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ORIGINAL ARTICLE

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Reflex inhibition during muscle fatigue in endurance-trained and sedentary individuals

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Abstract Reflex inhibition of the motoneuron pool following fatiguing contractions may be mediated by the build-up of byproducts of fatigue. Endurance training is accompanied by neuromuscular adaptations that would alter the production and/or clearance of metabolic substrates. The purpose of the study was to determine the extent of reflex inhibition during and after fatigue in endurance-trained individuals compared to sedentary controls. Subjects produced isometric ankle plantarflexion contractions at 30% of maximal voluntary contraction (MVC) until their MVC torque declined by 30%. H-reflexes were measured during a brief rest period every 3 min as well as superimposed upon the contraction every minute. Both groups of subjects experienced a similar amount of reflex inhibition by the end of the fatiguing protocol, although the endurance time was twice as long for the endurance-trained subjects. The endurance-trained subjects showed a greater reduction in H-reflex amplitude early in the fatiguing protocol compared to the sedentary subjects. These experiments have demonstrated that the neuromuscular processes associated with fatigue-related reflex inhibition must be multi-faceted and cannot be explained solely by small-diameter afferents responding to the byproducts of muscle contraction.

Keywords Human · Muscle fatigue · H-reflex · Submaximal contraction

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Introduction

Muscular fatigue has been associated with reflex inhibition of the motoneuron pool (Garland 1991; Woods et al. 1987). The mechanism underlying this reflex inhibition is unknown; however, one theory points to the activity of small-diameter type III/IV afferents. Hayward and colleagues (1988) used isolated cat preparations to show that force inhibition was increased by stimulation of small-diameter afferents. Others have found the discharge rate of these afferents to increase in the presence of ischaemia (Adreani and Kaufman 1998) or metabolic substrates found after muscular contraction or fatigue (Rotto and Kaufman 1988). In addition, stimulation of the small-diameter afferents resulted in increased after-hyperpolarization duration of alpha motoneurons (Windhorst et al. 1997), indicating inhibition of the motoneuron pool.

Endurance training is known to result in neuromuscular adaptations that would alter the production and/or clearance of metabolic substrates. For instance, endurance-trained individuals utilize more free fatty acids and produce less lactate than sedentary individuals when working at the same absolute capacity (Hurley et al. 1986). Saltin and Karlsson (1971) and Lucia and coworkers (2000) also demonstrated that endurance-trained individuals produced less lactic acid than sedentary individuals for a given submaximal workload. In addition, circulating potassium levels are lower in trained than in untrained individuals following fatiguing work at a similar workload (McCoy and Hargreaves 1992). This could be related to the greater Na^+/K^+ pump activity in the fibre membrane of endurance-trained individuals (McKenna et al. 1996). Furthermore, the improved capillarization of muscle following endurance training could result in improved metabolite clearance (Brodal et al. 1977). Thus, we postulated that there would be less inhibition stemming from small-diameter afferents in endurance-trained than sedentary individuals with fatigue.

The purpose of the present study was to determine the extent of reflex inhibition during and after fatigue in endurance-trained individuals. The maximal H-reflex and maximal M-wave in the endurance-trained runners were compared to those in sedentary controls following a fatiguing submaximal isometric plantarflexor contraction. It was hypothesized that the endurance-trained group would show less reflex inhibition of the soleus muscle when fatigued to the same degree as a sedentary group of individuals with otherwise similar characteristics.

Methods

Subjects

Subjects were healthy, non-smoking volunteers (aged 22–53 years). Endurance-trained individuals ran at least 40 km/week for at least 1 year prior to the study. Sedentary individuals participated in no formal exercise program. Group assignment was confirmed by having subjects perform a predictive $\dot{V}O_{2max}$ test using a modified Astrand 6-min submaximal cycle ergometer protocol (Astrand and Rodahl 1977). Subjects were included in the sedentary group if they had a predicted $\dot{V}O_{2max}$ equal to or below the "low" range for their age (approximately 28 ml/kg per min for women, 37 ml/kg per min for men) and were included in the endurance-trained group if they were found to have a predicted $\dot{V}O_{2max}$ equal to or above the "high" range for their age (approximately 47 ml/kg per min for women, 56 ml/kg per min for men; see Astrand and Rodahl 1977). Subjects in the mid-range were excluded from the study.

Subjects were excluded if they had any musculoskeletal or neuromuscular disorder affecting the lumbar spine or lower extremities. All subjects were asked to refrain from consumption of alcohol, caffeine or drugs for at least 2 h preceding the experimental session. All subjects gave their signed informed consent.

Experimental protocol

Subjects attended the laboratory on two separate occasions. The first visit included an orientation to the laboratory and an explanation of the experiment. They were asked to perform one or two "practice" maximal voluntary contractions (MVCs) in the experimental apparatus. This was done because subjects who have never performed an isometric plantarflexion MVC require some practice for peak performance on this task. The experimental protocol was performed during the second visit. For the endurance group, the experiment was scheduled to be on, or immediately following, a rest day from training. The temperature in the laboratory was maintained at a comfortable 21°C.

Subjects were seated in a comfortable chair with their hips and knees flexed to 90° and the ankles in neutral position, perpendicular to the lower leg. The right leg was placed into a metal support apparatus with the foot strapped to a plate under which a transducer was mounted to measure plantarflexion torque. A padded metal clamp was secured above the knee to prevent the heel from moving off the foot-plate during an ankle plantarflexion contraction. A second clamp in front of the tibia prevented any forward movement of the heel on the foot-plate. Non-compliant straps were used to reinforce the movement restrictions imposed by the clamps, as well as to prevent any backward movement of the tibia. A lap belt was used to maintain a stable hip position.

Surface electromyographic (EMG) electrodes (8 mm diameter) were placed over the soleus muscle belly in a bipolar arrangement, with one approximately 20 mm distal to the gastrocnemius muscle–tendon junction, and the other approximately 10 mm distal to the first. Stimulating electrodes for the tibial nerve were positioned with the cathode (2 cm×2 cm) in the popliteal fossa and the anode (10 cm×5 cm) just superior to the patella. Both electrodes were held in position using a 5-cm-wide neoprene sleeve. A ground electrode was wrapped around the lower leg between the stimulating and recording electrodes.

Single square-wave pulses of 50–100 μs duration were used for maximal M-wave testing, and 1,000 μs duration for H-reflex testing. The stimuli were generated by a constant-voltage stimulator (Digitimer type 3072) for maximal M-wave testing and by a constant-current stimulator (Digitimer DS7) for H-reflex testing. EMG responses were amplified and filtered (13 Hz–10 kHz) using EMG amplifier/filters (Coulbourn Instruments V75-01) before being displayed on a storage oscilloscope (Tektronix R5103N). EMG output was also displayed on a second storage digital oscilloscope (Tektronix TDS 224) with a 50-ms window that was used for monitoring the small M-wave shape and amplitude. Force output was amplified using a force transducer coupler (Coulbourn Instruments S72-25). Force production was also displayed on a storage oscilloscope. Force and EMG responses were recorded on videotape for off-line analysis using a digital PCM recording adaptor (Vetter 3000A) and a hi-fi stereo VCR (JVC HR-D75OU).

The protocol is summarized in Fig. 1. During the prefatigue phase subjects performed two MVCs, each lasting for 3–5 s. To ensure maximal descending drive in response to voluntary effort during fatigue, the twitch occlusion technique described by Merton (1954) was used. A supramaximal double pulse at 100 Hz was delivered once the force output reached a plateau. Any superimposed increase in force with the double pulse indicated that the subject did not perform a true MVC. In this case, the MVC was repeated after a 1-min rest until there was no interpolated twitch with the double pulse. This peak torque was recorded as the MVC value.

Seven maximal H-reflexes were recorded at a frequency of 0.2 Hz (Hugon 1973). A maximal H-reflex was reached when an increase in the stimulation intensity led to an increase in peak-to-peak amplitude of the small M-wave, and decrease in the H-reflex. One representative H-reflex recording was stored on the digital oscilloscope. The small M-wave was kept stable throughout the experiment and was monitored to ensure a constant volley along the peripheral nerve during H-reflex testing. Two maximal M-waves were elicited and recorded.

Subjects were then asked to maintain a non-fatiguing plantarflexion isometric contraction of 30% MVC for approximately 10–15 s while three H-reflexes were elicited. The subjects rested and

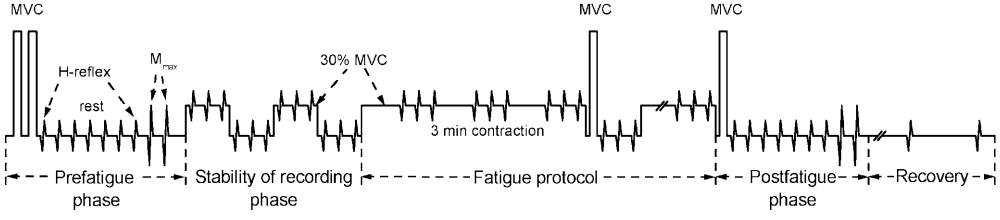


Fig. 1. Diagram of the experimental protocol with five different phases – pre-fatigue, stability of recording, fatiguing, post-fatigue and recovery. During the fatigue protocol only one cycle, consisting of a 3-min contraction and the H-reflexes taken during the contraction and at rest, is presented. The cycle was repeated until the subject's maximal voluntary contraction (MVC) was reduced by 30% from the pre-fatigue value

three more H-reflexes were elicited at rest. This was repeated twice to test the stability of the recordings. This stability of recording phase was incorporated because the amplitude of the soleus H-reflex is depressed when an agonist muscle relaxes from a previous voluntary contraction (Schieppati et al. 1986). This procedure enabled us to determine the extent to which any decline in H-reflex amplitude during the protocol was related to fatigue or training status as opposed to the voluntary termination of the fatiguing contraction.

To fatigue the ankle plantarflexors, a target line corresponding to 30% of the MVC torque was displayed on an oscilloscope that was placed in front of the subject at eye level. Subjects were asked to produce a 30% MVC of the ankle plantarflexion muscles for 3-min intervals. After every minute three H-reflexes, superimposed upon the contraction, were recorded using the same stimulation parameters as those found for the previous maximal H-reflexes. At the end of the 3rd min, the subject released the contraction and immediately performed an MVC with a superimposed double pulse. As long as the MVC force was above 70% of that found pre-fatigue, three H-reflexes were recorded while the subject was resting. During this period, only the small M-wave was being monitored in order to blind the tester to the H-reflex responses. At times, adjustments needed to be made to the stimulation parameters to match the shape and amplitude of the small M-wave with that of the pre-fatigue one. Three stable recordings were taken at least 5 s apart, and the subject was then asked to continue producing the 30% MVC force for another 3 min. The rest period usually lasted 15–20 s. This protocol continued until the MVC with superimposed double pulse fell to or below 70% of the pre-fatigue value.

During the post-fatigue phase, seven H-reflexes with stable small M-waves and two maximal M-waves were recorded immediately following the final MVC. Subjects remained resting in the chair during recovery while H-reflexes were elicited every 15–20 s. The H-reflexes were compared to the stored pre-fatigue one. When the amplitude returned to the pre-fatigue values, the experiment was terminated. This was performed to ensure that the stimulating electrodes or recording conditions had not changed during the fatiguing protocol.

Data analysis and statistics

Peak-to-peak amplitude of maximal H-reflex, small M-wave, and maximal M-wave was measured off-line using custom adapted Spike 2 software (CED Ltd.) after being digitized at a sampling rate of 10,000 Hz. H-reflexes were excluded if the small M-wave differed more than 20% from the pre-fatigue value. This was done only for those H-reflexes recorded while the subject was at rest (i.e. every 3 min). Every superimposed H-reflex was used during the analysis because the background EMG made it impossible to compare the small M-waves. The superimposed H-reflexes during fatigue were expressed as a percentage of the mean H-reflex amplitude found during the two brief 30% MVC the stability of recordings phase.

To determine if subjects had a significant post-contraction depression of the H-reflex, the mean of the pre-fatigue H-reflex was compared to the mean of the six H-reflexes (three H-reflexes taken after each of the two brief contractions at 30% MVC) from the stability phase. If the post-contraction H-reflexes were significantly lower than those measured pre-fatigue but had a comparable small M-wave (i.e. if post-contraction depression of the H-reflex was present), then the lower of the two values was taken as the pre-fatigue value.

Because endurance time was different from subject to subject, all data could not be pooled in absolute time and therefore data were compared against percent of endurance time. For the endurance-trained group, individual subject's values at 10% intervals of endurance time were determined through the use of an interpolation algorithm from Origin 6.0 software (Microcal Software Inc.). For the sedentary subjects who had shorter endurance times, the values at 20% intervals were determined using the same algorithm.

Student's *t*-test for independent samples between groups was done on the following variables: age (years), mass (kg), predicted $\dot{V}O_{2max}$ (ml/kg per min) and endurance time (minutes). Paired *t*-tests were done on the H-reflex amplitude in the stability of recording phase for each individual subject and for the percent difference in recovery H-reflex amplitude between the groups.

Gender differences were analysed using two-way ANOVA with group (endurance-trained or sedentary) and gender as the factors on the following measures: endurance time (minutes), pre-fatigue MVC torque (Nm), and MVC torque post-fatigue (% pre-fatigue). In addition, two-way ANOVA was performed on MVC torque and maximal M-wave data with group (endurance-trained or sedentary) and time (pre- or post-fatigue) as the factors. Bonferroni's post hoc test was done on significant interactions from the two-way ANOVA testing.

Two-way repeated measures ANOVA with group as one factor and time as a repeated factor was performed on those measures that were repeated throughout the experiment: resting and superimposed H-reflexes and MVC torque. These were analysed at intervals of 20% endurance time and absolute time (every 3 min for the first 12 min). Again, Bonferroni's post hoc procedure was performed on significant interactions. Because the aforementioned two-way ANOVA excluded half of the data from the endurance subjects, one-way repeated measures ANOVA with time as a repeated factor was performed on this group at 10% intervals of endurance time. This additional analysis confirmed the validity of the results from the two-way ANOVA.

The data throughout the text are presented as mean (SD), except when otherwise noted. The significance level was set at $P < 0.05$ for all analyses.

Results

A total of 29 subjects gave informed consent to participate in the study. Of these, five subjects did not fall into either the "low" or "high" categories on predicted $\dot{V}O_{2max}$ testing, two subjects had highly variable H-reflexes across recordings and two subjects had very small or non-existent H-reflexes. Therefore the data for a total of 20 subjects (10 endurance-trained and 10 sedentary) are reported. Table 1 contains the subject characteristics of the two groups including age, mass, predicted $\dot{V}O_{2max}$ and gender.

Post-contraction depression

Seven subjects (three endurance-trained, four sedentary) had a significant post-contraction depression of the

Table 1. Subject characteristics. Data presented as mean (SD)

Characteristic	Endurance-trained	Sedentary
Age (years)	37.1 (10.8)	29.7 (9.3)
Mass (kg)	60.7 (10.0)	69.2 (18.5)
Predicted $\dot{V}O_{2max}$ (ml/kg per min)	62.0 (14.0)	27.6 (5.91)*
Gender		
Male	6	5
Female	4	5
Time to fatigue (min)	31.3 (7.4)	17.6 (7.5)*
Peak MVC (Nm)		
Male	123.6 (46.9)	135.7 (29.8)
Female	72.6 (19.8)	67.1 (14.9)
Total	103.2 (45.3)	101.4 (42.5)

*Measures that were significantly different between the two groups ($P < 0.05$)

H-reflex peak-to-peak amplitude following a non-fatiguing 10–15 s contraction at 30% MVC ($P < 0.05$). For subjects whose H-reflex amplitude changed, the post-contraction value of the H-reflex from the stability of recording phase was taken as the pre-fatigue value against which subsequent H-reflex recordings would be compared. Figure 2 is an example of H-reflex recordings from one subject under pre- and post-fatigue conditions. It can be seen that maximal H-reflex amplitude is notably facilitated when superimposed on top of 30% contraction (Fig. 2, bottom). This subject also shows some evidence of a post-contraction depression of the H-reflex (Fig. 2 top left, dotted line), and pronounced depression following fatigue (Fig. 2, top right).

Endurance time

Table 1 shows the absolute endurance time in minutes for the two groups. Two-way ANOVA revealed no gender differences; therefore the reported results were collapsed across genders for the two groups. The sedentary group was able to produce at least 70% of their original MVC torque without interpolated twitch for 17.6 (7.5) min, ranging from 6 to 18 min in nine subjects and one subject holding for 33 min. The endurance-trained group did not decline to 70% of pre-fatigue MVC torque until 31.3 (±7.4) min, with a range from 21–43 min. The difference in the endurance time between groups was significant ($P = 0.002$). Due to the large range of endurance time, measures that were repeated throughout the fatiguing protocol were reported in both absolute time (minutes) and relative time (% endurance time). When reporting in absolute time, only the first 12 min in each experiment were compared. After the 12th min, there were three sedentary subjects without data. Note that there was one missing data point at 9 and 12 min owing to the very short endurance time of one sedentary subject.

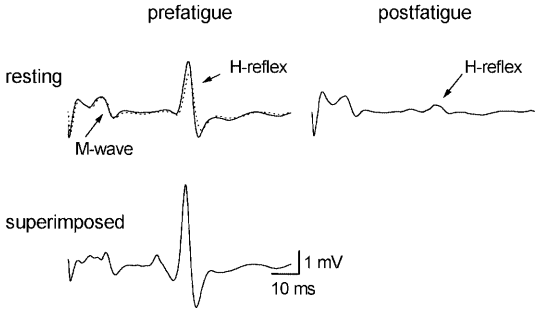


Fig. 2. H-reflex recordings from one subject. In the *top row*, H-reflexes taken at rest are presented – pre-fatigue (*left*) and post-fatigue (*right*). In the same panel with the pre-fatigue H-reflex at rest is the H-reflex evoked after a brief (15 s) contraction at 30% MVC (*dotted line*), demonstrating slight post-contraction depression. Note that the small M-waves on the recordings have similar shape and amplitude. The post-fatigue H-reflex shows considerable depression. The second row presents the superimposed H-reflex evoked during the stability of recordings phase. Note the increase in peak-to-peak amplitude in this subject

Maximal voluntary contractions

The peak plantarflexion MVC torque for the groups is also presented in Table 1, with distinction made between the genders. Although the mean peak MVC torque for the males was significantly larger than that of the females [129.7 (38.7) Nm males, 70.3 (16.3) Nm females], when combined, the means of the sedentary and endurance-trained groups were virtually identical (Table 1, last line).

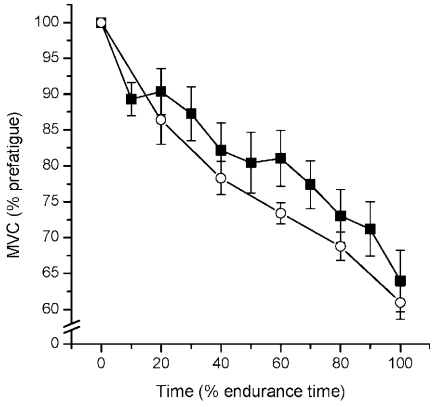
Two subjects had a decrease in the MVC torque less than 30% of pre-fatigue although they were unable to continue the fatiguing protocol. One of them was an endurance-trained subject with an endurance time of 43 min whose MVC torque remained at 79.5% of the pre-fatigue value despite exhibiting signs of fatigue such as tremor and sweating. The other subject was in the sedentary group with an endurance time of 18 min. The MVC torque was 75.4% of the pre-fatigue value yet the subject was visibly and subjectively fatigued. Note that both of these subjects were at the high end of the endurance-time range for their group.

Figure 3a shows the MVC data for the sedentary and endurance-trained groups plotted against percent of endurance time. Both groups showed a similar quasi-linear drop over time. The MVC torque decreased to 60.9 (7.3)% and 63.9 (12.8)% of the pre-fatigue value in sedentary and endurance-trained groups, respectively. There was no significant difference between the groups.

The group means for the MVC torque were plotted against absolute time over the first 12 min of contraction in Figure 3b. After the first 3 min of fatiguing contraction, both groups showed a similar decrease in MVC torque. Divergence of the two groups was observed at the 6th min and became significantly different at the 9th min of fatiguing contraction, at which time the MVC torque of the sedentary group had dropped to 73.4 (10.1)% of their pre-fatigue value while the endurance-trained group was still able to produce 87.6 (12.0)% of their pre-fatigue MVC torque ($P = 0.032$). There was no significant difference between the groups at the 12th min of contraction.

H-reflexes and M-waves

Figure 4a depicts the relationship between the H-reflex peak-to-peak amplitude and the endurance time when compared between the sedentary and endurance-trained groups. The sedentary group showed a steady decline in amplitude over time whereas the endurance-trained group showed a steep decline that appeared to plateau after 20% of endurance-time. Both groups demonstrated a significant depression of the H-reflex over time. Interestingly, post-hoc analyses revealed that the sedentary



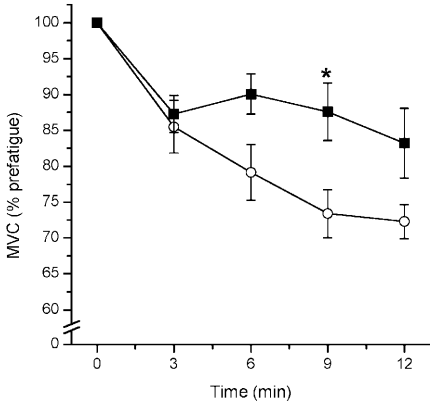
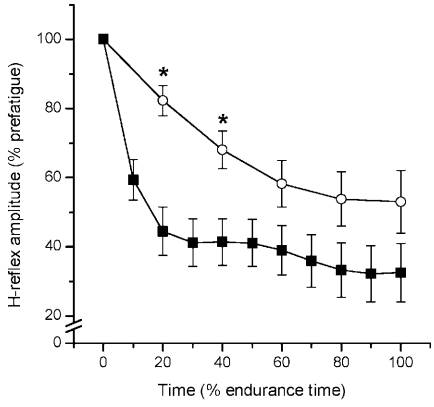


Fig. 3A, B. Peak torque during MVCs, performed every 3 min throughout the fatiguing protocol. **A** The MVC peak torque, as a percentage of pre-fatigue, is plotted against the percentage of endurance time. Data (mean, SE) for the endurance-trained subjects (*filled squares*) are presented for every 10% of endurance time. For the sedentary subjects (*open circles*), the interval is 20% of endurance time. The comparison between the two groups was performed for every 20% of endurance time. **B** MVC data presented for the first 12 min of each experiment. *Significant difference ($P < 0.05$)



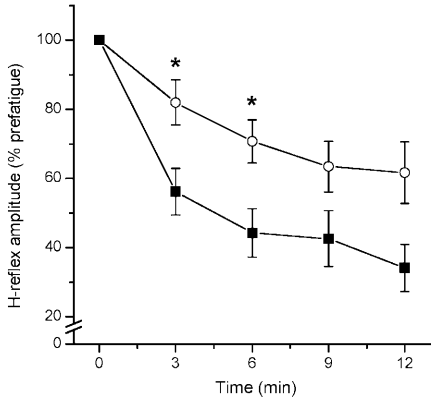


Fig. 4A, B. Amplitude of the H-reflex evoked every 3 min throughout the fatiguing protocol. **A** The H-reflex amplitude, as a percentage of pre-fatigue, is plotted against the percentage of endurance time. **B** H-reflex data presented for the first 12 min of each experiment. Data are mean (SE) for endurance-trained (*filled squares*) and sedentary subjects (*open circles*); for details, see Fig. 3. *Significant difference ($P < 0.05$)

group showed significantly *less* decline in H-reflex amplitude than did the endurance-trained group at 20% and 40% of endurance time. There were no significant differences after 40% of endurance time. The mean post-fatigue amplitude was 53.0 (28.6)% of the pre-fatigue amplitude for the sedentary group and 32.6 (26.6)% for the endurance-trained group, a non-significant difference.

Following fatigue, there were no significant differences in maximal M-wave amplitude within or between the two groups. The peak-to-peak amplitude of the maximal M-wave was 94.2 (18.0)% and 100.8 (18.8)% of the pre-fatigue values in the endurance-trained group and sedentary group, respectively.

To be sure that the relationship seen in Fig. 4a was not simply due to the markedly different endurance times between the two groups, a comparison was also done on the H-reflex data over the first 12 min of contraction (Fig. 4b). Analysis revealed that again the sedentary group demonstrated a significantly smaller depression of the H-reflex over this time ($P < 0.001$). Post hoc analyses showed a significantly smaller drop in the sedentary group than the endurance-trained group at the 3rd min [82.0 (20.8)% and 56.6 (20.2)%, respectively] and at the 6th min [70.8 (19.7)% and 44.3 (21.0)%, respectively]. There were no significant differences between the groups at either the 9th or 12th min.

Superimposed H-reflexes

Figure 5 shows the superimposed H-reflex amplitudes, normalized to the stability phase, plotted as a percent of endurance time. There was no statistically significant difference in the superimposed H-reflex amplitude between or within groups.

Recovery H-reflexes

The endurance-trained group demonstrated recovery of their H-reflex amplitude to 96.3 (15.3)% of the pre-fatigue value. The sedentary group showed recovery to 98.3 (10.5)% of the pre-fatigue value. No significant differences were present within or between the groups.

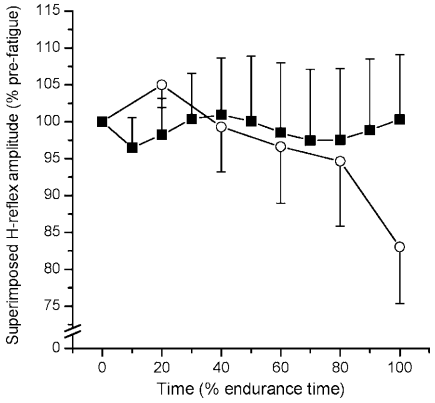


Fig. 5. Amplitude of the superimposed H-reflexes evoked while subjects maintained the fatiguing contraction. Values are normalized to the H-reflexes taken during stability of recordings phase and are mean (SE) for endurance-trained (*filled squares*) and sedentary subjects (*open circles*); for details, see Fig. 3

Discussion

Endurance-trained subjects had significantly longer endurance times in the submaximal isometric fatigue protocol than sedentary subjects. This indicated that the endurance-trained subjects possessed neuromuscular adaptations that allowed for delayed fatigue on a low-intensity isometric task. It can be seen from Table 1 that the subjects in both groups were quite similar with respect to age, mass and MVC peak plantarflexion torque production. Subjects in both groups were producing similar absolute torque outputs during the fatigue task. Therefore, the torque output per se was not a factor underlying the different behaviour of H-reflexes between the two groups. Furthermore, the experimental design enabled the separation of the effect of post-contraction depression (which is not related to fatigue) from fatigue effects by controlling for the changes in H-reflex amplitude upon relaxation from non-fatiguing contractions at the beginning of the experiment.

By the end of the fatiguing contraction, the post-fatigue decline in H-reflex amplitude in the current study was 47.0 ($\pm$28.6)% and 67.4 ($\pm$26.6)% in the sedentary and endurance-trained groups, respectively. Neuromuscular propagation failure had a very small impact on the decrease in H-reflex amplitude because of the small change in the maximal M-wave as compared to the H-reflex. The H-reflex findings are similar to those of Garland and McComas (1990), who fatigued the triceps surae musculature using electrical stimulation and reported a mean decrease in H-reflex amplitudes of 47.9 ($\pm$7.6%).

Garland (1991), as well as other investigators (e.g. Bigland-Ritchie et al. 1986), suggested that the reflex inhibition post-fatigue resulted from chemically sensitive small-diameter group III/IV afferents from the periphery. In the present study, if we had only measured the pre- and post-fatigue H-reflexes, we might have concluded that because the endurance-trained subjects contracted for twice as long to achieve 30% decline in MVC torque, they would have accumulated metabolites by the end of the fatiguing protocol and hence experienced a similar amount of reflex inhibition. However, the detailed analysis over time enables us to draw a somewhat different conclusion.

Despite the finding that the MVC peak torque was not significantly different between the endurance-trained and sedentary subjects at the 3- and 6-min marks, the H-reflex amplitude showed significantly greater *decline* in the endurance-trained than the sedentary group. When compared across percent endurance time, the sedentary group demonstrated consistently less reflex inhibition than did the endurance-trained group. Although metabolites were not measured in this study, it would stand to reason that the steep decline in the H-reflex in the first 20% of endurance time could not be associated with accumulation of metabolites in the endurance-trained subjects. Two potential explanations for this somewhat unexpected finding are proposed.

One possible explanation is that endurance-trained subjects require less central drive to the motoneuron pool to maintain a relatively simple task of 30% MVC plantarflexion contraction as compared to their sedentary counterparts, especially early in the fatiguing protocol. The endurance-trained group showed a very early and quick amplitude reduction in their H-reflex, manifesting by 10% of endurance time. After the 20% of endurance time point, there appeared to be a plateau in the amplitude. The non-significant drop in the superimposed H-reflex amplitude that is evident in the first 10% endurance time is consistent with the notion of decreased central drive; thereafter the endurance-trained subjects were able to maintain their level of motoneuron pool excitability throughout the fatiguing contraction.

Interestingly, Loscher et al. (1996) demonstrated a progressive increase in H_{max}/M_{max} ratio in gastrocnemius muscle throughout a fatiguing contraction (30% MVC) of the ankle plantarflexor muscles. This increase was only evident in the soleus muscle in five of eight subjects. In the present study, the H-reflex amplitude also increased in some subjects but there was no significant change in this parameter when the data from all subjects were combined.

Growing evidence suggests that neuromuscular adaptations are occurring in endurance-trained subjects. Maffiuletti et al. (2001) recently demonstrated that the absolute amplitude of the H-reflex was larger in endurance-trained than in either sedentary or strength-trained subjects, whereas the peak torque of the twitch evoked by that stimulation was lower in the endurance-trained group. In addition, the trained muscle fibre has greater density and sensitivity of acetylcholine receptors at the motor endplate (Desaulniers et al. 1998), thus augmenting the generation of a post-synaptic potential. Similarly, a greater density of Na^+/K^+ pumps in the muscle fibre membrane of endurance-trained muscle (McKenna et al. 1996) may allow action potentials to

propagate along the muscle fibre membrane with less distance-related decay in amplitude. It is possible that such peripheral adaptations could necessitate a reduction in the central drive to prevent endurance-trained subjects from overshooting the required force.

The second possible explanation is that the endurance-trained subjects were simply able to relax more than the sedentary group when at rest. Every effort was made to control for this by disregarding those H-reflexes that were recorded when there was evidence of EMG on the oscilloscope just before the stimulation was delivered. However, although all subjects may have been at rest in the soleus muscle, it is possible that the sedentary subjects were less comfortable with the protocol and therefore had a higher level of overall "tension" in the body. The influence that this can have on reflex gain is evidenced by the Jendrassik manoeuvre, where tension in the muscles of the upper extremity can lead to higher reflex gain in the lower extremity, and vice versa (Bussel et al. 1978; Garland et al. 1994).

In the present study, regardless of the mechanism underlying the H-reflex findings in the first 40% endurance time, it appeared as though the endurance-trained group had developed an adaptation whereby they were able to maintain a submaximal contraction with a level of reflex inhibition that was greater than a comparable group of sedentary individuals.

In conclusion, this study was the first to demonstrate a progressive decline in H-reflex amplitude as submaximal isometric fatigue was approached. Endurance trained subjects had more reflex inhibition of the motoneuron pool than sedentary subjects. It is quite possible that by the end of the fatiguing contraction, sufficient metabolites could have built up in the muscle in both groups and be contributing to the H-reflex inhibition. However, there are likely additional factors at play during the fatiguing contractions that affect the reflex inhibition of the motoneuron pool. These experiments have demonstrated that the neuromuscular processes associated with fatigue-related reflex inhibition must be multi-faceted and cannot be explained solely by small-diameter afferents responding to the byproducts of muscle contraction.

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