Increase in Neuromuscular Activity and Oxygen Uptake during Heavy Exercise

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In order to examine the contribution of neuromuscular activity to the slow increase in $\dot{V}O_2$ during heavy exercise, integrated electromyogram (iEMG) of dominant working muscle and $\dot{V}O_2$ was compared in seven subjects during constant-load cycling exercise at the intensity of 10\% below and 30\% above ventilatory threshold (VT) for seven minutes.

$\dot{V}O_2$ and iEMG after 4th min in above VT test was significantly correlated ($r = 0.53, p < 0.01$) and $\dot{V}O_2$/iEMG was constant after 4th min, indicating coupling of iEMG with $\dot{V}O_2$. The results suggested that the slow increase in $\dot{V}O_2$ during heavy exercise may result from the changes in the recruitment pattern of motor units.


Key words: $\dot{V}O_2$, iEMG, Motor unit recruitment, Ventilatory threshold

Compared to light exercise below ventilatory threshold (VT), oxygen uptake ($\dot{V}O_2$) during constant-load heavy exercise above VT slowly increases as exercise continues (Whipp and Wasserman, 1972, 1987; Roston et al., 1987; Henson et al., 1989) and could reach maximal oxygen uptake ($\dot{V}O_2$ max) if the exercise is prolonged until exhaustion (Camus et al., 1988).

Recently Poole et al. (1991) demonstrated that the increased $\dot{V}O_2$ reflected predominantly the increased $\dot{V}O_2$ of exercising legs and precluded the dominant role for factors such as ventilatory muscle work (Hagberg et al., 1978; Casaburi et al., 1987), metabolic stimulation at sites outside the exercising limbs by the effect of catecholamines (Kalis et al., 1988), and lactate (Roston et al. 1987; Henson et al. 1989; Poole et al., 1988). They further suggested the possible involvement of serial recruitment of fast-twitch fibers, which are less efficient than slow-twitch fibers (Crow and Kushmerick 1982).

In consistent with this idea, neuromuscular fatigue, as evidenced by the increase in iEMG, is observed during constant-load cycle exercise if the work intensity is relatively high (devries et al., 1982). Therefore the purpose of this study was to examine if the increase in $\dot{V}O_2$ during heavy exercise is associated with the increase in neuromuscular activity as evidenced by integrated electromyogram (iEMG) increase.

METHODS

The experiments were performed by seven healthy males whose mean (SD) values of age, height, and weight were 27.4 (6.9) years, 168.0 (3.5) cm, and 61.0 (7.2) kg, respectively.

Initially, each subject performed an incremental exercise test which started with a 2-min period of unloaded cycling, followed by an initial 60W and sequential increase in work rate of 20W each minute. The test was stopped when $\dot{V}O_2$ plateaued or levelled off in spite of further increment of work rate, and $\dot{V}O_2$ max was determined as the peak $\dot{V}O_2$.
achieved. VT was determined independently by both of the authors by the criteria examined by Caiazzo et al. (1982).

From the incremental exercise test, work rates were calculated to elicit \( \dot{V}O_2 \) corresponding to 10 % below VT or 30 % delta above VT, where delta is the difference between VT and \( \dot{V}O_2 \) max for each subject. Constant-load exercise tests of these work rates were performed on separate days from the incremental exercise test and consisted of a 2-min rest period followed by abrupt exercise at the constant work rate of below or above VT for 7 minutes.

During all the exercise tests the subjects exercised on an electromagnetically braked cycle ergometer (Aerobike 800 COMBI, Tokyo) and a constant pedal frequency of 60 rpm was maintained throughout the tests, cued by a metronome and a speedometer on the handlebars.

Ventilatory and gas exchange parameters were analyzed during all the exercise tests by the procedure described in detail elsewhere (Moritani et al. 1987). The subjects wore a noseclip and breathed through a low-resistance 2-way valve (2700 series, Hans Rudolph, MO) via mouthpiece. The expired gas passed through a pneumotachograph (no. 2S/H S353 Fleisch, Validyne, CA), connected to a respiratory flow transducer. The gas sample was analyzed for \( CO_2 \) and \( O_2 \) content (expired gas monitor 1H21B Sanei, Tokyo). The electrical outputs of the flow and \( CO_2 \) and \( O_2 \) transducers underwent analog-to-digital conversion, and then transmitted to the computer (PS-9020F TEAC, Tokyo) by which \( \dot{V}O_2 \) and \( CO_2 \) production (\( \dot{V}CO_2 \)) in STPD and minute ventilation (\( \dot{V}e \)) in BTPS were calculated over 20-s period. Data were stored on disk for later retrieval and further analysis.

During constant-load exercise tests, myoelectric signal was obtained from the bipolar silver/silver chloride electrodes (6 cm interelectrode distance) filled with conducting jelly on the lateral portion of the dominant quadriceps femoris muscle and the reference electrode over the iliac crest. Each electrode was attached after careful abrasion of the skin.

Thus obtained signal was analyzed following procedure described elsewhere (Moritani et al. 1986). The signal was amplified (MEG-6100 Nihon Kohden, Tokyo), band-pass filtered (15-500 Hz), digitized and stored on a hard disk in a computer (IMS 286 Intelligent Micro System, TX) for subsequent analysis. Myoelectric waveforms were monitored by a digital storage oscilloscope (VC-6025 Hitachi Tokyo) to assure the absence of artifact. After the test, 20-s iEMG were consecutively calculated over the exercise period.

To minimize the errors among the subjects and electrode placement, iEMG of each subject was normalized by the 4th-min value and expressed in arbitrary unit (AU) since observation of the data revealed that iEMG at 4th min was the lowest in most of the subjects during exercise above VT.

Statistical analysis was performed by Student's paired t-test and regression analysis. \( P < 0.05 \) was considered to be significant. The values are presented by mean(SE).

RESULTS

\( \dot{V}O_2 \)max and VT of the subjects were 3.42 (0.35) l min\(^{-1}\) and 2.18 (0.41) l min\(^{-1}\), respectively. VT was 63.7 % of \( \dot{V}O_2 \)max on average. Work rates below and above VT, and the results of each test are compared in Table and Figure 1. The difference in work rate between the tests were around 40 W.

\( \dot{V}O_2 \) reached steady value in 4min during below VT test, while slow increase was observed after 4min during above VT test. iEMG decreased for the initial 4 min in both tests, and it increased thereafter to 106.0 % in above VT test, while it did not change (98.6%) in below VT test.

Correlation of \( \dot{V}O_2 \) and iEMG after 4 min of grouped data showed significant (\( P < 0.01 \)) linear relationship although the correlation coefficient (\( r = 0.53 \)) was not so high (Figure 2).
Table  Mean (SE) values of work rate below and above VT tests, and $\dot{V}O_2$, iEMG at 7th min of each test. % of $\dot{V}O_2$ max represents the mean (SE) values of [$\dot{V}O_2$ at 7 min divided by $\dot{V}O_2$ max of each subject times 100].

<table>
<thead>
<tr>
<th>below VT</th>
<th>mean</th>
<th>SE</th>
<th>above VT</th>
</tr>
</thead>
<tbody>
<tr>
<td>Work Rate (W)</td>
<td>121.1</td>
<td>8.9</td>
<td>163.0</td>
</tr>
<tr>
<td>$\dot{V}O_2$ at 7 min (1·min⁻¹)</td>
<td>1.92</td>
<td>0.16</td>
<td>2.64</td>
</tr>
<tr>
<td>% of $\dot{V}O_2_{max}$ (%)</td>
<td>56.82</td>
<td>5.93</td>
<td>77.54</td>
</tr>
<tr>
<td>iEMG at 7 min (AU)</td>
<td>106</td>
<td>1.7</td>
<td>98.6</td>
</tr>
</tbody>
</table>

Fig. 1 Mean (SE) values of $\dot{V}O_2$ (upper) and iEMG (lower) during below VT (○) and above VT (●) tests. iEMG is normalized by the individual 4th-min value of each test, and the values of the initial minute are out of the range. In below VT test, there were no significant (p > 0.05) differences in both $\dot{V}O_2$ and iEMG after 4 min as compared with 4th min value. In above VT test, $\dot{V}O_2$ on and after 5.6 min were significantly higher (p < 0.05) than the 4th-min value, and iEMG on and after 4.3 min were significantly higher (p < 0.05) than the 4th-min value.

Fig. 2 Correlation between $\dot{V}O_2$ and iEMG after 4 min in above VT test of all the subjects. iEMG is normalized by the individual 4th-min value. Solid line represents the regression line. $\dot{V}O_2$ and iEMG are significantly correlated ($r = 0.53$, $p < 0.01$).

Fig. 3 Mean (SE) values of $\dot{V}O_2$/iEMG during below VT (○) and above VT (●) tests. $\dot{V}O_2$ and iEMG are normalized by the individual 4th-min value of each test. $\dot{V}O_2$/iEMG = 1 represents the constant ratio of $\dot{V}O_2$ to iEMG at 4th min. In both tests, there were no differences between the values after 4 min and 4th-min value.

In order to examine the coupling of $\dot{V}O_2$ with iEMG, $\dot{V}O_2$ were normalized by 4th min and divided by iEMG, which could virtually represent the oxygen equivalent for the neuromuscular activity (Fig-
ure 3). $\dot{V}O_2/iEMG$ after 4 min were not different between the tests, and kept constant in both tests indicating $\dot{V}O_2$ after 4 min are closely coupled with iEMG.

**DISCUSSION**

Previous studies (Roston et al., 1987; Henson et al., 1989) have observed no increase in $\dot{V}O_2$ after 3rd min when the exercise intensity is below VT. In this study, however, 3 min was not long enough to achieve steady value. The difference in exercise intensity and in the condition before the exercise could be responsible for this discrepancy. The exercise intensity employed in the present study was just 10% below VT of each subject and exercise started abruptly from resting condition instead of unloaded cycling. The exercise intensity very close to VT and the lack of warm-up may have slowed the response of $\dot{V}O_2$.

When the work intensity is high enough to lead to fatigue, iEMG is known to increase with time, which could be utilized for the evaluation of physical working capacity (deVries et al., 1982; Matsumoto et al., 1991). Although this was the case after 4 min in above VT test, iEMG dramatically decreased (about 7%) for the initial 3 to 4 minutes in both tests (Figure 1). The increase in the muscle temperature during the initial several minutes of exercise (Asmussen and Boje, 1945; Saltin et al., 1968) and its effect on the EMG signal (Petrofsky et al., 1979) might explain the decrease in iEMG. However, considering the results of those studies, that the only small decrease in iEMG (4%) was observed by 5°C increase in muscle temperature (Petrofsky et al., 1979), and that the increase in muscle temperature was less than 2°C in the exercise periods of less than 5 min (Asmussen and Boje, 1945; Saltin et al., 1968), the large decrease of iEMG in the present study could not be fully explained. In fact, iEMG of the initial minute increased with time in the present study (data not shown). One of the possible reasons for the decrease in iEMG except for the muscle temperature change might be that at the onset of heavy exercise, the larger MUs are recruited for the initial several minutes when oxygen delivery is rather limited, and as $\dot{V}O_2$ increases the smaller MUs are recruited in turn. This is based on the hypothesis that the MU recruitment is dependent not only on the level of force developed, but on the oxygen availability at the working muscle.

Although the increased $\dot{V}O_2$ may predominantly reflect the increase in leg $\dot{V}O_2$ (Poole et al., 1991), the process of increased $\dot{V}O_2$ utilization in the legs is unclear. Increased muscle temperature could enhance the increased leg $\dot{V}O_2$ by $Q_12$ effect (Hagberg et al., 1978), but it merely facilitates the extraction of $O_2$. Increased leg $\dot{V}O_2$ should represent the increased $O_2$ demand or decreased efficiency of the exercising muscle. $O_2$ required for 1 W of WR ($\dot{V}O_2$/WR) at 4th and 7th min are presented in Figure 4. $\dot{V}O_2$/WR at 4th min of both tests and at 7th min of below VT test were not different. However, $\dot{V}O_2$/WR at 7th min of above VT test was significantly higher ($p < 0.01$) than the 4th-min value in above VT test and both values in below VT test.

**Fig. 4** Mean (SE) values of $\dot{V}O_2$/WR at 4th min and 7 th min in below VT and above VT tests. $\dot{V}O_2$/WR at 7th min in above VT test was significantly higher ($p < 0.01$) than the 4th-min value in above VT test and both values in below VT test.

In the present study, the decreased efficiency, or increased $O_2$ demand during constant power output after 4th min during above VT test was coupled.
with the increased iEMG (Figure 3). Since increased iEMG represents changes in MU recruitment and/or MU firing frequency, the increased $\dot{V}O_2$ may be explained by the progressive recruitment of additional motor units (MUs) of fast twitch fibers for the compensation of the reduced power output by the fatigued MUs.

During heavy exercise, the decreased pH as a result of lactate accumulation may interfere with the excitation-contraction coupling by affecting Ca$^{2+}$ binding to troponin and the affinity of sarcoplasmic reticulum for Ca$^{2+}$ with a subsequent deficit in the developed force (Fuchs et al., 1970; Nakamaru and Schwartz, 1972; Fitts and Holloszy, 1976). Also, Vollestad et al (1988) suggested the impairment of excitation-contraction coupling during fatiguing process under small changes in the metabolic state. To maintain the constant power output under the impaired excitation-contraction coupling, more energy is needed for the recruitment of fatigued MUs and/or for the progressive recruitment of additional MUs. According to the well-known "size principle" (Henneman et al., 1965), non-recruited MUs should be of larger size, which necessarily requires more energy for the recruitment. As a consequence, more type II fibers are progressively recruited as exercise proceeds (Vollestad et al., 1984). Furthermore, there is a good evidence to support that the fast-twitch fibers are less efficient in terms of energy cost (Crow and Kushmerick 1982; Katz et al. 1986).

From these it is suggested that the neuromuscular activity during heavy exercise increases with time as a result of progressive recruitment of fatigued or larger MUs innervating fast-twitch fibers, which needs more energy and $\dot{V}O_2$. The finding that the increased iEMG is coupled with the increased $\dot{V}O_2$ after 4th min (Figure 3) is in consistent with these consideration.

In conclusion, this study demonstrated the coupling of iEMG and $\dot{V}O_2$ during heavy exercise above VT, which suggests that the slow increase in $\dot{V}O_2$ may be related to the recruitment pattern of motor units.

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(Received March 5, 1992)