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Loss of power during fatigue of human leg muscles

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1. We have investigated the loss of power seen during high-intensity exercise of human leg muscles such as might occur during sprinting. Subjects exercised the quadriceps and hamstring muscle groups using a Cybex dynamometer at an angular velocity of 90 deg s^{-1} once a second for 6 min. At 1 min intervals the quadriceps were electrically stimulated via the femoral nerve to produce an isometric contraction which was then released into an isokinetic shortening contraction at 90 deg s^{-1}.

2. The extent of central fatigue was assessed by comparing the force of a voluntary isokinetic contraction with that elicited by electrical stimulation during isokinetic releases. Two subjects were repeatedly tested. In the first series of experiments, exercising the quadriceps of one leg, the instantaneous power fell to about 50% over the course of 2 min and remained constant for the rest of the exercise. For one subject the voluntary and electrically stimulated forces declined in parallel while for the second subject the voluntary force was 10% less than the stimulated force at the end of the exercise. These results show that central fatigue represented a minor factor contributing no more than one-fifth of the total loss of power in these circumstances.

3. In a second series of experiments the subjects alternately contracted the quadriceps and the hamstrings of both legs in an exercise which had a high rating of perceived exertion and entailed considerable respiratory and cardiovascular effort. The time course and proportionate loss of power were very similar to those seen with the one-leg exercise and neither subject showed evidence of significant central fatigue. The pattern of force loss was very similar for the hamstrings. We conclude that, for determined subjects, afferent feedback from muscles, tendons and joints or from the respiratory and cardiovascular systems does not have a major role in inhibiting voluntary activation of the quadriceps during heavy exercise.

4. In both series of experiments the power output during electrically stimulated isokinetic contractions was reduced to 50% of the initial value after 2 min of exercise while the isometric force, measured immediately before the release, fell to only 75%. This suggests that fatigue affects isometric and shortening contractions to different extents and the loss of power may be due to a combination of factors, only one of which is evident in the loss of isometric force.

A high power output is required during sprinting first to accelerate the body and then to maintain the running speed by overcoming air resistance and other frictional losses. Measurements of power output during isokinetic cycling have shown that after a peak in the first few seconds power falls rapidly, so that by 30 s it is reduced to 50 or 60% of the maximum value (Sargeant, Hoinville & Young, 1981), and athletes sprinting on a free running treadmill showed a similar rapid loss of power during all-out exercise (Cheetham, Boobis, Brooks & Williams, 1986). This loss of power is about twice the extent of fatigue seen during sustained isometric contractions (e.g. Bigland-Ritchie, Jones, Hosking & Edwards, 1978; Cady, Jones, Lynn & Newham, 1989). During an isometric contraction, typically, there is a loss of about 20–30% of the initial force by 30 s. It is important to understand the reasons for the difference between the two types of activity since most experimental work on fatigue has concentrated on isometric contractions whilst everyday and athletic activities generally consist of dynamic movements involving shortening and lengthening contractions.

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The discrepancy between performance of isometric and isokinetic contractions might result from an inability to maintain motor drive during the execution of complex tasks, often referred to as 'central fatigue'. Merton (1954) was the first to use electrical stimulation to study the question of central fatigue and concluded that full activation could be maintained in the adductor pollicis during a maximal voluntary isometric contraction sustained for 3 min. This has been confirmed with well-motivated subjects making contractions of the adductor pollicis (Bigland-Ritchie, Johansson, Lippold & Woods, 1983) and for contractions of the quadriceps lasting at least 30 s (Bigland-Ritchie *et al.* 1978). For muscles of the lower leg such as the foot plantar flexors (Belanger & McComas, 1981), dorsiflexors (Grimby, Hannerz & Hedman, 1981) and soleus muscles (Kukulka, Russell & Moore, 1986), there can be an appreciable component of central fatigue. Central fatigue might come about as a result of conscious or unconscious mechanisms. The subject may decide that the sensations are unacceptable and deliberately reduce the level of activity. Alternatively, afferent information from working muscles, joints or tendons may inhibit motor activity at spinal or supraspinal levels, leading to an obligatory loss of performance that no amount of voluntary effort can overcome. An example of this type of reflex inhibition might be the slowing of motor unit firing frequency that occurs during sustained isometric contractions (Bigland-Ritchie, Dawson, Johansson & Lippold, 1986).

There is very little information about central failure during dynamic exercise, although Newham, McCarthy & Turner (1991) applied the technique of superimposing a short tetanus on isokinetically contracting quadriceps muscle fatigued by repeated maximal isokinetic contractions and concluded that loss of central drive during isokinetic exercise was no greater than during isometric contractions. In the first part of the work described here we have carried out similar experiments using femoral nerve stimulation to activate maximally the quadriceps and have expanded the investigation to include exercise of a much larger bulk of muscle. The experiments were designed to see whether there is any evidence of an obligatory mechanism leading to loss of motor drive which well-motivated subjects are unable to overcome by voluntary effort.

Preliminary reports of this work have been communicated to The Physiological Society (James & Jones, 1990; James & Sacco, 1992, 1993).

METHODS

Subjects

The bulk of the work described here was carried out on two of the authors (P. S. and C. J.), aged 27 and 39 years, who were both fit male recreational runners. Four other subjects (23–55 years, one female) participated in a preliminary study examining their ability to activate simultaneously two legs during isometric and isokinetic contractions. The investigation was approved by the local ethics committee and all subjects gave their informed consent after first experiencing the methods to be used.

Muscle strength testing

A Cybex II+ dynamometer was modified by attaching two silicon strain gauges (Kulite Sensors), arranged in a half-Wheatstone bridge formation, midway along the lever arm. The amplified output was processed by a data handling package (Microscope; Amplicon Liveline, Brighton, UK) using an IBM compatible PC. This arrangement bypassed the mechanical linkages of the Cybex force transducing system. A bracing arm was fitted to the base of the dynamometer housing to stabilize the Cybex motor assembly. Mechanical oscillation due to the loose attachment of the standard lever arm to the axle was reduced by bolting the lever to the axle. A rotary potentiometer was fitted directly to the centre of the axle shaft to provide measurements of angle that were fed through the digital system mentioned above and displayed as a second channel on the PC.

Subjects were seated in the chair, adjusted to give maximum support to the upper leg, and firmly restrained by two straps, one placed at 45 deg across the hips and the other around the chest. The axle of the dynamometer was aligned to the centre of the knee joint with the lower leg at approximately 90 deg flexion and the lever arm adjusted to attach just above the malleoli of the ankle. The angle of the knee was then set to 90 deg using an external goniometer to calibrate the angle channel. In reporting leg position the convention was adopted that full extension was 0 deg and degrees of flexion were measured from the horizontal so that when the lower leg of the seated subject was vertical the angle was reported as 90 deg of flexion.

Muscle stimulation

The quadriceps were stimulated via the femoral nerve in the groin using a long probe cathode with a hemispherical end (about 15 mm diameter) placed over the inguinal canal, just lateral to the insertion of the adductor longus. The anode was a strip of aluminium foil, 15 × 3 cm, placed over the proximal third of the quadriceps and held in place by an elasticated fabric strap. Square wave pulses from a Devices variable frequency generator triggered a Devices dual high voltage stimulator, producing 100 μs square wave pulses at 50 Hz. The electrical circuit was completed by a switch operated by the subject, giving him ultimate control over the stimulation. The supramaximal stimulating voltage varied from 140 to 240 V. Subjects were first accustomed to the uncomfortable procedure of femoral nerve stimulation. Initially, the stimulating voltage was set at a mild 40 V and was then increased in 10 V steps until the isometric force no longer increased with further increments in voltage.

Isokinetic measurements, femoral nerve-stimulated releases (FNR)

The quadriceps were stimulated via the femoral nerve whilst held with the knee flexed at 90 deg until maximal isometric force was achieved, after which the leg was released into an isokinetic contraction at 90 deg s^{-1}. The isometric force generated before the release was measured. Force measurements during the isokinetic contractions were made as the leg passed 60 deg flexion. Modifications to the Cybex dynamometer, the rationale for using FNR contractions and many of the details of making the measurements have been described elsewhere (James, Sacco

& Jones, 1994). The angle at which the measurement was made during the isokinetic contraction was a compromise between the desire to leave sufficient time for the initial oscillations associated with the release to subside and to minimize any contribution by the series elastic components, while remaining close to the peak of the angle–tension relationship of the muscle. Sample records of fresh and fatigued muscles are given in Fig. 1 showing the angle at which measurements were made. Forces were measured from the baseline immediately before the start of stimulation for the isometric portion of the trace. For the isokinetic phase, the same baseline was used but the measurements were corrected for the weight of the limb plus lever arm at 60 deg (Winter, Wells & Orr, 1981).

Experimental protocols

Fatigue of one quadriceps muscle (Series 1). The electrically evoked FNR contractions were recorded from the fresh muscle and then the quadriceps of one leg were fatigued by repeated maximal voluntary isokinetic contractions at 90 deg s^{-1}. The range of movement was 90 deg so the contraction lasted 1 s, with 1 s recovery while the leg returned passively to the starting position; the exercise continued for 6 min. At the end of each minute the exercise was briefly interrupted to record a test FNR contraction at a velocity of 90 deg s^{-1}. This protocol was carried out by two subjects, each repeating the exercise on five occasions.

Fatigue of four muscle groups (Series 2). The experiments in Series 1 were repeated, except that the fatiguing exercise consisted of alternate contractions of the quadriceps and hamstrings of both legs working to extend and then to flex the knees. The foot attachment of the Cybex was extended so that both legs could be exercised, but when it came to testing the muscle at the end of each minute the adapted bar was replaced with the usual attachment and only one quadriceps was tested with an FNR contraction. Consequently the voluntary force of both legs was recorded while the stimulated force was that of one leg. Detachment and reattachment of the extension bar took only a few seconds.

Respiratory gas measurements were made during both series of experiments, minute samples being collected into Douglas bags during the exercise. Venous blood samples were taken for the measurement of lactate before and 5 min after the exercise. Heart rate was recorded throughout the test with a telemetric monitor and at the end of each minute the subject was asked to rate the perceived exertion on a conventional Borg scale (Borg, 1970).

Statistics

Values are given as the means ± S.E.M and the significance of differences between mean values was determined using Student's *t* test at the 5% level (unless otherwise indicated). In the figures, standard error bars are shown where these are greater than the size of the symbol.

RESULTS

Isokinetic fatigue of one quadriceps muscle group (Series 1)

Figure 2*A* shows records of both voluntary and stimulated contractions taken before the start of exercise and Fig. 2*B* shows records at the end of the first minute. A clear loss of force of the voluntary and FNR contractions can be seen. Every 30 s during the exercise three consecutive voluntary isokinetic contractions were recorded and the averages of these values are shown in Fig. 3*A* and *B*. Also shown in Fig. 3 are the isokinetic forces generated during the stimulated FNR contractions that were interposed at 1 min intervals during the exercise. The forces have been normalized to the values obtained in the fresh muscle. The subjects were encouraged to make maximal efforts throughout the exercise which they found moderately difficult. Perceived exertion was reported to be between 12 and 16 and heart rates were around 110–120 beats min^{-1} (Fig. 4*A* and *B*).

For both subjects the stimulated and voluntary contractions fatigued in a similar fashion with a fall in the first 2 min to 50–60% of the initial values, after which the forces remained relatively constant. After 6 min of exercise by Subject 1 (Fig. 3*A*) the decrease in voluntary force was slightly (and significantly) more than that of the stimulated contractions; the difference amounted to approximately 10% of the initial force. Since the total loss

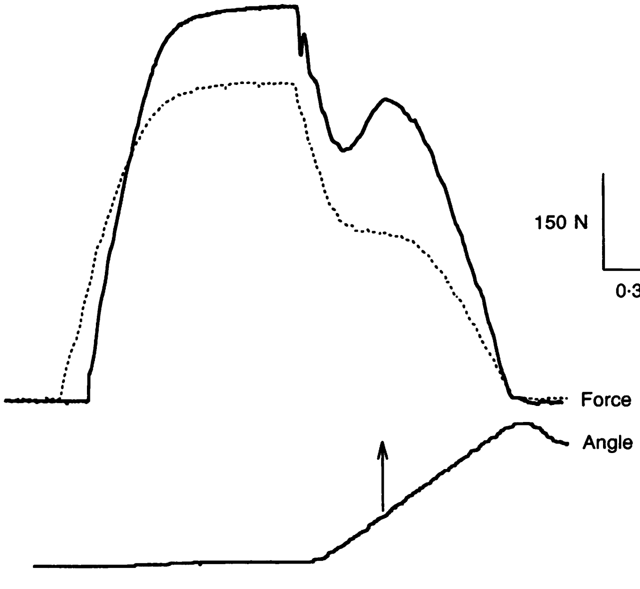

Figure 1. Quadriceps force and knee angle recordings from one subject (P. S.)

Femoral nerve-stimulated isometric contractions and isokinetic releases at 90 deg s^{-1} in the fresh state (continuous line) and after 6 min of exercise (dotted line). The lower trace gives the angle at the knee moving from 90 to 0 deg flexion. The arrow indicates 60 deg, the angle at which force was measured during the isokinetic phase of the contraction.

of force was of the order of 50%, the component due to central fatigue was approximately one-fifth of the total. For the second subject (Fig. 3*B*) there was no significant difference between the changes in stimulated and voluntary force after 3 min of exercise. At earlier times the stimulated force was slightly lower than the voluntary force.

Fatigue of four muscle groups (Series 2)

This series of experiments investigated the ability of the two subjects to activate the quadriceps during isokinetic exercise whilst subjected to high levels of afferent stimulation from a large bulk of working muscle and from the cardiovascular and respiratory stress of heavy exercise.

Preliminary experiments were carried out to determine the extent to which subjects were capable of voluntarily activating both legs in a combined contraction in the fresh state. Using the attachment for two legs, the subjects made both isometric and isokinetic contractions of first one leg, then the other, and finally both legs together. Most healthy subjects can fully activate the quadriceps of one leg (Jones & Rutherford, 1987; James *et al.* 1994) so that if subjects contract both legs the force might be expected to equal the sum of the two separate legs. Figure 5 shows the results of four subjects, measuring the strength of the two legs separately and then when working together. For isometric contractions the combined forces were equal to the sum of the two legs. With isokinetic

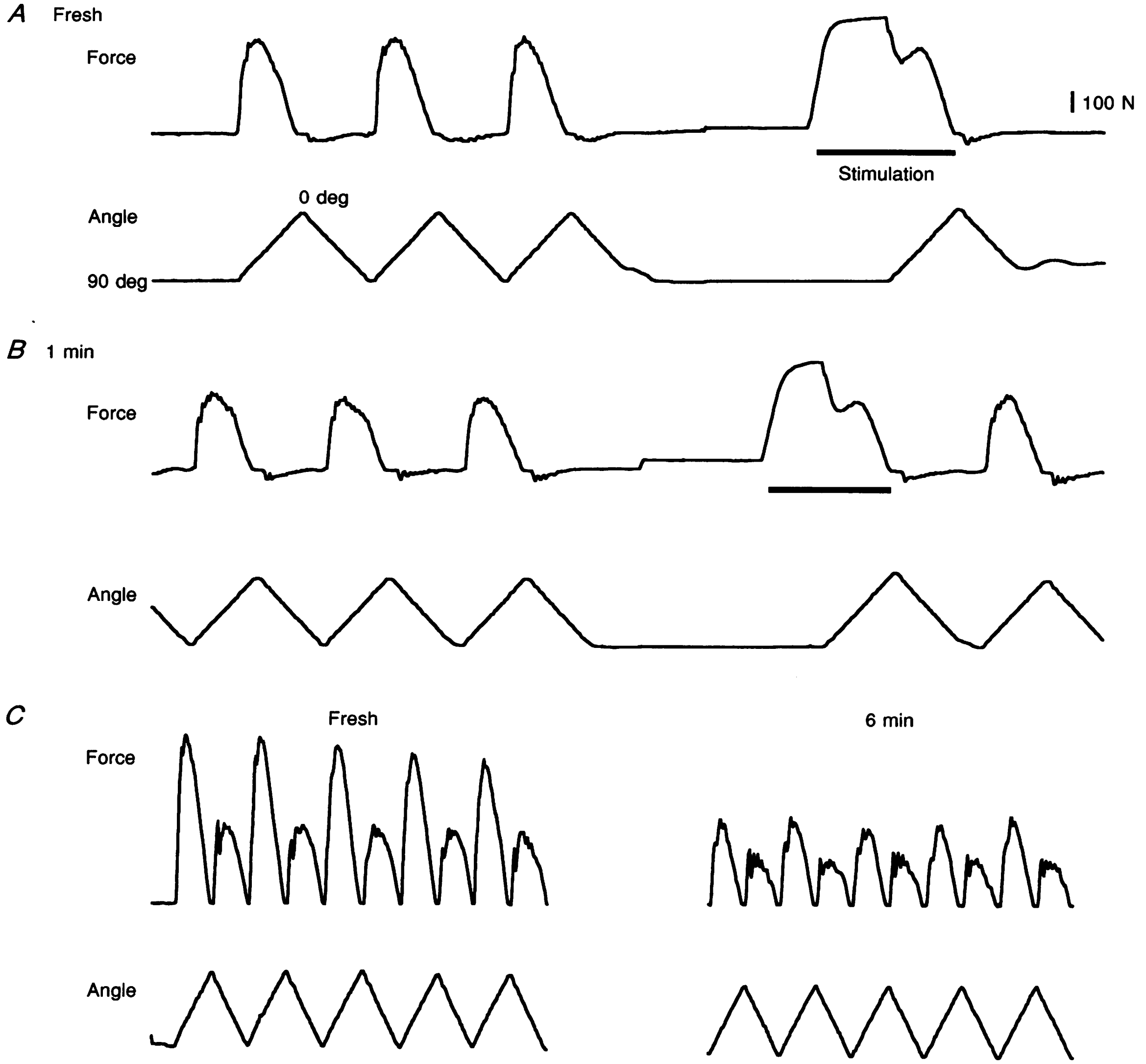

Figure 2. Force and knee angle records from exercise protocols in one subject

Voluntary single-leg extensions and FNR contractions at 90 deg s^{-1} in the fresh state (*A*) and 1 min into the fatigue protocol (*B*). Electrical stimulation via the femoral nerve is indicated by the horizontal bar. *C*, voluntary bilateral alternate quadriceps and hamstring isokinetic contractions at the beginning and end of the 6 min fatigue protocol; the force traces have been rectified. For the time scale, an angle excursion of 90 deg represents 1 s.

contractions the combined forces were approximately 12% less than the sum of the individual leg forces.

The two subjects (C. J. and P. S.) repeated the experiments carried out in Series 1 with the difference that they worked the quadriceps of both legs in extending, and the hamstring muscle groups of both legs in flexing, the knees (see Fig. 2*C*). The voluntary forces of *both* the quadriceps and hamstrings were measured at 30 s intervals and the quadriceps of *one* leg was tested with an FNR contraction at 1 min intervals, as in the previous Series 1 experiments.

The exercise was perceived to be much more severe than the single-leg exercise of Series 1. Ratings of exertion towards the end of exercise were around 19 and heart rates were between 130–150 beats min^{-1} (Fig. 4*C* and *D*). Ventilation rose progressively throughout the exercise in Subject 1, reaching 120 l min^{-1} after 6 min. For Subject 2, the ventilation was fairly constant at around 80 l min^{-1}. In both cases the oxygen consumption during the exercise was approximately two-thirds $V_{O_2,\text{max}}$, as determined by cycle ergometry. Resting blood lactate concentration was 0·96 mM for Subject 1 and 1·0 mM in Subject 2. The blood

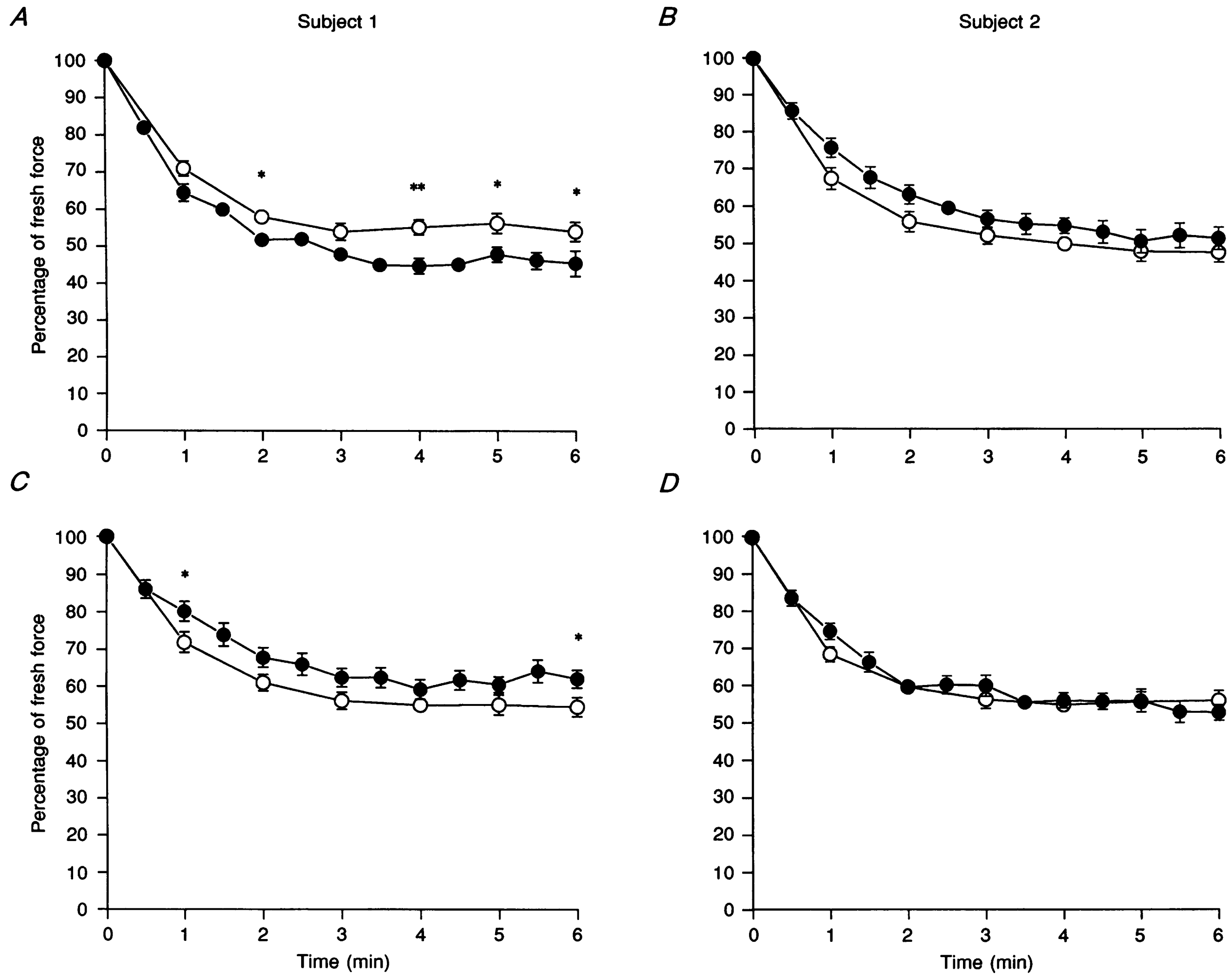

Figure 3. Isokinetic force changes during 6 min of exercise

A and *B*, subjects made maximal voluntary isokinetic contractions of the left quadriceps at 90 deg s^{-1}, with 1 s rest; values are shown at 30 s intervals and forces of the FNR contractions, interposed at 1 min intervals, measured during the isokinetic release phase. *C* and *D*, subjects exercised the quadriceps and hamstring muscle groups of both legs, alternately extending and flexing the knees. The voluntary force of the isokinetic contractions of both quadriceps was measured at 30 s intervals and the FNR contraction of one quadriceps was measured every minute during the isokinetic release phase. The mean values for two subjects are shown, each repeating the exercise on five different occasions. ●, voluntary contractions; ○, FNR contractions. The forces are expressed as a percentage of the fresh muscle forces. Significant differences between the voluntary and stimulated forces: $^{*}P < 0{\cdot}05$; $^{**}P < 0{\cdot}01$.

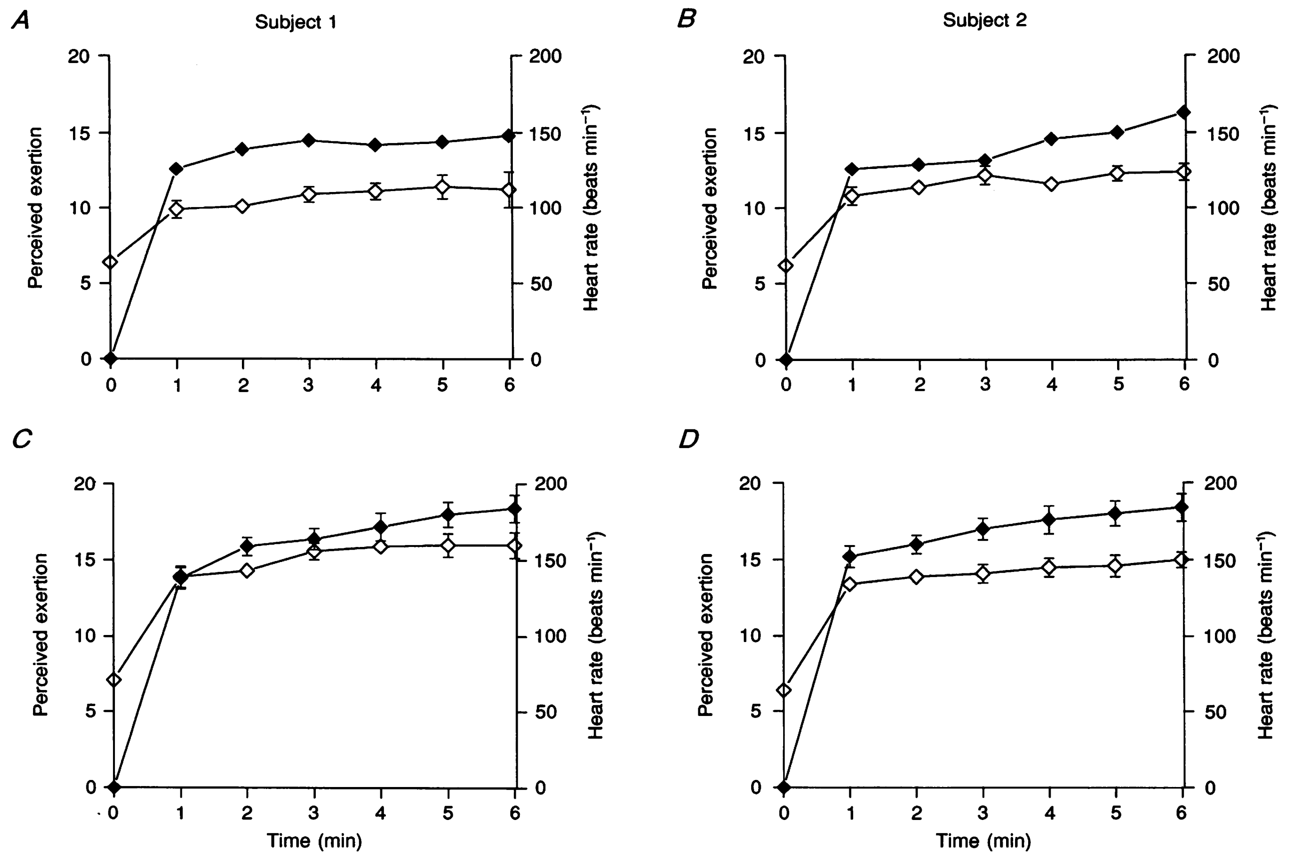

Figure 4. Heart rate and perceived exertion during exercise

A and *B*, two subjects exercised with one quadriceps, as described in the legend to Fig. 3*A* and *B*. *C* and *D*, the same subjects exercised quadriceps and hamstrings of both legs as described in the legend to Fig. 3*C* and *D*. Heart rate (◇) and ratings of perceived exertion (◆) using a Borg scale were recorded at 1 min intervals.

lactate values 5 min post exercise were 5·3 ± 1·6 and 6·7 ± 0·6 mM for Subjects 1 and 2, respectively.

The forces generated by the quadriceps are shown in Fig. 3*C* and *D*. There are two notable features of these results. First, the decline in voluntary performance of the two quadriceps, as a proportion of the initial force, was very similar to, and in neither subject was it greater than, the decline in force measured during the FNR contraction of one quadriceps (compare *A* and *B* in Fig. 3), indicating that central fatigue could not account for the loss of performance. For Subject 1 the voluntary force was slightly greater (relative to the performance of the fresh muscle) than the stimulated force during the exercise, a phenomenon that was noted for Subject 2 in the previous

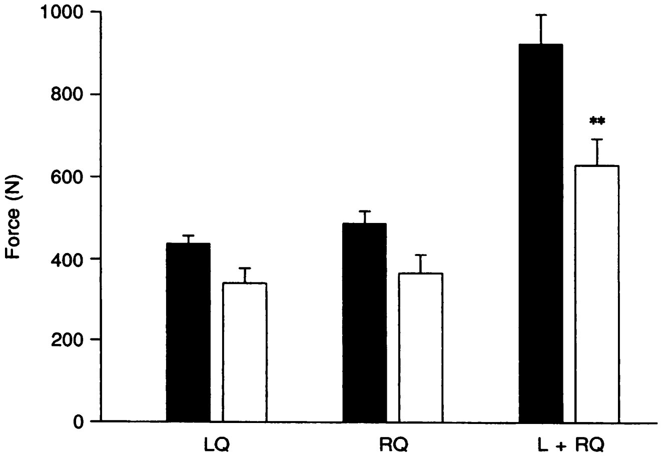

Figure 5. Forces developed during one- and two-leg exercise

Four subjects made maximal voluntary contractions of either the left (LQ) or right (RQ) quadriceps and then both together (L + RQ). Forces were measured during either isometric contractions or isokinetic contractions at 90 deg s^{-1}. **$P < 0·01$ for the differences between forces generated by two legs together compared with the sum of the individual legs. ■, isometric contractions; □, isokinetic contractions.

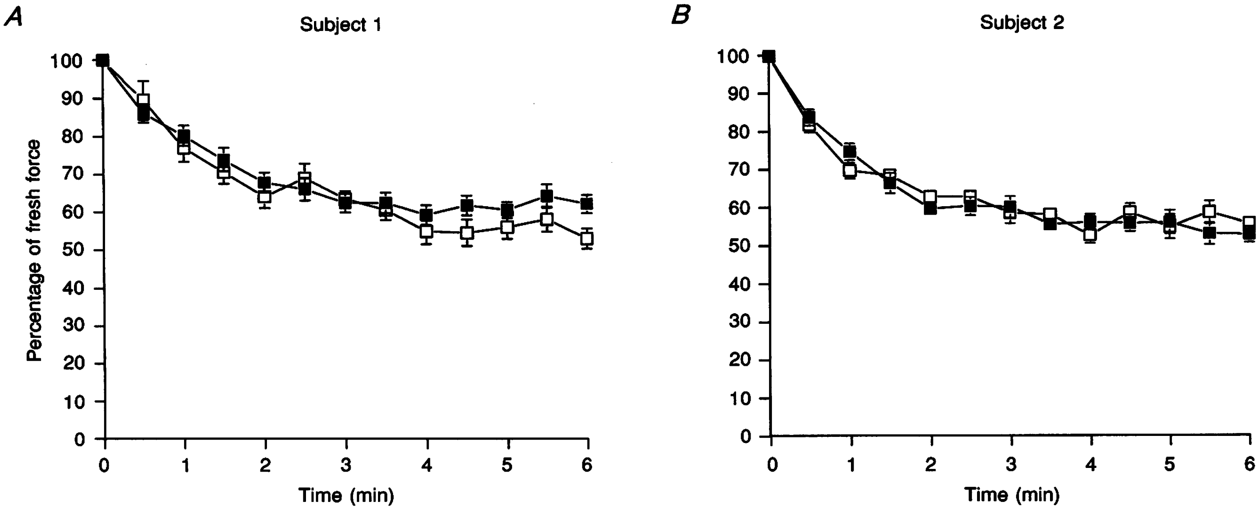

Figure 6. Isokinetic forces generated by quadriceps and hamstring muscle groups

Two subjects exercised the quadriceps and hamstring muscle groups of both legs as described in the legend to Fig. 3. Maximal isokinetic forces of both quadriceps (■) and both hamstrings (□) are shown measured every 30 s during the exercise.

series of experiments. The second feature is that the extent and time course of force loss were very similar to that seen when exercising just one quadriceps (Fig. 3*A* and *B*); indeed the voluntary forces were slightly better maintained during the two-leg exercise.

The time course of fatigue of the hamstrings, contracting whilst flexing the knees, is shown in Fig. 6, compared with that of the voluntary forces of the quadriceps. For both subjects there was an almost identical decline in performance of the two muscle groups. It was not possible to electrically stimulate the hamstring muscles in these experiments.

Changes in isometric and isokinetic forces

Figure 7 compares the decline in isometric and isokinetic forces measured during the fatiguing protocol in Series 1 and shows that, while the isokinetic forces fell by approximately 50% during the exercise, the isometric forces declined by only about 25%. Similar results were seen with the experiments in Series 2. In these experiments the isometric force was measured at 90 deg flexion while

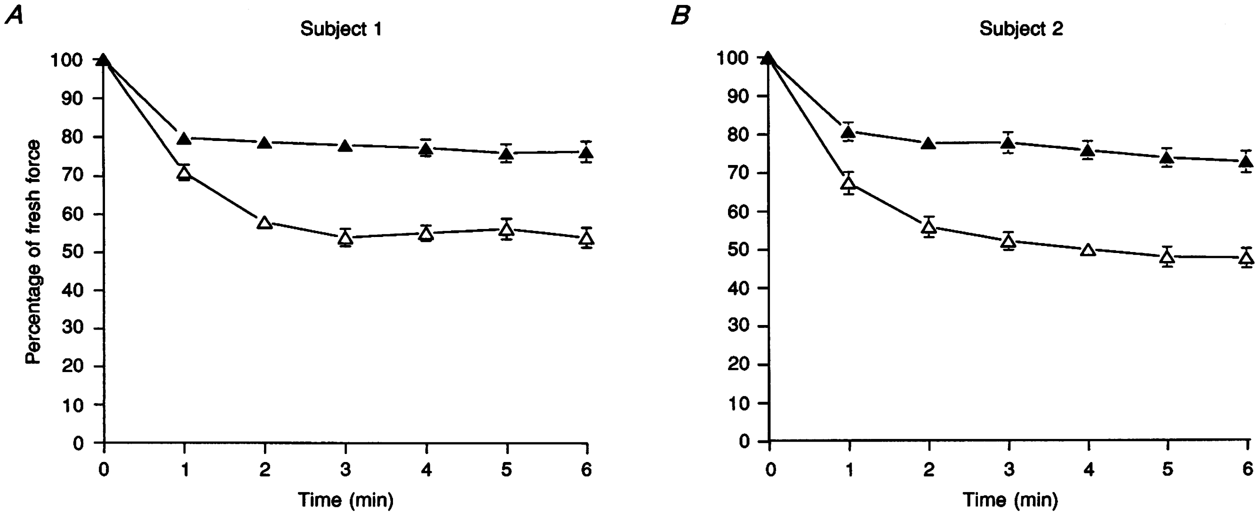

Figure 7. Changes in isometric and isokinetic force during one-leg exercise

Two subjects exercised one leg, as described in the legend to Fig. 3*A* and *B*, and were tested at 1 min intervals with a femoral nerve-stimulated release. Isometric force (▲) was measured before the release and isokinetic force (△) during the isokinetic phase of the contraction. Isometric and isokinetic forces were significantly different at all times after the first minute of exercise.

the isokinetic force was determined as the lower leg passed though 60 deg flexion. As a control, two subjects repeated the experiment in Series 1 with the difference that the FNR was replaced with an isometric contraction measured at 60 deg of flexion. The extent of fatigue was the same as for the isometric contractions measured at 90 deg, indicating that the differences seen between isometric and isokinetic contractions were a result of the mode of testing and not the muscle lengths at which the measurements were made.

DISCUSSION

During intense dynamic exercise there is a rapid loss of muscle power that is much more pronounced than the loss of force seen during fatigue involving isometric contractions, and the investigations described here have examined this discrepancy. The first possible explanation is that during dynamic exercise it may be increasingly difficult to maintain full muscle activation by voluntary effort, especially when the exercise involves several large muscle groups and appreciable cardiovascular and respiratory stress. A second possible explanation is that the process of muscular fatigue may affect the ability of a muscle to shorten, and therefore develop power, to a greater extent than its ability to generate isometric force.

In the fatiguing protocols of Series 1 and 2, the isokinetic force declined to about 50% of the initial values. Since the contractions were made at a constant velocity, the changes in force may be taken to reflect changes in power output, and the degree of fatigue seen in these experiments was similar to that reported during intense cycling (Sargeant *et al.* 1981) and sprinting (Cheetham *et al.* 1986) exercise.

We have investigated the possibility of central fatigue by comparing voluntary contractions with electrically stimulated contractions, a technique that has been widely used in studying fatigue during isometric exercise. Using this technique with isokinetic contractions is technically difficult, mainly because of the limited time available during the movement and the fact that the muscle is continually changing length. Activation of a part of the muscle using percutaneous stimulation is well tolerated and gives information that, for isometric contractions, is similar to that obtained by stimulating the whole muscle via the femoral nerve (Bigland-Ritchie *et al.* 1978). However, we have found that the volume of muscle stimulated percutaneously varies with the position of the leg and so, for an isokinetic contraction, it is impossible to be sure that the stimulated portion of the muscle remains constant (James *et al.* 1994). Consequently we have used the FNR procedure, which has the advantage of ensuring full activation of the whole muscle before the shortening contraction begins as well as providing a relatively smooth force record from which it is possible to measure the force as the leg passes a standardized position (60 deg flexion) during the isokinetic phase. Our subjects suffered no ill effects from the procedure, although it is equally true to say that neither found femoral nerve stimulation a pleasant experience.

The two subjects who took part in the Series 1 experiments were able to activate the quadriceps muscle fully when fresh, as judged by comparison of the voluntary and stimulated forces, and for Subject 2 this remained the situation throughout the 6 min of exercise. During this time the isokinetic force declined by 40–50% for both voluntary and stimulated contractions. There was no indication of central fatigue in this subject (Fig. 3*B*). Subject 1 (Fig. 3*A*) showed a small but consistent shortfall in voluntary force after 2 min of exercise, but the discrepancy between stimulated and voluntary contractions in this subject could account for no more than one-fifth of the isokinetic force loss so that central fatigue was a minor component of the overall loss of performance.

Exercise of one muscle group, albeit with dynamic contractions, is not an ideal model for high-intensity, whole-body exercise such as sprinting or cycling, since the exercise was perceived to be of only moderate intensity. Consequently the study was expanded in Series 2 to include a larger mass of muscle so that the respiratory and cardiovascular loads and the general afferent sensory input would approximate that of heavy exercise. However, despite the fact that heart rates, ventilation and blood lactates were comparable to values expected of exercise at around 80% of maximum capacity, the pattern of force loss was very similar to that seen in the Series 1 experiments, with even less evidence of central fatigue (Fig. 3*C* and *D*). During the two-leg voluntary exercise it was possible to stimulate only one leg so that in Series 2 the comparison was between the voluntary force generated by *two* quadriceps and the FNR contraction of *one* leg, but this does not invalidate the conclusions since there is no reason to think that the electrically stimulated responses of one leg were not representative of the function of both legs.

During the two-leg exercise the loss of force over the 6 min was a little less than that seen during the one-leg exercise. This finding may be explained by the fact that the initial intensity of the exercise with two legs was probably 85–90% of maximal. It appears that when using both legs together subjects can fully activate the quadriceps during isometric contractions but they have some difficulty doing so during isokinetic contractions at 90 deg s^{-1} (Fig. 5).

On occasions the voluntary force was found to be greater than that evoked by electrical stimulation of the femoral nerve (Subject 2 in Series 1, Subject 1 in Series 2) despite the fact that care was taken to keep the stimulating voltage supramaximal. Although the maximal voluntary and stimulated forces were the same in the fresh muscle we have observed that during voluntary contractions it is possible for the seated subject to arch the back and extend the hips, thereby stretching the rectus femoris and generating greater forces (James *et al.* 1994). This does not happen during stimulated contractions where the tendency is for the hips to flex and the trunk to come forward. During the fatiguing exercise the subjects adopted various strategies to try and maintain the power output and arching the back may account for the unexpected finding.

It might be objected that whilst it is possible to activate fully the quadriceps by voluntary effort during high-intensity exercise, other muscle groups, which are important during sprinting, may be more sensitive to central fatigue. Measurements of the hamstrings during the fatiguing exercise of the Series 2 experiments showed a pattern of force loss that was identical to that of the quadriceps. It was not possible to electrically stimulate the hamstrings and directly measure the extent of central fatigue, but the close similarity between the behaviour of the quadriceps and hamstrings argues against there being any significant central fatigue in the hamstrings during the heavy exercise undertaken in the Series 2 experiments.

The small differences between the subjects and the high voluntary force compared with the stimulated force seen on some occasions are minor considerations when set against the major observation that most, if not all, the loss of power during 6 min exercise, of one or two legs, was due to failure of peripheral rather than central processes. The athletic background of our two subjects, the amount of muscle exercised and the respiratory and cardiovascular loads imposed in our experiments were sufficiently similar to those used in the experiments of Sargeant *et al.* (1981) and Cheetham *et al.* (1986) to suggest that during this type of activity the rapid loss of power during whole-body exercise was not primarily due to central fatigue but in major part represents a change in the contractile properties of the locomotor muscles.

We do not argue that central fatigue during dynamic contractions is never a cause of loss of performance, since it is a common observation of daily life that most people make a conscious decision to limit their effort and minimize the discomfort of exercise. However, our present results indicate that the desire to reduce activity can be largely overridden by determined subjects and thus we have found very little evidence of an *obligatory* mechanism by which the voluntary activation of skeletal muscle is limited by sensory inputs as fatigue sets in. In this respect the present results agree with the conclusions of Beelen, Sargeant, Jones & de Ruiter (1995), obtained using a motor-driven cycle ergometer.

The second objective of the work described here was to investigate the differential effects of fatigue on isometric and isokinetic force output in human muscle. During the FNR contraction it was possible to measure both the isometric force before the release as well as the force generated at a given angle during the isokinetic phase of the contraction, so that a direct comparison could be made of the effects of fatigue without any question arising about the extent of voluntary activation. Figure 7 compares the two forces for the Series 1 experiments where the decrement in the isometric force was approximately half that seen with the isokinetic force measurements, demonstrating that the differential sensitivity of the two types of contraction is a major factor accounting for the loss of power during intense exercise.

One reason for the difference between the two modes of contraction may relate to the slowing of the contractile properties of the muscle. Slow relaxation is a feature of fatigued muscle and it has been argued that if this is due to a slower turnover of actomyosin cross-bridges then a reduction in shortening velocity and power output would be expected which would be proportionately greater than the loss of isometric force (Jones & Bigland-Ritchie, 1986; de Haan, Jones & Sargeant, 1989). Further studies are needed to determine whether the difference in the time course of fatigue between power and isometric force, which became apparent during the first minute of exercise, was paralleled by a change in the relaxation from an isometric tetanus, as was the case in the animal experiments of de Haan *et al.* (1989).

In summary, we have investigated two aspects of fatigue during high-intensity dynamic exercise. The first concerns the role of central fatigue and our conclusion is that healthy and determined male subjects can sustain a high level of voluntary activation during dynamic contractions of large muscle groups for periods of at least 6 min. The second aspect of the work has drawn attention to the loss of power that cannot be accounted for by the loss of isometric strength and we speculate that this phenomenon is associated with slow relaxation from an isometric contraction.

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