Lower extremity muscle activation during horizontal and uphill running

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Sloniger, Mark A., Kirk J. Cureton, Barry M. Prior, and Ellen M. Evans. Lower extremity muscle activation during horizontal and uphill running. J. Appl. Physiol. 83(6): 2073–2079, 1997.—To provide more comprehensive information on the extent and pattern of muscle activation during running, we determined lower extremity muscle activation by using exercise-induced contrast shifts in magnetic resonance (MR) images during horizontal and uphill high-intensity (115% of peak oxygen uptake) running to exhaustion (2.0–3.9 min) in 12 young women. The mean percentage of muscle volume activated in the right lower extremity was significantly (P < 0.05) greater during uphill (73 ± 7%) than during horizontal (67 ± 8%) running. The percentage of 13 individual muscles or groups activated varied from 41 to 90% during horizontal running and from 44 to 83% during uphill running. During horizontal running, the muscles or groups most activated were the adductors (90 ± 5%), semitendinosus (86 ± 13%), gracilis (76 ± 20%), biceps femoris (76 ± 12%), and semimembranosus (75 ± 12%). During uphill running, the muscles most activated were the adductors (83 ± 8%), biceps femoris (79 ± 7%), gluteal group (79 ± 11%), gastrocnemius (76 ± 15%), and vastus group (75 ± 13%). Compared with horizontal running, uphill running required considerably greater activation of the vastus group (23%) and soleus (14%) and less activation of the rectus femoris (29%), gracilis (18%), and semitendinosus (17%). We conclude that during high-intensity horizontal and uphill running to exhaustion, lasting 2–3 min, muscles of the lower extremity are not maximally activated, suggesting there is a limit to the extent to which additional muscle mass recruitment can be utilized to meet the demand for force and energy. Greater total muscle activation during exhaustive uphill than during horizontal running is achieved through an altered pattern of muscle activation that involves increased use of some muscles and less use of others.

exercise; magnetic resonance imaging; skeletal muscle function

ELECTROMYOGRAPHY (EMG) (3, 4, 13, 21, 25–27, 37) and muscle glycogen depletion (9–11) have been used extensively to determine lower extremity muscle activation during running. However, the restricted sampling area and invasive nature of these techniques limit their usefulness, and a quantitative assessment of the muscle activated is not possible.

Recently, exercise-induced contrast shifts in proton magnetic resonance (MR) images have been used to quantify muscle use during exercise (1, 2, 14, 16, 23, 33, 36, 42, 43). MR images provide unparalleled visualization of muscle and associated tissues. More importantly, muscles actively involved in exercise show increased signal intensity and “light up” in MR images, permitting active and inactive muscle to be distinguished (15). Increased signal intensity results primarily from increases in skeletal muscle proton spin-spin relaxation times (T2) and is most evident in T2-weighted MR images (15). The exact cause of the exercise-induced increase in T2 is unknown, but it is hypothesized to reflect complex changes in the fractions of extracellular and bound and unbound intracellular water, resulting from muscle recruitment and metabolic activity (5, 6, 14, 16). Although application of this new technology to study muscle activation patterns has been limited, in part because there still is no agreement on the mechanism underlying and on the physiological meaning of exercise-induced T2 increases, considerable data indicate that the method provides valuable practical information about muscle use. The magnitude of exercise-induced elevations in T2 are directly related to EMG activity, force and rate of work (1, 5, 14, 23), and estimates of the cross-sectional area of muscle showing increased T2 increase in direct proportion to force and exercise intensity (2, 33). By quantifying the amount of muscle showing a T2 increase, it is possible to estimate the portion of individual muscles activated (2, 7, 33).

We recently reported that muscle activation in the entire lower extremity was greater during exhaustive uphill vs. horizontal running (39). However, the extent of individual muscle activation during exhaustive horizontal and uphill running has not been reported, and the contribution of individual muscles to the greater overall muscle activation during uphill running is unknown. Therefore, the specific aims of the present study were 1) to determine the extent of individual muscle or group activation during exhaustive horizontal and uphill running and 2) to assess their contribution to the greater overall muscle activation during uphill vs. horizontal running. Exhaustive running was selected because 1) it provided a common physiological condition under which horizontal and uphill running could be compared; 2) the highest level of muscle activation during dynamic, ballistic, low-resistance movement like running is unknown; and 3) to understand the basis for differences in metabolic responses, it is important to know whether muscle activation is greater during exhaustive uphill vs. horizontal running (29, 39). We hypothesized that because running involves dynamic, ballistic, low-resistance movements, that individual muscles in the lower extremity would not be fully activated and that extent of activation would vary depending on function. Uphill running was expected to show increased activation of the hip and knee extensors, and plantar flexors.

METHODS

Subjects. The subjects were 12 young women involved in recreational running for conditioning at the time of the study. Mean (± SD) physical characteristics of the subjects were age (23.8 ± 2.7 yr), mass (59.7 ± 8.2 kg), %fat (20.0 ± 4.9%), and
peak oxygen uptake ($V_\text{O}2_{\text{peak}}$; 2.91 ± 0.52 l/min or 48.6 ± 5.2 ml·kg$^{-1}$·min$^{-1}$). After an explanation of the time commitment and procedures involved in the study, each subject provided written consent and completed medical history and training background questionnaires. The study was approved by the Institutional Review Board.

Testing procedures. Subjects completed five test sessions on separate days. Two of these sessions were used to determine $V_\text{O}2_{\text{peak}}$ and muscle activation during horizontal running and two were used to obtain the same measurements during uphill (10% grade) running. The order of test sessions was balanced. During the first test session, subjects completed a discontinuous, speed-incremented treadmill test to exhaustion under one of the two experimental conditions to determine $V_\text{O}2_{\text{peak}}$. Subjects completed a series of 6-min bouts of treadmill running in which treadmill speed was increased until the subject could not finish a 6-min bout. Treadmill speeds ranged from 7.9 to 17.1 km/h and from 5.3 to 9.8 km/h for the horizontal and uphill conditions, respectively. During the bouts of running, metabolic measurements were obtained by using a computer-automated system. The volume of inspired air was measured by a Rayfield (Rayfield Equipment, Waitsfield, VT) model 9200 mechanical flowmeter. The concentrations of carbon dioxide and oxygen in the expired air were measured by Ametek CD-3A and S-A/I electronic gas analyzers. Standard gases analyzed by the micro-Scholander chemical gas analyzer were used to calibrate the analyzers before the test. One-minute averages of oxygen uptake ($V_\text{O}2$) and other metabolic measurements were calculated every 15 s by using modified Vista (Rayfield Equipment) software. Maximal heart rate (HR) was determined with a Polar Vantage XL HR monitor. The highest $V_\text{O}2$ obtained on the test was operationally defined as the $V_\text{O}2_{\text{peak}}$ if there was a plateau in heart rate (HR) was determined with a Polar Vantage XL HR monitor. The highest $V_\text{O}2$ obtained on the test was operationally defined as the $V_\text{O}2_{\text{peak}}$ if there was a plateau in HR between the last two stages of the test, as assessed by an increase in $V_\text{O}2$ of <2.1 ml·kg$^{-1}$·min$^{-1}$ (40), or if peak HR was at least 90% of age-predicted maximum and respiratory exchange ratio was >1.0.

The second test session under each condition involved collection of MR images by using a 1.5-T superconducting magnet (General Electric, Milwaukee, WI). These data were used to assess right lower extremity exercise-induced contrast shifts in MR images. After a 10-min period of rest, preexercise MR images were obtained of the right lower extremity muscle volume and T2 at rest, measured on 3 separate days, were 0.90 and 0.47, respectively; the within-subjects SD values of replicate measurements were 53 cm$^3$ for muscle volume and 0.49 ms for T2. The reliability of T2 was low from one-way analysis of variance) for the right lower extremity muscle volume and T2 at rest, measured on 3 separate days, were 0.90 and 0.47, respectively; the within-subjects SD values of replicate measurements were 53 cm$^3$ for muscle volume and 0.49 ms for T2. The reliability of T2 was low because the range of values was extremely small (28.5–30.7 ms). There were no significant differences among the three means (29.7 ± 0.6, 29.7 ± 0.4, and 29.6 ± 0.5 ms). Three separate measurements of the cross-sectional area of the same muscle region of interest at rest were obtained for 30 individual muscles. Based on these data, the single-trial reliability for repeated determinations of a muscle cross-sectional area was 0.99. The within-subjects SD of replicate measurements was 0.53 cm$^2$.

Running velocity ranged from 8.9 to 11.9 km/h for uphill and 14.0–19.0 km/h for horizontal running. Immediately after exercise, MR images of the right lower extremity were once again obtained after procedures used at rest. For each individual, the time between termination of exercise and completion of the postexercise image attainment was the same from one test session to the next and ranged from 10.9 to 12.3 min.

MR images were analyzed by using a modified version of the public-domain National Institutes of Health (NIH) Image program (written by Wayne Rasband and available from the internet at http://zippy.nimh.nih.gov or on floppy disk from NTIS, 5285 Port Royal Rd. Springfield, VA 22161, part no. PB93–504868). For each image, regions of interest were defined by tracing each muscle or muscle group in the cross section. The 13 muscle regions of interest were iliopsoas, gluteus maximus-medius-minimus, sartorius, rectus femoris, vastus lateralis-medialis-intermedius, adductor magnus-longus-brevis, gracilis, biceps femoris, semitendinosus, semimembranosus, gastrocnemius, soleus, and tibialis anterior plus all remaining calf musculature. After spatial calibration, muscle cross-sectional area and transverse relaxation times T2 were determined for each region of interest. A T2 (½ of the signal decay time) was calculated for each pixel within a region of interest by using the formula $T2 = (t_b - t_a)$ln($\rho_b/\rho_a$), where $t_a$ and $t_b$ are spin-echo collection times and $\rho_a$ and $\rho_b$ are signal levels. Pixels with T2 values between 20 and 35 ms were used to represent muscle at rest, based on reports in the literature that resting T2 of muscles is <28 ms with a SD of =3 ms (2). Mean T2 values at rest were 29.7 ± 0.6 and 29.7 ± 0.4 ms for horizontal and uphill running, respectively. Pixels with T2 values out of this range were considered nonmuscle. The muscle cross-sectional area was later subtracted from the postexercise cross-sectional areas for the same test session. In the postexercise images, active muscle and total muscle cross-sectional areas for each region of interest were determined. Pixels with T2 greater than the resting mean plus 1 SD were assumed to represent muscle that had recently performed contractile activity (2, 33).

Active and total muscle volumes were calculated by summing the products of the cross-sectional areas and the thickness of each section (10-mm thickness plus 20-mm space) for each region of interest (18). The active muscle volume was divided by the postexercise muscle volume to obtain the percentage of muscle volume that was active. The volumes for the 13 regions of interest were summed, and the same calculation was made for the entire lower extremity. Postexercise muscle volumes for the lower extremity were not different (P > 0.05) between horizontal and uphill conditions.

The single-trial reliabilities (intraclass correlation coefficient from one-way analysis of variance) for the right lower extremity muscle volume and T2 at rest, measured on 3 separate days, were 0.90 and 0.47, respectively; the within-subjects SD values of replicate measurements were 5.3 cm$^3$ for volume and 0.49 ms for T2. The reliability of T2 was low because the range of values was extremely small (28.5–30.7 ms). There were no significant differences among the three means (29.7 ± 0.6, 29.7 ± 0.4, and 29.6 ± 0.5 ms). Three separate measurements of the cross-sectional area of the same muscle region of interest at rest were obtained for 30 individual muscles. Based on these data, the single-trial reliability for repeated determinations of a muscle cross-sectional area was 0.99. The within-subjects SD of replicate measurements was 0.53 cm$^2$.

At the final test session, a whole body scan was obtained for each subject by using dual-energy X-ray absorptiometry
(Hologic QDR 1000-W, software version 5.5) to determine total percent body fat.

Statistical analysis. A t-test for dependent samples was used to determine the significance of differences between dependent variables measured during uphill and horizontal running. A significance level of \( P < 0.05 \) was used for the total set of 14 comparisons (total lower extremity and 13 muscle regions of interest), with the significance level for individual comparisons \( (P \leq 0.004) \) adjusted by using the Bonferroni technique.

RESULTS

During horizontal running, the percentage of the volume of individual muscles or groups activated varied from 41 to 90% (Fig. 1). Those most activated were the adductors (90 ± 5%), semitendinosus (86 ± 13%), gracilis (76 ± 20%), biceps femoris (76 ± 12%), and semimembranosus (75 ± 12%). The least activated were the soleus (41 ± 18%), vastus group (53 ± 11%), sartorius (53 ± 22%), and iliopsoas (59 ± 15%).

Mean T2 values, which reflect the intensity of muscle use, ranged from 32.1 to 37.2 ms during horizontal running (Fig. 2). The muscles showing the most intense use were the gluteal group (37.3 ± 1.4 ms), adductor group (36.9 ± 1.2 ms), semitendinosus (36.9 ± 1.8 ms), and semimembranosus (35.0 ± 1.0 ms). The least intensely used were the iliopsoas (32.1 ± 1.1), rectus femoris (32.2 ± 1.9), and vastus group (32.8 ± 1.1). Mean T2 and the percentage of muscle volume activated during horizontal running were only moderately correlated \((r = 0.63)\) and, therefore, provided somewhat different information.

During uphill running, the percentage of individual muscle volume activated ranged from 44 to 83% (Fig. 1). The muscles most activated were the adductors (83 ± 8%), biceps femoris (79 ± 7%), gluteal group (79 ± 11%), gastrocnemius (76 ± 15%), and vastus group (76 ± 14%). The least activated muscles were the rectus femoris (44 ± 20%), soleus (55 ± 14%), tibialis anterior (58 ± 16%), and gracilis (59 ± 16%).

Mean T2 values varied from 30.1 to 37.9 ms during uphill running. The muscles with the most intense use were the gluteal group (37.9 ± 3.5 ms), adductors (36.2 ± 1.4 ms), biceps femoris (35.8 ± 2.3 ms), gastrocnemius (35.6 ± 2.3 ms), and semimembranosus (35.5 ± 2.3 ms). The least intensely used muscle was the rectus femoris (30.1 ± 2.0 ms). Under the uphill condition, mean T2 and the percentage activation results for the 13 muscle regions of interest were quite highly correlated \((r = 0.86)\).

As reported previously (39), the mean percentage of the right lower extremity muscle volume activated was significantly \((P < 0.004)\) greater during uphill (73 ± 7%) compared with horizontal (67 ± 8%) running. The mean percentage of muscle volume activated increased significantly \((P \leq 0.004)\) from horizontal to uphill running for the vastus group (23%) and for soleus (14%) and decreased significantly \((P \leq 0.004)\) for the rectus femoris (29%), gracilis (18%), and semitendinosus (17%).

Mean lower extremity T2 values were not significantly \((P < 0.004)\) different between horizontal (34.0 ± 0.9 ms) and uphill (34.2 ± 1.0 ms) running. Mean T2 increased significantly \((P \leq 0.004)\) from horizontal to uphill running for the vastus group (1.6 ms) and
DISCUSSION

Knowledge of muscle use during physical activity is important in understanding the basis of movement; in diagnosing disease; in normalizing metabolic and cardiovascular responses during exercise; and in understanding the effects of training, muscle disuse, and rehabilitative treatments such as electromyostimulation. EMG has provided extensive information on the temporal pattern and intensity of individual muscle activation during physical activities, but this technique is limited because only small areas of selected muscles can be studied, and EMG signals are affected by a host of factors that can make interpretation of data difficult (3). Insight into muscle use during physical activity also has been obtained from studies measuring glycogen depletion in different fiber types (9–11). However, muscle biopsies are usually obtained only from a small area of a one or a few muscles and, therefore, do not provide comprehensive information on the amount of muscle activated and the pattern of activation in different muscles.

We used the powerful technique of MR imaging to quantify the activation of individual muscles in the lower extremity during exhaustive horizontal and uphill running. MR imaging provides unparalleled visualization of the muscle groups and most individual muscles in a given limb segment. Exercise-induced contrast shifts in T2-weighted MR images reflect muscle recruitment and intensity of use (1, 14, 15, 23, 31, 38, 43). Furthermore, the absolute cross-sectional area and volume of muscle that show the contrast shift (2, 33, 39) can be quantified, providing unique information on the proportion of available muscle that is activated, which is not available through other approaches. This method has been used to quantify muscle recruitment during acute voluntary physical activity (2, 7, 32, 38) and electrical stimulation of muscle (2) and consequent to muscle unweighting (35) and training (8, 33). Our interests were in quantifying individual lower extremity muscle activation during exhaustive running to determine whether muscles are maximally activated at the point of fatigue and in determining the contribution of individual muscles to the greater overall muscle activation during uphill compared with horizontal running to fatigue.

The primary finding was that muscles of the lower extremity were not uniformly and maximally activated during exhaustive horizontal and uphill running. The percentage of the volume of 13 individual muscles or muscle groups activated varied from 41 to 90% during horizontal running and from 44 to 83% during uphill running. Similarly, the intensity of muscle use as reflected by the T2 values for individual muscle regions of interest varied from 30 to 38 ms. Thus, even during exhaustive exercise in which the energy demand could not be sustained, some involved muscles were quite heavily used, whereas others were not. This is not surprising given the varying roles of different muscles in the lower extremity in producing force at various phases of the gait cycle during running (27). However, even muscles that were most heavily involved were not maximally activated during either horizontal or uphill running. Less than complete activation of involved muscle may reflect the ballistic, dynamic nature of movements during running and the fact that near-maximum levels of force are not needed. Furthermore, in a 2- to 3-min effort, the maximal rate of power output is less than during shorter efforts (28), which should result in less muscle mass activated, assuming muscle activation is proportional to power output. Failure to recruit all available muscle is consistent with the fact that in large muscle activity motor units rely primarily on recruitment and less on rate coding to modulate force (12). However, because the exercise was carried to the point of exhaustion, these data suggest that there is a limit to the extent to which additional muscle mass recruitment can be utilized to meet the demand for force and energy.

The incomplete activation of all available muscle is consistent with studies involving exhaustive, heavy-resistance exercise by using the same MR imaging technique. In these studies involving leg extension by electromyostimulation (2) or voluntary effort in the squat or neck movements (7, 32, 33), five sets of 10 muscle actions to exhaustion (100% maximal load) were accomplished by activating 70–85% of the involved muscle. As in the present study, the range of individual muscle activation varied from 40% or below to 90% or above. These studies involving heavy-resistance exercise are consistent with the concept that there may be a neural limitation to motor unit recruitment in some forms of exercise that prevents the full force potential of muscle from being utilized during voluntary contractions (12). Our data suggest that this phenomenon exists for exhaustive horizontal and uphill running of 2- to 3-min duration.

Our data seem to conflict with studies on cycling that have suggested that all fibers in some muscles are activated during supramaximal exercise to exhaustion. Glycogen depletion data on supramaximal cycling at approximately the same relative intensity [122% maximal VO₂ (VO₂max)] and duration as in the running in the present study have suggested that all type I and type II fibers in the lateral portion of the vastus lateralis are activated (41). However, at higher intensities resulting in exhaustion in 1 min (150% VO₂max) and 30 s (194% VO₂max), respectively, higher rates of glycogen depletion were observed, suggesting that muscle use was not maximal at the lower intensity and implying that increased frequency of stimulation must have accounted for the increased work output at higher intensities. However, differential activation of seven muscles involved in force production during incremental cycling, with the gluteus maximus showing the greatest relative activation at high intensities, has been found (see Ref. 19a). Thus the extent to which the data from lateral portion of the quadriceps can be used to represent muscle recruitment and metabolic changes in other
muscles of the lower extremity during cycling can be questioned. In addition, data from cycling cannot be generalized to running because of the marked differences in movement pattern.

EMG studies have provided considerable information on the phase of the gait cycle during which individual muscles are active during horizontal running (27), but quantitative information comparing the degree of activation of different muscles has not been possible. We have shown that during exhaustive horizontal running, the muscles with the highest percentage of their volume activated were the adductor group (90%), hamstrings [semimembranosus (86%), biceps femoris (76%), semitendinosus (75%)], gracilis (76%), rectus femoris (74%), gluteal group (72%), and gastrocnemius (68%). All of these muscles except the rectus femoris had relatively high T2 values (>34 ms), reflecting a high intensity of use. The gluteal group had the highest T2 (37 ms), indicating that the portions of this muscle group that were activated were used very intensely. Our findings supplement those from EMG studies by indicating that muscles involved in hip stabilization and adduction (adductors and gracilis), hip extension (gluteal and hamstrings), knee and hip flexion-extension (hamstrings, rectus femoris, and gastrocnemius), and plantar flexion (gastrocnemius) were the most intensely used during horizontal running.

We previously reported that the percentage of the lower extremity muscle volume activated was greater during uphill compared with horizontal running by 9% (39). The present study shows that not all of the lower extremity muscles were activated to a greater extent during this condition; instead, the greater overall muscle activation during uphill running was achieved through increased activation of some muscle groups (vastus and soleus) and less activation of others (rectus femoris, gracilis, and semitendinosus). It is interesting that the range of individual muscles/muscle group activation was less during uphill running (44–83%) than during horizontal running (41–90%), perhaps reflecting the slower, more restricted movements performed. T2 changes were similar to changes in the volume of muscle activated, as reflected by the relatively high correlation between the two measurements (r = 0.86) during uphill running.

We are aware of only one other study comparing lower extremity muscle utilization between horizontal and uphill running. Costill et al. (10) determined glycogen depletion of the vastus lateralis, gastrocnemius, and soleus muscles during horizontal and uphill running. Subjects completed 2-h bouts of horizontal and uphill (6% grade) treadmill running at 75% of mode-specific VO2max. Mean treadmill speeds were 8.3 and 13.8 km/h for uphill and horizontal conditions, respectively. They reported that muscle glycogen was depleted to a greater extent during uphill running for all three muscles evaluated. Glycogen depletion for the soleus and gastrocnemius increased 30% from horizontal to uphill running, whereas the increase for the vastus lateralis was approximately threefold. In the present study, the percentage of the muscle volume activated increased significantly from horizontal to uphill (10% grade) running for the vastus (43%) and soleus (35%) muscles/muscle groups, whereas the increase for the gastrocnemius (11%) was not significant (P > 0.004). The vastus lateralis was analyzed with the vastus medialis and vastus intermedius as one group (vastus); therefore, the change in activation for the vastus lateralis alone could not be distinguished. The results of the two studies are consistent in showing that activation of the soleus and quadriceps muscles increased with uphill running.

The interpretation of our values for the percentage activation of muscles depends in part on the validity of the criterion used to classify whether muscle is active. Adams et al. (2) first proposed that a T2 increase greater than the resting mean +1 SD be used as the criterion for classifying pixels of muscle active. Although arbitrary, this criterion has been used in a number of previous studies (2, 7, 33, 39), and its validity is supported by several observations. 1) The mean T2 of resting skeletal muscle is consistently 28–29 ms, with an SD of ~3 ms or less in various studies (2). Only a small amount of low-intensity exercise is needed to significantly increase T2 values (43). For example, Yue et al. (43) found that only five repetitions of elbow flexion-extension exercise at 25% maximal voluntary contraction or two repetitions at 80% maximal voluntary contraction were necessary to detect a statistically significant (3–4%) increase in T2. Moderate-to-heavy rates of work produce relative large increases in T2, averaging 7–35% (7, 15, 17, 35, 36, 43), and the magnitude of increase in T2 is independent of muscle size (7, 36). Furthermore, exercise does not alter the shape of the distribution of T2 values but simply shifts the distribution to higher values (35). Thus the T2 increase is a sensitive index of muscle activity. 2) Elevations in T2 within the range observed in the present study are directly related to EMG activity, force, and rate of work (1, 14, 23), and estimates of the cross-sectional area of muscle activated increase in direct proportion to force and exercise intensity (2, 33). Thus these indexes of muscle activity accurately reflect intensity of muscle use. 3) Estimates of the percentage of individual muscles activated by using this criterion are reasonable, ranging from ~25% to over 90% (2, 7, 32, 33). Use of a different T2 cut-off point as the criterion for “activated” muscle would obviously change the absolute values, but any large change would result in values that are implausible (35).

It is possible that the estimates of activated muscle are slight underestimates, because increases in T2 in some pixels may be too small to be considered active and some T2 increases that may have exceeded the criterion immediately after exercise may have dropped below the criterion because of the time required to complete the scans. The latter effect would be greater for muscle in the leg, because it was always scanned after the thigh and the time after exercise until the second scan was completed was longer than usual. However, the mean T2 for muscles in the leg were over 3 SDs above the criterion, indicating that there would be few pixels that
initially exceeded the criterion that were not counted as active because the T2 had fallen below the criterion during the first 10–12 min of recovery. Thus, whereas the absolute accuracy of the estimates of the percentage of muscle volume activated cannot be known for certain, large error is unlikely, and the comparisons of the relative activation of individual muscles or muscle groups during horizontal and uphill running should be valid.

The exact cellular mechanisms underlying the exercise-induced contrast shifts in transverse relaxation times (T2) of MR images are unknown (1, 23, 43). Because proton-weighted MR images are based on signals from hydrogen atoms and because the primary source of hydrogen in the human body is water, exercise-induced changes in muscle T2 have been hypothesized to be caused by movement of water into and among compartments in muscle (15). This issue is complex; multiple water fractions with different T2 values (extracellular water T2 = 196 ms, intracellular free water T2 = 40–45 ms, and intracellular bound water T2 = <16 ms) contribute to the T2 of skeletal muscle (20, 24), and all probably change with exercise. However, simple movement of water into the muscle does not fully explain T2 changes with exercise, because increased muscle cross-sectional area due to venous occlusion (14), head-down tilt (6), or external leg negative pressure (34) is associated with little, if any, increase in T2. The T2 change with lower body negative pressure is fundamentally different than that observed during exercise (34). Increased muscle perfusion also is an unlikely cause, because muscle T2 increases after exercise with vascular occlusion (15). These findings suggest that complex intracellular events are probably responsible for the exercise-induced T2 increase. Decreased pH and/or lactate accumulation after exercise may contribute to the T2 increase after exercise. Patients with McArdle’s disease, who lack phosphorylase, the enzyme needed for breakdown of muscle glycogen, and who do not experience lactate accumulation during heavy exercise, have little T2 increase after exercise (16, 22). Studies showing that T2 is negatively correlated with pH support this suggestion (22, 42). This association is apparently not due to an osmotic effect of lactate accumulation, because patients with mitochondrial myopathies, who display high lactate but little pH change, show little T2 change during exercise (22).

Decrease in pH may decrease intracellular water bound with macromolecules and increase free intracellular water (19, 34). However, Cheng et al. (5) have shown that the time course of the increase in T2 at the beginning of exercise and the decrease during recovery are faster than for pH. Thus the increase in T2 with exercise appears to be related to the biochemical events associated with muscle recruitment and increased energy metabolism, but the precise role of pH change remains to be clarified.

We conclude that during high-intensity horizontal and uphill running to exhaustion lasting 2–3 min muscles of the lower extremity are not maximally activated, suggesting there is a limit to the extent to which additional muscle mass recruitment can be utilized to meet the demand for force and energy. Greater total muscle activation during exhaustive uphill than horizontal running is achieved through an altered pattern of muscle activation that involves increased use of some muscles and less use of others.

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