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Quadriceps Fatigue Alters Human Muscle Performance during a Novel Weight Bearing Task

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Abstract

Limited information is currently available regarding muscle synergistic patterns and triggered reflex responses during dynamic weight bearing activities in the presence of muscle fatigue.

Purpose—The purpose of this study was to examine the effects of quadriceps muscle fatigue on patterns of muscle activation and performance in response to sudden, unexpected perturbations during a weight-bearing task.

Methods—Motion of the knee was measured as subjects were asked to track a visual target as accurately as possible while performing a resisted single leg squat task. Random perturbations were delivered in 20% of the trials by unexpectedly releasing the resistance during the flexion phase of the exercise. Absolute and constant errors were calculated to evaluate target tracking performance. Quadriceps and hamstring muscle activity was recorded during both perturbed and unperturbed trials. Twelve healthy females were tested before and after completing a repetitive submaximal eccentric quadriceps fatigue protocol. A second group of 12 females served as controls. Unexpected perturbations elicited long latency responses characterized by facilitation of the quadriceps and inhibition of the hamstrings.

Results—Muscle fatigue increased the amplitude of the long latency response in vastus lateralis by 4.3% maximum voluntary isometric contraction ($p=.004$). Changes in tracking error occurred in response to perturbations after fatigue in spite of significantly increased quadriceps muscle activity, especially during the extension phase of the exercise.

Conclusion—Quadriceps muscle fatigue alters the patterns of coordinated muscle activity and may render subjects less able to cope with unexpected perturbations during weight bearing tasks.

Keywords

long latency responses; muscle activation; perturbation; eccentric exercise

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Conflict of Interest

None. The results of the present study do not constitute endorsement by ACSM.

INTRODUCTION

Though largely anecdotal, studies have reported that more injuries tend to occur near the end of a sporting event, when athletes may experience muscle fatigue (7,12). These observations suggest that muscle fatigue may be a predisposing factor that contributes to lower extremity injuries. By altering the force producing capability of the muscles surrounding the joint, fatigue may contribute to injuries by exposing ligaments and other static restraints to excessive loads.

While muscle fatigue has been shown consistently to manifest detrimental effects on performance during exercise, the majority of studies have focused on a single joint under static conditions(1,4,5,15). Much less attention has been given to the effect of fatigue on multisegmental dynamic weight bearing activities. In these more complex movements, the reduction in force producing capability and alterations in voluntary activation patterns that accompany fatigue could affect the ability of a muscle to fulfill its role as a dynamic joint stabilizer. Some evidence supporting this notion is available in a study by Nyland and colleagues (29) who examined the effects of an eccentric isokinetic hamstring fatigue protocol on a crossover cutting maneuver. Kinematic and kinetic analysis revealed an increase in internal rotation velocity of the tibiofemoral joint just after heel strike. Because selective hamstring muscle fatigue increased internal tibial rotation, excessive stress may have been placed on the anterior cruciate ligament (ACL), predisposing it to injury.

In addition to negatively influencing muscle activation patterns and force output, muscle fatigue alters proprioceptive (20,27) and long latency “reflexive” (1,4,17) aspects of neuromuscular control. With few exceptions (22,35), findings have suggested that muscular fatigue impairs both joint position sense and kinesthesia at the shoulder (3,27,30), elbow (16), spine (38), knee (20), and ankle (8) joints. Conclusions regarding the nature and extent to which fatigue affects a muscle’s response to sudden unexpected perturbation, however, show much less agreement.

Testing under isometric conditions, Darling and Hayes (4) and Kirsch and Rymer (17) reported enhancement of the response to muscle stretch at the elbow after fatigue, suggesting that the gain of the long and short latency triggered responses are increased as a compensation for the loss of force producing capability. In contrast, Balestra (1) reported a significant reduction in response amplitude after voluntary isometric fatigue of a distal hand muscle. Fatigue induced by stretch-shortening cycle exercise has shown both increased (10,17) and decreased (17) amplitude of the short and long latency components of the stretch reflex. The type and level of muscle fatigue, as well as the characteristics of the perturbation induced may explain the varied responses observed across studies. Our understanding of the effects of localized muscle fatigue on neuromuscular control strategies during functional weight bearing tasks is limited.

Therefore, the purpose of this study was to examine the effects of quadriceps muscle fatigue on patterns of muscle activation and performance in response to sudden, unexpected perturbations during a weight-bearing task. We hypothesized that quadriceps muscle fatigue would alter long latency responses and negatively affect the accuracy of target tracking performance and patterns of neuromuscular recruitment during the weight bearing task.

METHODS

Subjects

Twenty-four healthy adult females (21-31 years of age) were invited to participate in this study. Subjects were physically active, but not currently participating in any formal physical

exercise or sports program. Subjects were asked to refrain from any strenuous exercise for 24 hours preceding any test session. Subjects with a history of knee injury that required diagnosis or treatment by a medical practitioner were not allowed to participate. In addition, subjects with visual or hearing impairment, those who reported a history of spinal surgery or balance problems, or those who currently were experiencing knee pain during activity or at rest were excluded. Prior to participation, subjects read and signed a consent form approved by the university institutional review board.

Instrumentation

A custom-built device was used to provide controlled resistance to the lower extremity as subjects performed the single leg squat (SLS) weight bearing task. The device consists of a modified standing frame with a rack and pinion gearbox mounted to the frame between the two side supports (Fig. 1). At one end of the horizontal shaft of the gearbox is a padded plate. During the SLS task, the plate was positioned such that the anterior aspect of the patella was located at the center of the pad. The lower extremity was secured to the pad by an inelastic Velcro strap that extended around the knee. Thus, as the task was performed, horizontal linear displacement of the shaft occurred as the knee joint moved forward and backward during each flexion and extension phase of the exercise. The horizontal position of the knee joint was measured by a potentiometer mounted to the shaft of the pinion gear of the device.

Resistance during the SLS task was provided by an electromechanical braking system mounted to the shaft of the pinion gear. Subjects encountered constant resistance throughout the range of motion in both the flexion and extension phases of the exercise. However, software controlling the braking system allowed for the abrupt release of resistance. The timing of the release of resistance was adjusted such that the perturbation occurred at a consistent point in the range of motion. The duration of the perturbing event during the task was set to 500 ms. Following the period of release, the resistance of the brake returned immediately to the previously specified level. Release of the brake occurred randomly in 20% of the repetitions within each set of the exercise.

Experimental Procedures

Preliminary Training Session—Each subject attended a preliminary training session 24-48 hours prior to actual testing to familiarize them with the testing device and to ensure that they learned the task correctly. During the training session, subjects performed 5 sets of 10 repetitions of the resisted SLS exercise. Resistance of the testing device was set to 15% of the subject's body weight and remained constant throughout the training session. Thus, no perturbations were delivered in any repetition while subjects were learning the task.

Real-time visual feedback indicating the horizontal position of the shaft of the testing device was made available to subjects as the task was performed. Feedback was presented on a computer monitor located in front of the subject at eye level. A target in the form of a sine wave (period = 2.5 s) also appeared on the screen, which subjects were instructed to track as accurately as possible with the position trace of the device during each repetition of the exercise. Peak-to-peak amplitude of the target waveform corresponded to a 15 cm horizontal displacement of the shaft of the testing device. Linear displacement of the shaft was highly correlated to anatomical knee flexion range of motion (0-40°; $r = 0.98$).

The task was performed with subjects in unilateral stance on a 20 cm step. Subjects were positioned with the medial border of the supporting foot within 3 cm of the edge of the step and the outline of the foot was traced. A strap was placed around the waist as subjects performed the SLS task to remind them to only bend at the knee while keeping the back

straight. In addition, subjects were allowed minimal upper extremity support by placing two fingers of the right hand on the edge of the tray covering the top of the testing device. Subjects were cautioned not to exert significant downward pressure on the fingers at any time during the task. Preliminary data recorded from a force sensor in 4 subjects indicated that less than 2-3 Newtons of force were used to perform the weight bearing task, both before and after fatigue.

Each set of exercise began with the foot of the supporting limb on top of the step with the knee extended. Subjects were required to maintain their trunk erect for the duration of the exercise in each set. The exercise was initiated when the target waveform began to progress across the computer screen. Subjects were then required to track the target as accurately as possible during 10 repetitions (1 set) of the exercise. Brief rest intervals (30-60 s) separated each set of the exercise to avoid fatigue during the training session. Recordings of perceived exertion supported that no additional fatigue was induced during training or testing sessions as a result of these procedures.

Testing Session—Prior to data collection, preamplified (35x) bipolar surface electrodes (Ag/AgCl; 8 mm diameter, 20 mm interelectrode center-to-center distance) were attached to the skin overlying the muscle bellies of vastus medialis (VM), rectus femoris (RF), vastus lateralis (VL), medial hamstring (MH), and lateral hamstring (LH). EMG electrodes were placed at four-fifths the distance along a line from the anterior superior iliac spine (ASIS) to the medial joint line for VM, at one-half the distance along a line from the ASIS to the superior pole of the patella for RF, and at two-thirds the distance along a line from the ASIS to the lateral joint line for VL. (34) For the hamstring muscles, EMG electrodes were placed at one-half the distance along a line from the ischial tuberosity to the medial and lateral femoral condyles for MH and LH, respectively(18). The reference electrode was placed over the head of the fibula. Raw EMG signals were collected online and subsequently analyzed using Datapac II software (version 3.0; Run Technologies Inc., CA). EMG signals were sampled at 2000 Hz via differential amplifiers (Model EMG-55 driver amplifier; CMRR (common mode rejection ratio) = 87 dB at 60Hz, bandwidth = 20-4000Hz, input impedance = 15 M Ω at 100Hz; Therapeutic Unlimited, Iowa City, IA) with a gain of 1000.

EMG data collected during these experiments were expressed as a percentage of the EMG activity produced during a maximum voluntary isometric contraction (MVIC). Maximum contractions were performed with subjects seated on the chair of a Kin-Com isokinetic dynamometer (Kin-Com 125E+; Chattex Corp.; Chattanooga, TN) with the knee joint positioned in 45° of flexion. Subjects performed 3 maximum isometric contractions in extension followed by 3 maximum contractions in flexion. The trial with the highest recorded peak EMG was used to normalize the activity of each muscle during the resisted SLS task.

After performing maximum contractions, subjects were placed in the SLS testing device to perform a series of random perturbation trials. These trials consisted of 5 sets of 10 repetitions of the exercise during which the resistance of the device was unexpectedly released to 0% BW in 20% of the repetitions within each set during the knee flexion phase. The software controlling the electromechanical brake was adjusted such that the perturbations occurred when the horizontal shaft of the device had translated 5 cm from the start of the flexion phase of the exercise for 500 ms. During unperturbed tracking, knee joint angular velocity was estimated to be approximately 40°/sec. Peak knee joint angular velocity resulting from perturbations was estimated to reach approximately 90°/sec. Subjects rested briefly between sets and again after completing all 5 sets.

Following random perturbation trials, subjects were randomly assigned to either the fatigue or control group. Table 1 summarizes the demographic information describing the subjects in each group. Independent t-tests confirmed that no baseline differences existed between groups. Subjects assigned to the fatigue group completed a repetitive eccentric isokinetic exercise protocol on the dynamometer. The fatiguing exercise protocol was designed to selectively fatigue the quadriceps muscles to a point at which maximum voluntary eccentric (MVEC) knee extension force was reduced by at least 25%. To determine MVEC forces, subjects performed 3 maximum eccentric quadriceps contractions at a constant angular velocity of 14°/s. The repetition in which the highest peak force occurred was used to determine the 25% criterion level of fatigue.

The fatiguing exercise protocol began with the knee flexed at 90°. The knee was passively extended to 20° of flexion at an angular velocity of 7°/s while the subject relaxed. Extension was limited to 20° of flexion to avoid the discomfort of initiating a strong eccentric contraction of the quadriceps with the knee joint locked in terminal extension. During the eccentric phase of the exercise, the subject contracted the quadriceps to resist knee flexion, which occurred at an angular velocity of 14°/s. The target force level for each contraction (75% of MVEC) was displayed as a horizontal line on a computer monitor. Visual feedback of the eccentric force produced by the subject was displayed as a vertical bar. Subjects were required to reach and maintain the target level of force for as long as possible during each repetition of the exercise until the criteria for fatigue was met. Repetitions continued until the peak force remained below the 75% MVEC target level during three consecutive eccentric contractions in spite of maximal effort on the part of the subject and strong verbal encouragement from the investigator. Subjects were unaware of the criterion for stopping the exercise during the fatigue protocol. A preliminary study verified that this fatigue protocol induced a long duration fatigue consistent with low frequency fatigue.

Subjects in the control group underwent a similar exercise protocol on the dynamometer consisting of 75 repetitions of passive knee flexion and extension using the same angular velocities. The duration of this period of exercise (20 minutes) closely approximated the average duration of the exercise performed by the fatigue group, although no muscle fatigue was induced. Maximal eccentric quadriceps contractions, however, were performed prior to the passive exercise protocol in the same manner as described for the fatigue group.

Immediately following the isokinetic exercise protocol (Fatigue or Control), subjects were returned to the SLS testing device to perform a final bout of random perturbation trials. Subjects completed an additional 5 sets of 10 repetitions of the SLS exercise as previously described. Subjects then returned to the dynamometer to perform a single maximum eccentric quadriceps contraction to confirm the status of their post-exercise fatigue.

Motor Control Assessment

Accuracy of Performance—Error in tracking the visual target was evaluated in those repetitions in which a perturbation was delivered during the flexion phase of the exercise. Thus, a total of 20 repetitions (10 prior to fatigue and 10 after fatigue) were analyzed from each subject. Each repetition consisted of a flexion phase, during which the perturbation occurred, followed by an extension phase. Flexion and extension phases were analyzed separately by dividing each phase of the exercise into 10 equal intervals (125 ms each).

Within each 10% interval of the flexion and extension phase of the exercise, error in tracking the target was calculated as the difference between the sinusoidal target waveform and the position trace recorded from the potentiometer of the testing device. This difference represented constant error (CE), which served as a measure of directional bias. A positive difference indicates that the position of the horizontal shaft of the testing device was leading

the target (an overshoot). Absolute error (AE) was calculated as the absolute value of the difference between the target and position traces. During both the flexion and extension phase of the exercise, the mean CE and AE within each 10% interval was used to assess performance during these perturbed trials.

Muscle Activation Patterns—A similar analysis was performed to examine the effect of quadriceps fatigue on the patterns of muscle activity. Following RMS (root-mean-square) processing (50 ms time constant), the mean EMG within each 10% interval of the flexion and extension phase of the exercise was determined for each muscle. The amplitude of the EMG within each interval was normalized and expressed as a percentage of the activity obtained from the MVIC.

Long Latency Responses to Perturbation—Signal averaging was used to extract the long latency muscle responses to perturbation under fatigued and non-fatigued conditions. During both perturbed and unperturbed repetitions of the exercise, an event marker was recorded as the potentiometer of the testing device passed a specified threshold voltage. For perturbed trials, the event marker corresponded to the onset of the perturbation. For unperturbed trials the marker served to indicate the point at which a perturbation would have occurred if the software had allowed for it. This event marker was used as the reference for signal averages created separately for perturbed and unperturbed trials within and between each of the 5 sets of the exercise before and after fatigue.

A total of 10 perturbed and 40 unperturbed repetitions were available from each subject under fatigued and non-fatigued conditions from which signal averages were constructed. Averaging began 50 ms prior to the event marker and continued until 250 ms after the event for both perturbed and unperturbed repetitions. To account for potential fatigue-related changes in the level of background muscle activity at the time of the perturbation, long latency muscle responses were extracted by subtracting the averaged signal of the unperturbed repetitions from the averaged signal of the perturbed repetitions. The peak amplitude of the residual signal from 50-150 ms following the event marker was used to represent the magnitude of the response to perturbation. A representative example of the signal averages extracted for the LLR in VL from one set trials before and after fatigue is presented in Figure 2. To further take into account any possible changes in motoneuron excitability that might contribute to the amplitude of the response, an LLR ratio was calculated by dividing the peak amplitude of the long latency response by the mean background level of EMG present during the 50 ms that immediately preceded the perturbation for both fatigued and non-fatigued conditions.

Statistical Analysis

Normality of the data was confirmed using the Kolmogorov-Smirnov test. The influence of quadriceps muscle fatigue on AE, CE, and EMG was analyzed using a series of three-factor repeated measures analyses of variance. The within-subject factors were Condition (Pre-fatigue, Post-fatigue) and Interval (1-10). The between-subject factor was Group (Fatigue, Control). Flexion and extension phases of the exercise were analyzed separately. Although Interval was included in the overall model, any significant main effect due to this variable was of no interest in this analysis since comparisons between intervals were not related to the hypotheses of this study. Significant interaction effects were further analyzed within each interval of the exercise using Bonferroni-adjusted t-tests when appropriate. The effect of fatigue on eccentric torque and long latency response amplitude was analyzed using two-factor (Condition $\times$ Group) repeated measures analyses of variance followed by Bonferroni-adjusted t-tests as appropriate. The level of significance was established at $\alpha \leq 0.05$, and all statistical analyses were performed using SPSS software (version 10.0 for PC).

RESULTS

Effect of Fatigue on Eccentric Torque

The fatigue protocol used in this study was intended to induce a significant and long-lasting impairment in force producing capability of the quadriceps. Maximum voluntary eccentric knee extension torque was measured in all subjects prior to the fatigue protocol (pre-fatigue) and again at the end of the experiment (post-fatigue). The effectiveness of the fatigue protocol was confirmed by comparing pre-fatigue and post-fatigue eccentric torque measurements within and between groups. Analysis of these data revealed a significant Group $\times$ Condition interaction ($P < .001$). Within the fatigue group, there was a significant difference before and after eccentric exercise ($P < 0.001$), with an average 24.2% (SD $\pm$ 9.8) reduction in maximum eccentric torque. No difference existed between pre-fatigue and post-fatigue eccentric torque values for the control group ($P = 0.895$). A difference between groups was found only in the post-fatigue condition ($P = .024$), indicating that the groups were similar with regard to muscle performance prior to the eccentric exercise protocol. Mean torque values before and after fatigue are displayed in Figure 3A for both groups.

The number of repetitions completed by subjects in the fatigue group before meeting the criteria for fatigue (25% reduction in MVEC) ranged from 51 to 139, with a mean of 91.6 (SD $\pm$ 27.6). A representative example of maximal and submaximal eccentric torque values recorded from one subject during the fatigue protocol is presented in Figure 3B. This particular subject completed a total of 89 repetitions before meeting the criterion level of fatigue. In the final repetition of the exercise, eccentric torque reached only 67.3% MVEC, in spite of maximum effort on the part of the subject. At the end of the experiment, approximately 15 minutes after completing the eccentric exercise protocol and SLS task, maximum voluntary torque recovered somewhat but remained 16.7% below the pre-fatigue value. These findings confirmed that fatigue was long lasting and present during the completion of the SLS task.

Effect of Fatigue on Long Latency Muscle Responses

Regardless of fatigue status, long latency muscle responses to the perturbation were characterized by increased activation of the quadriceps muscles followed shortly by a reduction in activity of the hamstrings. Figure 4A shows the mean amplitude of the long latency responses from each of the muscles tested for both groups before and after fatigue. The amplitude of each response represents the increase (or decrease) in peak normalized EMG following the onset of the perturbation after subtracting the averaged EMG signal of the unperturbed trials. When comparing LLR amplitude under fatigued and non-fatigued conditions, only vastus lateralis showed a significant increase in EMG after fatigue. For subjects in the fatigue group, muscle activity in VL increased by 4.3 %MVIC ($P = 0.004$), to reach an overall amplitude of 15.1% MVIC (SD $\pm$ 6.9). No difference was found between conditions within the control group ($P = 0.803$) or between groups prior to fatigue ($P = 0.584$). Further analysis of these data revealed that under both conditions, the amplitude of the LLR for each muscle represented a constant proportion of the background level of EMG at the time of the perturbation (Fig 4B). For example, prior to fatigue the peak of the LLR for VL was 1.62 times greater than baseline muscle activity. After fatigue, the ratio remained essentially unchanged at 1.68 ($P = 0.41$), suggesting a general increase in the level of excitability of the motoneuron pool.

Effect of Fatigue on the Accuracy of Performance

Figure 5A displays the absolute error observed during the SLS task before and after fatigue. Prior to the perturbation during the flexion phase (intervals 1-3), tracking errors were generally within ± 2 cm of the target. After the perturbation, errors progressively increased,

reaching a maximum of more than 4 cm by interval 8 under both pre- and post-fatigue conditions. Statistical analysis revealed a significant Group $\times$ Condition interaction ($P = 0.022$), with a 1.4 cm difference between groups ($P < 0.001$) in the post-fatigue condition within interval 10. AE in the subsequent extension phase of the exercise was much smaller, with no differences identified between groups or conditions.

Constant error is summarized in Figure 5B for both phases of the exercise. Prior to release of the resistance, CE was near zero, indicating that tracking errors were not biased in either direction at the start of the flexion phase. However, perturbations caused subjects to lead (overshoot) the target throughout the remainder of the flexion phase of the exercise. During this portion of the task, no differences in CE were found between groups or conditions. In the absence of muscle fatigue, subjects continued to lead (overshoot) the target during much of the extension phase that followed the perturbation as well. After completing the fatigue protocol, however, subjects were no longer able to maintain this strategy. Instead, quadriceps muscle fatigue caused subjects to lag behind the path of their original performance during this phase of the exercise. A significant Group $\times$ Condition interaction ($P = 0.022$) was found, with post-hoc tests revealing differences between groups in the post-fatigue condition during intervals 1 through 5 ($P < 0.001$ at each interval). Between-group differences ranged from 1.4 cm to 1.6 cm over this portion of the extension phase.

Effect of Fatigue on Muscle Activation Patterns

Mean EMG within each interval of the SLS task before and after fatigue for all muscles is presented in Figure 6. Similar patterns of activity were seen among the quadriceps muscles throughout the exercise (Fig. 6A, B and C). Quadriceps activity gradually increased from the beginning to the end of the flexion phase, followed by a gradual decline during the extension phase. Overall, vastus lateralis was the most active of all the muscles tested in both the flexion and extension phases of the exercise (Fig. 6C). This muscle was also the one most affected by fatigue. In the flexion phase, average VL activity across all intervals increased from 24.8% MVIC prior to fatigue to 31.4% MVIC after fatigue. Statistical analysis of these data revealed a significant Group $\times$ Condition interaction ($P = 0.002$). In the post-fatigue condition, significant differences between groups were found in intervals 4 through 10. The magnitude of these differences ranged from 5.4 % MVIC to 15.3% MVIC ($P < 0.001$ at each interval), depending on the interval. Similar results were seen in the extension phase of the exercise, with significant differences between groups in the post-fatigue condition in intervals 1 through 8 ($P < 0.001$ at each interval). Smaller, but significant ($P < 0.006$) increases in muscle activity were observed in RF in both the flexion and extension phases of the exercise as well. Significant effects related to fatigue in VM were found only in the first three intervals of the extension phase of the exercise ($P < 0.048$ at each interval).

The extent to which the hamstring muscles were utilized in the SLS task showed considerable variability between individuals, particularly among subjects in the fatigue group. Although a significant main effect for Condition was identified in both the flexion ($P = 0.002$) and extension ($P = 0.021$) phases of the exercise for the MH muscles, the magnitude of the difference between pre- and post-fatigue conditions was less than 3.5% MVIC in both cases (Fig. 6D). Similar results were obtained for LH in the flexion phase of the exercise (Fig. 6E), with an overall difference of 3.0% MVIC between conditions ($P = 0.013$). No differences were significant for LH in the extension phase of the exercise.

DISCUSSION

Development and maintenance of knee stability is of paramount importance to enhancing performance, minimizing the risk of injury, and returning young athletes to pre-injury levels of activity after rehabilitation. Yet limited information is currently available regarding the

influence of muscle fatigue on neuromuscular control in response to unexpected and potentially destabilizing forces at the knee in functional environments. In the present study, the primary effects of localized eccentric quadriceps muscle fatigue on neuromuscular control during the resisted SLS task were 1) an increase in the overall level of quadriceps activation required to perform the exercise, 2) an increase in the amplitude of the long latency muscle response in vastus lateralis following unexpected perturbations during the flexion phase of the exercise, and 3) an inability to maintain pre-fatigue levels of performance in tracking a target late in the flexion phase of the exercise that continued into the first half of the subsequent extension phase after the perturbation.

The fatigue protocol in this study utilized repetitive submaximal eccentric exercise to induce a significant and long-lasting impairment of force producing capability of the quadriceps. The substantial deficit in maximum voluntary eccentric knee extension torque at the end of these experiments supports the assertion that fatigue was present throughout the post-fatigue testing period. This fatigue model was selected primarily to replicate the functional demands placed on the quadriceps during the flexion phase of the single leg squat task, since it was during this portion of the exercise that perturbations were delivered. In addition, eccentric quadriceps activation occurs routinely in many daily and athletic activities that require rapid deceleration and energy absorption.

As expected, the reduction in voluntary force production resulting from the fatigue protocol was accompanied by an increase in activation of the quadriceps during the resisted SLS task. Similar increases in surface EMG have been reported with fatigue during submaximal isometric (17) and dynamic (17,25) contractions. During visually-guided tracking movements of the arm, Miller et al. (25) demonstrated that the increase in surface EMG that accompanied fatigue was due primarily to recruitment of additional motor units. The increase in EMG is suggestive of an increase in excitatory drive to the motoneuron pool as the central nervous system (CNS) attempts to compensate for the reduced force output. Alternatively, it is feasible that changes in muscle fiber conduction velocity contributed to changes in the summation of the EMG signal.

During the SLS task, the influence of fatigue on muscle activation was most pronounced in RF and VL, with significant between-group differences found in both phases of the exercise. The magnitude of these differences ranged from 3.6 to 7.9 %MVIC in RF and from 5.4 to 15.3 %MVIC in VL, depending on the interval. In contrast, an increase in VM activity (2.4 to 7.1 %MVIC) was observed only during the early intervals of the extension phase, suggesting that VM may not have experienced fatigue to the same extent as RF and VL, or that the CNS differentially modulates parts of the quadriceps after fatigue (2). Because EMG data were not recorded during the fatigue protocol, we were unable to evaluate the relative extent to which individual muscles were fatigued.

The finding that hamstring activity was reduced in the post-fatigue condition for both groups was unexpected. While the differences are small, the result suggests that subjects in both groups may have altered their strategy somewhat when they returned to the SLS exercise device after completing their respective protocols. It appears, however, quadriceps muscle fatigue itself did not influence the change in hamstring activation. Therefore, the difference may simply represent the normal variability in the strategies used to accomplish this particular task.

In the present study, fatiguing intermittent eccentric exercise of the quadriceps resulted in a significant increase in the amplitude of the triggered response from vastus lateralis to an unexpected perturbation during the resisted SLS task. The time frame of the muscle response appears to be consistent with what has come to be referred to as a long latency

stretch reflex (23). Overall the peak increase in the averaged EMG signal following the perturbation occurred at 125 ms ($SD \pm 4.9$). Muscle responses at shorter latencies were minimal or absent in all subjects tested. The lack of short latency responses most likely stems from the lower velocities associated with the perturbations triggered in this study.

Long latency responses to muscle stretch have been shown to be task-dependent and are thought to make important contributions to joint stiffness (31) and corrective reactions to maintain positional accuracy (23). Recent evidence from the lower extremity in humans strongly suggests that these responses are mediated mainly by spindle group II afferent fibers through polysynaptic spinal pathways (11,36). However, later components of the response may also reflect a transcortical pathway originating from larger diameter group Ia afferents as well (21,31).

Many conflicting reports have been presented concerning the influence of muscle fatigue on the amplitude of long latency muscle responses to unexpected perturbation. Depending on the type and intensity of the contraction used to induce fatigue, responses have been shown to increase (1,4,10), decrease (1,5), or remain unchanged (6). In all cases, the exact mechanism responsible for the excitatory or inhibitory response remains uncertain.

Prior to fatigue, VL muscle activity increased by 10.8 %MVIC within 150 ms of the onset of the perturbation. After fatigue the amplitude of the response increased even further to an average of 15.1% MVIC. The increase in muscle activity appears at first to suggest that the loss of voluntary force producing capability was accompanied by an increase in the excitability of the reflex loop in response to muscle stretch. Such an increase in reflex excitability could be mediated by any one of several mechanisms including alterations in peripheral afferent sensitivity, changes in alpha-gamma motor linkage, and changes in the level of central drive or presynaptic inhibition (10). However, when the amplitude of the evoked response was expressed as a percentage of the background level of EMG, the increment was found to be a nearly constant proportion of the muscle activity present at the time of the perturbation. This finding is consistent with the principle of automatic gain compensation described by Matthews (24), and likely reflects a general increase in the level of activation across the entire motoneuron pool as a result of an increase in descending input. These conclusions are in agreement with others who have reported enhancement of long latency responses to muscle stretch in other muscles (4,17).

While muscle fatigue was accompanied by an increase in the amplitude of the LLR to perturbation in VL, the efficacy of reflexive neuromuscular responses in protecting a joint from injury has been called into question (19,32). It has been suggested that if reflex activity is to be effective at preventing injury, a response large enough to oppose the disturbance must be delivered within approximately 70 ms (39). However, studies on which this information is based were done with muscles relaxed at the time of loading; a situation that likely does not represent the conditions under which most injuries occur. Since muscle stiffness is directly related to the extent of cross-bridge formation (33), the amount of muscle activity present at the time of the perturbation would seem to be an important factor to consider when evaluating the adequacy of these reactive muscular responses. In the present study, VL activity increased by more than 60% within 150 ms after the onset of a perturbation. Such an increase in activation would be expected to provide at least some greater measure of active stiffness to oppose the perturbation.

Although muscle activity increased as a result of fatigue in both VM and RF during unperturbed trials of the SLS task, neither of these muscles showed a change in LLR amplitude suggesting that long latency responses might be modulated differently among this group of synergistic muscles. Recent studies in the non-fatigued state have also reported that

the gain of the long latency stretch reflex may be modulated differently among synergist muscle groups (26). For example, during the later part of stance phase, Mrachacz-Kersting (26) reported that the amplitude of the LLR of RF was significantly smaller than that of either of the two vasti muscles. These findings suggest that the gain of spinal reflexes might be modulated independently, even among synergist muscles, to meet the demand of the motor task.

For RF, the absence of an effect may reflect the different functional role of this muscle in dynamic lower extremity activities, since activation contributes to moments concurrently at both the knee and the hip. While an increased extension moment at the knee resulting from a larger LLR might assist in arresting the motion caused by the sudden release of resistance, a larger hip flexion moment would oppose any effort by the hip extensors to prevent further displacement. Therefore, an increase in the gain of the LLR from RF may reduce the efficiency of the overall response to restore lower extremity stability.

One factor to consider in explaining the results in VM and RF is the possibility that over the course of repeated trials subjects developed an adaptive preparatory response strategy to cope with unexpected events after the first few exposures to the perturbation. For example, short-term adaptations have been revealed in studies of reflexes controlling postural sway (28) and in reactions to unexpected loading of the low back (37). If such a change in strategy had occurred in this situation, the process of averaging might have masked a larger response in these muscles that was present only in the first one or two trials. This possibility was investigated by comparing the patterns of muscle activity and errors seen during the cycle of the exercise that immediately preceded the first perturbation with those recorded just prior to the last perturbation. This analysis revealed no differences in the timing or magnitude of the EMG, no changes in the level of coactivation, and no differences in the direction or extent of the errors measured. In addition, there was no difference in the amplitude of the LLR itself between the first and last perturbation presented. Therefore, it appears that subjects did not alter their strategy in response to repeated exposure to perturbations during the SLS exercise. The requirement to maintain accuracy during the task and familiarity with the exercise from the training sessions may have contributed to the use of a consistent strategy throughout the exercise.

Release of the resistance caused subjects to overshoot the target throughout the remainder of the flexion phase of the exercise. The magnitude of the overshoot reached a peak of nearly 4 cm at about 80% of the flexion phase, a pattern that was unaffected by the fatigue protocol. Prior to fatigue, subjects continued to lead (overshoot) the target during the extension phase that followed the perturbation. Presumably, subjects adopted this strategy so as to compensate for the error at the end of the flexion phase and to avoid the occurrence of even larger errors during subsequent cycles of the exercise. After fatigue, however, subjects were no longer able to maintain this strategy, and instead lagged slightly behind their pre-fatigue performance throughout most of the extension phase.

Although considerable evidence has been presented that muscle fatigue negatively affects the ability to accurately sense joint position and movement (3,20,27), the availability of visual information provides adequate compensation, even in patients with a complete loss of proprioception (9). Because visual information was available regarding movement errors throughout the task, it seems unlikely that disruption of proprioceptive afferent information was responsible for the larger absolute error and the reversal in the direction of the error during the extension phase. Rather, the alteration might be better explained by the mismatch between descending drive to the motoneuron pool and the forces produced by the knee extensor musculature after the fatigue protocol. As previously mentioned, EMG of the quadriceps was increased after fatigue, particularly in the extension phase. It appears,

however, that the additional recruitment of motor units was insufficient to provide the muscle power necessary to compensate the larger absolute error at the end of the flexion phase, causing subjects to alter their strategy in tracking the target during the extension phase. These results seem to suggest that muscle fatigue might render subjects less able to cope with unexpected perturbations during a task that requires a high degree of consistency. One could speculate that such errors in controlling knee position during sporting activities might compromise dynamic joint stability and increase the risk of injury, particularly to someone with a history of instability, such as from ACL deficiency.

We believe that the controlled SLS task used in this study provides a potentially useful method of examining lower extremity neuromuscular control. However, there are several limitations that must be considered when interpreting the results of our study. First, our findings apply only to uninjured females. One of the reasons for choosing only female participants was to examine the extent to which muscle fatigue influences neuromuscular control of the knee in a population known to have a higher incidence of knee injuries. In addition, recent evidence suggests that females may respond differently to similar fatigue protocols than males(13,14). As a result, the magnitude of fatigue induced in men by the fatigue protocol may not have been the same magnitude of fatigue induced in women, the effect of gender versus fatigue would have become the issue. Direct comparisons between males and females and between injured and uninjured populations will be the focus of future studies in our laboratory. Second, because eccentric muscle contractions were used to induce fatigue, the possibility that muscle damage might have contributed to the observed changes in neuromuscular control cannot be eliminated. However, none of the subjects who experienced exercise-induced muscle soreness experienced symptoms beyond 48 hours and symptoms were mild.

In summary, a novel method was used to assess neuromuscular control in response to sudden, random perturbations delivered during a commonly prescribed unilateral weight bearing exercise. These responses were evaluated in the presence of muscle fatigue in order to gain insight into the strategies used to restore and maintain dynamic lower extremity stability. The key finding of the study was that quadriceps muscle fatigue increased the amplitude of the long latency response in vastus lateralis, which appears to reflect an increase in the gain of the reflex in response to muscle stretch. The gain enhancement is consistent with an increase in the general level of excitability of the motoneuron pool as a compensation for the impairment in muscle force output. Despite the increase in muscle activity, however, the response was not sufficient to maintain prefatigue levels of performance in tracking a target. The observed increase in error suggests that muscle fatigue might render subjects less able to cope with unexpected perturbations, making it more difficult to maintain consistent levels of performance during skilled movement and perhaps increasing the likelihood of injury. Therefore, exercise programs for patients and athletes should be carefully monitored for signs of fatigue to avoid deficits that might compromise dynamic joint stability. More research is needed in this area to better understand the functional consequences of muscle fatigue and the role of long latency responses in the restoration and maintenance of joint stability.

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Fig. 1.
Testing device used to provide resistance during the single leg squat task.

Fig. 2. Representative example of the averaged EMG signal from vastus lateralis (VL) within the long latency response period from one set of fatigued (*solid line*) and non-fatigued (*dotted line*) trials in a single subject.

Fig. 3.

A: Mean (SD) maximum voluntary eccentric knee extension torque before and after fatigue for the fatigue group (*closed circles*) and the control group (*open circles*). *Significant difference between conditions within the fatigue group. †Significant difference between groups. **B:** Representative example of eccentric knee extension torque from one subject in the fatigue group before, during, and after a series of eccentric contractions. The horizontal line indicates the target level of eccentric torque during the fatigue protocol based on the subject's maximum voluntary eccentric contraction (MVEC) torque prior to fatigue.

Fig. 4.

A: Mean (SD) normalized long latency response (LLR) amplitude for pre-fatigue (*closed symbols*) and post-fatigue (*open symbols*) conditions for the fatigue group (*circles*) and for the control group (*squares*). *Significant difference between conditions within the fatigue group. †Significant difference between groups in the post-fatigue condition. B: Mean (SD) amplitude of the LLR for subjects in the fatigue group expressed as a proportion of background muscle activity at the time of the perturbation for pre-fatigue (*closed symbols*) and post-fatigue (*open symbols*) conditions.

Fig. 5. Effect of quadriceps muscle fatigue on (A) absolute error and (B) constant error during the flexion phase (*left panel*) and extension phase (*right panel*) of the SLS task. Mean (SD) errors for pre-fatigue (*closed symbols*) and post-fatigue (*open symbols*) conditions for the fatigue group (*circles*) and for the control group (*squares*). The cycle interval within which the perturbation was delivered is indicated by the vertical dashed line in the flexion phase. *Significant difference between groups in the post-fatigue condition.

Fig. 6. Effect of quadriceps muscle fatigue on (A) vastus medialis (VM), (B) rectus femoris (RF), (C) vastus lateralis (VL), (D) medial hamstring (MH), and (E) lateral hamstring (LH) EMG activity during the flexion phase (left panel) and extension phase (right panel) of the SLS task. Mean (SD) normalized EMG for pre-fatigue (closed symbols) and post-fatigue (open symbols) conditions for the fatigue group (circles) and for the control group (squares). The cycle interval within which the perturbation was delivered is indicated by the vertical dashed line in the flexion phase. *Significant difference between groups in the post-fatigue condition.

Subject characteristics**Table 1**

	Fatigue	Control
<i>n</i>	12	12
Age, yr	23.3 ± 2.7	22.9 ± 1.0
Height, cm	166.6 ± 7.5	170.8 ± 7.6
Body mass, kg	61.9 ± 7.7	66.1 ± 10.7

Values are means ± SD