ORIGINAL PAPER

Frequent alternate muscle activity of plantar flexor synergists and muscle endurance during low-level static contractions as a function of ankle position

Hiroyuki Tamaki · Hikari Kirimoto · Kengo Yotani · Hiroaki Takekura

Received: 9 April 2011/Accepted: 23 May 2011/Published online: 9 June 2011 © The Physiological Society of Japan and Springer 2011

Abstract We have investigated the appropriate joint angle for detecting frequent alternating activity in synergistic muscles and the relationship between muscle activation patterns and endurance during static low-level contractions. Eleven healthy men performed prolonged static plantar flexion of the ankle at 10% of the maximal voluntary contraction, with the ankle flexed at 100°, 110°, or 120°, while seated with the right leg in full extension. The onset of muscle activation and/or inactivation was detected using quantitative analysis, and alternate activity among muscles was detected using a threshold criterion of $\times e$ or $\times 1/e$ multiplied by the levels of mean electromyograms (EMG) calculated at 1-min intervals. Surface EMG revealed frequent alternations of activity among the lateral and medial gastrocnemius and soleus muscles at an ankle flexion of 110°. The first alternation occurred after approximately 15 min of exercise. The number of alternations per hour was four- to sevenfold higher at 110° than at 100° or 120°. Endurance was longest and shortest at 110° and 120°, respectively. These findings suggest that synergistic motor pools activated at a specific joint angle (110°) affect muscle endurance during static low-level fatiguing tasks.

Keywords Isometric contraction · Trade-off · Fatigue · Triceps surae

H. Tamaki (⊠) · H. Kirimoto Institute for Human Movement and Medical Sciences, Niigata University of Health and Welfare, 1398 Shimami, Kita-ku, Niigata City, Niigata 950-3198, Japan e-mail: hiroyuki-tamaki@nuhw.ac.jp

K. Yotani · H. Takekura National Institute of Fitness and Sports, Kanoya, Kagoshima 891-2393, Japan

Introduction

The nervous system uses various muscle recruitment strategies to prolong muscle contractions with constant submaximal force production. During prolonged lowlevel static contraction, increases in the recruitment and/ or rate coding of motor units generally compensate for decreases in the contraction force of the acting motor units, resulting in a gradual increase of electromyographic activity. Alternate activity in one muscle or in synergistic muscles during prolonged muscle contraction is another strategy [1-8]. The system of rotational activity among muscles provides muscles with time to recover from the fatigue that develops during prolonged static muscle work and may contribute to improved muscle endurance. The relevant studies suggest that maximal endurance might actually be related to this alternation. Individuals with an endurance of >2 h frequently show episodes of alternate activity of motor units during prolonged isometric contractions at 10% maximal voluntary contraction (MVC) [1]. Moreover, alternate activity in synergistic muscles occurs during static contractions under a constant load at 10% MVC for >3 h [3]. Kouzaki and Shinohara [8] reported that alternate muscle activity between synergists attenuates muscle fatigue during low-level sustained knee extension. However, alternate muscle activity seems to emerge under specific conditions of force and joint angle, since the recruitment threshold [9] and activation pattern of motor units [10] for synergistic muscles that involves complex neural interactions in humans are likely to change with joint angle and force levels. Alternation is frequent when very low workloads are applied at 5-10% MVC. However, the appropriate joint angle for detecting frequent alternation remains unclear.

We postulated that different patterns of muscle activity, as a function of joint angle, are associated with muscle endurance. Emphasis has been placed on the fact that the emergence of alternate activity would be related to joint angle; in particular, alternate activity among synergists would serve as a means of minimizing fatigue in a given set of motor units when the activity occurs at a specific joint angle. Muscle fatigue and endurance have been thoroughly investigated in terms of muscle metabolism and type characteristics. Knowledge of the appropriate angle for detecting alternation in muscle activity would enable muscle endurance to be investigated in terms of the neural control system, thus contributing to improved endurance performance.

In the study reported here, we focused on recording surface electromyograms (EMG) from the triceps surae muscle at different joint angles with the aim to detect frequent alternating activity in synergists. The relationship between muscle activation patterns as a function of joint angle and endurance time during low-level static contractions was also examined.

Methods

Subjects

Eleven healthy men with no history of neurological disorders or orthopedic problems provided written, informed consent to participate in the study after receiving a detailed explanation of the experimental procedures and possible risks involved. The participants were given the opportunity to familiarize themselves with the experimental equipment at our laboratory before the study started. Practice MVC tasks were repeated several times using the plantar-flexion device, and all participants precisely followed the experimental protocol and procedures. The Ethics Committee of the National Institute of Fitness and Sports in Kanoya approved the study protocols, which conformed to the Declaration of Helsinki. The mean \pm standard deviation (SD) of the physical characteristics of the participants were as follows: age, 23 ± 3 years; height, 172.6 ± 4.8 cm; body mass, 65.3 ± 5.8 kg.

Procedures

The participants performed prolonged isometric contraction of the triceps surae muscle against a constant workload that corresponded to 10% MVC at ankle joint angles of 100°, 110°, or 120° of plantar flexion (at 90°, the foot is considered to be perpendicular to the leg). Workloads of 10% MVC at each angle were equivalent to 123, 94, and 66 N (mean values), respectively. The order of joint angles was randomized, and the participants rested for at least 2 weeks between tests. The trials were conducted with each participant seated in a custom-designed chair with the right leg fully extended, as previously described [11, 12]. Sirin and Patla [12] demonstrated that the trade-off of EMG activities between individual muscles of the plantar flexors is more evident when the knee is extended rather than flexed. In our study, both the knee and thigh were fixed using a clamp to avoid limb movement and changes in muscle length. The right foot was placed on a footplate attached to a resistance arm, which was counterbalanced at 100°, 110°, or 120°. A custom-designed weight-loading device comprised a wheel connected to a weight by means of a stainless-steel wire [13]. The participants could produce a constant load throughout the experiment by rotating the wheel with the foot attached to the footplate, as previously described [3, 13].

Before and after each experiment, the maximal isometric force of the ankle plantar flexors was measured at 100°, 110°, or 120° using an isometric dynamometer (model 1269F; Takei, Niigata, Japan). The MVC task involved a gradual increase in ankle plantar-flexor force from baseline to maximum over a time interval of approximately 3 s, with maximal force held for 2-3 s. The largest of three maximal efforts at each joint angle was considered to be the MVC force and was used as the reference to determine the target force for fatiguing contractions. Each trial was separated by a rest period of >3 min to minimize the effects of muscle fatigue. To confirm EMG recruitment of the lateral gastrocnemius (LG), medial gastrocnemius (MG), and soleus according to ankle joint angle, three brief (5 s) isometric contractions were performed at a constant load that corresponded to 10% MVC, at ankle plantar-flexion angles that increased at 10° increments between 90° and 130° . Maximal force and EMG at MVC were also measured at each angle to calculate the normalized %EMG. The angle of ankle plantar flexion was determined using an electrogoniometer mounted on the wheel, and joint angle signals were displayed on an oscilloscope screen to provide visual feedback to the participant and to ensure the quality of the contraction. The participant was required to match the target angle (within $\pm 5\%$ of the plantar-flexion angle) on the oscilloscope screen, and an indication was given to match the target angle when the ankle angle fell outside this range. The endurance test was terminated when the participant was unable to maintain the target angle for 5 s despite encouragement from the investigator or when the endurance period exceeded 180 min, which was observed only for the 110° ankle angle.

EMG recordings

Surface EMG recordings were obtained from the LG, MG, soleus, and tibialis anterior (TA) muscles. We also confirmed EMG activity in the TA to check the co-activation of each muscle in the triceps surae and the influence of crosstalk from the TA during prolonged static contractions. Bipolar Ag/AgCl surface electrodes (diameter 8 mm) were placed 25 mm apart (center-to-center) between the medial or lateral side of the Achilles tendon insertion (morphologically confirmed by ultrasonography) and the innervation zone (electrically confirmed with a linear array electrode) of the LG and MG, and on the medial prominence of the soleus along the longitudinal axis of each muscle, running parallel to the fibers.

The reference electrode was placed over the lateral condyle of the femur for all EMG measurements. Skin electrode impedance was reduced by first shaving the skin above the muscle and then abrading it with sandpaper, followed by cleaning with an alcohol wipe. Raw EMG signals were amplified, full-wave rectified, and smoothed (time constant 300 ms) (rsEMG) using a bioelectric amplifier and integrator unit (models AB-261G, EI-601G, respectively; Nihon Kohden, Tokyo, Japan). Amplifier gains were adjusted so that peak rsEMG values fell within the range of 50–200 μ V during the test to confirm EMG recruitment in each muscle according to ankle joint angle. All EMG, force, and joint angle signals were monitored on an oscilloscope and continuously displayed on a thermal array recorder (model RTA-1200; Nihon Kohden). Signals from each measurement were stored on a tape recorder (model RD-135T; TEAC, Tokyo, Japan) and subsequently digitized at a sampling frequency of 2 kHz using a 16-bit A/D converter (PowerLab; AD Instruments, Tokyo, Japan) for later analysis. Each instrument was calibrated immediately before data collection.

Whether or not alternating EMG activity in the triceps surae is due to small changes in force direction and the position of the ankle or toe (that is, inversion or eversion force, toe flexion, or extension force) and changes in plantar-flexed or dorsiflexed positions have been investigated [3]. We therefore confirmed that alternating EMG activity cannot be voluntarily achieved by altering joint angles and force directions of the foot. Muscle movement below the electrode can alter amplitude values. However, whether the geometric artefacts and/or crosstalk are sufficient to continue to cause alternations to EMG activity at a level of $\times 2.7(e)$ or $\times \frac{1}{2}.7(1/e)$ is unclear. We therefore adopted the more stringent level ($\times e$, $\times 1/e$) in our study (Statistical analysis) to show clear increases and decreases in the magnitude of electromyographic activity.

Electrodes were placed between innervation zones and tendons to avoid contributing to geometric artefacts [14].

The innervation zone of each muscle was electrically confirmed with EMG signals recorded during an isometric contraction for 5 s using a linear array of 10 electrodes (silver bars; 1 mm diameter, 10 mm apart; Unique Medical, Fukuoka, Japan) located along the direction of the muscle fibers. The direction of muscle fascicles was checked using a B-mode ultrasound apparatus (SSH-140A; Toshiba, Otawara, Japan) operating the transducer. According to the methods described by Rainoldi et al. [15], the location of the innervation zone was detected as the channel with minimal amplitude. The estimated innervation zone was $48.9 \pm 4.5\%$ of the distance between the MG-Achilles tendon insertion point and the medial side of the popliteus cavity for MG, 59.1 \pm 6.6% of that from the LG-Achilles tendon insertion point to the lateral side of the popliteal cavity for LG, and $68.3 \pm 3.9\%$ of that from the medial side of the Achilles tendon insertion to the soleus line level with the tibia for the soleus.

Statistical analysis

Data are expressed as the mean \pm SD. The effects of joint angle on each parameter were analyzed by repeatedmeasures analysis of variance (ANOVA) non-parametric (Friedman) tests. Differences between groups were assessed by Dunn's test. Differences were considered to be statistically significant at P < 0.05. The amplitude of rsEMG obtained at each angle was normalized according to the value of the EMG amplitude at MVC (%EMG_{max}). Normalized rsEMG data were quantitatively and qualitatively analyzed to detect the onset of muscle activation (ON) and/or inactivation (OFF) as well as alternating activity among muscles, using the scheme of multiple fixed-size test windows and the threshold criteria reported by Staude and Wolf [16] (Fig. 1). The rsEMG data sequence was initially divided into constant 60-s fragments (test window). Mean rsEMG level (m) was then calculated for each window. Different threshold levels were set to detect the onset of ON and OFF in the test window (Window_k), that is, (1) the threshold of 1/e (where e is the base to natural logarithm used to measure the time constant) multiplied the magnitude of *m* in the previous fragment (Window_{k-1}) when the acting muscle turns off and (2) the threshold of e multiplied by the magnitude of m in the previous fragment (Win dow_{k-1}) when the resting muscle turns on. "Binary events" were defined as rsEMG in test windows_(k) that exceeded these thresholds [17]. Alternation of EMG activity among triceps surae muscles was defined when the onset of ON and OFF events within the test window overlapped for more than 0 s (Fig. 1) [18]. At least two consecutive windows were required to visually verify event detection.

Fig. 1 Test windows for event detection of alternate activity among muscles. Two consecutive windows (Window $_{k-1}$, Window $_k$) are displayed for each muscle (LG lateral gastrocnemius, MG medial gastrocnemius, Sol soleus muscle). m Mean rsEMG [raw electromyogram (EMG) signals that had been amplified, full-wave rectified, and smoothed (time constant 300 ms)] level in the previous Window $_{(k-1)}$ with a period of 60 s. The threshold for the offset was set at 1/e while that of the onset was set at e time m (Window_k). Binary events detecting the active (ON) and inactive (OFF) periods are shown in the three muscles. The typical EMG overlap period is also shown (below left) See Statistical analysis for a detailed definition of parameters



Results

Force, ankle joint angles, and EMG activity in individual triceps surae muscles

The MVC forces significantly decreased (P < 0.05) with increasing joint angle (Table 1). To confirm recruitment of LG, MG, and the soleus for static low-level tasks, EMG signals from these muscles were recorded during sustained constant loading, corresponding to 10% MVC, with plantar flexion of the ankle at 10° increments between 90° and 130°. No EMG activity was evident in LG at angles <120°. The LG started to become active at 130° in 9 of the 11 participants, and EMG evidence of MG and soleus recruitment was identified at joint angles between 90° and 130°. As joint angles increased, rsEMG amplitude and %EMG_{max} values between 100° and 130° increased in the MG, but decreased in the soleus (Table 1).

Alternation frequency in triceps surae muscles and endurance

EMG activity was identified at all angles in the MG and soleus, but not in the LG at the start of prolonged static exercise at 100°, 110° or 120°. However, differences in joint angle affected endurance time, ratio (%) of maximal force to initial value, and the number of alternate activity events in the triceps surae muscle per hour. At 110°, increased and relatively silent EMG activity alternated in synergists of the triceps surae muscles (Figs. 1, 2b), whereas EMG activity was silent in the TA, and a co-activation pattern with the triceps surae muscles was absent. Frequent alternation of muscle activity was observed in the three muscles throughout the entire duration of exercise (Fig. 3a). This included the first alternation, which occurred after approximately 15 min of exercise (mean 16.5 ± 4.5 min; Fig. 4a). The number of alternations per hour was four- to sevenfold higher at 110° (P < 0.05) than at either 100° or 120° (Fig. 3a). The tendency for percentage

 Table 1
 Force and electromyographic parameters at 10 and 100% of maximal voluntary contraction

Force and electromyographic parameters	Ankle joint angle				
	90°	100°	110°	120°	130°
At MVC					
Force (N)	1220.4 ± 162.6 a,b	1226.1 ± 160.4 a,b	936.8 ± 142.0 a	664.3 ± 173.1	486.1 ± 101.8
Average rsEMG (µV)					
Lateral gastrocnemius (LG)	89.3 ± 37.7 c,d	109.4 ± 43.4	112.6 ± 43.9	108.9 ± 41.6	110.4 ± 44.6
Medial gastrocnemius (MG)	151.3 ± 48.8 a,b,c	171.1 ± 42.2	170.8 ± 39.3	169.0 ± 47.9	175.8 ± 51.3
Soleus muscle (Sol)	109.9 ± 32.9 a,b	95.4 ± 27.4 a	86.9 ± 32.3	84.2 ± 37.8	75.5 ± 32.9
At 10% MVC					
Target force (N)	$122.0 \pm 16.3 \text{ a,b}$	$122.6 \pm 16.0 \text{ a,b}$	93.7 ± 14.2 a	66.4 ± 17.3	48.6 ± 10.2
%EMG _{max} (%)					
LG	0.0 ± 0.0 a	0.0 ± 0.1 a	0.0 ± 0.1 a	0.2 ± 0.2 a	4.3 ± 4.9
MG	6.1 ± 6.5 a,b	6.0 ± 5.3 a,b	9.8 ± 5.4 a	15.1 ± 8.7	19.1 ± 12.6
Sol	8.6 ± 4.2	14.9 ± 4.4 a	11.9 ± 5.2	8.7 ± 6.0	7.6 ± 4.4

MVC Maximal voluntary contraction, *rsEMG* raw electromyogram (EMG) signals that had been amplified, full-wave rectified, and smoothed (time constant 300 ms), $\% EMG_{max}$ amplitude of rsEMG obtained at each angle normalized according to the value of the EMG amplitude at MVC Values are presented as the mean \pm standard deviation (SD)

Values followed by a, b, c, and d are significant different from values at 130°, 120°, 110°, and 100°, respectively

maximal force and endurance time in relation to joint angle was also the same. That is, the values were highest at 110° (Fig. 3b, c). Duration from the start of exercise to the first recruitment of LG was 80.5 ± 43.2 , 16.5 ± 4.5 , and 9.5 ± 6.5 min at 100° , 110° and 120° , respectively (Fig. 4b). Prolonged static contractions at 100° resulted in a significantly longer time to the first recruitment of LG (P < 0.05) compared with static contractions at 110° and 120° .

Continuous EMG showed that various combinations of muscles became active with increasing duration of exercise. Complementary activity between muscles characterized EMG during static contractions at 100° and 120°; for example, the LG was recruited or increased in activity whenever the activity of the MG and/or soleus decreased (Fig. 2a, c). Alternate activity events were rare in the triceps surae muscle at 100° and 120°.

The ratio of total activation time (%Ta) during the entire endurance exercise increased in the LG with increasing joint angle (P < 0.05), but decreased in the soleus (P < 0.05; Fig. 5). The %Ta was significantly lower at 110° (P < 0.05) than at 100° or 120° for MG activity The total sum of %Ta in the three muscles at 110°, 100° and 120° was 189 ± 13, 143 ± 35 and 217 ± 47%, respectively. The rate of total activation time in the triceps surae muscle was shorter at 110° (P < 0.05) than at 100° or 120°.

Discussion

The major findings of this study were as follows. Firstly, the appropriate ankle position for detecting frequent alternations of activity in triceps surae muscles was 110° during static contractions at 10% MVC. Secondly, maximal voluntary force decreased when the ankle joint angle was increased from 100° to 120° , and the recruitment of synergistic muscles differed as a function of ankle angle. Thirdly, endurance was the longest at 110° , which was also the angle at which alternate activity in synergistic muscles was the most frequent and the rate of the total sum of %Ta was the lowest.

Joint angle and recruitment patterns of synergistic muscles

Our results show that isometric plantar flexion at joint angles of 100°, 110°, and 120° continued without LG activity at the start of contractions. Thus, the activation and time to the first recruitment of LG differed in an angledependent manner with increasing contraction time. If muscles with a larger mechanical advantage receive larger activation [10], then the LG would seem to be less active in terms of electrophysiological function [19]. Thus, the LG could conceivably play a complementary role with triceps surae muscles since the function of other synergistic muscles was impaired under the conditions used in our study.

At least one inactive muscle is required at the start of exercise to generate alternate activity in the triceps surae muscles. Moreover, the oscillation range of the recruitment angle threshold [1] is notable since this range is related to the repetitive appearance and disappearance of motor unit activity and to the occurrence of alternate activity during

Fig. 2 Simultaneous EMG recordings from the lateral gastrocnemius (LG), medial gastrocnemius (MG), and soleus (Sol) muscle during static contractions at 10% maximal voluntary contraction (MVC). The bottom line (angle) indicates ankle joint angles. Continuous EMG recordings during static contractions at an ankle joint angle of 100° (a) and 120° (c), respectively. Note the difference in time to first recruitment of LG between 100° and 120°. Few events of alternating muscle activity were shown, although each muscle showed repeated fluctuations in EMG activity with increasing time. b An example of clear alternation of EMG activity during static contractions at 110°. Note that EMG activities are switched from MG to LG + Sol with increasing duration of contractions. All traces (a-c) were obtained from the same subject



prolonged static contractions. Our findings show a longer time to first recruitment of the LG at 100° and a longer total period of LG activity and reduced repetition of high and lower activity at an ankle angle of 120° than at 110°. We speculate that the recruitment threshold in the LG for the joint angle might vary between approximately 20° and 30° during prolonged low-level static plantar flexion. Prolonged static muscle contractions at 110° might cause repetitive alternating high and low activity in the LG associated with frequent alternating muscle activity.

Appropriate joint angle for frequent alternations of activity in synergistic muscles and force–angle relationships

Our results show that alternate activity was more frequent at 110° than at 100° or 120°. The recruitment threshold for human motor units reportedly varies with joint angle [9, 10] and with prolonged low-level muscle contraction. Moreover, the disappearance (derecruitment) and reappearance (re-recruitment) of motor unit activity during prolonged low-level static contraction [1] indicates oscillation of the recruitment threshold with increasing contraction time. The threshold for muscle spindle activation also varies during isometric voluntary contractions [20]. The appropriate joint angle for the oscillation range of the recruitment angle threshold in each muscle could thus conceivably result in repetitive high and low activity, reflecting complex neural interactions [3]. Although the physiological mechanisms underlying alternate activity among synergists remain unknown, I_a afferents would be one possible route for neural interactions, as selective impairment of I_a afferents originating from a muscle that is inactive at the beginning of exercise results in frequent alternations of activity in quadriceps femoris muscles [5]. Force fluctuation is also modulated by the alternate muscle





Fig. 3 a The influence of ankle joint angle on number of events of alternate activity among synergistic muscles per hour. **b** The influence of ankle joint angle on endurance time and maximal force level normalized to initial value after fatiguing exercise. A higher force level for maximal plantar flexion is maintained at an angle of 110° compared to 100° or 120°. Values are given as the mean \pm standard deviation (SD). $^{#}P < 0.05$, $^{*}P < 0.05$, Significantly different from the value at 110°

activity of knee extensor synergists, suggesting that I_a inhibitory connections between the gastrocnemius and soleus muscles [21] represent the mechanism for adjusting activity between synergists. Muscle spindle afferents also reportedly vary with muscle length and joint angle [22]. These results suggest differences in appropriate joint angle for mechanical properties and frequent alternations of muscle activity. Different neural control strategies might exist between the exertion of greater muscle force and maintenance of a required force.

On the other hand, activity in groups III and IV sensory afferents might have excitatory effects, particularly on static and dynamic gamma-motoneurons [23]. These effects are powerful enough to increase firing in muscle spindle afferents, which in turn will raise the activation level in the pool of alpha-motoneurons projecting to the extrafusal muscle fibers [24]. This reflex is mediated by chemical factors associated with muscle pain [25] that increase during fatigue, such as bradykinin, potassium, lactate, and phosphate [26]. Possible neural circuits could

Fig. 4 a A comparison of time to first alternation of activity among muscles during static contractions at each joint angle. The first alternation of muscle activity is observed early in all exercise times during static contractions at an angle of 110° . **P* < 0.05, Significantly different from the value at 110° , **P* < 0.05, significantly different from the value at 100° . **b** A comparison of time to first recruitment of the lateral gastrocnemius (*LG*) during static contraction at each joint angle. Note that LG is hardly recruited at an angle of 100° , i.e., far from the recruitment threshold of LG (approximately 130°). There is no significant difference between values at the ankle angles of 110° and 120° . **P* < 0.05, Significantly different from the value at 100° .

also be investigated through a study of the metabolite substance.

Angle-dependence of muscle activity and endurance

The relationship between muscle endurance and muscle length reportedly depends on joint angle, with endurance time being inversely related to muscle length as a function of the ankle or knee joint angle [27, 28]. Many investigators have suggested that several factors related to muscle length and/or joint angle can affect endurance. The metabolic cost of contractions at relatively shorter muscle lengths assessed by ³¹P-nuclear magnetic resonance spectroscopy resembles that at longer muscles [29]. Weir et al. [11] therefore postulated that differences in fatigue resistance relative to muscle length do not appear to result from differences in metabolic demand. Differences in total blood flow might lead to angle-dependent fatigue [9], since



Fig. 5 Percentage of total activation (%Ta) and inactivation (%Ti) time during the whole endurance exercise in the lateral gastrocnemius (*LG*), medial gastrocnemius (*MG*), soleus muscle (*Sol*)

tension varies with muscle length and joint angle even when relatively equal workloads are applied at each joint angle. Another important factor is the neural control system underlying the electromyographic behavior. Continuous muscle contraction at a constant force generally requires a compensatory increase in de novo recruitment and/or rate coding of motor units to maintain the given load—and ultimately leads to exhaustion [30]. The length of muscle endurance generally depends on the type of motor unit recruited. In our study, the %Ta was related to ankle joint angle in the LG, but it was inversely related in the soleus. Longer utilization of the fatigue-resistant soleus at an ankle angle of 100° might prolong the endurance limit, although a low frequency of alternate activity did emerge. Moreover, despite maximal effort during a low-force contraction, net motor unit activity at the endurance limit, as indicated by interference EMG, often does not achieve the maximal values recorded before the onset of fatiguing contraction [31]. The degree of this deficit was found to be inversely related to the level of sustained submaximal force. The presence of a deficit in activation at exhaustion suggests that endurance time could be prolonged if the size of the deficit could be altered.

In our study, endurance was longest at a joint angle of 110°, at which alternate activity was the most frequent and the rate of the total sum of %Ta was the lowest in synergistic muscles. These findings suggest that the specific muscle activation at 110° was linked to endurance time during static contraction. Static muscle contractions might be more effectively prolonged if periods of muscle inactivity are provided to enable recovery, in comparison with stereotypical performance of the same task where muscle activity increases in a simple progressive manner. Manipulation of the joint angle and weight loading, namely a joint angle of 110° and an ankle angle of 10% MVC, facilitates frequent alternate activity among synergistic muscles, resulting in a shorter rate of total muscle activation period and possibly contributing to minimizing and/or delaying muscle fatigue in the synergist.

Electrical contamination of EMG recordings (crosstalk)

Crosstalk has often been discussed in terms of results potentially indicating muscle "co-activation" in synergists. However, our results demonstrate "reciprocal" muscle activity among synergists of the triceps surae muscles, such as when one muscle began to increase activity, while others became inactive or decreased in activity and vice versa. Solomonow et al. [32] showed that crosstalk does not constitute a technical problem regarding neighboring synergists unless the amount of adipose tissue over the muscle is substantial. None of the participants in our study were obese, and their mean body mass index was 21.9 ± 1.3 [33].

In conclusion, we found that the appropriate joint angle for detecting frequent alternations of activity in triceps surae muscles is around 110° during static contractions at 10% MVC. This result suggests that alternate muscular activity in the synergist would be related not only to force, but also to the characteristics of muscle architecture and/or afferent activity as a function of joint angle. In addition, rotational activity in a muscle and/or synergistic muscles is an important strategy under neural control that prolongs low-level muscle contractions accompanied by longer total inactive periods in individual muscles. In our study, the type of muscle predominantly used and the emergence of alternate activity in synergistic muscles would have influenced muscle endurance as a function of joint angle. Further study of the complex neural processes that control the activity of motoneurons would improve understanding of the motor control mechanisms that enable new recruitment strategies to sustain prolonged low-level tasks, such as alternate activity in synergistic muscles.

Acknowledgments This work was supported in part by a Grant-in-Aid for Scientific Research (C, project nos. 18200512 and 22500611) from the Japan Society for the Promotion of Science, by the Sasakawa Research Foundation of The Japan Science Society (#11-284), and by a Grant-in-Aid for Developed Research (B) from the Niigata University of Health and Welfare.

References

- Fallentin N, Jørgensen K, Simonsen EB (1993) Motor unit recruitment during prolonged isometric contractions. Eur J Appl Physiol Occup Physiol 67:335–341
- Sjøgaard G, Kiens B, Jørgensen K, Saltin B (1986) Intramuscular pressure, EMG and blood flow during low-level prolonged static contraction in man. Acta Physiol Scand 128:475–484
- Tamaki H, Kitada K, Akamine T, Murata F, Sakou T, Kurata H (1998) Alternate activity in the synergistic muscles during prolonged low-level contractions. J Appl Physiol 84:1943–1951
- Semmler JG, Kutzsuher DV, Enoka RM (2000) Limb immobilization alters muscle activation patterns during a fatiguing isometric contraction. Muscle Nerve 23:1381–1392
- Kouzaki M, Shinohara M, Fukunaga T (2000) Decrease in maximal voluntary contraction by tonic vibration applied to a single synergist muscle in humans. J Appl Physiol 89:1420–1424
- Kouzaki M, Shinohara M, Masani K, Kanehisa H, Fukunaga T (2002) Alternate muscle activity observed between knee extensor synergists during low-level sustained contractions. J Appl Physiol 93:675–684
- Kouzaki M, Shinohara M, Masani K, Fukunaga T (2004) Force fluctuations are modulated by alternate muscle activity of knee extensor synergists during low-level sustained contraction. J Appl Physiol 97:2121–2131
- Kouzaki M, Shinohara M (2006) The frequency of alternate muscle activity is associated with the attenuation in muscle fatigue. J Appl Physiol 101:715–720
- Miles TS, Nordstrom MA, Türker KS (1986) Length-related changes in activation threshold and wave form of motor units in human masseter muscle. J Physiol 370:457–465
- Van Zuylen EJ, Gielen CCAM, Van Der Denier Gon JJ (1988) Coordination and inhomogeneous activation of human arm muscles during isometric torques. J Neurophysiol 60:1523–1548
- Weir JP, McDonough AL, Hill VJ (1996) The effects of joint angle on electromyographic indices of fatigue. Eur J Appl Physiol Occup Physiol 73:387–392
- Sirin AV, Patla AE (1987) Myoelectric changes in the triceps surae muscles under sustained contractions. Evidence for synergism. Eur J Appl Physiol Occup Physiol 56:238–244
- Tamaki H, Kitada K, Akamine T, Sakou T, Kurata H (1997) Electromyogram patterns during plantarflexions at various angular velocities and knee angles in human triceps surae muscles. Eur J Appl Physiol Occup Physiol 75:1–6
- Rainoldi A, Nazzaro M, Merletti R, Farina D, Caruso I, Gaudenti S (2000) Geometrical factors in surface EMG of the vastus medialis and lateralis muscles. J Electromyogr Kinesiol 10:327–336

- Rainoldi A, Melchiorri G, Caruso I (2004) A method for positioning electrodes during surface EMG recordings in lower limb muscles. J Neurosci Methods 134:37–43
- Staude G, Wolf W (1999) Objective motor response onset detection in surface myoelectric signals. Med Eng Phys 21:449–467
- 17. Kirimoto H, Gotoh Y, Kotake N, Kitada K, Ogita F, Tamaki H (2006) Electromyogram patterns during sustained low-level plantar flexions and changes of blood flow at alternate activity among the triceps surae muscles. Jpn J Fit Sports Med 55:393–402
- Tamaki H, Kitada K, Kirimoto H, Wagatsuma A, Ogita F, Takekura H, Shibayama H (2004) Differences in electromyographic behavior of the synergistic muscles during prolonged isometric contractions at different loads. Jpn J Physiol Anthrop 9:53–58
- Duysens J, van Wezel BM, Prokop T, Berger W (1996) Medial gastrocnemius is more activated than lateral gastrocnemius in sural nerve induced reflexes during human gait. Brain Res 727:230–232
- Burke D, McKeon B, Westerman RA (1980) Induced changes in the threshold for voluntary activation of human spindle endings. J Physiol 302:171–181
- Schieppati M, Romanò C, Gritti I (1996) Convergence of Ia fibres from synergistic and antagonistic muscles onto interneurones inhibitory to soleus in humans. J Physiol 431:365–377
- Vallbo ÅB (1974) Afferent discharge from human muscle spindles in non-contracting muscles. Steady state impulse frequency as a function of joint angle. Acta Physiol Scand 90:303–318
- Kaufman MP, Hayes SG, Adreani CM, Pickar JG (2002) Discharge properties of group III and IV muscle afferents. Adv Exp Med Biol 508:25–32
- 24. Sjøgaard G, McComas AJ (1995) Role of interstitial potassium. In: Gandevia SC, Enoka RM, McComas AJ, Stuart DG, Thomas CK (eds) Fatigue: neural and muscular mechanisms. Plenum, New York
- Mense S (1977) Nervous outflow from skeletal muscle following chemical noxious stimulation. J Physiol 267:75–88
- Dawson MJ, Gadian DG, Wilkie DR (1980) Mechanical relaxation rate and metabolism studied in fatigued muscle by phosphorus nuclear magnetic resonance. J Physiol 299:465–484
- Gandevia SC, McKenzie DK (1998) Activation of human muscles at short muscle lengths during maximal static efforts. J Physiol 407:599–613
- Ng AV, Agre JC, Hanson P, Harrington MS, Nagle FJ (1994) Influence of muscle length and force on endurance and pressor responses to isometric exercise. J Appl Physiol 75:2551–2559
- Baker AJ, Carson PJ, Green AT, Miller RG, Weiner MW (1992) Influence of human muscle length on energy transduction study by 31P-NMR. J Appl Physiol 73:160–165
- Petrofsky JC, Phillips CA (1985) Discharge characteristics of motor unit and the surface EMG during fatiguing isometric contractions at submaximal tensions. Aviat Space Environ Med 56:581–586
- Bigland-Ritchie B, Furbush F, Woods JJ (1986) Fatigue of intermittent submaximal voluntary contractions: central and peripheral factors. J Appl Physiol 61:421–429
- Solomonow M, Baratta R, Bernardi M, Zhou B, Lu Y, Zhu M, Acierno S (1994) Surface and wire EMG crosstalk in neighbouring muscles. J Electromyogr Kinesiol 4:131–142
- Bernardi M, Solomonow M, Sanchez JH, Baratta RV, Nguyen G (1995) Motor unit recruitment strategy of knee antagonist muscles in a step-wise, increasing isometric contraction. Eur J Appl Physiol Occup Physiol 70:493–501