Alternate activity in the synergistic muscles during prolonged low-level contractions

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Tamaki, H., K. Kitada, T. Akamine, F. Murata, T. Sakou, and H. Kurata. Alternate activity in the synergistic muscles during prolonged low-level contractions. J. Appl. Physiol. 84(6): 1943–1951, 1998.—The purpose of this study was to investigate the functional interrelationship between synergistic muscle activities during low-level fatiguing contractions. Six human subjects performed static and dynamic contractions at an ankle joint angle of 110° plantar flexion and within the range of 90–110° (anatomic position = 90°) under constant load (10% maximal voluntary contraction) for 210 min. Surface electromyogram records from lateral gastrocnemius (LG), medial gastrocnemius (MG), and soleus (Sol) muscles showed high and silent activities alternately in the three muscles and a complementary and alternate activity between muscles in the time course. In the second half of all exercise times, the number of changes in activity increased significantly (P < 0.05) in each muscle. The ratios of active to silent periods of electromyogram activity were significantly higher (P < 0.05) in MG (4.5 ± 2.2) and Sol (4.3 ± 2.8) than in the LG (0.4 ± 0.1), but no significant differences were observed between MG and Sol. These results suggest that the relative activation of synergistic motor pools are not constant during a low-level fatiguing task.

The muscles continue to exert force corresponding to the load during prolonged static contractions. Force output of a muscle is regulated by recruitment and/or rate coding of motor units, and it appears that all of the motor units that innervate a muscle rarely are recruited simultaneously in a given muscle. Moreover, during prolonged contractions, it has been reported that the increase in the electromyogram (EMG) activity maintaining a given force level is accomplished by recruiting more motor units or activating them at a higher frequency to compensate for the decrease in the contraction force in the fatigued muscle (8). The work of Person and Kudina (24) would suggest that this compensatory event is due to part recruitment, because the frequency of activation of a motor unit burst tends to decline with prolonged contractions. For example, Kurata (18) found that the relative threshold of activation of single motor unit in the vastus medialis varied during prolonged very low-level contractions. Moreover, Fallentin et al. (9) reported that previously acting motor unit activity disappeared for a moment and then reappeared minutes later during prolonged elbow flexion at 10% maximal voluntary contraction (MVC). Sjøgaard et al. (28) obtained the EMG recordings and intramuscular pressure in the vastus lateralis and the rectus femoris, which showed complementary changes during prolonged static knee extensions. Although there are several reports of alternating activity of motor units in the homonymous muscle, little information is available on the whole-muscle level in the activation of synergistic muscles such as the triceps surae muscules during prolonged contractions.

The triceps surae muscles are a synergy composed of three muscles, i.e., lateral gastrocnemius (LG), medial gastrocnemius (MG), and soleus (Sol) muscles. These muscles seem to function as synergists in many movements, but they differ in fiber type composition and structural properties. That is, the Sol muscle is the monoarticular muscle that has its origin at the head of the fibula and a predominance of type I muscle fibers (~90%), whereas the LG and MG muscles are biarticular muscles that arise from the condyles of femur and have similar proportions of type I and II fibers (16, 23). Moreover, the extent of recruitment in each muscle can differ depending on the ankle angle. For example, the MG and Sol are mainly recruited in plantar flexion, but the LG is not active at ankle angles between 90 and 120° at 10% MVC during ankle plantar flexions (30).

Therefore, these studies demonstrated differential recruitment of the ankle extensors, i.e., facilitation of the LG and MG and depression of the slow ankle extensors (Sol). It appears that complex neural interactions within the spinal motoneuron pool can modify the pattern of synaptic input, i.e., the relative excitability of groups of motoneurons, depending on the type of motor tasks. Thus it is conceivable that these marked differences in functional and structural properties in the triceps surae muscles could be associated with unique recruitment strategies.

The purpose of this study was to investigate, by recording the surface EMG from the triceps surae muscles, the functional interrelationships between the individual muscles in the synergy during prolonged low-level static and dynamic contractions, with special notice taken of the existence of another new strategy to prolong muscle contractions.

METHODS

Subjects. Six healthy men [mean age 25.0 (22–27) yr] with no history of neurological disorders participated in the experiments. Voluntary consent was obtained from the subjects after the explanation of the experimental procedures and
possible risks involved. The study was approved by the local ethics committee.

Protocol. In the condition of static contractions, the subjects were placed in a specially designed chair with the right leg secured in full extension. The knee joint was fixed by a clamp to avoid limb movement and changes in muscle length. The foot was placed at 110° of plantar flexion (90° equalling the right angle of the ankle) and rested on a footplate. The subjects performed isometric contractions of the triceps surae muscles against a constant load for 210 min.

Before the experiments, isometric force at MVC of the ankle plantar flexors was measured at 110° of ankle angle with an isometric dynamometer, and the highest one of three maximal efforts was determined as MVC force. The experiments were conducted at relatively constant workloads corresponding to 10% MVC. A specially designed weight-loading device was used, with a wheel that was connected to a weight by means of a stainless steel wire (30). The foot of the subject was attached to a footplate that was connected to the wheel so that the rotational axis of the ankle approximated that of the wheel. This device enabled subjects to produce a constant force by means of the ankle plantar flexors. The foot of the subject was secured in full extension. The knee joint was fixed by a clamp to avoid limb movement and changes in muscle length.

The ankle plantar flexors were measured at 110° of ankle angle of 110° while the direction of force was changed toward inversion-eversion and plantar-dorsiflexion. To measure the voluntary force outputs during inversion-eversion and toe flexion-extension, force transducers (LM-10KA, KYOWA) were attached under the first metatarsal head and the first toe of the foot. EMGs in each muscle were recorded during sustained contractions at an ankle angle of 110° while the direction of force was changed toward inversion-eversion and plantar-dorsiflexion (Fig. 1A). During the dynamic condition, the ankle angle was at 110°, and for determination of the joint angle were the same used in static measurements.

In the condition of dynamic contractions, the subjects performed repetitive concentric and eccentric plantar flexions against a constant load (10% MVC) in the direction of dorsiflexion (90°–110°) and synchronized with a metronome. This movement lasted ~210 min at the angular velocity of 30°/s marked as the target velocity on the monitor oscilloscope in front of the subject to ensure the quality of the contraction.

In the condition of dynamic contractions, the subjects performed repetitive concentric and eccentric plantar flexions against a constant load (10% MVC) in the direction of dorsiflexion (90°–110°) and synchronized with a metronome. This movement lasted ~210 min at the angular velocity of 30°/s marked as the target velocity on the monitor oscilloscope in front of the subject. The devices for weight loading and for determination of the joint angle were the same used in the static contractions.

EMG recordings. The myoelectric signals were recorded from the LG, MG, Sol, and tibialis anterior (TA) muscles by using bipolar surface electrodes (10 mm in diameter) with an interelectrode distance of 30 mm along the longitudinal axis of the muscle. Silver-silver chloride electrodes were used and placed on the belly of the LG, MG, and TA and on the medial and lateral aspect of the Sol. Electrode diameter was 10 mm, and the interelectrode distance was 30 mm for bipolar recordings. Even though it appeared that the surface bipolar electrodes picked up only a few of the total number of motor units activated within a muscle, similar activation patterns were recorded (EMG 1 and 2). However, alternate activity was recorded between synergistic muscles (Fig. 1D).

Data and statistics. Integrated EMG (iEMG) values at 10-s intervals in each muscle were measured in dynamic contractions, and total values of iEMG in the first half and in the second half of all exercise periods were compared. EMG data of 6,300 trials were collected for all exercise times (12,600 s). Repetitive concentric and eccentric plantar flexions were performed every 2 s. In static contractions, the rate of total activation period (TA) and silent or little-activation period (TS) in the three muscles were calculated for each complete exercise period (210 min) as the index of the relative activation time in each muscle.

Standard statistical methods were used for the calculation of means ± SD of the parameters examined. The statistical significance of differences between mean values was tested by Student’s t-test. Significance was accepted at P < 0.05.

Fig. 1. Simultaneous recordings of force outputs in the direction of inversion-eversion (A), toe extension-flexion (B), and plantar flexion-dorsiflexion (C). Two EMG recordings from different sites in each muscle (EMG 1 and 2) during static plantar flexions at 10% maximal voluntary contraction (MVC) are shown. Relatively constant EMG signal in medial gastrocnemius (MG) and soleus (Sol) muscles are evident from each electrode of each muscle in A, B, and C. Lateral gastrocnemius (LG) muscle was not active during inversion-eversion (A) or in toe extension-flexion (B) but became active after ~20 min during isometric contractions at 10% MVC (D). An important point to note in D is that the EMG from both electrodes within each muscle changed at about the same time, and direction of change was in opposite direction for MG and LG.
RESULTS

Activation pattern in the synergistic muscles. In static contractions, a typical example of EMG records in the triceps surae muscles for 210 min is shown in Fig. 2. Large amplitudes and silent or little EMG activity occurred alternately in each muscle during the 210-min time course of each isometric task. Alternate activity among the synergist of the triceps surae muscles was evident, with some muscles becoming more active while others became inactive or less active. Complementary activities often occurred whereby the LG EMG increased when the MG became inactive. When the subjects perceived pain while exercising, sudden changes in activity often occurred. The disappearance of the pain was indicated by the end of these changes in EMG activity.

EMG activity in Sol and MG was always present at the start of the prolonged static exercise, but different combinations of muscles became active with increasing time (Fig. 3A). Muscle activity most frequently took the form of MG + Sol and relatively infrequently occurred in combination with LG (Fig. 4).

In dynamic contractions, MG and Sol were recruited, but LG was not active during concentric and eccentric plantar flexions in ankle angles between 90 and 110° at the beginning of exercise. However, LG was recruited whenever MG and/or Sol were inactive or decreased in activity with increasing times (Fig. 3B). Alternating iEMGs occurred in the order of frequency as follows: LG < Sol < MG. Moreover, these changing EMG amplitudes often complemented one another by becoming more or less active.

Comparisons of the activation pattern in the first and the second half of all exercise times. In the static conditions, the mean number of events of alternate activities between the synergistic muscles was 28 ± 8 in the first half of all exercise times and 36 ± 7 times (27% greater) in the second half. The number of EMG changes (alternating between activation and silence) in the individual muscle in the second half of all exercise times was greater than in the first half by ~60% in LG (P < 0.05), 24% in MG (P < 0.05), and 34% in Sol (Fig. 5).

In dynamic conditions, 1,032 alternating events occurred in the LG in the first half and 1,223 occurred in the second half of all exercise times (total 6,300 trials); i.e., the number was 19% greater (P < 0.05) in the second half. The total value of iEMGs in the second half of all exercise times tended to increase in LG (P < 0.05) and Sol, but to decrease in MG (P < 0.05) compared with the first half (Fig. 6).

Changes in the EMG activity in the individual muscle. EMG recordings showed alternation between activation and inactivation in individual muscles during prolonged static contractions. To investigate the changes in the EMG amplitudes during the activation period within a burst in each muscle, the rectified and smoothed EMGs (rsEMGs) at the time points corresponding to 10, 50, and 90% of the activation period (100% equaling the time period from the start point to the end point of activation) were measured at the constant sampling period of 10% activation period (Fig. 7A). Continual changes in the rsEMG at 10, 50, and 90% of the activation period, namely the former, the middle, and the latter period, respectively, showed various patterns. For example, they showed linear, exponential, and logarithmic increases as well as slight decreases occasionally. The EMG amplitudes during the activation period in each muscle tend to increase.

Fig. 2. Continuous EMG recordings for 210 min during which static contractions were maintained at 10% MVC. EMGs and rectified and smoothed EMGs (rsEMGs) in LG, MG, and Sol are shown. Note that EMG recordings in each muscle show very active and silent periods throughout 10% MVC for plantar flexion. Note that LG and Sol activity tends to occur during silent period for MG, but LG and Sol are not always activated during same MG silent period. Bottom line (Angle) indicates ankle joint angles.
especially at the middle and the latter periods: this pattern appeared for \( \sim 90\% \) of all cases. The rsEMGs for the middle and the latter periods were higher (\( P < 0.01 \)) than for the former period, but there was no difference between the middle and the latter periods (Fig. 7B).

TA/TS values in each muscle. The ratio of TA and TS with EMG activity were calculated. These values were
higher (P < 0.05) in MG (4.5 ± 2.2) and Sol (4.3 ± 2.8) than in LG (0.4 ± 0.1), but no significant differences were observed between MG and Sol.

**DISCUSSION**

Alternate activity in the synergistic muscle. Although it has been suggested that the recruitment of motor units may alternate among synergistic muscles during fatigue from prolonged low-level contractions, there has been little evidence to support it. Kurata (18) found single motor units that vary the relative threshold of activation in the vastus medialis muscle and suggested that the rotation of motor units was caused by changes in the relative threshold of activation of motor units. Furthermore, Fallentin et al. (9) reported that activity of previously acting motor units disappeared for a moment and then reappeared minutes later during prolonged elbow flexion at 10% MVC. It is conceivable that the amount of muscle activity obtained from the surface EMG would show little change during static contractions at a constant load because the total amounts of whole muscle activity may not change, even if there is rotation of motor units in a muscle. As shown in this study, however, the individual muscles of triceps surae alternated high activation and silent periods, and these synergistic muscles rotated in a complementary pattern to maintain a constant torque. These findings suggest that the three muscles did not perform in a stereotypical manner (all muscles were recruited at the same movement and time and increased their activities gradually and similarly during the development of fatigue). In general, it has been reported that muscle recruitment strategies are stereotyped during prolonged low-level tasks such as gradual increase in the recruitment of motor units (2, 15). The lower threshold motor units, i.e., slow units, are more likely to be activated at the lower force thresholds and then the higher threshold motor units are more likely to be fast-fatigue resistant and fast-fatigable units, assuming orderly recruitment with increasing demands of relative muscle output. On the other hand, Smith et al. (29) have observed that Sol was mainly recruited during the slow movement, whereas LG was active without slow Sol during the fast movements, and suggested that type-matched selective recruitment of motor units was executed so as to suit the demand of motor tasks. It appears that fatigue may be another condition that results in selective recruitment at any given time and, therefore, alternate activity occurs among the synergistic muscles studied.

Agonist muscle during static and dynamic ankle plantar flexions. As shown in Fig. 2, the MG and Sol were recruited but the LG was not activated at the start of the exercise. Moreover, two parameters, the frequency of the combination of acting muscle throughout the whole exercise period and the Tα/Ts ratios, were
Much higher in the MG and Sol than in the LG, both indicating that the recruitment of the synergists was not stereotypical under the constant torque conditions of this study. Tamaki et al. (30) reported no EMG activity in LG when generating 10% MVC with ankle plantar flexions at ankle angles between 90 and 120°. This result suggests that the MG and Sol play a more important role in prolonged low-level (10% MVC) contractions at the ankle angle of 110° than did the LG. It has been reported previously that the recruitment threshold of human motor units in the synergistic muscles can vary with joint angle (20, 32). Although one subject showed a higher Ta/Ts value in the MG than in the Sol in the present study, it is conceivable that the relative contributions of a synergistic muscle could be determined not only by the physiological properties of muscle fibers but also by joint angle and sensory feedback incidental to that angle.

EMG activity in the first and the second half of the exercise periods. There are few reports concerning the number of the alternating cycles of high and low activities during prolonged contractions. Fallentin et al. (9) reported that the subjects with very long endurance times (>2 h) frequently showed episodes of alternating activity of motor units during prolonged low-level contractions. The individual ability or capacity for motor unit rotation seemed to be related to maximal endurance time. Although the mean number of alternate activities between synergistic muscles was observed, i.e., 64 times in all exercise times in the present study, these frequent alternations of activity might facilitate the maintenance of the ankle extensor tasks for as long as 210 min. Moreover, the interval between occurrences of alternate activity tended to be shorter and the number of alternations more frequent in the second than in the first half of all exercise periods (Fig. 5). If the alternating of recruitment serves as a means of minimizing fatigue of a given set of units, the occurrence of the rotational activity would be expected to occur as the exercise continued. The more frequent alternations of activity in the latter half of all exercise times are consistent with a fatigue-related phenomenon.

EMG changes within one activation period. It has been well documented for several muscles that the EMG amplitude increases with increasing time of the continuous submaximal contractions (7, 8, 25, 26). This is due to de novo recruitment and/or rate coding of motor units to compensate for the decrease in contractile force of acting motor units. In prolonged low-level contractions, especially, the surface EMG amplitude may reflect the relative number of recruited motor units (8). In the present study, rsEMG of the middle period was significantly higher than that of former period, but there was no significant difference between middle and latter periods. Values are means ± SD. **Significance at P < 0.01.

Fig. 7. A: schematic representation of methods used to measure rsEMGs in each burst activity. EMG amplitudes at 5–15% (former), 45–55% (middle), and 85–95% (latter) activation period within a burst during a static contraction of 10% MVC are shown. B: rsEMGs at former, middle, and latter phase in each burst activity during static contractions. Note that rsEMG of middle period is higher than that of former period, but there is no significant difference between middle and latter periods. Values are means ± SD. **Significance at P < 0.01.

Synaptic input to spinal motoneurons. It is not easy to explain how the alternate activity occurs in the synergistic muscle. At a minimum, the relative activation of motor units could vary if the efficacy of the synaptic inputs originating from central and peripheral nerves during prolonged low-level contractions varied with times. Furthermore, there are some type-dependent differences of synaptic input to α-motoneurons, i.e., synaptic input from red nucleus and fast-type pyramidal tract neuron and cutaneous nerve cause a facilitative influence on fast-type motoneurons but cause an inhibitory influence on slow-type motoneurons (1, 3, 4). Inhibitory inputs from Renshaw cell and excitatory inputs from group Ia fibers were generally larger in slow-type motoneurons than in fast-type motoneurons (5, 11). The magnitude of these differential inputs also may vary with prolonged efforts. Fur-
Moreover, group III and IV fibers can be activated by chemical substances associated with muscle pain (17, 19) that have been shown to increase during fatigue, e.g., bradykinin, potassium, lactate, and phosphate (6, 10, 27); these afferents cause an inhibitory influence on α-motoneurons and EMG activities (12–14). In the present study, although most of the subjects often had pain in the acting muscle at the time of the alternate activity in the synergistic muscle, the activation threshold of α-motoneurons innervating each muscle might be modified by chemical substance associated with muscle pain through the above-mentioned pathways.

In the present study, the organization of the synaptic inputs that influenced the muscle activity reflects complex temporal-dependent neural interactions within and among spinal motoneuron pools. It is obvious that recruitment strategies are not stereotyped during low-level prolonged motor tasks. A clear and specific recruitment strategy was to alternate activity among the synergists during prolonged low-level muscle contractions. Motor control mechanisms to account for these sudden and frequent changes in the combinations of motor units and motor pools that will contribute to a prolonged low-level force effort remain unknown at this time.

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