Local blood circulation among knee extensor synergists in relation to alternate muscle activity during low-level sustained contraction

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The relation between local circulation and alternate muscle activity among knee extensor synergists was determined during low-level sustained knee extension at 2.5% of maximal voluntary contraction for 60 min in seven subjects. Blood volume of rectus femoris (RF) and vastus lateralis (VL) was assessed by using near-infrared spectroscopy. Surface electromyogram (EMG) was recorded from RF, VL, and vastus medialis (VM). Alternate muscle activity was observed between RF and either VL or VM. Cross-correlation analysis was used to investigate the relation between blood volume and integrated EMG (iEMG) sequences throughout the task. One negative peak in the cross-correlation function was seen between the iEMG and blood volume with time lag of 30–60 s, indicating that muscle activity increases (or decreases) with the decrease (or increase) in local circulation with the corresponding time lag. Two cases in the emergence of alternate muscle activities, i.e., an increase in the EMG of RF accompanied by a decline of EMG in VL (case I) and vice versa (case II) were further analyzed. The time lag between iEMG and blood volume was longer in case I than that in case II. These results were statistically significant in the RF but not in the VL. It is concluded that even during low-level sustained contraction, local circulation is modulated by the alternate muscle activity of knee extensor synergists, and a negative correlation between the muscle activity and blood volume sequences was found in only RF but not in VL.

Near-infrared spectroscopy; electromyogram; synergistic muscles

SUFFICIENT CIRCULATION OF blood to exercising muscles is essential for maintaining muscle contractions by supplying oxygen and substrates while removing metabolic wastes. Blood flow is determined by the integrated results of cardiac output, blood pressure, vasoconstriction, vasodilatation, mechanical compression, and so forth (22). It is known that the blood flow during sustained isometric contraction is strongly affected by the intensity of the contraction and that the relation between them depends on the muscle groups (22). In the knee extensors, blood flow measured at the femoral vein is maintained at a sufficient level and does not show any signs of occlusion during low-intensity sustained contraction below 10% of maximal voluntary contraction (MVC) (38). In contrast, during contraction above 10% of MVC, blood flow is not maintained at a sufficient level and is eventually occluded (13, 38). The existence of a threshold in contraction intensity has been demonstrated in other muscle groups such as forearm muscles (20) and plantar flexors (5). These dependencies of blood flow on the contraction intensity seem mostly due to the effects of intramuscular pressure (25, 38).

It has been reported that intramuscular pressure is linearly related to contraction intensity during knee extension (25, 32, 37, 38), elbow flexion (25), and plantar flexion (3, 25). Intramuscular pressure has mostly been compared with the total force of synergistic muscles when muscle activation is assumed to be relatively constant. Through the observation of electromyogram (EMG), however, an unusual pattern of muscle activation has often been demonstrated when sustained contraction at low-level intensity is prolonged for >30 min; the individual synergistic muscles are not continuously activated, but rather they alternate between periods of activity and silence (19, 29, 30, 37, 40). This unique pattern of muscle activation has been called “alternate muscle activity of synergistic muscles” (19, 40). Enoka and Stuart (12) suggested that alternate muscle activity would be effective for minimizing muscle fatigue. This has been reported in a variety of muscle groups, including knee extensors (19, 37), plantar flexors (35, 40), and elbow flexors (29, 30). Recently, we examined the changes in EMG activity of the quadriceps muscle during low-level sustained contractions (2.5–10% of MVC) (19). During the sustained force matching task at 2.5 or 5% of MVC in total knee extension force, alternating muscle activity of knee extension force, alternating muscle activity of knee extension force, alternating muscle activity of knee extension force, alternating muscle activity of knee extension force, alternating muscle activity of knee extension force, alternating muscle activity of knee extension force, alternating muscle activity of knee extension force, alternating muscle activity of knee extension force, alternating muscle activity of knee extension force, alternating muscle activity of knee extension force, alternating muscle activity of knee extension force, alternating muscle activity of knee extension force, alternating muscle activity of knee extension force.
extensors increased the amplitude of EMG in the rectus femoris muscle, which reached 15–20% of that seen during MVC. Based on a previous study that found an impedance of blood supply to the knee extensors during contraction at 15% of MVC (38), it is possible therefore that intramuscular pressure of the individual muscles of the synergists fluctuates because of the effects of the alternate muscle activity and that the fluctuations in intramuscular pressure affect the local circulation. Indeed, one study (37) has demonstrated fluctuations in the intramuscular pressure of rectus femoris and vastus lateralis muscle during sustained contractions at 5% of MVC. However, in their study, Sjøgaard et al. reported constant blood flow to the femoral vein, and local blood circulation in the individual heads of knee extensors was not examined. Hence, the effects of alternate muscle activity on the local circulation in the individual muscles remain as yet unknown. We hypothesized that, even during low-level contraction below 10% of MVC, blood circulation is locally altered because of the effects of alternate muscle activity.

Invasive measurement of blood flow in the femoral vein has been commonly employed to examine the blood circulation during knee extension (13, 37, 38). The blood flow so measured cannot distinguish the local circulation among individual muscles, but it indicates the average value for several muscles. With near-infrared spectroscopy (NIRS), however, one can measure total Hb content in the capillary bed of individual muscles (7, 21), including the knee extensor muscles (4, 15, 24, 34). Thus the local circulation in the individual knee extensor synergists can be examined by using NIRS.

To test the above-mentioned hypothesis, local circulation in individual muscles was examined by NIRS during alternate muscle activity of knee extensor synergists. We predicted that fluctuations in the blood circulation of individual muscles are correlated with alternate muscle activity.

METHODS

Subjects. Seven subjects (5 men and 2 women) voluntarily participated in the experiment. Their mean age, height, and body mass were 25.7 ± 2.4 (SD) yr, 167.1 ± 8.1 cm, and 61.0 ± 6.9 kg, respectively. They had no significant medical history or signs of neurological disorders, and they had not participated in any programs of regular exercise. All subjects gave their written informed consent for the study after receiving a detailed explanation of the purposes, potential benefits, and risks associated with participation in the study. All procedures used in this study were in accordance with the ethical standards of the Committee for Human Experimentation at the Department of Life Sciences, The University of Tokyo, and its protocol was consistent with their requirements for human experimentation.

Recording techniques. The basic setup for the knee extension procedure was the same as that described elsewhere (18, 19). Each subject was required to perform a static unilateral knee extension exercise in a seated position with the hip and knee joint angles of 100 and 90° flexed (full extension = 0 deg), respectively. The subject’s upper body was firmly fixed on a chair by a seat belt. The force of isometric contraction of the knee extensors was measured by a strain-gauge force transducer that was coupled with a strain amplifier and attached by a strap to the subject’s ankle. The force was displayed on a storage oscilloscope in front of the subject to provide visual feedback regarding the produced force and target. Surface EMG from skin surface over the rectus femoris (RF), vastus lateralis (VL), and vastus medialis (VM) muscles was recorded by using Ag-AgCl electrodes with a diameter of 5 mm and an interelectrode distance of 20 mm. After careful abrasion of the skin, the electrodes were placed over the muscle belly of the respective muscles. The reference electrode for the EMG was placed on the iliac crest. The electrodes were connected to a preamplifier and a differential amplifier having a bandwidth of 5 Hz to 1 kHz (model 1253A, NEC Medical Systems, Tokyo, Japan). All electric signals were stored with a sampling frequency of 1 kHz on the hard disk of a personal computer using a 12-bit analog-to-digital converter (Lab-PC+®, National Instruments, Austin, TX).

To estimate the local circulation of individual synergists, the present study utilized NIRS (NIRO-300, Hamamatsu Photonics, Hamamatsu, Japan) equipped with dual-channel near-infrared laser diodes. The NIRS probes were firmly placed on each muscle belly of the RF and VL near the EMG electrodes. We focused on the RF and VL muscles, because we have already found that alternate muscle activity emerges between RF and either VL or VM but not between VL and VM (19). The light was generated by four laser diodes operating at 775, 810, 850, and 905 nm. The detector in the NIRS probe was separated from the light source by 40 mm. The penetration depth of NIRS corresponds to ~20 mm because penetration depth has been reported to equal half the distance between the light source and the detector (9, 16). The absorption of light at the different wavelengths was analyzed according to the modified Beer’s law, and the changes in oxygenated Hb and Hb were quantified. The sum of known wavelengths is susceptible to the changes in the total Hb (change in oxygenated Hb + change in deoxygenated Hb), which reflects the changes in blood volume under the NIRS probe (6). The algorithm requires the actual pathlength of the light between the light source and detector, but because of the technical inability to measure the pathlength in human muscles, blood volume is expressed in units that involve the pathlength factor. The blood volume measured by the NIRS is different from the blood flow, but it can be used as an index of the local blood circulation because a good correlation has been reported between the data measured by NIRS and blood flow measured by plethysmography (10, 11). The details of this technique and principle of this instrument have been described elsewhere (39). NIRS signals were continuously stored on a personal computer connected via a RS-232C cable with a sampling frequency of 1 Hz.

Experimental protocol. The MVC for knee extension was the largest force of three trials that could be sustained for at least 2 s. After a sufficient rest period, at least for 10 min after completion of the MVC measurement, the subject performed a sustained knee extension for 60 min at a level corresponding to 2.5% of MVC. Immediately after sustained contraction, the MVC measurement was performed. The target force production in the present study was lower than that employed in the previous study (37) because the alternate muscle activity clearly emerged when the force level decreased from 5.0 to 2.5% of MVC (19).

Data analysis. The EMG signals were full-wave rectified and integrated over 1 s to yield integrated EMG (iEMG). The torque at the knee joint was calculated on the basis of the measured force multiplied by the length of the leg. The iEMG
was expressed relatively as a percentage of the corresponding value during MVC (%iEMG max).

Maximal value, mean value, SD, and coefficient of variation of iEMG sequences in the individual muscle heads were calculated for 60 min of sustained contraction (3,600 sample points). iEMG immediately after the onset of sustained contraction was also calculated over 10 s as an unfatigued value. For the blood volume fluctuation, the range and SD of sequences were calculated.

To evaluate the extent of correlation and the time relation between the iEMG and blood volume sequences of each muscle, we calculated the normalized cross-correlation function (CCF) between the two time series. Before this calculation, the two time series were low-pass filtered (cutoff frequency = 0.01 Hz) by using a fourth-order Butterworth filter employing a zero phase lag (45) to eliminate the high-frequency component. Data for a 20-min period in the early (between the 10th and the 30th min) and later stage (between the 40th and the 60th min) of the sustained contraction were selected for analysis. When the iEMG and blood volume series were written as \( x(t) \) and \( y(t) \) (\( t = \) time), respectively, the normalized CCF \( R_{xy}(\tau) \) was calculated as

\[
R_{xy}(\tau) = \frac{x(t + \tau)y(t)}{\sqrt{x^2(t)}\sqrt{y^2(t)}}
\]

where \( \tau \) is time lag. The actual calculation was performed in discrete form using a 1,024 points fast Fourier transform calculation. Thus it should be noted that the CCF was for a time window of 1,024 s and that the time resolution of CCF was determined as 2 s. The peak value was used to evaluate the similarity of the two time series, and the time lag was used to evaluate the temporal relation between them.

Furthermore, we paid special attention to the responses of the blood volume around the two epochs at which alternate muscle activity emerged (Fig. 1); the epoch at which the iEMG of RF abruptly increased with the decrease in the iEMG of VL and VM (case I in Fig. 1), and the epoch at which the iEMG of RF dramatically decreased with an increase in the iEMG of VL and VM (case II in Fig. 1). The alternate muscle activities that involved case I and case II were extracted in the following way. For each case, a data set for the ~240-s period that included the most abrupt change of RF in the iEMG of RF was then given as a result of the time derivative of the low-pass filtered iEMG of RF (Fig. 1, bottom). The extracted data were aligned to the positive and negative peaks of the iEMG\(_{d/dt}\) of RF for case I and case II, respectively. Blood volume at each epoch was expressed as the differences from the reference value (change in blood volume) in which the iEMG of the RF abruptly changed (Fig. 1, dashed lines). Thereafter, iEMG and blood volume were averaged for every 5-s period. All the data are presented as means ± SE.

Statistical significance in the measurement of iEMG (%iEMG max) and blood volume (\( \mu \)M-cm) sequences among synergistic muscles was tested by using a one-way ANOVA with repeated measures followed by a Tukey’s post hoc test. To find significant differences in blood volume from the time at which iEMG of RF abruptly changed, blood volume data were also statistically using a repeated measurement one-way ANOVA with a Tukey’s post hoc test. A paired Student’s \( t \)-test was used to compare peak value of the normalized CCF in the early and the later stages. The significance level for all comparisons was set at \( P < 0.05 \).

RESULTS

The MVC was 173.2 ± 8.9 N·m, and 2.5% of MVC was equivalent to 4.3 ± 0.2 N·m. All subjects could perform completely the knee extension task at 2.5% of MVC for 60 min. The MVC after the sustained contraction fell to 85.2 ± 4.4% of the initial MVC measurements without fatigue. This is similar to our previous study (19).

A typical example of the changes in the iEMG and blood volume in the individual heads of knee extensor muscles is shown in Fig. 2. Alternate muscle activity emerged between RF and both VL and VM in all subjects. The total number of alternate muscle activities for 60 min (RF-VL: 8.5 ± 1.6, RF-VM: 8.0 ± 1.9, VL-VM: 1.0 ± 0.4) was consistent with the finding in our previous study (19). Fluctuations in iEMG and
blood volume appeared to be larger in RF than in other synergists.

Table 1 summarizes basic statistics of the iEMG and blood volume sequences in each muscle head of the knee extensors. The iEMG of each head is expressed in relative values normalized to the MVC values of each head except for coefficient of variation. This measurement revealed more pronounced changes for iEMG and blood volume in RF compared with VL or VM. The iEMG at the onset of sustained contraction is significantly higher in VL than that in RF and VM \((P < 0.05)\). It is noteworthy that the iEMG in the RF is much lower than the value of 2.5% (percentage of total knee extension force relative to MVC). The average iEMG value across the three muscle heads is approximately equivalent to the contraction intensity \((2.6 \pm 0.1\% \text{EMG}_{\text{max}})\). The maximal iEMG in VM was only one-half the value of RF. SD of iEMG in RF was more than twice as large as that in VL and VM \((P < 0.05)\). Similar differences among the heads are found in coefficient of variation of iEMG, an index for fluctuations of muscle activity. The similar tendency in differences between SD and coefficient of variation of iEMG reflects no difference in the mean iEMG among the individual heads of the knee extensors. Blood volume was measured in RF and VL. Similar to the results in iEMG, the range and SD of blood volume sequence were significantly larger in RF than those in VL.

Figure 2. Typical example of torque, iEMG of RF, VL, and VM over 1-s period, and blood volume of RF and VL during sustained knee extension at 2.5% of maximal voluntary contraction for 60 min. %iEMG max, maximal iEMG.

Table 1. Fluctuation of iEMG and blood volume in each head of knee extensors during sustained contraction for 60 min

<table>
<thead>
<tr>
<th></th>
<th>RF</th>
<th>VL</th>
<th>VM</th>
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<tbody>
<tr>
<td>iEMG</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Onset, (\mu V \cdot s)</td>
<td>3.2 ± 0.7</td>
<td>10.9 ± 1.7</td>
<td>7.3 ± 2.7</td>
</tr>
<tr>
<td>%EMG_{max}</td>
<td>1.1 ± 0.1</td>
<td>4.7 ± 0.6*</td>
<td>2.0 ± 0.1†</td>
</tr>
<tr>
<td>Maximal, (\mu V \cdot s)</td>
<td>76.5 ± 10.5</td>
<td>32.6 ± 2.4</td>
<td>43.0 ± 5.8</td>
</tr>
<tr>
<td>%EMG_{max}</td>
<td>27.6 ± 4.4</td>
<td>13.3 ± 1.7*</td>
<td>10.4 ± 2.2*</td>
</tr>
<tr>
<td>Time, min</td>
<td>50.3 ± 2.1</td>
<td>52.0 ± 2.0</td>
<td>50.2 ± 3.6</td>
</tr>
<tr>
<td>Mean, (\mu V \cdot s)</td>
<td>24.4 ± 3.7</td>
<td>19.1 ± 1.6</td>
<td>17.2 ± 2.4</td>
</tr>
<tr>
<td>%EMG_{max}</td>
<td>8.4 ± 1.4</td>
<td>7.5 ± 1.0</td>
<td>4.2 ± 3.9</td>
</tr>
<tr>
<td>SD, (\mu V \cdot s)</td>
<td>18.5 ± 3.1</td>
<td>5.5 ± 1.0</td>
<td>7.3 ± 1.2</td>
</tr>
<tr>
<td>%EMG_{max}</td>
<td>6.7 ± 1.3</td>
<td>2.4 ± 0.3*</td>
<td>1.8 ± 0.3*</td>
</tr>
<tr>
<td>Coefficient of variation, %</td>
<td>77.8 ± 3.9</td>
<td>32.0 ± 3.1*</td>
<td>43.6 ± 5.6*</td>
</tr>
<tr>
<td>Blood volume</td>
<td></td>
<td></td>
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</tr>
<tr>
<td>Range, (\mu M \cdot cm)</td>
<td>175.6 ± 34.2</td>
<td>129.0 ± 30.7*</td>
<td></td>
</tr>
<tr>
<td>SD, (\mu M \cdot cm)</td>
<td>29.0 ± 6.2</td>
<td>21.8 ± 4.9*</td>
<td></td>
</tr>
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</table>

Values are means ± SE. Onset indicates integrated electromyogram (iEMG) immediately after sustained contraction start as unfatigued state value. Time indicates the time at which the iEMG in each muscle reached maximal value (iEMG_{max}). See text for further explanation. RF, rectus femoris; VL, vastus lateralis; VM, vastus medialis. *Significant difference from RF muscle, \(P < 0.05\). †Significant difference from VL muscle, \(P < 0.05\).
From each subject, two epochs of dramatic changes in iEMG are randomly extracted for the duration of 240 s: one in which EMG activity switched from VL to RF (case I in Fig. 4A) and the other in which the converse occurred (case II in Fig. 4B). iEMG and blood volume are aligned to the time of abrupt change in iEMG of RF (Fig. 1, dashed lines). In both epochs, the inverse relation between iEMG and blood volume was found only in the RF with some delay but not in VL. In case I, the blood volume significantly decreased 62.5 s

Fig. 3. Group-averaged normalized cross-correlation function (CCF) between iEMG and blood volume in RF (top) and VL (bottom) during sustained knee extension exercise at 2.5% of the subjects’ maximal voluntary contraction for 60 min. A: early stage (from 10th to 30th min). B: later stage (from 40th to 60th min). Solid lines, means; dashed lines, SE. Positive time lag means that change in iEMG sequence occurred before blood volume response.

Fig. 4. Mean values (± SE) from 7 subjects of iEMG of RF, VL, VM, and blood volume over 5-s period obtained from RF and VL in case I (A) and case II (B). ●, RF; ○, VL; △, VM. iEMG and blood volume expressed as the differences (∆) from the reference value in which iEMG of RF abruptly changed (Fig. 1, dashed lines). *Significant difference (P < 0.05) of blood volume from the time at which iEMG of RF abruptly changed (∆time = 0 min).
after iEMG started to increase. In case II, however, the increase in blood volume was followed by a decrease in iEMG with shorter time delay (27.5 s) compared with case I. In VL, the change in iEMG was small, and the blood volume was almost constant in both cases.

DISCUSSION

The main findings of the present study were that 1) local circulation assessed by blood volume was negatively correlated with muscle activity in the RF, 2) changes in RF muscle activity preceded local circulation, 3) the time lag between the muscle activity and circulation sequences was different between case I and case II, and 4) such prominent results were found in RF but not in VL. These results support the hypothesis that, even during low-level contraction below 10% of MVC, blood circulation is locally occluded due to the effects of alternate muscle activity in the RF.

Negative correlation between local circulation and muscle activity. The alternate muscle activity of the knee extensors emerged during sustained contraction at 2.5% of MVC for 60 min (Fig. 2), and this is consistent with the reports by Sjøgaard et al. (37), who employed 5% of MVC. In the present study, we focused on the local circulation of the individual synergistic muscles in relation to the alternate muscle activity. As a result, blood volume fluctuated rather than maintaining a constant value throughout the sustained contraction. Cross-correlation analysis clearly demonstrated that blood volume sequence was negatively correlated with iEMG sequence. This negative correlation indicates that iEMG increases with the decrease in blood volume or that iEMG decreases with the increase in blood volume. It was shown that, during prolonged contraction at 5% of MVC, blood flow in the femoral vein was maintained, on average (38). Closer examination of their data, however, tells us that the variation of the blood flow was progressively increased to a great extent as the exercise prolonged. On the basis of the present results, local circulation of blood may be modulated by the alternate muscle activity even during low-level sustained contraction at 2.5% of MVC.

The possibility for regional temporal hypoperfusion of the blood during low-level isometric contraction has been reviewed by Rowell (22). Although the mean intramuscular pressure seems to be well below systolic, diastolic, or mean arterial pressure during low-level contraction (32, 38), spatial distribution of intramuscular pressure is complex depending on the architecture of the muscle (muscle fiber orientation, thickness, curvature of the fibers) (31). The major effect of the intramuscular pressure during low-level contraction is thought to be venous compression, which would be expected to impede blood flow (22). In addition, impedance to flow may be caused not only by the effect of the compression on vascular radius and resistance but also by the twisting of arteries (14). The femoral venous blood flow at 15% of MVC is already reduced below the highest flow at 5% of MVC (38). Marked postcontraction hyperemia after 10–15% of MVC (38, 42) would suggest that blood flow was low because the contraction had caused a hypoperfusion relative to metabolic rate somewhere within the quadriceps muscle. In the present study, iEMG of RF reached above 20% of iEMGmax during the alternate muscle activity and close relations have been shown between EMG and intramuscular pressure during fatiguing exercise (8, 25). Thus the negative correlation between the muscle activity and blood volume of the RF may be interpreted as follows: the blood supply to the working regions fluctuated as a result of the dramatic increase or decrease in the muscle activity and consequent changes in the intramuscular pressure even during low-level sustained contraction at 2.5% of MVC.

It is of interest that a clear negative correlation between the iEMG and blood volume sequences was found in only RF but not in VL (Fig. 3). There are three major possibilities that may be related to the different results between these muscles: 1) larger changes in muscle activity, 2) higher muscle force, and 3) higher fatigability in RF.

The larger changes in muscle activity in RF were evident from the comparison of changes in iEMG and the coefficient of variation of iEMG (Table 1). The maximum change of iEMG relative to the onset value amounted to ~25 times in RF, whereas it was only 3–5 times in vasti muscles. Despite the low-level contraction at 2.5% of MVC, iEMG of RF amounted to excess of the values above 20% of iEMGmax. In contrast, iEMG was always <20% of iEMGmax in VL or VM. The coefficient of variation of iEMG, an index of the fluctuations of muscle activity, was also considerably larger in RF than that in VL or VM. These results suggest that the larger change in the muscle activity of RF than vasti muscles during sustained contraction at 2.5% of MVC alters the local circulation of the RF.

Intramuscular pressure depends on the muscle fiber force and differences in the muscle force per physiological cross sectional area (force/PCSA) of each muscle head reflect the differences in the muscle fiber force. From the previous studies on young Japanese with similar physical characteristics and MVC to the present subjects, PCSA of each muscle head can be estimated as 230–238% for VL, 154–159% for VM, and 171–185% for vastus intermedius (VI) compared with RF (1, 2). Alternate muscle activity is not observed between the VL and VM (19), and most of the VI is fused to the VL (43, 44). Hence alternate muscle activity is likely to emerge between the RF and all of the vasti muscles. On the basis of this information, compared with the force/PCSA of RF during the condition in which only the RF is active, the force/PCSA of vasti muscles (VL, VM, and VI) would be 17.2–17.7% during the condition in which only the vasti muscles are activated (even if the activity of VI is neglected, the force/PCSA of VL and VM would be 23.6–24.6% compared with RF). Thus the marked difference in the muscle fiber force between RF and other synergists may have induced heterogeneity of intramuscular pressure and thus the heterogeneity of the local circulation among...
the knee extensor synergists even during low-level sustained contraction.

During sustained low-level contraction in which EMG activity increases with time, the increase in EMG activity matches the increase in the intramuscular pressure (8, 25). The increase in EMG activity is regarded as a measure of muscle fatigue, i.e., decline in the ability of muscle of motor unit to produce force. Hence some process that occurs in concurrent with the development of muscle fatigue has been discussed as a possible cause of the increased intramuscular pressure. Accumulation of intramuscular water, which was observed during knee extension at 5% of MVC (36), was suggested other than the effect of increased motor unit activity (8). In the present study, MVC force was decreased by 15%. It is of note that RF is more susceptible to muscle fatigue compared with VL and VM (17, 33, 41). Thus it is possible that the enhanced negative relation between iEMG and blood volume of RF in the later stage is related to the development of fatigue. With these points taken into account, it is most likely that the negative correlation of normalized CCF between iEMG and blood volume observed in only the RF is attributable to the divergence of the force levels and the fatigue state among the knee extensor muscles during sustained contraction at 2.5% of MVC.

**Time lag between iEMG and blood volume.** In the RF muscle, the cross-correlation analysis resulted in the inverse relation between iEMG and blood volume sequences with a time lag of ~50 s. This indicates that the local circulatory change generally occurs after 50 s of the fluctuations in muscle activity. To examine this time delay in more detail, the data of the two epochs of alternate muscle activity were further analyzed: data around the increase in iEMG of RF accompanied by the decline in iEMG of VL (case I) and vice versa (case II).

In case I, blood volume of RF started to decrease 50–60 s after the onset of the increase in iEMG of RF. This is probably related to the slow development of muscle force in RF, which is implied by the slow development of iEMG of RF. From the presence of marked postcontraction hyperemia after 10–15% of MVC (38, 42), hypoperfusion somewhere within the quadriceps muscle is suggested to exist around this level of contraction (23). In the present study, it required ~50 s for the iEMG of RF to exceed 15% of iEMG$_{\text{max}}$ on average. This amount of time may have been necessary for the muscle force and intramuscular pressure to be developed up to the level that could affect local blood circulation.

As the time proceeded with iEMG of RF maintained as high as 15–20% of iEMG$_{\text{max}}$, it is possible that muscle sympathetic nerve activity was enhanced. Responses in muscle sympathetic nerve activity depend not only intensity of exercise but also on exercise mode, and they are enhanced in accordance with the development of fatigue as well as the local sensation of fatigue (26–28). During sustained knee extension at 20% of MVC, muscle sympathetic nerve activity increased by 83% (26). Seals and Enoka (28) showed that the increase in muscle sympathetic nerve activity was related to the increase in EMG activity during sustained contraction, which was regarded as the index of fatigue. They further found that muscle sympathetic nerve activity was enhanced due to the prior fatiguing exercise and claimed the physiological link between EMG activity and muscle sympathetic nerve activity. Furthermore, increase in muscle sympathetic nerve activity is related to local sensation of fatigue during prolonged contraction (26, 27). Although it was anecdotal, subjects in the present study reported increased local sensation of fatigue in the RF when its iEMG was high. Thus it is likely that increase in muscle sympathetic nerve activity was developed when iEMG of RF was high.

In case II, when iEMG of RF dropped, there was a time delay for the blood volume to increase, although the amount of time was shorter compared with the delay for the decrease in case I. If muscle sympathetic nerve activity is enhanced, the delay in case I could be related to the delayed recovery of the muscle sympathetic nerve activity.

In conclusion, local circulation in the RF is modulated by the alternate muscle activity among the knee extensor synergists even during low-level sustained contraction.

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**REFERENCES**


11. Edwards AD, Richardson C, van der Zee P, Elwell C, Wyatt JS, Cope M, Delpy DT, and Reynolds EO. Measure-


