Acta of Bioengineering and Biomechanics
Vol. 14, No. 4, 2012

Original paper
DOI: 10.5277/abb120406

Effects of tendinous tissue properties on force output evoked by 2-pulse trains at different inter-pulse intervals in the human tibialis anterior muscle

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The aim of this study was to clarify the effects of tendinous tissue properties on origin of greater force output at short inter-pulse intervals in the 2-pulse trains compared to those at longer inter-pulse intervals. Thus, this study investigated the contributions of the second stimulus (C2) in 2-pulse trains with different inter-pulse intervals on the torque response and tendinous tissue properties of human skeletal muscle in vivo. The torque response and tendinous tissue elongation following single pulses and 2-pulse trains at different inter-pulse intervals (5, 10, 20, 30, 40, 50, 80, 100, 150, and 200 ms) were recorded in the tibialis anterior muscle using real-time ultrasonography. C2 with inter-pulse intervals of 5–100 ms invoked significantly greater torque responses than single pulses. In contrast, the elongation and compliance of tendinous tissue for C2 with inter-pulse intervals from 5–80 ms were significantly lower than those of the single-pulse response. A significant negative relationship between torque response and tendinous tissue compliance was observed in C2 with different inter-pulse intervals. The torque response as a result of C2 is greater at short inter-pulse intervals in which the force summation due to second stimulus coincides with the period of decreased tendinous tissue compliance due to the first stimulus.

Key words: *summation of contraction, doublet stimulation, muscle–tendon complex, electrical stimulation, ultrasonography*

1. Introduction

The summation of force induced by repetitive stimulation is a fundamental phenomenon in muscle physiology for increasing force. Previous studies report that the force response evoked by 2 closely spaced stimuli is larger than that of 2 and/or 3 single-twitch responses [1], [2]. This considerable force difference between single and 2-pulse trains indicates that the second pulse contributes more than the first pulse and that the second pulse has a facilitative effect on the force response. These previous findings suggest that the summation of force is nonlinear during the early phase of tetanic summation [2].

There are 2 possible mechanisms for the facilitative effects caused by the second stimulus on force response: one involves changes in the excitation–contraction coupling processes [3] and the other involves increased muscle stiffness [4], [5]. In human skeletal muscle, it is expected that this facilitative effect is not simply the result of changes in excitation–contraction coupling processes and muscle stiffness, because the process of force generation is coupled with elongation of elastic elements, which play a role in transmitting force from muscles. The changes in the properties of force-transmitting structures (i.e., tendons and aponeurosis) affect the capacity of force output. For example, increased tendon–aponeurosis stiffness augments the ability of the connective tissue to transmit contractile forces

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Received: March 3rd, 2012
Accepted for publication: September 4th, 2012

effectively [6]–[9]. Therefore, it is assumed that the tendinous tissue properties are related to the facilitative effect of force response with respect to the second stimulation.

Previous studies report that the force contribution of the second pulse (C2) in 2-pulse trains decreases with increasing inter-pulse interval [4], [10]. This phenomenon indicates that the facilitative effects of C2 on force response are altered due to different pulse duration between first and second pulse. If the tendinous tissue properties are related to the facilitative effect on the force response of C2, the C2 for tendinous tissue properties will be influenced by the duration of the inter-pulse interval. However, the effects of the inter-pulse interval of 2-pulse trains on tendinous tissue properties are unclear. The summation of contraction is a fundamental phenomenon in muscle physiology and is related to increases in muscle force. Clarifying the relationship between force response and tendinous tissue properties with different inter-pulse intervals during 2-pulse trains will enhance our basic understanding of the effects of force-transmitting structures on force output in human skeletal muscle.

Therefore, the present study investigated the effects of different inter-pulse intervals on C2 with respect to both force response and tendinous tissue properties using ultrasonography in human skeletal muscle. This was achieved by estimating the contribution of forces in response to C2 [2]. The purpose of this study was to clarify the effects of tendinous tissue properties on origin of greater force output at short inter-pulse intervals in the 2-pulse trains compared to those by longer inter-pulse intervals in the human tibialis anterior muscle (TA) in vivo.

2. Materials and methods

2.1. Subjects

Six males (mean ± SD: age = 27 ± 1.4 years; height = 166 ± 2.7 cm; weight = 73 ± 2.4 kg), with no history of neurological and musculoskeletal disorders, volunteered for this study. All of the selected individuals were normally active. Prior to the experiment, all of the subjects were given a full explanation of the purpose of the study based on descriptions approved by the Ethics Committee of Osaka University of Health and Sport Sciences. All subjects gave written informed consent before participation.

2.2. Experimental setup and signal detection

The subjects were seated in a custom-built isometric dynamometer with their right ankle positioned at 20° plantar flexion with both the hip and knee joints at 90°. A padded belt was strapped to a dynamometer to support the limb and maintain its position during the test. Each subject's foot was tightly secured to a footplate by 2 straps in order to maintain the ankle angle. The subjects' arms were folded in front of their chest. All of the subjects performed a few voluntary contractions of their dorsiflexor muscles as a warm-up prior to testing.

The isometric torque of the TA in response to electrical stimulation was measured by a dynamometer (Kin-Com, 500H, Chattecx, Inc., USA). The footplate was modified to provide a more stable and rigid attachment, and ensure the optimum transfer of force to the Kin-Com load cell. The torque was recorded by software at a sampling rate of 4 kHz via an analogue-to-digital (A/D) converter (PowerLab 8sp, ADInstrument, Australia); torque data were analysed by software (Chart v5.4.2, ADInstrument). Ultrasonic images of longitudinal TA sections were recorded using an electronic linear-array probe (wave frequency, 7.5 MHz; scanning length, 35 mm; PLM-703AT, Toshiba, Japan). The probe was attached to the skin over the TA 40% distally from the knee [11]. Real-time ultrasonic images of the TA during isometric contraction were continuously recorded on the computer memory of the ultrasonic apparatus at 63 Hz (SSA-500A, Toshiba, Japan). The relative physiological cross-sectional area contribution of TA (~60%) to all dorsiflexor muscle [12] was greater than relative contribution of gastrocnemius muscle (~18%) to all plantarflexor muscle [13] and relative contribution of vastus lateralis muscle (~22%) to quadriceps femoris muscles [14]. Thus, it is suggested that TA is a relatively suitable muscle to investigate relationship between output force and architectural change of muscle–tendon component.

2.3. Electrical stimulation

The electrical stimulations in 2-pulse trains at inter-pulse intervals of 5, 10, 20, 30, 40, 50, 80, 100, 150, and 200 ms were applied to the common peroneal nerve in a random order to record the evoked torque responses and ultrasonic images in the TA. A square wave (duration = 0.5 ms) was used for the electrical stimulation (S88k, Grass Telefactor, USA).

The cathode (1 cm diameter) and anode (1 cm diameter) were placed near the fibular head 5 cm apart. The stimulus intensity was 20% greater (supramaximal) than that required to produce a maximal twitch torque at the resting state. The torque and ultrasonic images were measured 3 times under each stimulation condition.

2.4. Analysis of experimental signals

The evoked twitch data recorded for each inter-pulse interval were used to determine the peak twitch torque. The changes in the crossing point between the TA fascicle and the deep aponeurosis were measured for each response using software (Frame-DIAS II, DKH, Japan) [15]. For the torque response and elongation of tendinous tissue, the contribution of the response to C2 was obtained by subtracting the response to the single stimulation from the response of the 2-pulse trains [2], [16]. The compliance of the tendinous tissue in the TA was estimated using the quotient of the maximal elongation of tendinous tissue to the peak tendon force (mm/N) for each response to the single pulse, 2-pulse trains, and C2. Tendon force (TF) was determined according to the twitch torque (TQ) during electrical stimulation. The TF transmitted through the tendinous tissue was calculated using the following equation [11]:

$$TF = k \bullet TQ/MA$$

where k is the relative physiological cross-sectional area contribution (0.57) of the TA to all dorsiflexor muscles [12] and MA is the length of the TA moment arm when the ankle is positioned at 20° plantar flexion, which was derived from RUGG et al. [17].

2.5. Statistical analysis

All data are presented as the mean ± standard error (SE). The changes in the peak torque, elongation of tendinous tissue, and compliance of tendinous tissue for 2-pulse trains with different inter-pulse intervals were analysed by one-way repeated-measures analysis of variance (ANOVA). Dunnett's post hoc test was used to determine the differences between stimulations with a single-pulse and 2-pulse trains with different inter-pulse intervals, and between single-pulse and C2. Pearson product moment correlation analyses were performed to determine whether the toque responses were associated with tendinous tissue elongation and tendinous tissue compliance with different inter-pulse intervals. The significance level was set at 5%. The Statistical Package for the Social Sciences (SPSS for Windows, version 11.0, USA) was used for all statistical analyses.

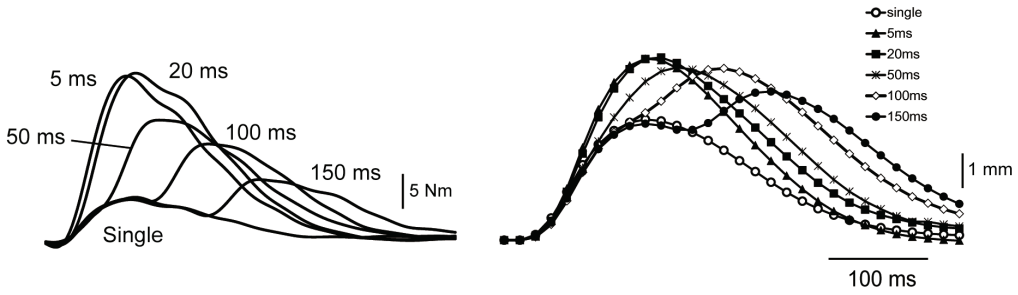

Fig. 1. Torque response (left) and tendinous tissue elongation (right) in response to a single pulse and 2-pulse trains at inter-pulse intervals of 5, 20, 50, 100, and 150 ms in a typical individual

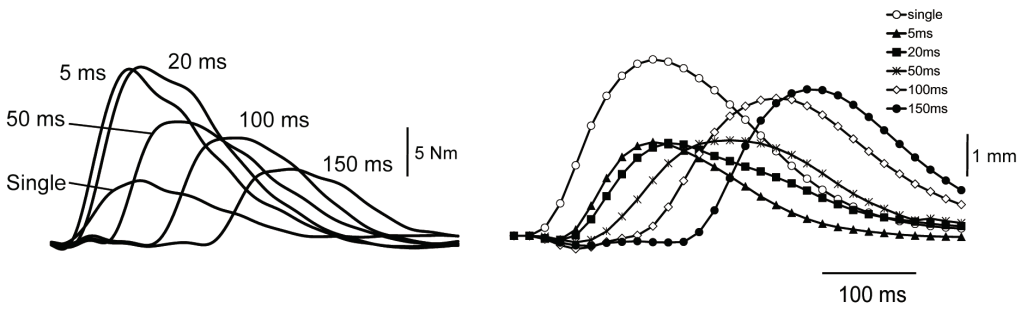

Fig. 2. Torque response (left) and tendinous tissue elongation (right) in response to a single pulse, and contribution of the second pulse (C2) in 2-pulse trains at inter-pulse intervals of 5, 20, 50, 100, and 150 ms in a typical individual

3. Results

Figure 1 shows a typical example of the torque and tendinous tissue elongation from 2-pulse trains with different inter-pulse intervals. Figure 2 shows a typical example of the C2 for the torque and tendinous tissue elongation with different inter-pulse intervals.

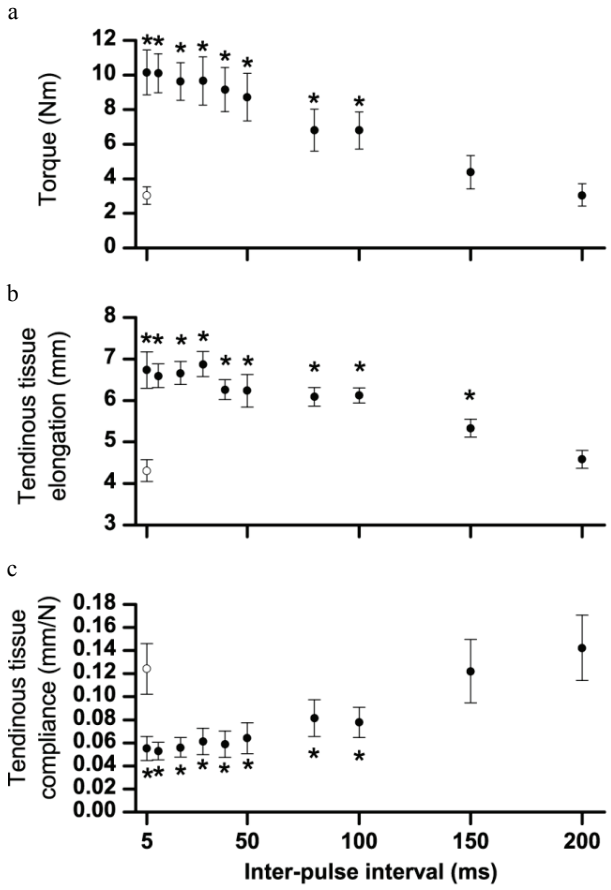

Fig. 3. Changes in the excursion of the peak torque (a), maximal elongation of tendinous tissue (b), and compliance of tendinous tissue (c) in response to a single pulse (○) and 2-pulse trains at different inter-pulse intervals. All values are expressed as the means ± SE of 6 individuals.
* Significantly different from a single pulse at $P < 0.05$

Figure 3 shows the peak torque (a), elongation of tendinous tissue (b), and compliance of tendinous tissue (c) for different inter-pulse intervals of 2-pulse trains. The mean peak torque values of 2-pulse trains with inter-pulse intervals of 5, 10, 20, 30, 40, 50, 80, 100, 150, and 200 ms were 10.1 ± 1.3, 10.1 ± 1.1, 9.6 ± 1.1, 9.7 ± 1.4, 9.2 ± 1.3, 8.7 ± 1.4, 6.8 ± 1.2, 6.8 ± 1.1, 4.4 ± 1.0, and 3.1 ± 0.6 Nm, respectively. The mean peak torque values of 2-pulse trains with inter-pulse intervals of 5, 10, 20, 30, 40, 50, 80, and 100 ms were significantly higher than that of the single-pulse response (3.0 ± 0.5 Nm) (figure 3a). The mean elongation of tendinous tissue for 2-pulse trains with inter-pulse intervals of 5, 10, 20, 30, 40, 50, 80, 100, 150, and 200 ms were 6.7 ± 1.3, 6.6 ± 1.1, 6.7 ± 1.1, 6.9 ± 1.4, 6.3 ± 1.3, 6.2 ± 1.4, 6.1 ± 1.2, 6.1 ± 1.1, 5.3 ± 1.0, and 4.6 ± 0.6 mm, respectively. The mean elongation of tendinous tissue for 2-pulse trains with inter-pulse intervals of 5, 10, 20, 30, 40, 50, 80, 100, and 150 ms were significantly higher than that of the single-pulse response (4.3 ± 0.3 mm) (figure 3b). The mean compliance of tendinous tissue for 2-pulse trains with inter-pulse intervals of 5, 10, 20, 30, 40, 50, 80, 100, 150, and 200 ms were 0.055 ± 0.010, 0.053 ± 0.008, 0.056 ± 0.008, 0.061 ± 0.011, 0.059 ± 0.011, 0.064 ± 0.013, 0.081 ± 0.016, 0.078 ± 0.013, 0.122 ± 0.027, and 0.142 ± 0.028 mm/N, respectively. The mean compliance of tendinous tissue for 2-pulse trains with inter-pulse intervals of 5, 10, 20, 30, 40, 50, 80, and 100 ms were significantly lower than that of the single-pulse response (0.124 ± 0.022 mm/N) (figure 3c).

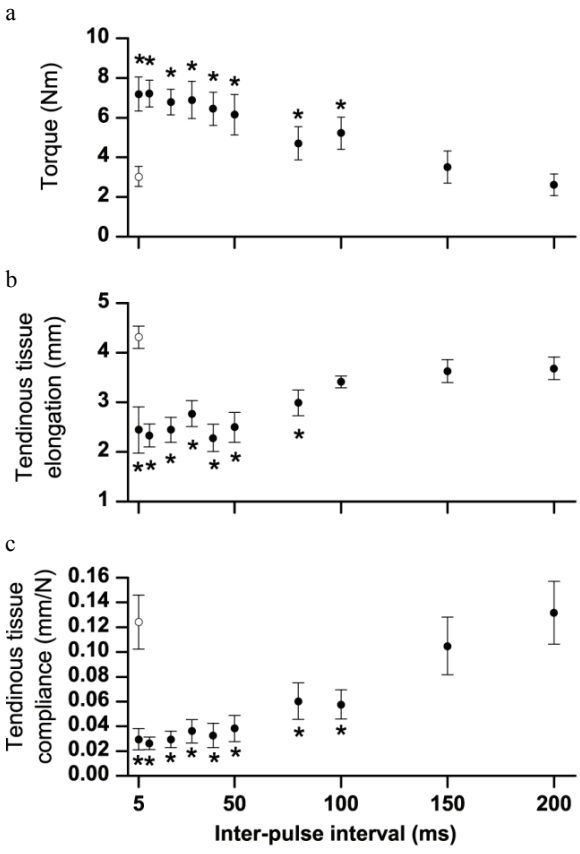

Fig. 4. Changes in the excursion of the peak torque (a), maximal elongation of tendinous tissue (b), and compliance of tendinous tissue (c) in response to a single pulse (○), and the contribution of the second pulse (C2) in 2-pulse trains at different inter-pulse intervals. All values are expressed as the means ± SE of 6 individuals.
* Significantly different from a single pulse at $P < 0.05$

Figure 4 shows the mean peak torque (a), elongation of tendinous tissue (b), and compliance of tendinous tissue (c) for C2. The peak torque values for C2 with inter-pulse intervals of 5, 10, 20, 30, 40, 50, 80, 100, 150, and 200 ms were 7.2 ± 0.9, 7.2 ± 0.7, 6.8 ± 0.6, 6.9 ± 0.9, 6.4 ± 0.8, 6.2 ± 1.0, 4.7 ± 0.8, 5.2 ± 0.8, 3.5 ± 0.8, and 2.6 ± 0.5 Nm, respectively. The mean peak torque values for C2 with inter-pulse intervals of 5, 10, 20, 30, 40, 50, 80, and 100 ms were significantly higher than that of the single-pulse response (3.0 ± 0.5 Nm) (figure 4a). The mean elongation of tendinous tissue for C2 with inter-pulse intervals of 5, 10, 20, 30, 40, 50, 80, 100, 150, and 200 ms were 2.4 ± 0.5, 2.3 ± 0.2, 2.4 ± 0.3, 2.8 ± 0.3, 2.3 ± 0.3, 2.5 ± 0.3, 3.0 ± 0.3, 3.4 ± 0.1, 3.6 ± 0.2, and 3.7 ± 0.2 mm, respectively. The mean elongation of tendinous tissue for C2 with inter-pulse intervals of 5, 10, 20, 30, 40, 50, and 80 ms were significantly lower than that of the single-pulse response (4.3 ± 0.3 mm) (figure 4b). The compliance of tendinous tissue for C2 with inter-pulse intervals of 5, 10, 20, 30, 40, 50, 80, 100, 150, and 200 ms were 0.030 ± 0.009, 0.026 ± 0.005, 0.029 ± 0.007, 0.036 ± 0.009, 0.033 ± 0.010, 0.038 ± 0.011, 0.060 ± 0.015, 0.058 ± 0.012, 0.105 ± 0.023, and 0.132 ± 0.025 mm/N, respectively. The compliance of tendinous tissue for C2 with inter-pulse intervals of 5, 10, 20, 30, 40, 50, 80, and 100 ms was significantly lower than that of the single-pulse response (4.3 ± 0.3 mm/N) (figure 4c).

The relationships between the torque response and tendinous tissue elongation and between the torque response and tendinous tissue compliance with different inter-pulse intervals are presented in figures 5 and 6, respectively. A significant positive linear relationship was observed between the torque response and tendinous tissue elongation during 2-pulse trains (figure 5a) (r = 0.974, P < 0.01). Meanwhile, a significant negative linear relationship was observed between the torque response and tendinous tissue compliance during 2-pulse trains (figure 5b) (r = –0.975, P < 0.01). A significant negative linear rela-

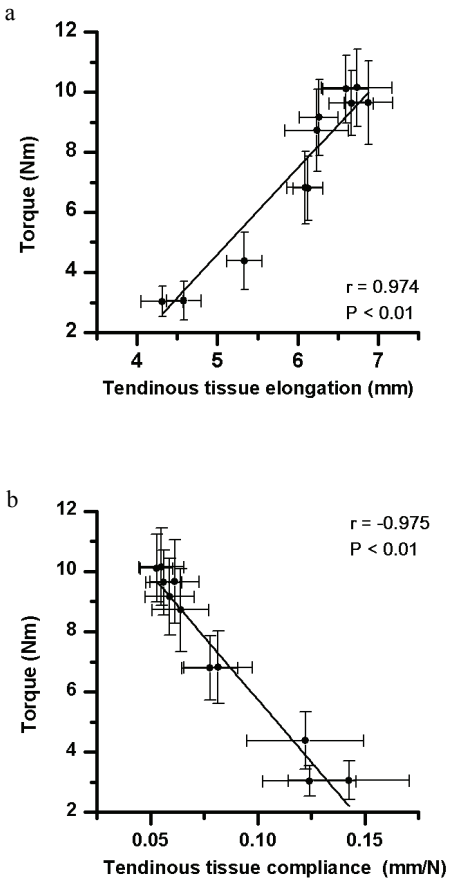

Fig. 5. Relationships between the torque response and tendinous tissue elongation (a), and between the torque response and tendinous tissue compliance (b) in response to 2-pulse trains with different inter-pulse intervals. Lines of best fit are shown

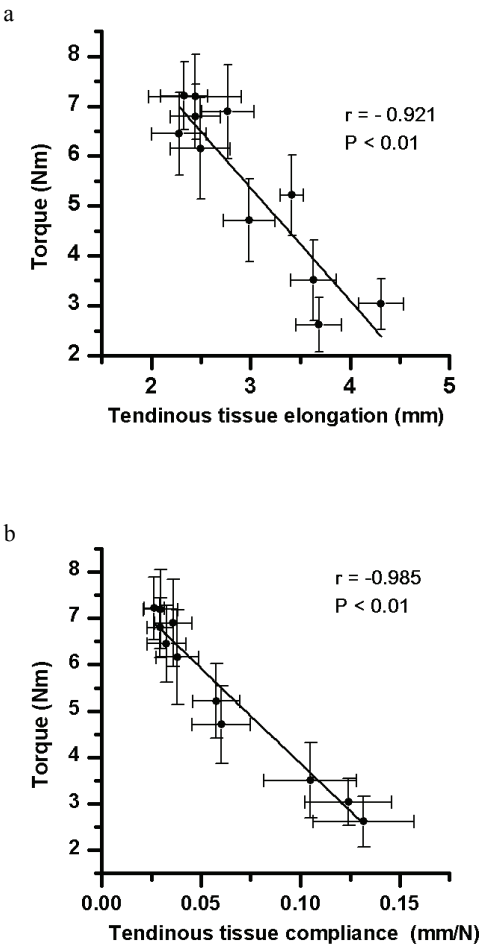

Fig. 6. Relationships between the torque response and tendinous tissue elongation (a), and between the torque response and tendinous tissue compliance (b) in response to the contribution of the second pulse (C2) in 2-pulse trains with different inter-pulse intervals. Lines of best fit are shown

tionship was observed between the torque response and tendinous tissue elongation for C2 (figure 6a) (r = –0.921, $P < 0.01$). Lastly, a significant negative linear relationship was observed between the torque response and tendinous tissue compliance for C2 (figure 6b) (r = –0.985, $P < 0.01$).

4. Discussion

To my knowledge, the present study is the first to analyse the effects of C2 in 2-pulse trains with different inter-pulse intervals on the torque response and tendinous tissue properties in human skeletal muscle *in vivo*. The main finding was that the greater torque produced by C2 compared to that by a single pulse was accompanied by lower elongation and compliance of the tendinous tissue at inter-pulse intervals less than 100 ms. Moreover, the results show that the tendinous tissue compliance for C2 was closely related to the force response for C2. This result suggests that the greater torque responses evoked by C2 at shorter inter-pulse intervals compared to those by longer ones occur because the second contraction is brought about when tendinous tissue compliance is lower at shorter inter-pulse intervals than longer ones.

It is well known that the peak torque responses to 2-pulse trains decrease with increasing inter-pulse interval (figure 3a). When the individual torque contributions as a result of C2 were analysed with different inter-pulse intervals, the present results revealed that the torque contributions of C2 with inter-pulse intervals from 5–100 ms were greater than the torque evoked by a single pulse (figure 4a). Moreover, the magnitude of the torque contribution of C2 decreased with increasing inter-pulse interval. These results indicate that the decreases in torque evoked by 2-pulse trains with increasing inter-pulse intervals are dependent on decrease of the torque contribution of C2. This decrease in the torque contribution of C2 with increasing inter-pulse interval is the result of lower muscle stiffness [4] and ionised calcium concentration in the cytosol [18].

The present results show that the elongation of tendinous tissue evoked by 2-pulse trains decreased with increasing inter-pulse interval while the tendinous tissue elongation of C2 increased with increasing inter-pulse interval. These results and the negative relationship between the torque and tendon elongation as a result of C2 (figure 6a) indicate that the torque contribution of C2 is greater when the elongation of tendinous tissue is low. ITO et al. [19] suggest that tendons are stretched more easily when the force is small and when the tendon becomes less compliant with increasing force. In the present study, the tendinous tissue compliance values with short inter-pulse intervals were lower than those with long ones (figures 3c and 4c). Furthermore, significant negative relationships between the torque and tendinous tissue compliance were observed in both 2-pulse trains and C2 (figures 5b and 6b). These results suggest that the greater torque produced by C2 with low tendinous tissue elongation at short inter-pulse intervals occurs because the second contraction is brought about when tendinous tissue compliance is lower at shorter inter-pulse intervals than at longer ones. In the long inter-pulse intervals, the decrease in torque and increase in tendinous tissue elongation in C2 may be due to the increase of tendinous tissue compliance caused by the long interval between the first and second stimulations.

In resting and non-acute stretching states, muscle–tendon complexes have slack. ODA et al. [11] observed a 10–30-ms time delay in the twitch torque generated in the presence of fascicle shortening in the TA at plantar-flexion angles of 10° and 30° during single stimulations. They suggest that this time delay could be due to the slack in the tendinous tissue. Because the present study used a 20° plantar-flexed position, the tendinous tissue may have had slack before the first electrical stimulations. It is likely that the elongation of the tendinous tissue induced by the first stimulation involved the taking-up of tendon slack. Therefore, the present results suggest that decreases in the taking-up of tendon slack as a result of the first stimulation are also related to the lower tendinous tissue elongation during C2 with a 100-ms inter-pulse interval compared to a single-pulse response. Moreover, the values of elongation and compliance with inter-pulse intervals exceeding 100 ms may near those of a single-pulse response because tendon slack is restored after the first stimulation due to the long inter-pulse interval. Thus, this suggests that the peak torque generated with inter-pulse intervals exceeding 100 ms nears that of a single-pulse response.

Measurement of contractile properties as a result of a single stimulation is a useful method for determining muscle output and muscle contractile fatigue without the influence of the voluntary neural drive. When a muscle–tendon component has a slack before the first electrical stimulation, the muscle contractile properties assessed by single-twitch torque are influenced by the slack of the muscle–tendon component. A previous study suggests that if the first response takes up most of the slack of the muscle–tendon component, the torque response and tendinous tissue elon-

gation during C2 would be minimally influenced by the muscle–tendon slack [16]. This is regarded as an important physiological and medical interpretation of the measurements of torque response and muscle architectural changes during C2 because neuromuscular function without the influence of muscle-tendon slack may be evaluated in the human skeletal muscle. In the light of the present results regarding the changes in the torque, tendinous tissue elongation, and tendinous tissue compliance during C2 with different inter-pulse intervals, this study propose that C2 measured with inter-pulse intervals less than 100 ms is useful for evaluating muscle contractile properties excluding the influence of tendon slack in the human skeletal muscle.

The limitation of the present study is that the results to tendinous tissue properties rely on analyses of two-dimensional images. In actual, the muscle has a complex three-dimensional structure. The previous study using three-dimensional analysis suggested that the muscle cell stress is approximately the same as in the tendon in TA [20]. Thus, this study could not rule out the possibility that interaction between muscle cell stress and tendon stress are related to the facilitative effect of force response with respect to the second stimulation. Therefore, future studies need to investigate the muscle architectural change using three-dimensional analysis, which can clarify more the relationship between extent of force summation and summation of contraction in human muscle as a muscle–tendon complex.

In summary, the results of the study show that the tendinous tissue elongations during C2 with inter-pulse intervals less than 80 ms are significantly lower than that of a single-pulse even though C2 with inter-pulse intervals less than 100 ms resulted in significantly higher torque responses compared to a single pulse. These results indicate that the summation pattern of tendinous tissue elongation is different from that of the torque response in the human TA during 2-pulse trains with different inter-pulse intervals. Moreover, the results show that the greater torque produced during C2 with inter-pulse intervals less than 100 ms compared to that with a single pulse is accompanied by lower elongation and compliance of tendinous tissue for C2. Furthermore, the tendinous tissue compliance for C2 is strongly negatively related to the force response for C2. Therefore, the present study revealed that the torque response generated by C2 is greatest where the force summation as a result of the second stimulation coincides with the period of decreased tendinous tissue compliance as a result of the first stimulus.

Acknowledgement

This work was supported by a Grant-in-Aid for Research Activity Start-up (No. 21800076) in Japan.

References

[1] COOPER S., ECCLES J.C., *The isometric responses of mammalian muscles*, J. Physiol., 1930, 69, 377–385.

[2] STEIN R.B., PARMIGGIANI F., *Nonlinear summation of contractions in cat muscles*. I. *Early depression*, J. Gen. Physiol., 1981, 78, 277–293.

[3] DUCHATEAU J., HAINAUT K., *Nonlinear summation of contractions in striated muscle*. I. *Twitch potentiation in human muscle*, J. Muscle. Res. Cell. Motil., 1968, 7, 11–17.

[4] PARMIGGIANI F., STEIN R.B., *Nonlinear summation of contractions in cat muscles*. II. *Later facilitation and stiffness changes*, J. Gen. Physiol., 1981, 78, 295–311.

[5] STEIN R.B., GORDON T., *Nonlinear stiffness – force relationships in whole mammalian skeletal muscles*, Can. J. Physiol. Pharmacol., 1986, 64, 1236–1244.

[6] BOJSEN-MOLLER J., MAGNUSSON S.P., RASMUSSEN L.R., KJAER M., AAGAARD P., *Muscle performance during maximal isometric and dynamic contractions is influenced by the stiffness of the tendinous structures*, J. Appl. Physiol., 2005, 99, 986–994.

[7] LIEBER R.L., LEONARD M.E., BROWN-MAUPIN C.G., *Effects of muscle contraction on the load-strain properties of frog aponeurosis and tendon*, Cells Tissues Organs, 2000, 166, 48–54.

[8] MAGANARIS C.N., NARICI M.V., REEVES N.D., *In vivo human tendon mechanical properties: effect of resistance training in old age*, J. Musculoskelet. Neuronal. Interact., 2004, 4, 204–208.

[9] MAGNUSSON S.P., HANSEN P., AAGAARD P., BROND J., DYHRE-POULSEN P., BOJSEN-MOLLER J., KJAER M., *Differential strain patterns of the human gastrocnemius aponeurosis and free tendon, in vivo*, Acta. Physiol. Scand., 2003, 177, 185–195.

[10] OHTA Y., SHIMA N., YABE K., *The effect of summation of contraction on acceleration signals in human skeletal muscle*, J. Electromyogr. Kinesiol., 2010, 20, 1007–1013.

[11] ODA T., HIMENO R., C HAY D., CHINO K., KURIHARA T., NAGAYOSHI T., KANEHISA H., FUKUNAGA T., KAWAKAMI Y., *In vivo behavior of muscle fascicles and tendinous tissues in human tibialis anterior muscle during twitch contraction*, J. Biomech., 2007, 40, 3114–3120.

[12] WICKIEWICZ T.L., ROY R.R., POWELL P.L., EDGERTON V.R., *Muscle architecture of the human lower limb*, Clin. Orthop. Relat. Res., 1983, 179, 275–283.

[13] FUKUNAGA T., ROY R.R., SHELLOCK F.G., HODGSON J.A., EDGERTON V.R., *Specific tension of human plantar flexors and dorsiflexors*, J. Appl. Physiol., 1996, 80, 158–165.

[14] NARICI M.V., LANDONI L., MINETTI A.E., *Assessment of human knee extensor muscles stress from in vivo physiological cross-sectional area and strength measurements*, Eur. J. Appl. Physiol. Occup. Physiol., 1992, 65(5), 438–444.

[15] OHTA Y., YABE K., *The effects of muscle architectural change with a pre-motion silent period on the subsequent muscular output during rapid voluntary movement*, J. Electromyogr. Kinesiol., 2010, 20, 136–141.

[16] OHTA Y., SHIMA N., YABE K., *Changes in force and tendinous tissue elongation during the early phase of tetanic*

summation in in vivo human tibialis anterior muscle, J. Biomech., 2010, 43, 998–1001.

[17] RUGG S.G., GREGOR R.J., MANDELBAUM B.R., CHIU L., *In vivo moment arm calculations at the ankle using magnetic resonance imaging (MRI)*, J. Biomech., 1990, 23, 495–501.

[18] DUCHATEAU J., HAINAUT K., *Nonlinear summation of contractions in striated muscle*, II. *Potentiation of intracellular Ca^{2+} movements in single barnacle muscle fibres*, J. Muscle. Res. Cell. Motil., 1986, 7, 18–24.

[19] ITO M., KAWAKAMI Y., ICHINOSE Y., FUKASHIRO S., FUKUNAGA T., *Nonisometric behavior of fascicles during isometric contractions of a human muscle*, J. Appl. Physiol., 1998, 85, 1230–1235.

[20] HIBLAR T., BOLSON E.L., HUBKA M., SHEEHAN F.H., KUSHMERICK M.J., *Three dimensional ultrasound analysis of fascicle orientation in human tibialis anterior muscle enables analysis of macroscopic torque at the cellular level*, Adv. Exp. Med. Biol., 2003, 538, 635–644; discussion 645.