Muscle use during dynamic knee extension: implication for perfusion and metabolism

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Ray, Chester A., and Gary A. Dudley. Muscle use during dynamic knee extension: implication for perfusion and metabolism. J. Appl. Physiol. 85(3): 1194–1197, 1998.—Dynamic one-legged knee extension (DKE) is commonly used to examine physiological responses to “aerobic” exercise. Muscle blood flow during DKE is often expressed relative to quadriceps femoris muscle mass irrespective of work rate. This is contrary to the notion that increased force is achieved by recruitment in large muscles. The purpose of this study, therefore, was to determine muscle use during DKE. Six subjects had magnetic resonance images taken of their quadriceps femoris before and after 4 min of DKE at 20 and 40 W. Muscle use was determined by shifts in T2. The cross-sectional area of quadriceps femoris that had an elevated T2 increased 11.4 ± 4% after 20- and 40-W DKE, respectively. Volume of quadriceps femoris increased 11.4 ± 0.2% (P = 0.006), from 2,230 ± 233 cm3 before exercise to 2,473 ± 232 cm3 after 40-W DKE. Extrapolation of these data indicates that 1.301 ± 111 cm3 of quadriceps femoris were engaged during 20-W DKE compared with 2,292 ± 154 cm3 during 40-W DKE. By using muscle blood flow data for submaximal DKE at 20 W (P. Andersen and B. Saltin, J. Physiol. (Lond.) 366: 233–249, 1985; and L. B. Rowell, B. Saltin, B. Kiers, and N. J. Christensen, Am. J. Physiol. 251 (Heart Circ. Physiol. 20): H1038–H1044, 1986) and estimating muscle use in those studies from our data (total muscle mass × 0.54, extrapolated blood flow to active muscle (263 and 278 ml·min⁻¹·100 g⁻¹, respectively) is comparable to that obtained during peak aerobic DKE when expressed relative to total muscle mass (243 and 250 ml·min⁻¹·100 g⁻¹, respectively). These findings indicate that increased power during aerobic DKE is achieved by recruitment. Additionally, they suggest that blood flow to the active quadriceps femoris muscle does not increase with increases in submaximal work rate but instead is maximal to support aerobic metabolism. Thus increases in muscle blood flow are directed to newly recruited muscle, not to increased perfusion of muscle already engaged.

The mechanism(s) by which humans meet the energy demand of “aerobic” exercise have been long examined. Once it became apparent that oxygen delivery and utilization were involved, studies were undertaken to assess their relative roles. Animal muscle preparations have routinely been used to study peripheral responses to increased contractile activity. Development of a comparable technique in humans proved fruitful when Andersen and Saltin (2) presented their dynamic knee extension (DKE) model. A variety of DKE studies have been conducted, and several have focused on perfusion and metabolism during aerobic exercise (2, 6, 9). The consensus of these studies is that blood flow per unit muscle mass increases with power output. As noted by Armstrong et al. (3), uncertainty about how much muscle is used during exercise complicates such estimates. In this regard, magnetic resonance (MR) imaging has been increasingly employed to assess muscle use during exercise (4). Therefore, the purpose of this study was to determine muscle use during DKE as assessed by exercise-induced contrast shift in MR images. It was hypothesized that muscle use would increase with power output. Additionally, MR imaging during DKE may help elucidate the relationship between blood flow and metabolism per unit of active muscle mass.

METHODS

Five men and one woman [ages, 30 ± 2 (SE) yr; weight, 70 ± 3 kg], who were recreationally active, participated in this study. The study was approved by The University of Georgia Institutional Review Board, and each subject provided written consent.

Subjects were familiarized to DKE four to five times over 1 wk as described previously (8). After 24 h of rest, each performed DKE for 4 min at 20 and at 40 W, in that order, with 1 h of rest between bouts. MR images were taken of both thighs before DKE and immediately (−1–2 min) after each bout.

MR image acquisition and analyses were done as described previously (1). Transaxial T2 weighted images of the thigh, 1 cm thick and 1 cm apart (repetition time, 2,000 ms; echo times, 30 and 60 ms; 256 × 256 matrix; 1 pulse sequence repeated per acquisition; 40-cm field of view), were collected from the knee joint to the head of the femur by using a 1.5-Tesla superconducting magnet (General Electric, Milwau-kee, WI). MR images were transferred to a computer for calculation of quadriceps femoris cross-sectional area (CSA) and the CSA of quadriceps femoris that showed an elevated T2, thereby indicating recent contractile activity. A modified version of the public domain NIH Image program (written by Wayne Rasband at the US National Institutes of Health, and available from the Internet by anonymous ftp from zippy.nimh.nih.gov or on floppy disk from National Technical Information Service, 5285 Port Royal Rd., Springfield, VA 22161) was used to calculate CSA.
22161) was used for these analyses. Briefly, after spatial calibration, the outline of quadriceps femoris was traced in serial images (17–19 per subject) to determine CSA. Subsequently, shifts in $T_2$ were determined. In preexercise images, pixels with a $T_2$ between 20 and 35 ms were assumed to represent resting muscle. Pixels with a $T_2$ greater than the mean $+1\sigma$ of quadriceps femoris from the preexercise image represented active muscle in matched pre- and postexercise images. The relative CSA of active muscle was calculated by averaging values over images, $\Sigma \text{[active muscle CSA/(active + nonactive muscle CSA)]}$ $\times$ 100/number of images. Total volume of quadriceps was estimated by summing CSA values for each 1-cm slice and doubling this to account for the 1-cm space between slices. Active volume of quadriceps femoris was estimated by multiplying total volume by the relative CSA of active muscle.

Dependent variables were analyzed by a one-way, repeated-measures analysis of variance. All variables are expressed as means $\pm$ SE.

RESULTS

DKE at 20 and 40 W evoked MR image contrast shift (Fig. 1). On average, 16 $\pm$ 1% of the CSA of quadriceps femoris had an elevated $T_2$ before DKE (Fig. 2). This increased to 54 $\pm$ 5 and 94 $\pm$ 4% after 20 and 40 W DKE, respectively ($P = 0.0001$; Fig. 2). Typical of this marked use of quadriceps femoris, its volume increased 11.4 $\pm$ 0.2% ($P = 0.006$), from 2,230 $\pm$ 233 cm$^3$ before exercise to 2,473 $\pm$ 232 cm$^3$ after 40-W DKE (Fig. 2). Extrapolation of these data indicates 1,301 $\pm$ 111 cm$^3$ of quadriceps femoris was engaged during 20-W and 2,292 $\pm$ 154 cm$^3$ was engaged during 40-W DKE (Fig. 2).

DISCUSSION

When we began this study, we expected muscle mass use to increase with power output on the basis of results from muscle biopsy, electromyography, and MR imaging studies (4, 5). Almost 100% of quadriceps femoris was engaged in nearly maximal aerobic DKE, and about one-half was engaged at 50% of this work rate. These results are corroborated by data reported for cycling exercise, which evoked glycogen depletion in about one-half of and all of the fibers examined in biopsies of vastus lateralis at work rates of 50 and 100% of maximal aerobic power, respectively (5).

Andersen and Saltin (2), Kim et al. (6), and Rowell et al. (9) using DKE have reported similar muscle blood flow responses to incremental aerobic exercise. Considering our data for muscle use and those of Andersen and Saltin (2) and Rowell et al. (9) for quadriceps femoris blood flow (142 and 150 ml·min$^{-1}$·100 g$^{-1}$, respectively) and mass (2.3 and 2.2 kg, respectively), it can be estimated that perfusion of active muscle for DKE at 20 W would be 263 and 278 ml·min$^{-1}$·100 g$^{-1}$ (Fig. 3). Similar values are obtained if 94% of quadriceps femoris was used for 40 W DKE. These estimated blood flows to active muscle for DKE at 20 and 40 W are comparable to those observed in the earlier studies (2, 9) during peak aerobic exercise (40–55 W), when perfusion was normalized to quadriceps femoris mass.
reduces force development, it allows full expression of a much lower rate (5). We speculate that, although this voluntary effort is achieved by recruiting motor units at generally evoked at a high frequency (e.g., 50 Hz), incremental muscle use and muscle blood flow. Results provide strong evidence for the tight coupling of increases in the mass of stimulated muscle (1), these shown that electromyostimulation would result in graded rate, oxygen uptake, and perfusion. Because it has been constant frequency evoked linear increases in work rate and is comparable to that reported for maximal aerobic DKE, when close to 100% of the muscle is active (Fig. 3). It should be noted that the estimated total muscle mass (2.2 and 2.3 kg) of the knee extensors used in the previous studies (2, 6, 9) is similar to the muscle mass found in the present study.

Does it seem reasonable that active muscle would be perfused at a rate that would support its maximal oxygen consumption during submaximal DKE? In addition, should this perfusion be independent of work rate? Neither of these assumptions is incongruent with our understanding of muscle recruitment and metabolism. Increments in power are achieved by recruiting new muscle, not by increasing the frequency of activation of already active motor units (5). This necessitates that increments in work rate are achieved by recruiting new muscle at a given frequency, as indicated by our findings and by Green and Patla (5). Recent work by Kim et al. (6), using DKE and electromyostimulation, showed that ramp increases in stimulation amplitude and with constant frequency evoked linear increases in work rate, oxygen uptake, and perfusion. Because it has been shown that electromyostimulation would result in graded increases in the mass of stimulated muscle (1), these results provide strong evidence for the tight coupling of incremental muscle use and muscle blood flow.

Unlike electromyostimulation, in which activation is generally evoked at a high frequency (e.g., 50 Hz), voluntary effort is achieved by recruiting motor units at a much lower rate (5). We speculate that, although this reduces force development, it allows full expression of the aerobic energy supply of the active fibers to meet the demands of contraction. Accordingly, perfusion is maximal to support aerobic metabolism. This is why our estimated blood flows to active muscle for submaximal DKE are comparable with those of Saltin’s group for DKE at peak aerobic power (2, 9). Approximately 100% of quadriceps femoris would be used at peak aerobic power for DKE. Thus dividing muscle blood flow by muscle mass should reflect maximal perfusion to support peak aerobic power. We estimate comparable blood flows per unit active muscle at submaximal work rates.

Limitations. Increases in power output by the muscle can be generated by recruitment of more muscle and/or by increased frequency of activation of already active fibers. At present, MR images do not provide a measurement of activation frequency. Thus we cannot be sure of the possible extent that changes in frequency of activation of the muscle played in power production. The dose relationship between muscle mass recruitment and power output suggests that alterations in frequency of activation were not significant. Additionally, the new concept that increases in skeletal muscle blood flow are directed to newly recruited muscle, not to increased perfusion to muscle already engaged, applies to human voluntary dynamic exercise of a large muscle mass at relatively high work intensities. It is likely that different exercise paradigm may produce other results (e.g., isometric contractions). Similarly, it is obvious from in situ and in vitro animal models of exercise that increases in blood flow can occur without increases in muscle recruitment (7). In these models, nearly all of the muscle is simultaneously recruited during stimulation protocols. However, these muscle contractions do not represent the normal pattern of muscle activation in humans. Finally, the results of this study are limited to quadriceps femoris and do not necessarily reflect activation patterns of other muscles in humans.

In summary, the present study clearly shows a strong relation between muscle use and work rate during aerobic DKE. The results, when considered in light of muscle biopsy and electromyographic data, suggest that incremental increases in aerobic work rate are achieved by recruiting “new” muscle that is designed to perform repetitive, low-power output activity. The frequency of activation of this muscle is not maximal but is set to minimize ATP cost per unit force while dictating full expression of aerobic energy supply. Accordingly, this is why we estimate blood flow to active muscle during submaximal DKE to be comparable to that found by Saltin’s group for peak aerobic DKE when essentially all of quadriceps femoris would be engaged in the activity.

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