Alternate muscle activity observed between knee extensor synergists during low-level sustained contractions

MOTOKI KOUZAKI, MINORU SHINOHARA, KEI MASANI, HIROAKI KANEHISA, AND TETSUO FUKUNAGA
Laboratory of Sports Sciences, Department of Life Sciences, Graduate School of Arts and Sciences, The University of Tokyo, Tokyo 153-8902, Japan
Received 20 July 2001; accepted in final form 23 April 2002

Kouzaki, Motoki, Minoru Shinohara, Kei Masani, Hiroaki Kanehisa, and Tetsuo Fukunaga. Alternate muscle activity observed between knee extensor synergists during low-level sustained contractions. J Appl Physiol 93: 675–684, 2002. First published May 3, 2002; 10.1152/japplphysiol.00764.2001.—To determine quantitatively the features of alternate muscle activity between knee extensor synergists during low-level prolonged contraction, a surface electromyogram (EMG) was recorded from the rectus femoris (RF), vastus lateralis (VL), and vastus medialis (VM) in 11 subjects during isometric knee extension exercise at 2.5% of maximal voluntary contraction (MVC) for 60 min (experiment 1). Furthermore, to examine the relation between alternate muscle activity and contraction levels, six of the subjects also performed sustained knee extension at 5.0, 7.5, and 10.0% of MVC (experiment 2). Alternate muscle activity among the three muscles was assessed by quantitative analysis on the basis of the rate of integrated EMG sequences. In experiment 1, the number of alternations was significantly higher between RF and either VL or VM than between VL and VM. Moreover, the frequency of alternate muscle activity increased with time. In experiment 2, alternating muscle activity was found during contractions at 2.5 and 5.0% of MVC, although not at 7.5 and 10.0% of MVC, and the number of alternations was higher at 2.5 than at 5.0% of MVC. Thus the findings of the present study demonstrated that alternate muscle activity in the quadriceps muscle (1) appears only between biarticular RF muscle and monoarticular vasti muscles (VL and VM), and its frequency of alternations progressively increases with time, and (2) emerges under sustained contraction with force production levels ≤5.0% of MVC.

DURING A SUSTAINED LOW-FORCE contraction, the development of fatigue is associated with an increase in surface electromyogram (EMG) amplitude that can be similar among individual synergist muscles (11). Such an increase suggests that more motor units are activated and that the firing frequency of motor units increases to compensate for the impairment of contractility of the fatigued muscles (13). However, when muscle contraction with low force production is sustained for a long time, the individual synergistic muscles are not continuously activated but alternate between periods of activity and silence, and these synergists most likely rotate in a complementary pattern to maintain the constant force of knee extensors (19), plantar flexors (18, 21), and elbow flexors (16, 17). This phenomenon has been called alternate muscle activity in synergistic muscles (21). Prior studies in which fine-wire electrodes were used have shown that alternating recruitment among motor units occurs during prolonged contraction of the biceps brachii (7) and the trapezius muscle (22). Enoka and Stuart (6) suggested that alternate muscle activity would be effective for minimizing fatigue. Furthermore, Semmler et al. (16, 17) suggested the possibility that elongated muscle endurance after immobilization is due to the observed alternate muscle activity among synergists. When these findings are considered, it is reasonable to assume that one of the causes of alternate muscle activity is related to the process of muscle fatigue. However, this phenomenon has not been thoroughly quantified, and the physiological mechanisms behind it remain as yet unknown. Therefore, the present study first aimed to quantify its features, i.e., frequency, timing, and combination of alternate muscle activity observed between synergists of the quadriceps muscle during low-level sustained knee extension (experiment 1).

Several previous studies on alternate muscle activity have utilized various experimental conditions with a single force production level, such as knee extension at 5% of maximal voluntary contraction (MVC) (19), plantar flexion at 10 or 50% of MVC (18, 21), and elbow flexion at 15% of MVC (16, 17). It is unclear whether alternate muscle activity depends on the intensity of the muscle contraction, given that most of the studies have examined the responses only at a single intensity. There is only one study that has demonstrated motor unit rotation during sustained elbow flexion at 10% of MVC but not at 40% of MVC (7). In addition, Sirin and Patla (18) examined the synergisms (coactivation or trade-off) of individual plantar flexors during sustained contraction under different conditions, and demonstrated that the trade-off of EMG activities be-

The costs of publication of this article were defrayed in part by the payment of page charges. The article must therefore be hereby marked “advertisement” in accordance with 18 U.S.C. Section 1734 solely to indicate this fact.
tween individual muscles of the plantar flexors were more evident in the knee-extended position than in the knee-flexed position. They postulated that alternate activity is related to the load placed on the muscle and to muscle effectiveness. With these findings taken into account, it is hypothesized that emergence of alternate muscle activity is dependent on the intensity of muscle contraction. To test this hypothesis, we investigated synergistic EMG activities of knee extensor muscles during sustained isometric contractions at different force production levels (experiment 2).

METHODS

Subjects. Eleven healthy male subjects [age 25.6 ± 2.0 (SD) yr, height 169.7 ± 2.7 cm, and body mass 70.1 ± 10.3 kg] voluntarily participated. They had no history of neurological disorders and had not participated in any programs of regular exercise. All subjects gave their written, informed consent to participate in the study after receiving a detailed explanation of the purposes, potential benefits, and associated risks. This study was approved by the office of the Department of Life Sciences, The University of Tokyo, and its protocol was consistent with their requirements for human experimentation.

General procedure and equipment. Each subject was required to perform a static unilateral knee extension exercise in a seated position with hip and knee joint angles of 100 and 90° flexed, respectively. The subject’s upper body was firmly set against the chair, which had an adjustable seat belt to prevent any movement of the hip joint. The isometric force was measured by a strain-gauge force transducer (model 274H, Minebea, Tokyo, Japan), which was coupled with a strain amplifier and attached by a strap to the subject’s ankle. The linearity of this measurement system was ensured by the manufacturer from 0 to 200 N. The force was displayed on the storage oscilloscope in front of the subject to provide visual feedback of the produced force and target. Surface EMGs from the muscle belly of the rectus femoris (RF), vastus lateralis (VL), vastus medialis (VM), and biceps femoris long head (BF) were recorded by using bipolar Ag-AgCl electrodes with a diameter of 5 mm and an interelectrode distance of 20 mm. The reference electrode for the EMG was placed on the iliac crest. The electrodes were connected to a preamplifier and differential amplifier with a bandwidth of 5 Hz to 1 kHz (model 1253A, NEC Medical Systems, Tokyo, Japan). For later analysis, all signals were stored on the hard disk of a personal computer by using a 12-bit analog-to-digital converter (Lab-PC+, National Instruments, Austin, TX) with a sampling frequency of 1 kHz.

Experiment 1. For 1 wk before the experiment, all subjects practiced sustaining a knee extension contraction at 2.5% of MVC so that they could produce stable force throughout the task. The MVC for knee extension was determined to be equal to the largest force of three trials, subjects were instructed to maintain the force for 60 min, and all subjects could complete the tasks without volitional exhaustion. With respect to the higher intensity tasks, subjects were instructed to maintain the prescribed force level for 60 min or up to the point of volitional exhaustion, if it happened before 60 min. In the task at 7.5% of MVC, three of the six subjects could not complete the 60 min. The mean duration for this task was 36.5 ± 6.9 min. In the task at 10.0% of MVC, no subject could complete the 60 min, and the mean duration resulted in 16.2 ± 3.1 min. The MVC after the exercises at 2.5, 5.0, 7.5, and 10.0% of MVC fell to 85.5 ± 5.9, 85.2 ± 5.3, 71.9 ± 7.4, and 72.3 ± 6.4% of the initial MVC measurements without fatigue, respectively. No feedback or encouragement by the investigators was provided throughout performance of the tasks to prevent any intentional changes in muscle contraction. Each subject performed only one task per day, and all tasks were performed on separate days with at least 1 wk in between tasks. The order of the tasks was pseudorandomized.

Data analysis. In the sustained knee extension at 2.5% of MVC, alternate EMG activity was observed between RF and both VL and VM (Fig. 1) in all subjects. The EMG of BF, the antagonist muscle for knee extension contraction, was substantially smaller than that of the quadriceps muscle group. We focused on the marked changes in the EMG sequences between the quadriceps muscles to quantify the alternate muscle activity among synergistic muscles. The EMG signals were full-wave rectified and integrated over 15 s to yield an integrated EMG (iEMG) (Fig. 2A, top). A calculation period of 15 s was employed based on the fact that it required at least 10 s for each muscle to develop a significant change during the alternate muscle activity. The torque at the knee joint was calculated from the measured force times the length of the lower leg and then averaged every 15 s. The iEMG and torque during sustained contraction were expressed as a percentage of the corresponding values obtained during the MVC.

Furthermore, the iEMG signals were analyzed to examine the alternate muscle activity in the quadriceps muscle. In this study, the time course of the frequency of alternation among the muscles was quantitatively evaluated on the basis of the differentiated iEMG. Detailed accounts of the analytic approach are given as follows.

1) As mentioned above, the iEMG of each muscle was calculated over 15 s (Fig. 2A, top).

2) iEMG measurements underwent a smoothing procedure with the moving average to remove high-frequency components (Fig. 2A, middle), by using the following equation

\[
y(n) = \frac{1}{M} \sum_{k=1}^{M-1} x(n+k), \quad k \leq n \leq N - 1 - k
\]

where \(y(n)\) is the calculated iEMG value at the number \(n\), \(x(n)\) is the original value of the iEMG at the number \(n\), \(N\) is the total number of samples, and \(M\) is the average point. Because we employed a five-point moving average, \(M\) is 5.

3) iEMG_dadt was given as a result of time differentiation of filtered iEMG sequences (Fig. 2A, bottom).

4) Eight sample points of iEMG_dadt immediately after the onset of exercise (<3 min after onset of exercise) were extracted because, during this period, no marked fluctuation of iEMG_dadt was observed in any of the subjects.

5) Three SDs during this period were determined as a normal fluctuation (Fig. 2A, bottom, dotted lines) because most samples fell within 3 SDs of the mean (14).
6) The criterion for an outlier was defined as iEMG$_{adj/dt}$ throughout the exercise that exceeds 3 SDs, including both upper and lower limits as a normal fluctuation (Fig. 2A, bottom, closed circles). Because the amplitude of the change in iEMG was different among muscles, we calculated SD as an assessment of the variability of the amplitude of the iEMG change.

7) The extracted outliers were classified into positive (+) and negative (−) outliers per muscle (Fig. 2B). The alternate muscle activity between knee extensors was defined as the case in which the positive and the negative outliers were simultaneously observed between the muscles (Fig. 2B, asterisks). The overlap in time for extraction of alternate muscle activity was accepted for a 15-s period.

8) The alternate muscle activity was counted in each muscle combination (RF-VL, RF-VM, and VL-VM) every 10 min.

The alternate muscle activity in the quadriceps muscle counted by this method (Fig. 2B) was consistent with that obtained by visual inspection (Fig. 2C).

Tests for possible natural cause of alternating EMG activity. A supplementary test was conducted to examine the possibility of involvement of changes in the hip joint angle or in the direction of the force that could produce drastic changes in EMGs similar to that seen in alternate EMG activity in knee extensor muscles. In addition, it was investigated whether the alternate EMG activity was consistently observed across the entire portion of each muscle. A triaxial force transducer (type 9251A, Kistler, Winterthur, Switzerland) (23) was attached to the ankle, and three force vectors, in the medial-lateral ($F_{L}$), upward-downward ($F_{V}$), and anterior-posterior ($F_{A}$) directions around the ankle, were measured (Fig. 3A). Two identical EMG electrode sets were attached to each muscle; one was at the proximal and the other at the distal portion. The subject performed sustained knee extension at 2.5% of MVC for 60 min, during which time the following instructions were given. First, the subject was asked to change the hip joint angle intentionally between 100 and 80° while maintaining the target force of the knee extension. Thereafter, the subject was asked to perform flexion, adduction-abduction, or external-internal rotation of the hip joint angle concurrently with the sustained knee extension. Additionally, sustained knee extension at 10.0% of MVC was performed under the same setup to compare EMGs from different portions and to monitor for possible changes in force direction.

Statistical analyses. Values are given as means ± SE. For experiment 1, a two-way ANOVA with repeated measures (3 × 6, combinations of alternating activity × time) with a Tukey's post hoc test was used. For experiment 2, a two-way ANOVA with repeated measures (4 × 6, contraction levels × time) with a Tukey's post hoc test was used. In each statistical analysis, the level of significance was set at $P < 0.05$.

RESULTS

Tests for possible natural cause of alternating EMG activity. The force vectors around the ankle and the changes in EMG from the proximal and distal portion of the muscles were examined during sustained knee extension 2.5% of MVC (Fig. 3, B−F) and 10% of MVC (Fig. 4). As demonstrated in Fig. 3B, no apparent changes were seen in the force of any vectors at the time when the alternating EMG activities emerged among the heads of the quadriceps muscle. Furthermore, even when the hip joint angle was changed intentionally between 100 and 80° during sustained knee extension, no marked changes in the EMG activity were observed (Fig. 3C). When the subject intentionally changed the force of the direction of flexion (Fig. 3D), adduction-abduction (Fig. 3E), and external-internal rotation (Fig. 3F) of the hip joint during sustained knee extension, small fluctuations in EMG amplitude could be observed, but these small changes were not systematic and quantitative changes were substantially smaller than those drastic changes seen in the alternate muscle activity (Fig. 3B). Furthermore, the subject could hardly maintain the target level of knee extension force when the direction of force...
was changed (Fz in Fig. 3, D–F), indicating that changing the direction of force while maintaining the target force in knee extension is less likely under natural conditions.

During the sustained contraction at 2.5% of MVC, similar activation patterns, including alternate muscle activity, were observed in both the proximal and distal portions in each muscle of the knee extensor muscles. Similar activation patterns across the two portions of the muscles and lack of marked change in force directions were also confirmed during the sustained contraction at 10% of MVC (Fig. 4). As it turned out, there was no alternate muscle activity at this intensity.

**Experiment 1.** The MVC was 193.0 ± 13.2 N·m, and 2.5% of MVC was equivalent to 4.8 ± 0.9 N·m. During the sustained contraction at 2.5% of MVC for 60 min, alternate muscle activity in the quadriceps muscle was found in all 11 subjects. The frequency of the alternate muscle activity between RF and either VL or VM was significantly higher (P < 0.05) than that between VL and VM throughout the sustained contraction (Fig. 5). The frequencies of alternation between RF and either VL or VM increased progressively with time after exercise had commenced. Consequently, the total number of alternations for 60 min between RF and VL, RF and VM, and VL and VM was 6.9 ± 0.5, 7.4 ± 0.8, and 0.7 ± 0.3, respectively.

**Fig. 2.** Successive stages of data processing in obtaining the alternate muscle activity among the heads of the quadriceps muscle. A: data of RF muscle are shown as an example. Top and middle: iEMG and smoothed iEMG during sustained contraction at 2.5% of MVC, respectively. Bottom: time differentiation of filtered iEMG sequences (iEMG_all/dt) calculated from smoothed iEMG sequence. Dotted lines, 3 SDs of iEMG_all/dt for 3 min after onset of exercise. ●, Outliers of the iEMG sequence. B: extracted positive (+) and negative (−) outliers of RF (top), VL (middle), and VM (bottom) muscles. *, Case in which an opposite relation of outliers (negative and positive) was found among the muscles. C: iEMG sequences of RF (top), VL (middle), and VM (bottom) during low-level sustained contraction are indicated for purposes of comparing the objective assessment (B) and visual inspection (C). %max, Percentage of maximum. See text for further explanation.

**Fig. 3.** Simultaneous recordings of medial-lateral (Fx), upward-downward (Fy), and anterior-posterior (Fz) force of a right leg, hip joint angle, and rectified electromyogram (EMG) obtained from RF, VL, VM, and BF during sustained knee extension at 2.5% of MVC. Two EMG recordings, from the proximal (P) and distal (D) sites of each knee extensor muscle, are shown. A: experimental setup for measurement of Fx, Fy, and Fz of the right leg. B: patterns of forces, angle, and rectified EMGs around the time at which alternate muscle activity emerged. C: forces, angle, and rectified EMGs when hip joint angle was changed intentionally from 100 to 80°. D–F: forces, angle, and rectified EMGs during hip flexion (D), hip adduction-abduction (E), and hip external-internal rotation (F). Horizontal scales are the same among the figures.

**J Appl Physiol • VOL 93 • AUGUST 2002 • www.jap.org**
Experiment 2. Six of the eleven subjects participated in an additional experiment employing different exercise intensities. The MVC value of these subjects was 185.9 \pm 13.1 \text{ N\cdot m}. Calculated values of 2.5, 5.0, 7.5, and 10.0% of MVC was equivalent to 4.6 \pm 0.3, 9.3 \pm 0.7, 13.9 \pm 1.0, and 18.6 \pm 1.3 \text{ N\cdot m}, respectively. Typical examples of knee extension torque and iEMG for knee extensors (RF, VL, and VM) and flexor (BF), and hip joint angle during sustained contraction at four different intensities are shown in Fig. 6. During contraction at 7.5 and 10.0% of MVC, no marked differences were found in the EMG behaviors among the three heads of the quadriceps muscle. As the task intensity decreased to 2.5 and 5.0% of MVC, the behavior of iEMG for knee extensors, especially for the RF, became dissimilar among individual heads despite constancy of the force. In the task at 2.5% of MVC, the iEMG of knee extensors seemed to increase or decrease more frequently than that in the task at 5.0% of MVC.

Figure 7 shows the changes in the frequency of alternate muscle activity across different intensities for every 10 min. The frequency of alternation was affected by intensity except in the relation between VL and VM, where no alternate muscle activity was observed at any intensity (Fig. 7C). For the task at 2.5% of MVC, the frequency of alternate muscle activity was significantly higher \((P < 0.05)\) than those at 7.5 and 5.0% of MVC after the -10th and -40th min, respectively. For 5.0% of MVC, the frequency of alternation was also significantly higher \((P < 0.05)\) than that in the task at 7.5% of MVC after the -30th min. Consequently, the total number of alternate muscle activities for 60 min was highest in the task at 2.5% of MVC (RF-VL: 8.0 \pm 0.6, RF-VM: 8.0 \pm 1.0), followed by that at 5.0% (RF-VL: 5.3 \pm 0.9, RF-VM: 5.0 \pm 0.4), at 7.5%
The findings of the present study showed that alternate muscle activity among knee extensor synergists emerged during prolonged isometric contractions, as evidenced by surface EMG recordings. Several studies in which surface EMG was used also reported that individual muscles of plantar flexors (18, 21), elbow flexors (16, 17), and knee extensors (19) repeated periods of high activation and silence, and these synergists appeared to rotate in a complementary pattern to maintain a requested force level. From the measurement of motor units using fine-wire electrodes, it has been found that newly recruited motor units can replace previous active motor units during prolonged elbow flexion at 10% of MVC (7). Recently, Westgaard and De Luca (22) reported that, despite almost constant surface EMG, low-threshold motor units showed inactive periods and were substituted by recruitment of higher threshold motor units during sustained contraction of the trapezius muscle at ~4% of MVC. From the viewpoint of motor unit rotation, it could be possible that the observed alternate muscle activity as assessed by surface EMG is dependent on the area of muscle that the attached EMG electrodes can monitor. To investigate this possibility, the surface EMG from the proximal and distal portions of each muscle was examined during 2.5% of MVC. It was observed that, throughout the sustained contraction, amplitude levels were apparently similar, and there seemed to be no obvious time lag between the surface EMG in the two discrete portions across the three heads of the quadriceps muscle (Figs. 3 and 4). This result clearly demonstrates that the alternate muscle activity emerges at the whole muscle level during prolonged contraction.

Alternate muscle activity between bi- and monoarticular muscles. In the present study, alternate muscle activity was found between RF and either VL or VM, but not between VL and VM. In a previous study that employed sustained plantar flexion (21), it seemed that the alternate muscle activity mainly emerged between the biarticular gastrocnemius medialis and the monoarticular soleus muscle. These findings suggest that the alternate muscle activity in synergistic muscles occurs between bi- and monoarticular muscles. Biomechanical and electromyographic studies by Buchanan et al. (2, 3) have indicated that, during static contraction of muscles across the elbow joint in various directions, the lack of a correlation between the EMG activities of the biceps brachii as a biarticular muscle and any other monoarticular muscle was found. Gritti and Schieppati (9) demonstrated a decreased amplitude of the soleus H reflex induced by the conditioning stimulus to the gastrocnemius medialis nerve. They found that prolonged vibration of the Achilles tendon abolished the inhibition of the soleus H reflex and that inhibition of the soleus H reflex was decreased by isometric leg flexion (activation of gastrocnemius muscles but not the soleus muscle). On the basis of these results, they suggested the existence of an inhibitory effect of Ia afferents from the gastrocnemius muscle on
the soleus motoneuron pool. Schieppati et al. (15) further suggested the possibility that the gastrocnemius and soleus muscles were not necessarily synergistic under all conditions but could be functionally antagonistic. These previous findings, taken together, suggest that it is likely that mono- and biarticular muscles function not only in synergistic but also in antagonistic ways. With these points taken into account, it is likely that the emergence of alternate muscle activity of synergistic muscles is related to the reciprocal complex physiological relations between bi- and monarticular muscles.

---

Fig. 6. Typical recording of torque, iEMG over 1-s period obtained from RF, VL, VM, BF, and hip joint angle during sustained knee extension at 2.5 (A), 5.0 (B), 7.5 (C), and 10.0% (D) of subject’s MVC.

Fig. 7. Values (means ± SE) from 6 subjects of frequency every 10 min of alternate muscle activity between RF and VL (A), RF and VM (B), and VL and VM (C) during sustained knee extension at 2.5, 5.0, 7.5, and 10.0% of MVC. †Significant differences from the sustained contraction at 5.0% of MVC, P < 0.05. *Significant differences from the sustained contraction at 7.5% of MVC, P < 0.05.
Frequency of alternate muscle activity increases with time. The frequencies of alternate muscle activities in the quadriceps muscle progressively increased with time. Sjøgaard et al. (19, 20) pointed out that fatigue during sustained knee extension at 5% of MVC for 60 min was associated with a decline in the muscle cell excitability, which was induced by a loss of potassium from the cells. This is in line with the present result that the impaired muscle contractility with time could be related to factors inducing alternate muscle activity during low-level sustained contraction. Tamaki et al. (21) suggested that the synaptic inputs to α-motoneurons among synergists might be modified by small-diameter afferents belonging to groups III and IV. These afferents are mostly polymodal and are sensitive to metabolites and chemicals associated with fatigue (10). Furthermore, Aymard et al. (1) evoked selective muscle fatigue of the biceps brachii and found a significant decrease in the inhibitory effect from fatigued muscle fatigue of the biceps brachii and found a significant decrease in the inhibitory effect from fatigued muscle on the nonfatigued neighboring finger muscles. According to these studies that examined the effects of muscle fatigue on the activation of synergistic muscles, development of impaired muscle contractility would induce heterogeneity of neuromuscular activity among synergists to compensate for the declined excitability of α-motoneurons of the fatigued muscles.

Alternate muscle activity depends on contraction intensity. The present examination at various contraction levels (experiment 2) showed that alternate muscle activity was observed in contractions with force production levels ≤5% of MVC by the quadriceps muscle. Previous studies on alternate muscle activity have employed various muscles and conditions with a given level of force production, such as knee extensors at 5% of MVC (19), plantar flexors at 10–50% of MVC (18, 21), elbow flexors at 10–15% of MVC (4, 7, 16, 17), or trapezius muscle at ~4% of MVC (22). Fallentin et al. (7) compared changes in action potentials of single motor units from the biceps brachii muscle between sustained contraction at 10 and 40% of MVC. They found an apparent lack of motor unit rotation when the higher intensity was employed. Sirin and Patla (18) demonstrated that the alternate EMG activities between individual plantar flexor muscles were more marked with the knee-extended position than with the knee-flexed position when the required force was identical between positions. Furthermore, Semmler et al. (17) reported that alternate EMG activities occurred during sustained elbow flexion after only 4 wk of limb immobilization that induced reductions in MVC. According to these previous findings, it is likely that the emergence of alternate muscle activity also depends on the contraction intensity.

As described earlier in Frequency of alternate muscle activity increases with time, we postulated that a possible factor for alternate muscle activity was the peripheral neural interaction of synergists, which is related to fatigue. In contrast to the sustained contractions at the lower contraction level (e.g., 2.5 and 5.0% of MVC), muscle blood flow was shown to be occluded, and marked metabolic change took place during sustained contractions at the higher level (e.g., 7.5 and 10.0% of MVC) in the quadriceps muscle (20). In this situation, increased neural input from both group Ia (12) and small-diameter afferents (8) to the motoneuron pool would be expected. This may appear to be inconsistent with the present result, because we found here that the frequency of the alternate muscle activity was reduced when the required level of force was increased. However, it should be remembered that the inhibitory effects between synergistic muscles were reported to disappear as the voluntary contraction levels increased (9, 15). These previous findings suggest that the alternation of muscle activity among synergists is related to the balance between neural inputs from the peripheral afferents and from the voluntary drive. In that case, the absence of alternate muscle activity above 5.0% of MVC could be explained as follows: the modulation of motoneurons elicited by the peripheral afferent activities was overcome by an increased descending command for knee extension with increased in contraction levels.

In conclusion, the alternate muscle activity in the quadriceps muscle emerged only between biarticular RF muscle and monoarticular vasti muscles (VL and VM). Moreover, the frequencies of alternation among synergistic muscles increased with time. The results of additional experiments investigating alternate muscle activity at the four intensities indicated that the alternation occurred in contractions with a force production level equal to or below 5.0% of the subject’s MVC and that the frequencies of the alternation increased with reductions in the required level of force production.

The authors are grateful to Dr. Kimitaka Nakazawa (National Rehabilitation Center for the Disabled, Saitama, Japan) for invaluable comments.

REFERENCES


