JOURNAL OF THE
JAPANESE PHYSICAL
THERAPY ASSOCIATION

REPORT

Task Dependent Motor Strategy of Human Triceps Surae Muscle

Kiyokazu AKASAKA[1], Hideaki ONISHI[2], Kouji IHASHI[3], Masayoshi ICHIE[4] and Yasunobu HANDA[5]

[1]Department of Physical Therapy, Saitama Medical School Junior College, Saitama 350-0495, Japan
[2]Department of Physical Therapy, Niigata University of Health and Welfare, Niigata 950-0932, Japan
[3]Department of Physical Therapy, Yamagata Prefectural University of Health Sciences, Yamagata 990-2212, Japan
[4]Department of Restorative Neuromuscular Surgery and Rehabilitation, Tohoku University Graduate School of Medicine, Sendai 980-8575, Japan
[5]New Industry Hatchery Creation Center, Tohoku University, Sendai 980-8579, Japan

Abstract. Even though many investigators have analyzed the functional difference of the three heads of triceps surae in human, none of them succeeded to clarify the distinctive functional difference of those three muscles. The aim of this study was to investigate whether the integrated EMGs (IEMGs) of the triceps surae muscle, gastrocnemius and soleus, were task dependent. IEMGs of the medial head of the gastrocnemius (GM), lateral head of the gastrocnemius (GL), and soleus (SO) were investigated at three different knee joint angles, at four different duration of ramp contraction, with the generation of a single ongoing force, from 0 to the maximum voluntary contraction (MVC). Three-way ANOVAs for repeated measures were used to estimate differences in IEMG values in each of the GM, GL, and SO, taken at four different durations of ramp contraction (5, 10, 15 and 20 s), at three different knee joint angles (0 deg, 30 deg and 90 deg), across ankle plantar flexion levels of force (10, 20, 30, 40, 50, 60 and 70% MVC). According to three-way ANOVAs for repeated measures, IEMG of the GM muscle showed a first-order interaction between force and knee joint angle. In addition, IEMG of the GL muscle showed first-order interactions between the level of force and knee joint angle, and between the level of force and duration of ramp contraction. Furthermore, IEMG of the SO showed a main effect only on level of force. These results suggest that the each head of the triceps surae may work task dependently.

Key words: duration of contraction, joint angle, force, triceps surae muscle, isometric contraction

(J Jpn Phys Ther Assoc 7: 15–22, 2004)

The functional distribution of motoneurons in the central nervous system may enable smoother muscle force generation and less fatigue during voluntary movement. The order in which muscles are recruited on the basis of the size principle and firing rate of motoneurons is reflected in the contraction property[1–3]. While muscles group such as the prime movers almost always consist of more than two different skeletal muscles, the combination of activities within individual muscles remains an exciting question in motor control.

Received: December 11, 2002
Accepted: December 6, 2003
Correspondence to: Kiyokazu Akasaka, Department of Physical Therapy, Saitama Medical School Junior Collgee, 38 Morohongou, Moroyama-machi, Iruma-gun, Saitama 350–0495, Japan.
e-mail: akasaka-smc@umin.ac.jp

The ankle plantar flexors consist of the triceps surae, plantaris, flexor hallucis longus, flexor digitorum longus, peroneus longus, and tibialis posterior[4]. Among these muscles, the triceps surae muscle is an interesting object for experimental investigation as it is viewed to constitute three unique muscles, the medial head of the gastrocnemius (GM), lateral head of the gastrocnemius (GL), and soleus (SO), all of which have been well identified histochemically and confirmed to function as agonists for ankle plantar flexion[5–9]. While the SO is composed mainly of slow twitch and fatigue-resistant muscle fibers, both the GM and GL have nearly the same proportions of slow and fast twitch muscle fibers. Because of these histochemical differences in the triceps surae muscle, the GM and GL should show fatigue characteristics different from those of the SO. Moreover, unlike the SO, a monoarticular muscle, the GM and GL are biarticular ones that cross the knee joint, hence the angle of the knee joint affects their contributions to plantar flexion torque. In addition to these difference, our previous study suggests that GL may have greater proportion of fast-fatigable twitch muscle fibers than GM[10]. Given these differences in the triceps muscles, their strategies in voluntary movements may differ[11–14].

Even though many studies indicate that the IEMG value of the prime mover is linearly increase with an increase in force under an isometric condition[15–18], some recent studies object to this opinion because the EMG amlitude increased nonlinearly with ensemble activation rate of a pool of motor units[19)20]. However, the increase in the IEMG value is commonly believed to due to increases in the amplitude and density of EMG signals resulting from the mutual influences of recruitment and firing rate. For this reason, many studies have used ramp contraction, defined as the generation of a single ongoing force from 0 to MVC[10,21–26]. To our knowledge, however, there have been no investigations on the activities of the prime mover at ramp contractions of various durations under an isometric condition and variable muscle length conditions. Within the human triceps surae, a muscle extensively studied by many investigators, the characteristic functional differences in the respective constituent muscles are not clearly distinguished. We hypothesized that activities of the triceps surae would be more clearly defined by three parameters of the constituent muscles, namely, duration of contraction, length of muscle, and plantar flexion performance. To look into this hypothesis, the present study investigated the behavior IEMG of each head of the triceps surae muscle during various ramp contraction durations (5, 10, 15 and 20 s), at three different knee joint angles (0 deg and flexed at 30 deg and 90 deg), across different ankle plantar flexion levels of force (10, 20, 30, 40, 50, 60 and 70% MVC).

Materals and Methods

Seven healthy men, (27.7 ± 5.6 years old; 168.4 ± 3.4 cm in height; 63.9 ± 12.8 kg in weight [mean ± S.D.]), volunteered for the present study. None had any history of musculoskeletal injury or orthopedic abnormality in the lower extremities. All of the subjects were fully informed of the nature of this research and gave their informed consent before participating in the experiments.

The subjects were positioned and secured on a dynamometer (KinCom AP; Chattanooga, TE, U.S.A.) for measurement of isometric ankle plantar flexion. The body was placed in a prone position on a test bench with the pelvis stabilized by belts. With the right foot firmly attached to the dynamometer, the knee angle was locked in a previously determined position with a turn-buckle type knee brace and attached to the bench (Fig. 1). To prevent

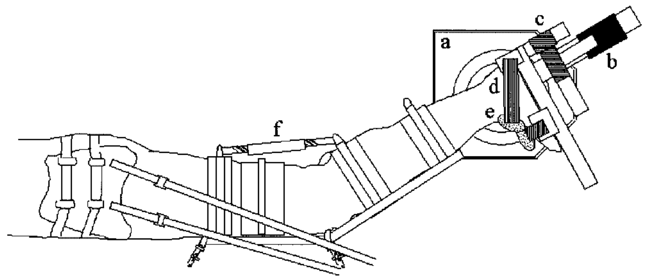


Fig. 1. The experimental arrangement for measurement of ankle plantar flexion force. The center of the ankle joint was set at the rotational center of the lever arm of KinCom (dynamometer). For a better view, the two belts to stabilize the pelvic are not shown. a. the head of KimCom; b. transducer of KimCom; c. adjustable parts of ankle device; d. elastic band; e. pads; f. turn-buckle knee brace.

the entire body upward, the pelvis of the subject was further stabilized by another belt, of the type usually used for indirect lumbar traction. EMG activity was recorded using Ag-AgCl surface electrodes (Blue Sensor, type NF-50-F, specially modified to a 16 mm diameter, MEDICOTEST, Ølstykke, Denmark). Before applying the electrodes, the skin was shaved and prepared to reduce skin resistance. Two pairs of electrodes were placed over each of the GM, GL and SO muscles of the right leg in a bipolar configuration parallel to the muscle fiber over the apparent belly of the muscles according to Delagi *et al.*[27]. Each pair of electrodes was positioned so that the central distance of the electrodes was set at 30 mm and held in place with adhesive tape to limit movement artifacts. Next, the ground electrode was placed over the greater trochanter of the femur. All EMG signals were pre-amplified with a gain of 2 by differential amplifiers (DPA-10P; Diamond Medical, Tokyo) and then amplified with a gain of 200 (Biotop 6R12; NEC San-ei, Tokyo). The best S/N ratio of either channel of EMG signals for each muscle was used for the subsequent filtering process.

Before the experiments, isometric ankle plantar flexion forces with the maximal effort were measured twice for a 5-sec period at an ankle joint angle of 0 deg (neutral position, the footplate of the dynamometer perpendicular to the tibia) and a knee angle of 0, 30, or 90 deg. The higher force between two maximal efforts was determined as the MVC at each knee joint angle. Subjects were allowed a 3-min rest between maximal efforts. For experimental measurements, we used a force trajectories system (KM-EMS101; Henry Japan, Hasuda) consisting of both hardware and software components. Because the force output of KinCom has linearity, we adjusted the gain with a weight of 100 N using the dial on the hardware controller after calibrating it to 0 without any weight. The hardware received force signals from the KimCom system and output four different signals,

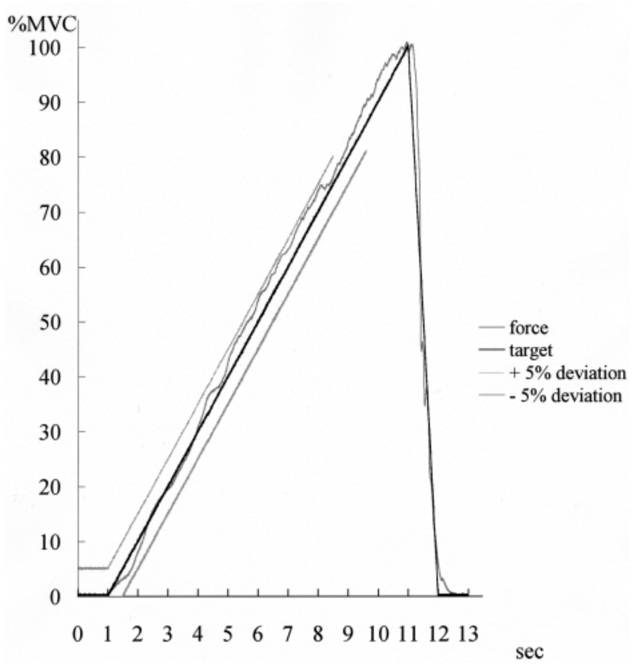


Fig. 2. Typical data from one subject: ankle planter flexion force and target line with 5% deviation lines during 5-s ramp contraction.

i.e., raw force, amplified force, target force, and trigger signals.

The experimental protocol consisted of four different ramp contraction durations (5, 10, 15 and 20 s) at three different knee joint angles. A ramp was defined as a single ongoing contraction with a linear increase in force from 0 to MVC. A 3-min rest period was allowed between each contraction. The subjects were provided visual feedback of their elicited force trajectories and a target force line on a computer monitor during all contractions. Twelve trials for each maneuver were repeated for each subject if the subject made good force trajectories compared to a target line on the computer monitor (Fig. 2). If the force elicited by the subject deviated more than 5 % of the maximal force from the target line upto 80% MVC, the subject was asked to repeat the trial after a 3-min rest.

The raw EMG signals and force signals from a dynamometer were simultaneously recorded on a 16-channel 8 mm data recorder (RX-800; TEAC, Tokyo) with a frequency range of DC-20 kHz. All signals were also continuously monitored on a pen-recorder, with a paper duration of 5 mm/sec. EMG signals were sampled at a frequency of 1.0 kHz and analogue-to-digital conversion with 12-bit accuracy over the range ± 5 V (AD12–16U(PC)EH; Contec, Osaka). The data were stored on an 8 mm tape for subsequent analyses.

The EMG signals were digital bandpass filtered between 10 Hz and 350 Hz (Bimtas2; Kissei Comtec; Matsumoto). IEMG values of the muscles were computed for 512 points of EMG signals, and each of its center was corresponding to the following levels of force: 10, 20, 30, 40, 50, 60 and 70% MVC, respectively. The IEMG values obtained from the four ramp contractions at three different knee joint angles at the same levels of force were used for the statistical analysis and graphical representation of the data.

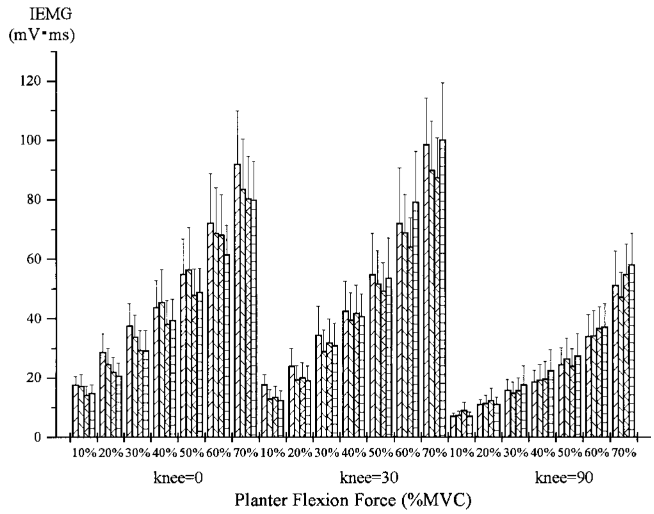
Statistical analyses

Three-way ANOVAs for repeated measure were used to estimate differences in IEMG values in each of the GM, GL, and SO, taken at four different ramp contraction durations (5, 10, 15 and 20 s), at three different knee joint angles (0, 30, and 90 deg), across levels of force (10, 20, 30, 40, 50, 60 and 70% MVC). As post hoc tests, Tukey's honestly significant difference (HSD) test and multiple comparison tests were performed. $p<0.05$ was assumed to indicate statistical significance.

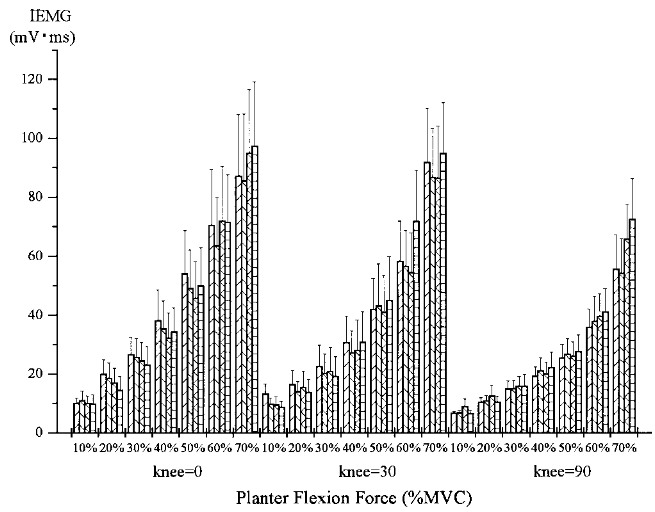
Results

The amplitude and density of raw EMG in each head of the triceps surae muscles were increased in all ramp contractions trials at increasing forces. Figure 3 shows the relationship between IEMG and force (% of MVC) for each of the three muscles at four different ramp contraction durations (5, 10, 15 and 20 s), at three different knee joint angles (0, 30, and 90 deg), at 10, 20, 30, 40, 50, 60, 70 % MVC were shown for GM, GL, and SO (Fig. 3). According to three-way ANOVAs, IEMG of the GM muscle showed a first-order interaction between the level of force and knee joint angle (df=12; F=8.96; $p<0.05$; Table 1). In addition, IEMG of the GL muscle showed first-order interactions between the level of force and knee joint angle (df=12; F=2.84; $p<0.05$), and between the level of force and duration of ramp contraction (df=18; F=1.93; $p<0.05$). Furthermore, IEMG of the SO showed a main effect only on the level of force (df=6; F=49.0; $p<0.05$).

For the multiple comparison tests for the GM, we combined and compared the ramp contraction durations as means because there were no significant interactions involving durations of contraction. Multiple comparison tests for the GM revealed that IEMG with the knee at 30 deg flexion showed the most sensitive increases as the ankle plantar flexion force was increased (Fig. 4). IEMG with the knee extended also increased under the same condition, but to a lesser extent. IEMG at 90 deg knee flexion was less sensitive to the increases in the levels of force. When IEMG of the GM was compared among all three knee joint angles, that obtained at 90 deg flexion was significantly smaller than those obtained at the knee extended and at 30 deg flexion positions at all levels of force investigated (Fig. 4). IEMG values at 30 deg knee flexion at 60 and 70% MVC of ankle plantar flexion force were significantly a



b



c

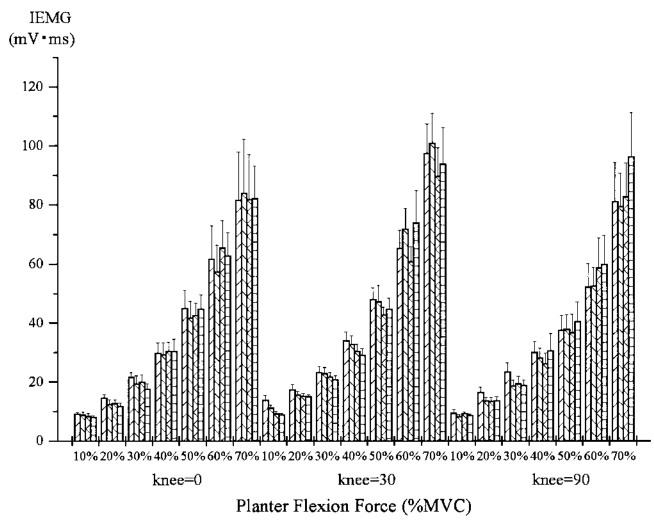


Fig. 3. The Relationship between the force (in % of MVC) and integrated EMG (mV·ms) at three different position of knee (extended, 30 deg and 90 deg in flexion) during four different durations of ramp contraction (5, 10, 15 and 20 s). a. medial head of the gastrocnemius (GM), b. lateral head of the gastrocnemius (GL) and c. soleus (SO). Durations of ramp contraction; 5 s (▨), 10 s (▧), 15 s (▩) and 20 s (▤) in rise time. The values represent the mean ± S.E. (n=7).

Table 1. Summary of three-way ANOVAs for each head of the triceps surae muscle

	C	A × C	B × C
GM			*
GL		*	*
SO	*		

A: 4 different durations of ramp contraction; B: knee joint angle; C: level of force. × indicates interaction between two factors; * indicates statistical significance ($p<0.05$).

larger than those at 0 deg and at 90 deg. In addition, IEMG values at 0 deg knee flexion at 60 and 70% MVC ankle plantar flexion force were significantly larger than those at 90 deg.

For the multiple comparison tests for the GL, the ramp contraction durations were combined and compared as means for a first-order interaction between level of force and knee joint angle, whereas the knee joint angles were treated as they were in the calculation for first-order interactions between the level of force and duration of ramp contraction. Multiple comparison tests on the first-order interaction between the level of force and knee angle for the GL showed that the IEMG of GL had an order of sensitivity to ankle plantar flexion force comparable to that of the IEMG of the GM (Fig. 5). As for angular differences of the knee, IEMG of the GL between at 90 deg knee flexion differed from that at the other two knee angles (Fig. 5). IEMG values at 0 deg knee flexion at 50 and 60% MVC ankle plantar flexion force were significantly larger than those at 30 deg and 90 deg, while IEMG values at 30 knee flexion at 60 and 70% MVC were significantly larger than those at 90 deg. Multiple comparison tests on another first-order interaction between the level of force and ramp contraction duration for the GL revealed almost the same results among the four ramp contraction durations (Fig. 6).

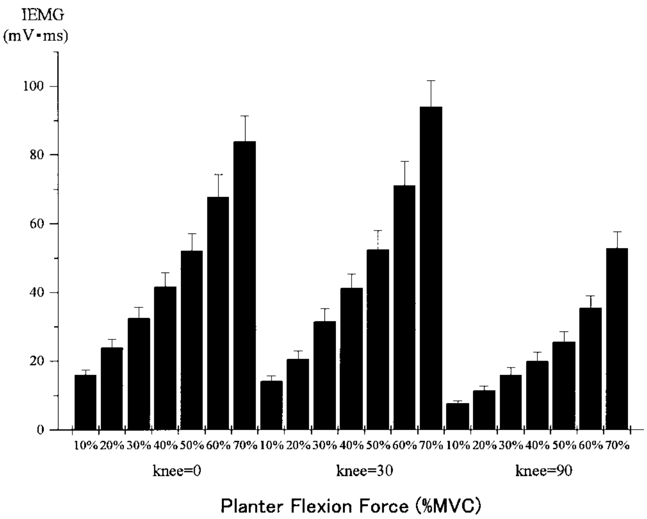


Fig. 4. The relationship between the force (in % of MVC) and integrated EMG (mV·ms) of medial head of the gastrocnemius muscle with the knee at 0, 30, and 90 deg flexion.

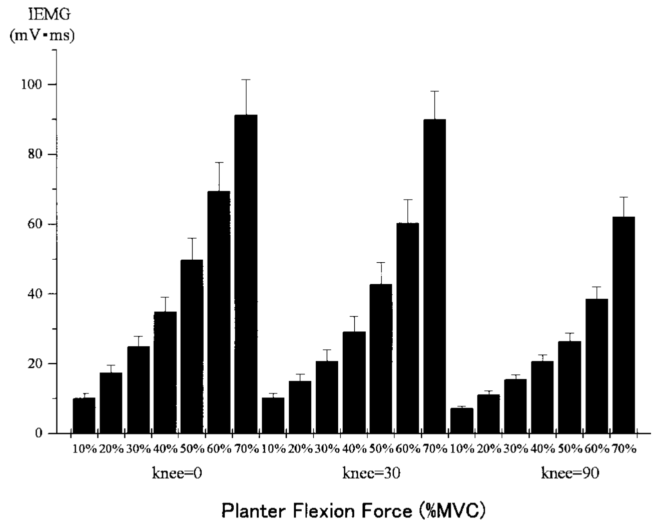


Fig. 5. The relationship between the force (in % of MVC) and integrated EMG (mV·ms) of lateral head of the gastrocnemius muscle with the knee at 0, 30, and 90 deg flexion.

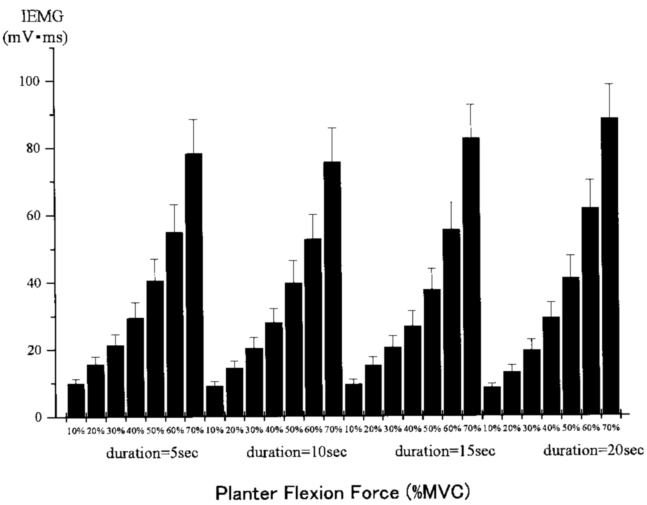


Fig. 6. The relationship between the force (in % of MVC) and integrated EMG (mV·ms) of lateral head of the gastrocnemius muscle during four different ramp contraction durations of 5, 10, 15, 20 s.

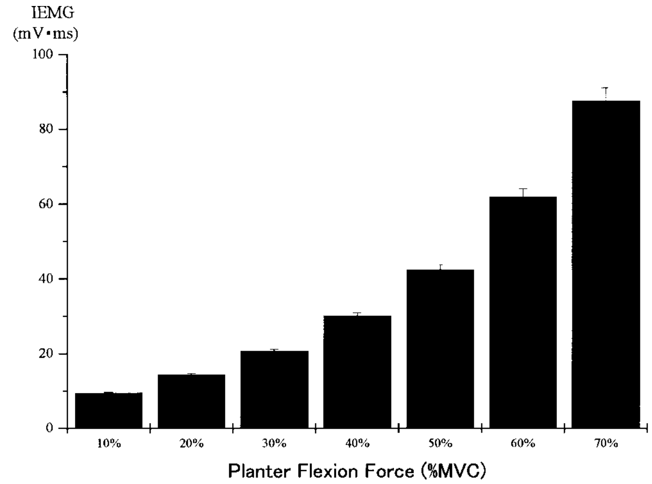


Fig. 7. The relationship between the force (in % of MVC) and integrated EMG (mV·ms) of the soleus muscle.

In the comparison among ramp contraction durations, IEMG obtained at an ankle plantar flexion force of 60% MVC was significantly different between ramp contraction durations of 10 and 20 s (Fig. 6). In addition, IEMG values obtained during 20 s ramp contraction at 70 % MVC were significantly different from those obtained during 5 and 10 s ramp contractions.

To analyze the main effect of levels of force by multiple comparison tests for the SO, we combined and compared the ramp contraction duration and knee joint angle as means since there were no significant interactions involving ramp contraction durations and knee joint angles. IEMG values at 60 and 70% MVC were larger than those at weaker ankle plantar flexion levels of force (Fig. 7).

According to our results, the constituent muscles within the triceps surae were clearly distinguished from each other with respect to the duration of contraction, length of muscle, and plantar flexion force.

Discussion

The triceps surae is generally considered to be the prime mover of ankle plantar flexion because of its muscular mass and the length of the lever arm of the moment on the ankle joint[28]. Many investigators have reported on different aspects of this muscle.

Positions of knee angle

As the GM and GL are biarticular muscles while the SO is a monoarticular one, differences of muscle activation in the former depend upon the angular positions of the knee[29]. According to their M-wave study on these three muscles, when subjects moved from a knee extended position to 90 deg knee flexion, the M-wave amplitudes decreased in the GM and GL (0.64 ± 0.14, 0.66 ± 0.16, respectively), while that of the SO (0.96 ± 0.05) remained unchanged. Our results indicated that the biarticular muscles, the GM and GL, showed a significant decrease in IEMG at higher levels of ankle plantar flexion force when the knee was flexed at 90 deg, whereas the monoarticular muscle, the SO, showed no significant difference at any angular position of the knee. Several factors could explain these results. First of all, neuromuscular transmission failure is likely to bring about decreases in IEMG values and the amplitude of M-wave. As the ramp contractions at three different knee angles were based on the MVC at each knee angle in our experiments, the central drive from the spinal motor neurons was considered to be unchanged. Second, the muscle length and tension also influenced the force production. Several differences have been reported in the activation of the gastrocnemius muscle (GA) and SO[30–33]. When the knee is flexed at 90 deg, both heads of the GA are placed at a mechanical disadvantage due to the shortened length of the muscle. On the other hand, during isokinetic ankle plantar flexion with the knee extended, the GA and SO were suspected to have different optimal lengths at different ankle joint angles[30]. As the ankle plantar flexion force was measured at three different knee angles with the ankle at a neutral angle in our experiment, the GA might have been subject to mechanical disadvantages as the knee angle increased. Third, as muscle itself serves as a conductor, the EMG signal characteristics depend on the number of muscle fibers within the recording volume of electrodes[34]. When we looked at the relationship between the diameter of a muscle fiber and muscle length in our study, the diameter of a muscle fiber decreased when the muscle was stretched, and vice versa. In other words, the numbers of muscle fibers of the GM and GL obtained by surface electrodes with the knee extended and flexed at 30 deg, may have far outnumbered those obtained with the knee flexed at 90 deg. Another factor that might have influenced the EMG of the triceps surae muscle was the thickness of skin layer. According to an earlier report, the skin layer thickness could act as a low-pass filter[35], hence the EMG of the triceps surae muscle obtained by surface electrodes might be influenced by the knee joint angle. This factor remains unclear in our experiment, as we did not measure thickness of the skin layer at any of the knee joint angles.

Ankle plantar flexion levels of force

Relating to the increase of IEMG during ramp contraction, EMG signals from all of the triceps increased in amplitude and firing rate with increasing levels of force. This result agrees with other literature that has dealt with prime movers[15–18]. In short, muscle force is graded primarily by increases in the number of active motor units and firing rate modulation[1–3].

Duration of ramp contraction

While IEMG of the GL exclusively showed significant increase during the longer duration of ramp contraction, this result can be imputed to be several factors. The first factor is the size of motor unit action potential. The progressive enlargement in the IEMG during submaximal contraction is thought to primarily reflect an increase in the number of recruited motor units and in their firing rates[36–38]. Compared to the GM, the GL has a significantly shorter mean contraction and half-relaxation time[39][40]. In addition to these contractile properties, spectrum analysis of EMG signals obtained by the GL showed that median frequency during step contraction exclusively increased as ankle plantar flexion force increased in our previous study[10]. These two findings may indicate that the GL consists larger proportion of fast-fatigable muscle among the type 2 fiber subgroups than GM. A recent study also indicated the possibility that the size of motor unit action potentials enlarge, especially on fast-fatigable muscles[41]. Compared to smaller sizes of motor unit action potentials, increased firing rate of the larger size of motor unit action potential by fast-fatigable muscle at higher force of ankle planter flexion during longer duration of contraction, may cause significantly increase the IEMG.

In addition to the number of recruited motor units and in their firing rates, the decreased conduction velocity of muscle fiber during prolonged contractions may influence the IEMG[42–44]. Muscle fiber conduction velocity was decreased mainly by peripheral mechanisms such as changes in the membrane excitability presumably due to hydrogen ion and metabolic accumulation[45][46], K^+ accumulation in the extracellular space[47] and the changes of pH[48]. A steeper decrease in the muscle fiber conduction velocity may account for the increase in IEMG.

Motor control

The last factor relating to muscle activation is motor control. Previous reports have speculated that the EMG signals may differ as a result of the actual role played by a muscle in a particular task[49][50]. It has been hypothesized that motor neuron pools are organized into task groups to help the CNS coordinate the activity of motor units in other synergistic muscles. Within the triceps surae muscle, the EMG of the GA increased while that of the SO decreased during faster isotonic contraction. In cases where the prime movers consist of more than two muscles, selective recruitment strategy to control the duration of contraction has been suggested. In addition to these recruitment strategy, a recent study relating to motor control, suggested that shortened GA muscle may be influenced by peripheral affarents capable of reducing the excitability of the motoneurone pool[51].

In conclusion, the present results suggest that each of the constituent muscles in the triceps surae has three distinctive functional characteristics, namely, the duration of contraction, muscle length, and plantar flexion force. These task-dependent motor strategies of human triceps surae muscle may contribute to the high functional precision of ankle plantar flexion performance.

REFERENCES

1) Basmajian JV, De Luca CJ: Muscle Alive. 5th ed, Baltimore, Williams and Wilkins, 1985.
2) Calancie B, Bawa P: Motor unit recruitment in humans. In: Binder MD, Mendell LM (eds) The Segmental Motor System. New York, Oxford University Press, 1990, pp 75–95.
3) Henneman E, Somjen G, Carpenter D: Functional significance of cell size in spinal motoneurons. J Neurophysiol 28: 560–580, 1965.
4) Salmons S: Muscle. In: Salmons S (ed) Gray's Anatomy. 38th ed, New York, Churchill Livingstone, 1995, pp 881–899.
5) Edgerton VR, Smith JL, Simpson DR: Muscle fiber type populations of human leg muscles. Histochem J 7: 259–266, 1975.
6) Elder GCB, Bradbury K, Roberts R: Variability of fiber type distributions in human muscles. J Appl Physiol Respirat Environ Exercise Physiol 53: 1473–1480, 1982.
7) Gollnick PD, Sjodin B, Karlsson J, Jansson E, Saltin B: Human soleus muscle: A comparison and enzyme activities with other leg muscles. Pflügers Arch 348: 247–255, 1974.
8) Green HJ, Daub B, Houston ME, Thomason JA, Fraser I, Ranney D: Human vastus lateralis and gastrocnemius muscles. A comparative histochemical and biochemical analysis. J Neurol Sci 52: 201–210, 1981.
9) Johnson MA, Polgar J, Weightman D, Appleton D: Data on the distribution of fibre types in thirty-six human muscles. An autopsy study. J Neurol Sci 18: 111–129, 1973.
10) Akasaka K, Onishi H, Momose K, Ihashi K, Yagi R, Handa Y, Hoshimiya N: EMG power spectrum and integrated EMG of ankle plantarflexors during stepwise and ramp contractions. Tohoku J Exp Med 182: 207–216, 1997.
11) Carpentier A, Duchateau J, Hainaut K: Velocity-dependent muscle strategy during plantarflexion in humans. J Electromyogr Kinesiol 6: 225–233, 1996.
12) Gravel D, Arsenault AB, Lambert J: Soleus-gastrocnemius synergies in controlled contractions produced around the ankle and knee joints: an emg study. Electromyogr Clin Neurophysiol 27: 405–413, 1987.
13) Jacobs R, Bobbert MF, Van Ingen Schenau GJ: Function of mono-and biarticular muscles in running. Med Sci Sports Exerc 25: 1163–1173, 1993.
14) Tamaki H, Kitada K, Akamine T, Sakou T, Kurata H: Electromyogram patterns during plantarflexions at various angular velocities and knee angles in human triceps surae muscles. Eur J Appl Physiol 75: 1–6, 1997.
15) Lippold OCJ: The relation between integrated action potentials in a human muscle and its isometric tension. J Physiol 117: 492–499, 1952.
16) Milner-Brown HS, Stein RB: The relation between the surface electromyogram and muscular force. J Physiol 246: 549–569, 1975.
17) Moritani T, deVries HA: Reexamination of the relationship between the surface integrated electromyogram (IEMG) and force of isometric contraction. Am J Phys Med 57: 263–277, 1978.
18) Weir JP, Wagner LL, Housh TJ: Linearity and reliability of the IEMG v torque relationship for the forearm flexors and leg extensors. Am J Phys Med Rehabil 71: 283–287, 1992.
19) Hulliger M, Day SJ, Guimaraes AG, Herzog W, Zhang YT: A new method for experimental simulation of EMG using multi-channel independent stimulation of small groups of motor units. Motor Control 5: 61–87, 2001.
20) Day SJ, Hulliger M: Experimental simulation of Cat Electromyogram: Evidence for algebraic summation of motor-unit action-potential trains. J Neurophysiol 86: 2144–2158, 2001.
21) Bernardi M, Felici F, Marchetti M, Montellanico F, Piacentini MF, Solomonow M: Force generation performance and motor unit recruitment strategy in muscles of contralateral limbs. J Electromyogr Kinesiol 9: 121–130, 1999.
22) Bilodeau M, Arsenault AB, Gravel D, Bourbonnais D: The influence of an increase in the level of force on the EMG power spectrum of elbow extensors. Eur J Appl Physiol 61: 461–466, 1990.
23) Bilodeau M, Arsenault AB, Gravel D, Bourbonnais D: EMG power spectra of elebow extensors during ramp and step isometric contractions. Eur J Appl Physiol 63: 24–28, 1991.
24) Bilodeau M, Goulet C, Nadeau S, Arsenault AB, Gravel D: Comparison of the EMG power spectrum of the human soleus and gastrocnemius muscles. Eur J Appl Physiol 68: 395–401, 1994.
25) Tanji J, Kato M: Recruitment of motor units in voluntary contraction of a finger muscle in man. Exp Neurol 40: 759–770, 1973a.
26) Tanji J, Kato M: Firing rate of individual motor units in voluntary contraction of abductor digiti minimi muscle in man. Exp Neurol 40: 771–783, 1973b.
27) Delagi EF, Petotto A, Iazzetti J, Morrison D: Leg. In: Perotto AO (ed) Anatomical Guide for the Electromyographer. 3rd ed, Charles C Thomas, 1994, pp 142–171.
28) Murray MP, Guten JM, Baldwin JM, Gardner GM: A comparison of plantarflexion torque with and without the triceps surae. Acta Orthop Scand 47: 122–124, 1976.
29) Cresswell AG, Löscher WN, Thorstensson A: Influence of gastrocnemius muscle length on triceps surae torque development and electromyographic activity in man. Exp Brain Res 105: 283–290, 1995.
30) Bobbert MF, Van Ingen Schenau GJ: Isokinetic plantar flexion: Experimental results and model calculations. J Biomech 23: 105–119, 1990.
31) Gregor RJ, Komi PV, Browning RC, Jarvinen M: A

comparison of the triceps surae and residual muscle moments at the ankle during cycling. J Biomech 24: 287–297, 1991.
32) Ito A, Komi PV, Sjodin B, Bosco C, Karlsson J: Mechanical efficiency of positive work in running at different durations. Med Sci Sports Exercise 15: 299–308, 1983.
33) Komi PV, Norman RW: Preloading of the thrust phase in cross-country skiing. Int J Sports Med 8(Suppl 1): 48–54, 1987.
34) Vigreux B, Cnockaert JC, Pertuzon E: Factors influencing quantified surface EMGs. Eur J Appl Physiol 41: 119–129, 1979.
35) Lindstrom L, Petersen I: Power spectrum analysis of EMG signals and its applications. Prog Clin Neurophysiol 10: 1–51, 1983.
36) Bigland-Ritchie B: EMG force relations and fatigue of human voluntary contractions. Exerc Sport Sci Rev 9: 245–250, 1981.
37) Fuglevand AJ, Zackowski M, Huey KA, Enoka RM: Impairment of neuromuscular propergation during human fatiguing contractions at submaximal forces. J Physiol 460: 549–572, 1993.
38) Maton B: Human motor unit activity during the onset of muscle fatigue in submaximal isometric isotonic contraction. Eur J Appl Physiol 46: 271–281, 1981.
39) Rice CL, Cunningham DA, Tayor AW, Paterson DH: Comparison of the histochemical and contractile properties of human triceps surae. Eur J Appl Physiol 58: 165–170, 1988.
40) Vandervoort AA, McComas AJ: A comparison of the contractile properties of the human gastrocnemius and soleus muscles. Eur J Appl Physiol 51: 435–440, 1983.
41) Chan KM, Andres LP, Polykovskaya Y, Brown WF: Dissociation of the electrical and contractile properties in single human motor units during fatigue. Muscle Nerve 21: 1786–1789, 1998.
42) Masuda K, Masuda T, Sadoyama T, Inaki M, Katsuta S: Changes in surface EMG parameters during static and dynamic fatiguing contractions. J Electromyogr Knesiol 9: 39–46, 1999.
43) Merletti R, Lo Conto LR, Orizzio C: Indices of muscle fatigue. J Electromyogr Kinesiol 1: 20–33, 1991.
44) Mortimer JT, Magnusson R, Petersen I: Conduction velocity in ischemic muscle: effect on EMG frequency spectrum. Am J Physiol 219: 1324–1329, 1970.
45) Nakamaru Y, Schwartz A: The influence of hydrogen ion concentration on calcium binding and release by skeletal mucle sarcoplasmic reticulum. J Gen Physiol 59: 22–32, 1972.
46) Wilkie DR: Muscular fatigue: effects of hydrogen ions and inorganic phosphate. Fed Proc 45: 2921–2923, 1986.
47) Sjogaard G: Muscle energy metabolism and electrolyte shifts during low-level prolonged static contraction in man. Acta Physiol Scand 134: 181–187, 1988.
48) Brody L, Pollock M, Roy S, De Luca C, Celli B: pH induced effects on median frequency and conduction velocity of the myoelectric signal. J Appl Physiol 71: 1878–1885, 1991.
49) Loeb GE: Motoneuron task groups: coping with kinematic heterogeneity. J Exp Biol 115: 137–146, 1985.
50) Tamaki H, Kitada K, Akamine T, Sakou T, Kurata H: Alternate activity in the synergistic muscles during prolonged low-level contractions. J Appl Physiol 84: 1943–1951, 1998.
51) Kennedy PM, Cresswell AG: The effect of muscle length on motor-unit recruitment during isometric planter flexion in humans. Exp Brain Res 137: 58–64, 2001.