contractile properties of a muscle difficult if not impossible.

To reduce these effects, an alternative approach for the evaluation of muscle contractile properties has been introduced through mechanomyographic methods based on measurements of lateral vibrations in resonant frequency and thickening of the muscle fibres. Several different sensors (transducers) have been evaluated, developed and tested: phonomyography (Maton, Petitjean & Cnockaert, 1990) and soundmyography (Barry, Geiringer & Ball, 1985; Orizio & Veicsteinas, 1992) use microphones to detect muscle sound as a consequence of muscle fibre mechanical oscillations; vibromyography (Zhang, Frank, Rangayyan & Bell, 1992) uses accelerometers and laser beams (Orizio, Baratta, Zhou, Solomonow & Veicsteinas, 1999 and 2000) to detect thickening and vibration of a whole muscle belly. Promising results have been obtained using the above methods, however, several difficulties – mostly of a technological origin – have been stated (Orizio, 2000; Wong, 2001): low signal to noise ratio and consecutively high variability, complex measuring set-up, expensive hardware adjustments and necessary post-processing of detected signals, etc.

Valenčič & Knez (1997) introduced another mechanomyographic method named Tensiomyography (TMG). TMG assesses muscle mechanical contractile properties with a linear displacement sensor applied directly on the skin surface above the muscle belly. The method has certain similarities with the intra-muscular pressure measurements (Hill, 1948; Parker, Körner & Kadefors, 1984; Sejersted et al., 1984) as well as other mechanomyographic measurements (Barry et al., 1985; Zhang et al., 1992; Orizio et al., 1999). The basic difference between the TMG method and other MMG type methods and similarity to the intramuscular pressure method is the slight pre-tension the displacement sensor exerts on the muscle belly before the measurement is performed. This pre-tension increases the muscle response amplitude when stimulated with an electrical pulse and increases the repeatability rate and the signal to noise ratio (Valenčič & Knez, 1997). The TMG method was used in several studies (Burger, Valenčič, Marinček & Kogovšek, 1996; Valenčič & Knez, 1997; Dahmane et al., 2000 and 2005; Kerševan, Valenčič, Djordjević & Šimunič, 2002; Grabljevec et al., 2004; Križaj, Šimunič & Žagar, 2008; Pišot et al., 2008). First evaluation of the TMG method was performed by comparing contraction time extracted from the transversal displacement of the muscle belly to the histological fibre typing analysis obtained from cadaver muscles (Dahmane et al., 2000 and 2005). A high correlation between the contraction time and the percentage of the type I muscle fibres was found (r = 0.93, Dahmane et al., 2000). The usefulness of the TMG method was further demonstrated in monitoring muscle atrophy of above-knee amputees (Burger et al., 1996), after 35 days of horizontal bed rest (Pišot et al., 2008), patients with spastic muscles (Grabljevec et al., 2004) and muscle adaptation on specific training process (Kerševan et al., 2002; Dahmane, Djordjević & Smerdu, 2007). The short-term repeatability rate of the TMG method has been found very high, making it a reliable estimator of muscle contraction properties (Križaj et al., 2008; Tous-Fajardo et al., 2010).

Despite several specific investigations and uses of the method has been demonstrated, so far no detailed explanation of the twitch mechanisms involved in the TMG response and its direct relation to the force/torque response of a muscle has been given. A goal of this study was to correlate the transversal response measured by the TMG method and the torque twitch response and to assess whether TMG may be used as an alternative method of the measurement of muscle contraction amplitude and its kinetics.

METHODS AND MATERIALS

Subjects

Fifteen male subjects (Table 1) with no history of neuromuscular disorders volunteered for this investigation. The study was approved by the Slovenian National Medical Ethics Committee and has therefore been performed in accordance with the ethical standards laid down in the 1964 Helsinki Declaration. Each subject was fully informed about possible risks and the nature of the experiments and signed the informed consent. Each subject was seated in a relaxed position on a straight back chair with elastic straps crossing their shoulders to fix their upper body. Their left arms were isometrically hung on a force transducer at 80º of elbow flexion (0º represents totally extended arm) in a pronated wrist position (palm rotated to face down direction).

Torque measurements

An analogue force transducer (FORT 5000, WPI Inc.) was mounted 26.7 ± 1.5 cm of the moment arm distally from the elbow joint axis. The forearm was hung on a force transducer, which was secured on the other side with a magnetic hand on a heavy metal stand. The torque signal was amplified using a DC amplifier (TGM4M, WPI Inc.).

Tensiomyographic measurements

The principle of the TMG method is presented in Figure 1. A custom-made digital displacement sensor (G40, RLS Inc.) was applied perpendicularly to the skin above the muscle belly to acquire the transversal response of the biceps brachii muscle. The sensor's sensitivity was 4 mm and the spring constant was 77 Nm^{-1}.

The measuring point was chosen carefully at the thickest part of the muscle belly from where also skin fold data was collected. The thickest part of the muscle belly was identified visually and through few measured transversal responses at different surrounding locations fixed at a position where the largest transversal response was

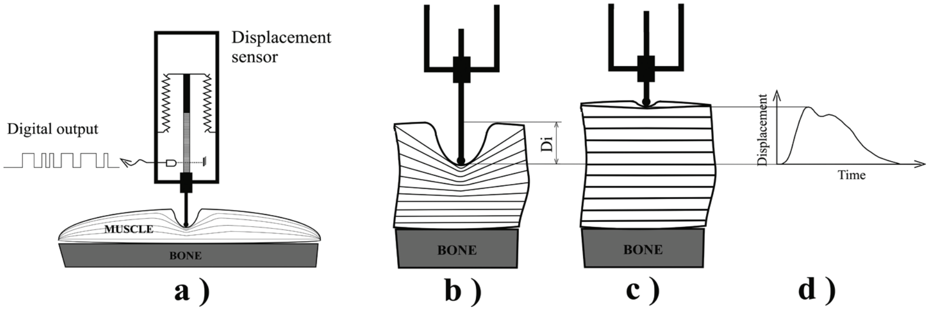

Figure 1: Principle of the Tensyomyographic method: linear displacement sensor (a) is pressed against resting muscle (b) and during twitch muscle contraction muscle belly thickens and vertically presses displacement rod (c) to measure a mechanical twitch response (d).

obtained. Two electrodes were placed 5 cm distally (cathode) and proximally (anode) from the measuring point. Passive (initial) muscle stiffness (Di) was evaluated in relaxed muscle as shown in Figure 1b and as it was previously proposed by Charles et al. (2001).

Signal recordings

The transversal and torque signals were simultaneously and continuously stored on a portable computer. Torque signal acquisition was performed through the interface and analogue/digital converter (DAQCard 1200, National Instruments, Inc.) and sampled with a Matlab Compiler Toolbox (The MathWorks, Inc.) with a sampling frequency of 1 kHz from the 16-bit up/down hardware counter storage. Torque signals were further smoothed using a digital low-pass Butterworth filter with a cut-off frequency of 25 Hz.

Both recorded signals were further analysed on the basis of seven extracted parameters presented in Figure 2.

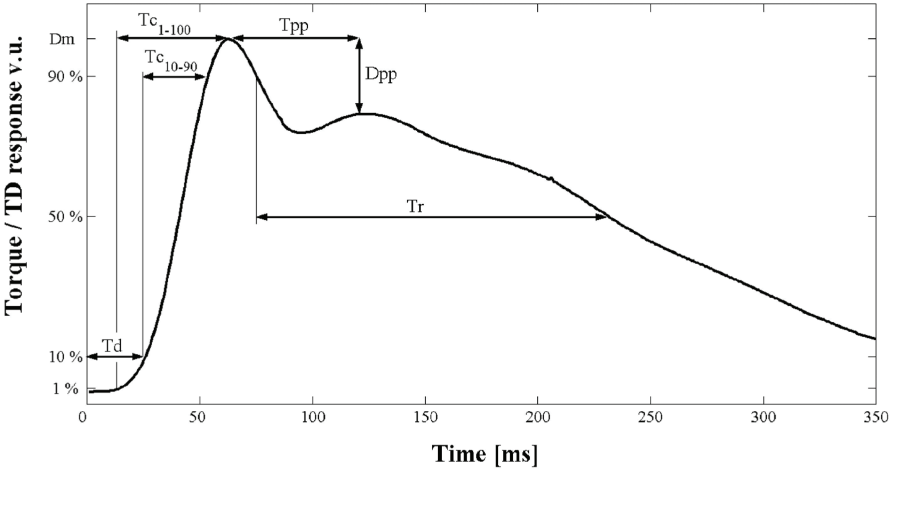

Figure 2: Explanation of the contractile parameters extracted from the twitch transversal displacement (TD) or torque response.

Contractile parameters were defined from the response as follows: Dm – maximal amplitude; Dpp – difference in the amplitude between both peaks; Tpp – time between both peaks; Td – delay time between stimulation and 10% of the Dm; Tc1-100 – contraction time from 1% and 100% of the Dm; Tc10-90 – contraction time from 10% to 90% of the Dm; Tr – half relaxation time from 90% to 50% of the Dm.

Experiment

Two rounded (5 cm diameter) self-adhesive electrodes (Axelgaard, Pulse) were placed bipolarly on the skin above the muscle belly. A cathode was placed distally while anode proximally to measuring point. Single monopolar rectangular pulses of 1 ms duration from the electro-stimulator (TMG-S1, Furlan & Co. Ltd.) were delivered to the electrodes. A single pulse (twitch) amplitude was increased every 15 s from the threshold to the maximal amplitude in steps of 5 mA. The threshold stimulation amplitude was determined as the amplitude necessary for evoking minimal detectable muscle response. Maximal stimulation amplitude was determined as minimum required stimulation pulse amplitude which elicited the largest transversal response. Further increase of the stimulation amplitude pulse would not result in the further increase of the transversal response. Typical threshold and maximal stimulation amplitude were around 10 mA and 65 mA, respectively.

Statistics

The torque peak amplitude values and the transversal peak amplitude values were correlated by the equation: $y = b + ax^2$, where y represents the transversal peak amplitude value, x represents the torque peak amplitude value, and a and b are the model constants (a is the regression coefficient expressing the change in y for a given change in x, b is the y-intercept).

Furthermore, a one-way ANOVA was used for comparing the means of two groups of data. A Pearson correlation coefficient (r) was used to test two series of data for its relations. An alpha of $p < 0.05$ was considered statistically significant for all comparisons.

RESULTS

Table 1 presents average data for relative displacement differences between peaks (relative Dpp), compression depth (Di) and contraction time (Tc_{10-90}) extracted from the transversal response together with anthropometrical (skin fold over biceps brachii muscle).

Table 1: Summary of subjects' personal, morphological, anthropometrical and transversal displacement characteristics.

Subject	**Age / years**	**Height / cm**	**Weight / kg**	**Skin fold / mm**	**Relative Dpp / %**	**Di / mm**	**Tc10-90 / ms**
1	22	181	80	2.5	44.5	8.7	26.9
2	27	184	85	2.6	24.3	9.5	30.9
3	30	183	95	5	17.7	9.3	28.6
4	26	176	86	6.5	31.3	7.7	25.5
5	23	187	83	3.7	27.0	8.7	29.5
6	22	175	72	3	26.0	5.8	28.1
7	20	184	90	3.5	25.3	8.9	30.4
8	19	188	76	4	21.3	8.7	32.6
9	20	186	75	4.2	45.4	8.3	28.7
10	23	181	72	3.5	21.0	5.2	28.0
11	27	171	78	5	27.9	7.2	28.4
12	25	179	73	3.1	0.0	8.7	34.3
13	24	188	75	4.6	23.8	9.5	25.0
14	28	193	110	5	19.5	8.0	25.3
15	20	189	76	2.7	20.7	8.4	25.9
Average	23.7	183.0	81.7	3.9	25.0	8.2	28.5
SD	3.4	5.9	10.4	1.1	10.7	1.3	2.7

Skin fold was measured above the biceps brachii muscle at the TMG measuring point. From transversal response initial muscle belly stiffness (Di) was assessed at relaxed muscle, relative peak-to-peak distance (Dpp) and contraction time (Tc10-90) were calculated by normalizing Dpp to Dm and as shown in Figure 2, respectively from maximal transversal response.

A typical example of the transversal and the torque responses is presented in Figure 3. Several differences in the responses can be qualitatively identified:

- The beginning of the muscle contraction appears sooner in the torque response.
- The peak of the response appears sooner in transversal response
- The relaxation phase of the torque response is shorter.
- Two peaks were identified only in the transversal responses. They were identified close to and at maximal responses in 14 subjects.

No statistically significant correlation was found between relative Dpp to the skin fold above the biceps brachii muscle belly (r = 0.056) nor to muscle stiffness Di (r = -0.043). The highest, but still not significant, correlation was found between the relative Dpp and Tc_{10-90} (r = -0.424).

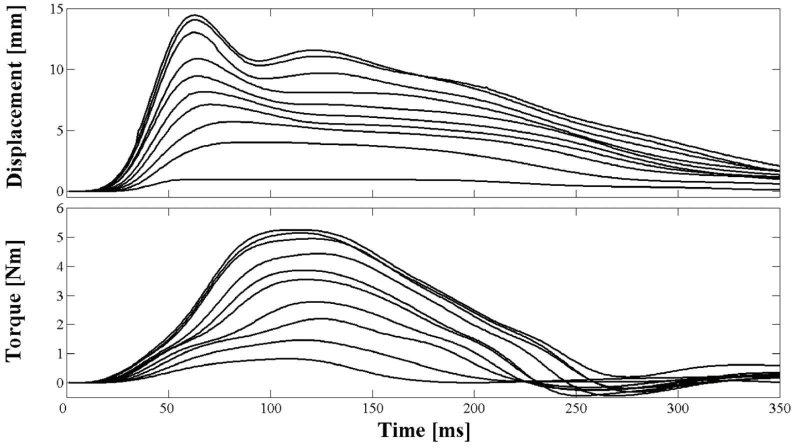

Figure 3: Transversal displacement (upper) and torque (lower) twitch muscle biceps brachii responses on graded electrical stimulation.

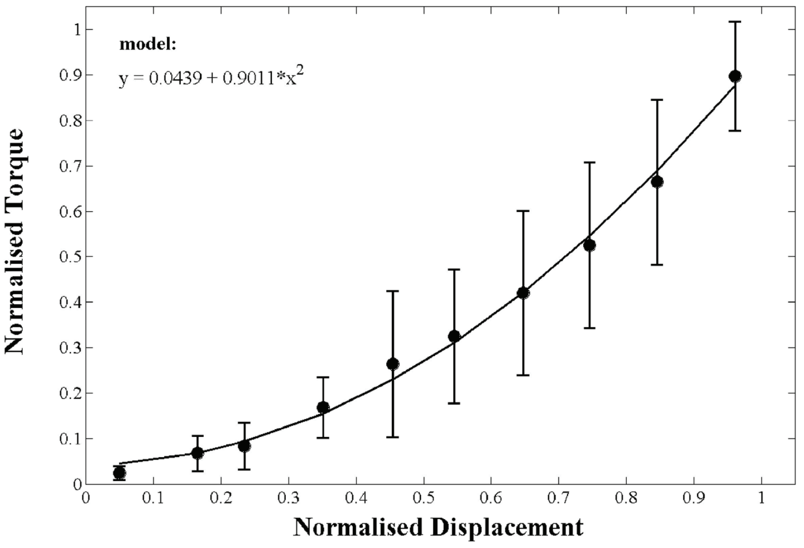

Figure 4: With model and experimentally determined relationship between normalized peak transversal displacement and corresponding peak torque twitch amplitude.

Parabolic trend curve models the relationship. The data were pre- normalized between threshold (0) and maximal (1) values for each subject and than averages with standard deviations presented.

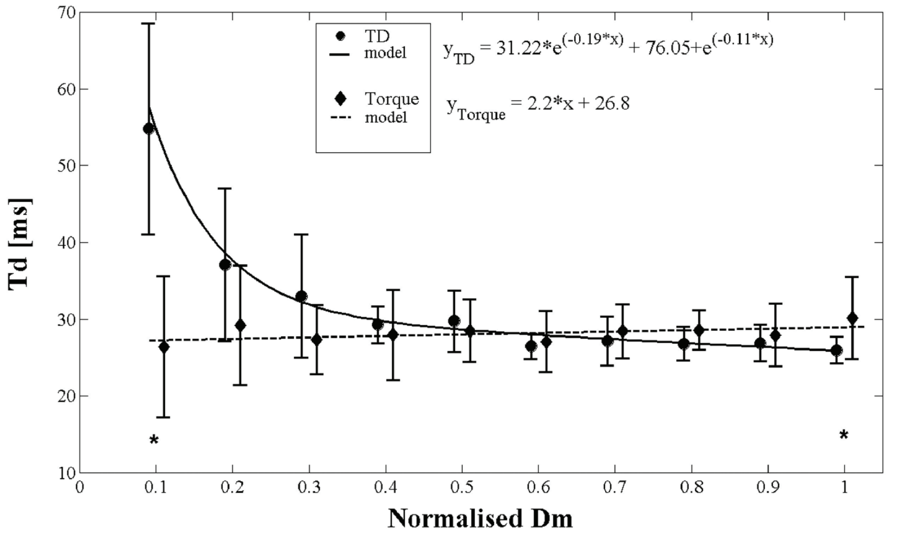

Figure 5: Delay time (Td) for transversal displacement (TD) and torque at different normalised response magnitudes (Dm).

Exponential trend for Td in TD response (yTD, circles and full line) and linear trend of torque response (yTorque, diamonds and dotted line) describing relation of the parameter Td values regarding to increasing magnitude of the responses. Statistical significant differences are presented with '' symbol.*

The relationship of the peak amplitude (Dm) of the transversal and torque responses is presented in Figure 4. Since the magnitudes of the transversal response and the torque response differ significantly from subject to subject, they were normalised between the threshold and the maximal values and classified into ten levels. The black circles represent experimental data with standard deviation at ten levels of different transversal amplitudes. At just-above-threshold stimulation we could notice a small increase in the torque compared to the transversal following with a comparable increase of both responses. Parabolic trend was found at 13 and a linear at two subjects, respectively. Parabolic curve appropriately models the relationship.

Different mechanisms influence transversal and torque twitch responses. Td was significantly longer at just-above-threshold transversal response than in torque response. At higher electrical stimulation amplitudes, Td in transversal response stabilises at lower value, those comparable to torque Td. Torque Td was found independent from electrical stimulation amplitude (Figure 5).

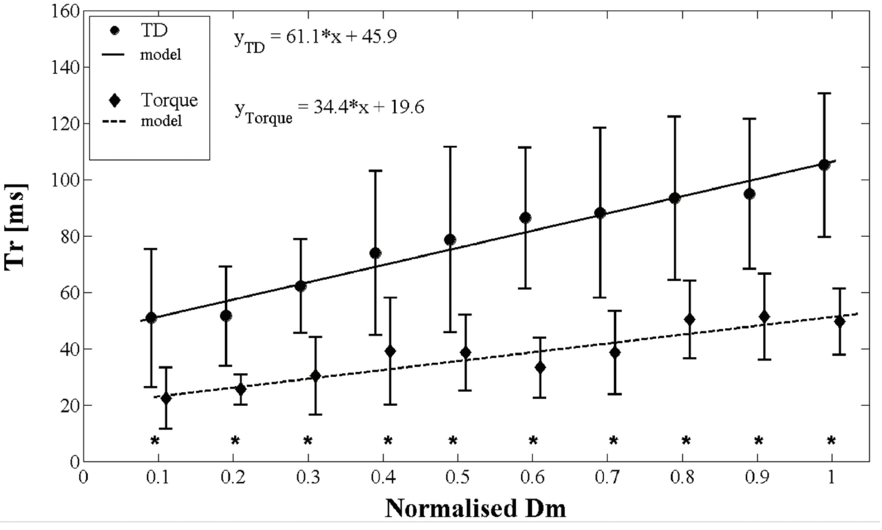

Figure 6: Half relaxation time (Tr) for transversal displacement (TD) and torque at different normalised response magnitudes (Dm).

Linear trends for Tr in TD response (yTD, circles and full line) and torque response (yTorque, diamonds and dotted line) describing relation of the parameter Tr values regarding to increasing magnitude of the responses. Statistical significant differences are presented with '' symbol.*

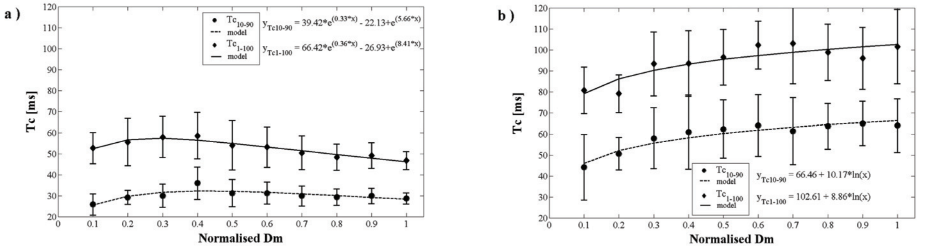

Figure 7: Contraction times (Tc1_100 and Tc10_90) for transversal displacement (TD) and torque at different normalised response magnitudes (Dm).

a.) Double exponential and logarithmic trends for both contraction times Tc10_90 (diamonds, full line) and Tc1_100 (circles, dotted line) for transversal displacement and b.) for torque, regarding to increasing magnitude of the responses.

Tr was longer in the transversal response than in the torque response for all subjects. Increasing electrical stimulation amplitude significantly prolongs Tr of both transversal and torque responses (Figure 6). The rate of increase of the Tr with increasing normalized displacement is about twice as large for the transversal than for the torque response.

Two different definitions of the twitch response contraction time were investigated Tc_{1-100} and Tc_{10-90}. Both Tc_{1-100} and Tc_{10-90} in transversal response were the shortest at the just-above-threshold electrical stimulation and were prolonged with increasing stimulation amplitude reaching maximum at approximately 40% of the maximal response (Figure 7a). With further increase of the transversal response magnitude at above 80%, both of them decrease and later stabilise (Figure 7a). These times could not be correlated to the torque contraction times, which are continually increasing with increasing stimulation amplitude (Figure 7b).

Absolute Tc_{10-90} in transversal response (being between 20 and 40 ms, average at maximal response 28.7 ms) was significantly smaller than in torque Tc_{10-90} (30 to 75 ms, average at maximal response 46.8 ms). Similar differences were found in Tc_{1-100} being from 45 to 70 ms (average at maximal response 64.0 ms) in transversal and from 70 to 120 ms (average in maximal response 101.6 ms) in torque.

From Figure 8 we did not observe a significant correlation (Figure 8a; r = -0.12) between Tc_{1-100} calculated from torque and transversal maximal responses in every participant. On the other hand we found significant correlation (Figure 8b; r = 0.82; p < 0.001) between torque Tc_{1_100} and the summation of transversal Tc_{1_100} and Tpp (occurrence of the second peak in transversal response) in fourteen participants with second peak occurrence.

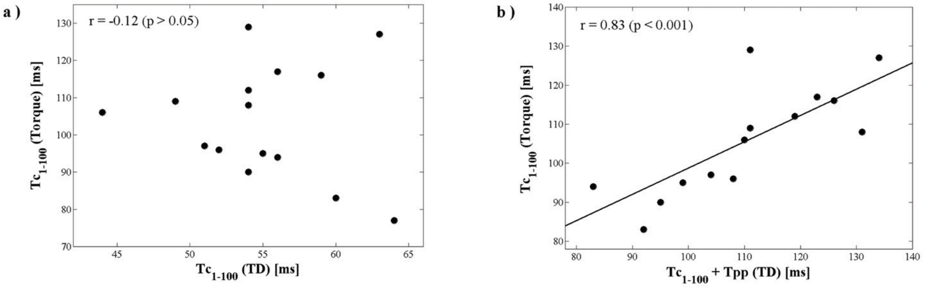

Figure 8: Correlation between torque and transversal displacement (TD) contraction time (Tc1_100) calculated from maximal biceps brachii response.

a.) Non significant correlation coefficient (N = 15; r = -0.12) between Tc1_100 of torque and TD maximal responses and b.) significant correlation (N = 14; r = 0.83) between Tc1_100 of torque and time of the TD second peak occurrence (Tc1_100 + Tpp) maximal responses.

DISCUSSION

The aim of this work was to check the potential differences in contractile properties being measured from the transversal and longitudinal direction of in-vivo twitch muscle contraction. We have found and explained significant differences between contractile parameters estimated from transversal and torque twitch response.

The sliding of actin and myosin filaments decreases the length of contractile elements reflecting in increased tension at the end of the serial elastic elements. In isometric twitch contraction both, tendon tension and changes of muscle belly diameter take place to compensate constant muscle volume. Zhang, Frank, Rangayyan & Bell (1996) explain that diameter changes are a mechanical reaction to the production of the muscle force but are not directly related to it. Muscle diameter changes have been thus far investigated with various transducers and could be explained by a summation of: slow bulk lateral muscle belly movement regarding the different regional distribution of the contractile elements; the excitation into fast ringing of the muscle fibres at its own resonant frequency, and pressure waves generated by the dimensional changes of the active fibres (Orizio, 1993).

The measurement technique for transversal response detection used in our investigation is very similar to the technique using a laser beam sensor with one important distinction. The high precision displacement sensor used in this study is a contact sensor and uses a spring to compress a relaxed muscle belly towards the bone where it compresses subcutaneous fat tissue as well as the muscle belly. By using this principle the amplitude of the measured transversal response is increased and the variability of the method is reduced (Križaj et al., 2008; Tous-Fajardo et al., 2010).

As demonstrated in Figure 1, at least two simultaneous phases of the transversal response can be identified during isometric contraction. In the first phase the muscle fibres' longitudinal force pulls the fibres into the horizontal position where the fibres push onto the sensor tip. In the second phase the sensor tip is further pushed due to the thickening of the muscle fibres.

Two obvious peaks of the transversal response (Figures 2 and 3) were not detected in other mechanomyographic investigations using laser beams (on isolated rat muscle, Orizio et al., 1999 and 2000). Knowing that contact sensors' mechanical properties could influence the results we first tried to seek out an explanation within them. The first peak was detected at contractions typically larger than 40 % of the supramaximal response (Figure 3). We did not observe any separation of the sensors' tip from the skin and no significant correlation between the skin fold and the relative Dpp. We further performed experiments in which the contact displacement sensor was used simultaneously with a laser beam sensor or a high-speed camera (1 kHz) (unpublished observations). Both methods clearly showed the occurrence of two peaks in transversal response of the human biceps brachii muscle. These observations are in contrast to experiments on animals made by Orizio et al. (1999 and 2000). On the other hand, Wetzel & Gros (1998) observed large differences in time to peak in isolated twitch response of fast twitch motor unit (29 ms) and slow twitch motor unit (151 ms) of rat muscles. Through modelling of these two fibre type characteristics, we anticipate that transversal response summates bi-modular muscle contraction, where in the first phase fast twitch fibres and in the second phase slow twitch fibres contribute to overall muscle transversal response (Šimunič, 2003).

A parabolic model was used to correlate the amplitude of the transversal response and the torque response. A similar model was found also by other investigators (Orizio et al., 1999) using a laser sensor. The correlation could be split into two components; the first with a large increment in transversal and low in force Dm and the second with small increment in transversal and large in force Dm. The latter occurs at approaching the maximal response (Figure 4). These phenomena could be explained with a "toe" region of stress-strain relationship in the soft tissues. Orizio et al. (1999) (demonstrated on isolated cat gastrochnemius muscle) that force generation takes place after muscle belly deformation at low activation level. However, Von Donkelaar, Willems, Muijtjens & Drost (1999) showed that during muscle-tendon complex isometric contractions in a rat muscle, muscle belly thickening is at some point linearly related to its shortening.

In agreement with Orizio et al. (1999) was also our finding on Td (Figure 5). Force twitch response at just above threshold stimulation amplitude has significantly shorter Td. With increasing stimulation amplitude Td from both methods equalises and stabilises.

Contraction times of the transversal and the torque response show different trends at increasing stimulation amplitude. Tc_{1-100} and Tc_{10-90} have the shortest values at just above threshold stimulation amplitude, largest at 40% of the stimulation amplitude and reduces at the maximal stimulation amplitude (Figure 7a). The same behaviour was found consistently in our previous study (Dahmane et al., 2005) in nine examined human muscles and was explained as a consequence of inhomogeneous fibre type distribution. A higher percentage of type 2 muscle fibres on the muscle surface were also reported by other authors (Edström & Kugelberg, 1968; Polgar, Johnson, Weightman & Appleton, 1973; Elder, Bradbury & Roberts, 1982).

Recruitment order at nerve and transcutaneous electrical stimulation is still very contradictive. Some experiments support reversal motor unit activation order (Heyters, Carpentier, Duchateau & Hainaut, 1994; Trimble & Enoka, 2001), while others are rather conflicting (Binder-Macleod, Halden & Jungles, 1995; Feiereisen, Duchateau & Hainaut, 1997; Knaflitz, Merletti & DeLuca, 1990). Similar to Dahmane et al. (2005) and Feiereisen, Duchtateau & Hainaut (1997) we assume that the nerve axons are directly activated and those that experience a higher electric field should be recruited more easily than those deeper in the muscle. However, contraction time of torque twitch response was found to have an incremental trend indicating that increased activation of motor units results in longer contraction times (Figure 7b). Assuming reversed recruitment order this could be explained through additional incremental recruitment of slower motor units. However, if we assume much more random recruitment order, then we must seek the explanation in non-isometric conditions within the whole muscle-tendon system during twitch contraction. Increased muscle activation results in shortening of the muscle belly. Non-isometric conditions during muscle contraction triggers muscle mass movement with torsion between active and the surrounding tissue and a consequential dumping effect of longitudinal mechanical muscle response. Such effects modify (right-shift) the force/torque mechanical response of intrinsic muscle belly.

Contraction times of transversal responses were found to be significantly shorter (more than two-fold) than those of torque twitch responses (Figure 7). This result is believed to indicate important differences in the dynamics between the investigated methods. Transversal twitch response carries more information on the velocity of the muscle contraction as it reaches peak values twice as soon as the torque twitch response. Experiments on isolated muscles using laser beams and a force transducer (Orizio et al., 1999 and 2000) or video analysis (Van Donkelaar et al., 1999) do not demonstrate such delay, which is believed to be due to a more controlled environment without interference from the surrounding tissue.

Our investigation indicates that the commonly proposed idea that a longer Tr indicates lower recruitment levels (Fang & Mortimer, 1991) is not necessarily correct. Savelberg (2000) also demonstrated that the composition of fibre type in a muscle affects Tr. Our findings are in agreement with Savelberg (2000). We both found that Tr increases with recruitment level when muscle fibres are orderly recruited (Figure 6). Tr increases with the recruitment rate in both approaches but with different slopes. In transversal response the Tr increase was steeper than in torque responses. Differences in absolute values were statistically significant for all recruitment levels.

In maximal transversal response we typically distinguished two peaks (Figure 2). The time occurrence of the second peak was found to correlate significantly to the (single) peak in the torque twitch response (Figure 8b). However, transversal responses comprise an additional (first) peak that does not correlate to the torque contraction time (Figure 8a). This probably demonstrates the loss of information in the torque twitch response and raises new questions for explanations of the double-peaked transversal twitch response. We previously modelled double peak occurrence in transversal response (Šimunič, 2003) and proposed a probable explanation of both peaks by integrative response of the fast- and slow- twitch fibres.

CONCLUSIONS

The aim of this investigation was to find explanation(s) for different mechanisms affecting the results of the transversal (tensiomyographic method) and the torque response on twitch contraction. Torque measurement is a well established method, widely used in the study of muscle physiology while a TMG method is a relatively novel method based on mechanomyographic methods. The results indicate different mechanisms that affect longitudinal and transversal twitch skeletal muscle deformations. Contractile properties extracted from the transversal response enable alternative insights in the kinetics of skeletal muscle contraction mechanics. The TMG method offers an additional insight into muscle physiology and can, with further development and analyses, become an alternative method for the evaluation of skeletal muscle contractile properties. Applications and areas where the method can be applied are wide; from studying muscle atrophy kinetics, hypertrophy after trauma or space travel, developmental muscle physiology, exercise physiology, etc.

Acknowledgements

This study was partly funded by the Ministry of Higher Education, Science and Technology of the Government of the Republic of Slovenia. We are grateful to Professor V. Valenčič (University of Ljubljana, Slovenia) and Srdjan Djordjević (University of Primorska, Slovenia) for supporting this study. We are indebted to TMG-BMC Ltd. Company for Biomedical Engineering for supporting us with a TMG device. We are thankful to our study participants for their willingness to participate in a study.

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