J Appl Physiol
90: 3–9, 2001.

Electrical and mechanical H_{max}-to-M_{max} ratio in power- and endurance-trained athletes

NICOLA A. MAFFIULETTI,[1] ALAIN MARTIN,[1] NICOLAS BABAULT,[1] MANUELA PENSINI,[1] BRIGITTE LUCAS,[2] AND MARCO SCHIEPPATI[1–3]
[1]*Groupe Analyse du Mouvement, Unité de Formation et de Recherche en Sciences et Techniques des Activités Physiques et Sportives, and* [2]*Groupe d'Etudes et de la Recherche sur le Handicap, Centre de Convalescence et de Rééducation, Université de Bourgogne, 21078 Dijon Cedex, France; and* [3]*Istituto di Fisiologia Umana, Università degli Studi di Pavia and Fondazione Salvatore Maugeri, I-27100 Pavia, Italy*

Received 15 June 2000; accepted in final form 31 July 2000

Maffiuletti, Nicola A., Alain Martin, Nicolas Babault, Manuela Pensini, Brigitte Lucas, and Marco Schieppati. Electrical and mechanical H_{max}-to-M_{max} ratio in power- and endurance-trained athletes. *J Appl Physiol* 90: 3–9, 2001.—The aim of this study was to compare the mechanical and electromyographic (EMG) characteristics of soleus motor units activated during maximal H reflex and direct M response among subjects with different histories of physical activity. Power-trained athletes produced stronger twitches, with a higher rate of twitch tension buildup and relaxation, than their endurance counterparts for both maximal H-reflex and maximal M-wave responses. The maximal H-reflex-to-maximal M-wave ratios for both force output (twitch) and EMG wave amplitude were significantly lower in power-trained than endurance-trained athletes. However, power-trained athletes exhibited a significantly greater twitch-to-EMG ratio for the reflexly activated motor units with respect to the entire motor pool, whereas endurance-trained athletes had comparable twitch-to-EMG ratios for both reflexly and directly activated units. Power training increases the force output of the whole ensemble of the motor units, thereby compensating for the lower efficacy of the reflex transmission between Ia spindle afferent input and soleus α-motoneuron. On the other hand, the lower level of force evoked by the reflexly activated units in endurance-trained athletes is associated with a greater motor pool reflex excitability. Therefore, endurance-trained athletes produce the necessary force by recruitment of more slow-twitch units than do other subjects for comparable levels of force and type of task.

soleus muscle; maximal H-reflex-to-maximal M-wave ratio; maximal H-reflex and maximal M-wave twitch; motor units; power training; endurance training

ELECTRICAL STIMULATION OF the posterior tibial nerve in the popliteal fossa at various intensities evokes two electromyographic (EMG) responses in the soleus muscle: the M and the H waves. Whereas the M wave is due to direct activation of the axons of the soleus α-motoneuron (MN) pool, the H wave is the reflex discharge of the same pool in response to the orthodromic afferent volley traveling in the large-diameter Ia fibers originating in the muscle spindles. The maximal H reflex (H_{max}) is elicited by submaximal nerve stimulation and is mainly due to the activation of the slow-twitch motor units (3, 5, 13, 18). The maximal M wave (M_{max}) is elicited by supramaximal nerve stimulation and is the electrical counterpart of the activation of all motor units of the pool, including the fast-twitch units.

The H_{max}-to-M_{max} ratio (H_{max}/M_{max}; henceforth also referred to as "EMG" ratio) is considered a suitable index for illustrating the level of reflex excitability of the motor pool, which, in turn, is dependent on the facilitation of the transmission between the Ia fibers and the α-MN (4, 13, 23). The H_{max}/M_{max} has been found to be significantly higher in athletes performing aerobic than anaerobic sports (22) and in athletes than in sedentary subjects (9). It increases after endurance-type training (21), indicating an association between endurance and the capacity to recruit a large proportion of the whole motor pool in response to the electrically elicited Ia afferent volley. The reflex excitability decreases instead in power-type athletes who have a lower H_{max}/M_{max} compared with sedentary subjects (6). The reflex excitability is also decreased by plyometric training in the rat (2), which induces a decrease in the percentage of type I soleus fibers, thereby suggesting a relationship between reflex excitability and muscle properties. Indeed, although the number and the type of motor units are genetically determined, systematic physical training (i.e., endurance or power type) can induce a transition in motor unit or fiber-type proportion (1, 2, 8, 10). It could, therefore, be hypothesized that long-term power or endurance training affects the H_{max}/M_{max} to a similar extent as the mechanical properties of the associated twitches evoked by the H and M waves.

The contractile properties of the twitch evoked by the M_{max} are different between power-trained and endurance-trained athletes or untrained subjects (20). The

Address for reprint requests and other correspondence: N. A. Maffiuletti, Groupe Analyse du Mouvement, UFR STAPS, Faculté des Sciences du Sport, Université de Bourgogne, BP 27877-21078 Dijon Cedex, France (E-mail: Nicola.Maffiuletti@u-bourgogne.fr).

The costs of publication of this article were defrayed in part by the payment of page charges. The article must therefore be hereby marked "*advertisement*" in accordance with 18 U.S.C. Section 1734 solely to indicate this fact.

first group has higher maximal twitch force and maximal rates of force development and relaxation, indicating an increase in overall force and adaptation of muscle units to power training. No studies have been made to investigate the effects of a different training procedure on the contractile properties of the twitch evoked by H_{max}. Knowledge of the capacity of force production by the motor units contributing to the H reflex would allow the realization of whether a given physical activity affects the various types of motor units to a similar or a different extent. The characteristics of the H_{max} twitch might then be compared with those of the H-reflex excitability, to assess whether plastic changes occur at both the spinal cord and muscle unit level. The aim of this study was, therefore, to compare the EMG and mechanical characteristics of the soleus motor units activated during H_{max} and direct M response among subjects with different histories of physical activity.

The mechanical response evoked by the tibial nerve stimulation at the strength that elicits the H_{max} is normally the sum of the torque contribution of both reflexly and directly activated soleus motor units, because H_{max} stimulus strength often produces a submaximal M wave (23). This fact precludes the evaluation of the characteristics of the twitch evoked by the H_{max} reflex response. In a previous study, however, our laboratory described a method to estimate the mechanical contribution of the H_{max} reflex response to the plantar-flexor torque, by subtraction of the mechanical contribution of the M wave preceding H_{max} (16). By using that procedure, we have compared the H_{max} EMG and force signal in power- and endurance-trained athletes and in untrained subjects. Matching up the "mechanical" to the EMG ratio has allowed us to get a picture of both central and peripheral plastic effects of long-term physical training on the capacity of force recruitment in the plantar-flexor soleus muscle.

METHODS

Subjects. The experiments were carried out on 24 healthy male individuals categorized into three groups. The first group was composed of eight power-trained athletes (21.4 ± 1.9 yr old, 180.6 ± 5.6 cm height, 75.9 ± 7.9 kg weight). They consisted of one high jumper, two long jumpers, two sprinters, and three basketball players, all engaged in activities requiring high-skill powerful contractions of the triceps surae muscle. The second group was composed of eight endurance-trained subjects, consisting of two triathletes, three endurance-trained swimmers, and three cross-country skiers (27.6 ± 4.0 yr old, 182.1 ± 3.4 cm height, 73.1 ± 4.2 kg weight). On average, power- and endurance-type athletes had trained 10–14 h every week for the previous 5 yr, and they were competing at national or regional levels. Eight nontrained subjects, with no history of regular participation in physical activities, composed the third group (24.6 ± 4.2 yr old, 177.3 ± 7.0 cm height, 77.9 ± 10.9 kg weight). All subjects were volunteers and read and signed informed consent before involvement in the investigation. Approval for the project was obtained from the University of Burgundy Committee on Human Research.

Stimulation. Subjects were examined under sitting conditions with the trunk inclined 60° with respect to the vertical. The limb under investigation (dominant leg) was fixed at ~90° of flexion at the hip, knee, and ankle joints. The posterior tibial nerve was stimulated by using a cathode ball electrode (0.5-cm diameter) pressed in the poplitea fossa. The anode was a large electrode (5 × 10 cm) placed on the anterior surface of the knee. The transcutaneous electrical stimulus was a rectangular pulse (1-ms duration) delivered by a Digitimer stimulator (DS7, Herthfordshire, UK). Each subject was initially familiarized with several submaximal electrical stimuli over a period of 10–15 min. The current was increased by 1-mA increments from 0 until a soleus M_{max} response was obtained. The stimulus intensity appropriate to obtain H_{max} was then carefully searched for. Five stimuli were delivered at each intensity, with a 5-s interval between stimuli.

Mechanical and electrical recording. The foot was secured to a footplate attached to an isokinetic dynamometer (Biodex, Shirley, NY) to measure the mechanical response of the plantar flexor muscles. Silver-chloride surface electrodes of 10-mm diameter, with an interelectrode (center-to-center) distance of 2 cm, recorded the EMG activity of the soleus muscle. The recording electrodes were placed along the middorsal line of the leg, ~5 cm distal from where the two heads of the gastrocnemius join the Achilles tendon. Low impedance (<2 kΩ) at the skin-electrode interface was obtained by abrading the skin with emery paper and cleaning with alcohol. EMG signals were amplified with a bandwidth frequency ranging from 1.5 Hz to 2 kHz. Both the single traces and the average of five electrical and mechanical signals were digitized on-line (sampling frequency, 5 kHz) and retained for further analysis.

Data analysis. For each subject, peak-to-peak amplitudes of the soleus H_{max} and M_{max} waves (Fig. 1) were recorded to calculate the H_{max}/M_{max} (the EMG ratio). The amplitude of the submaximal M wave preceding H_{max} was also recorded (M at H_{max} in Fig. 1). For the twitch torque associated with H_{max} and M_{max} (Fig. 1), the following variables were measured: *1*) peak twitch (P_t), the highest value of the plantarflexor twitch torque; *2*) twitch contraction time (CT), the time to twitch maximal force, calculated from the origin of the mechanical signal; *3*) the maximal rate of twitch tension development (RD), the first derivative of the torque signal; and *4*) the maximal rate of twitch tension relaxation (RR), the first derivative of the decline of torque. The relative contribution of the H_{max} wave and of the preceding submaximal M wave to the electrically evoked twitch were estimated with the method proposed by Maffiuletti et al. (16). $P_{t_{H\text{-}M}}$ was, therefore, obtained, i.e., the H_{max} peak torque value not contaminated by the M wave mechanical contribution. The $P_{t_{H\text{-}M}}$-to-P_t associated with M_{max} (P_{t_M}) ratio ($P_{t_{H\text{-}M}}/P_{t_M}$; i.e., the mechanical ratio) was then calculated.

Correction for the contamination of the H_{max} P_t by the preceding M wave. The contribution of the H_{max} to the P_t torque can be estimated if the contribution of the preceding M wave is known. Because *1*) total twitch torque evoked by nerve stimulation at H_{max} intensity (P_{t_H}) is the sum of the contribution of the units activated by both H and M waves, and *2*) the average ratio between the amplitude of the twitches selectively evoked by either wave has been described for a population of active normal young subjects (16), for each subject the relative contribution to the P_t of the units activated by the H wave was assessed using the following formula

$$P_{t_{H\text{-}M}} = P_{t_H}/(1 + M/H \times 0.8)$$

where M/H is the ratio of the amplitude of the two waves evoked by a given electrical stimulus to the nerve, and 0.8 is

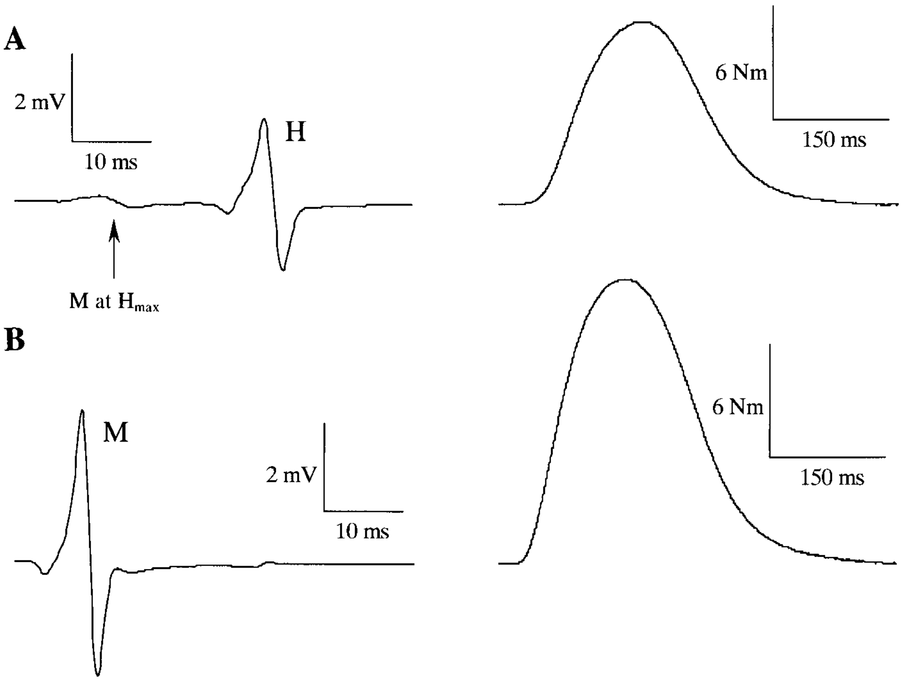

Fig. 1. Example of myoelectrical signal (*left*) and related twitch torque (*right*) associated with maximal H reflex (H_{max}; *A*) and maximal M wave (M_{max}; *B*) responses (average of 5 acquisitions for 1 representative subject). The submaximal M wave preceding H_{max} is indicated by the arrow (M at H_{max}).

the ratio of the amplitude of the twitches evoked by an equal-amplitude H or M wave. A new set of data points was thus obtained, with $P_{t_{H\text{-}M}}$ corresponding to the estimated amplitude of the twitch produced by the H_{max} reflex alone. Student's *t*-test showed that the $P_{t_{H\text{-}M}}$ values were indeed significantly smaller than the P_{t_H} values, both within groups (see Table 1) and in the whole population ($P < 0.001$). As a consequence of this calculation, one-way ANOVA showed no group effect for $P_{t_{H\text{-}M}}$ values. This shows that the small M wave associated with H_{max} produced a sizeable contribution to the resulting P_t, particularly in the power-trained athletes (see M at H_{max} in Table 1).

Statistical analyses. Differences in electrical and mechanical properties among the three groups of subjects were analyzed by means of one-way ANOVA followed by Newman-Keuls post hoc tests. Pearson's correlation test was carried out between mechanical (i.e., $P_{t_{H\text{-}M}}/P_{t_M}$) and EMG (i.e., H_{max}/M_{max}) ratios. Student's paired *t*-test was also used to compare P_{t_H} and $P_{t_{H\text{-}M}}$ within groups. The level of significance was fixed at $P < 0.05$ for all procedures.

RESULTS

M_{max} and H_{max} potentials. Tables 1 and 2 show the mean peak-to-peak values (SD) of soleus H_{max} and M_{max}, respectively, and the related plantar-flexor twitch contractile properties in the three groups. The amplitude of the M_{max} potentials was comparable among groups (Table 2). The amplitude of the H_{max} potential was highest in the endurance-trained and lowest in the power-trained athletes (Table 1). H_{max}/M_{max} significantly discriminated among the three groups of subjects (Fig. 2*A*). The ratio was highest in the endurance (67.2 ± 8.2%) and lowest in the power group (37.2 ± 13.2%).

M_{max} and H_{max} twitches. The peak amplitude of the twitch (P_t) produced by the M_{max} wave was significantly different among groups: power-trained athletes showed the highest values, followed by nontrained

Table 1. *Soleus H_{max} and related plantar-flexor twitch contractile properties*

	E	N	P	ANOVA *F*	ANOVA *P*
H_{max}, mV	4.15 ± 2.99	2.89 ± 1.50	2.37 ± 0.98	1.599	0.227
P_{t_H}, N·m	8.02 ± 1.96*	10.63 ± 1.22	13.31 ± 4.60	6.321	0.007
CT_H, ms	151.74 ± 10.59	141.46 ± 9.09	143.93 ± 11.93	2.051	0.154
RD_H, $N \cdot m \cdot ms^{-1}$	0.114 ± 0.028*	0.172 ± 0.049	0.214 ± 0.089	5.369	0.013
RR_H, $N \cdot m \cdot ms^{-1}$	0.078 ± 0.016†	0.118 ± 0.026	0.153 ± 0.076	5.065	0.016
M at H_{max}, mV	0.582 ± 0.491	0.478 ± 0.211	0.963 ± 0.498	2.723	0.090
$P_{t_{H\text{-}M}}$, N·m	6.93 ± 1.35‡	9.05 ± 1.16‡	10.26 ± 4.69‡	2.698	0.091

Values are means ± SD; $n = 8$ subjects/group. E, endurance-trained athletes; N, nontrained subjects; P, power-trained athletes; H_{max}, maximal H reflex; P_{t_H}, total twitch torque evoked by nerve stimulation at H_{max} intensity; CT_H, contraction time of H wave; RD_H, rate of twitch tension development of H wave; RR_H, rate of twitch tension relaxation of H wave; M at H_{max}, M wave preceding H_{max}; $P_{t_{H\text{-}M}}$, H_{max} estimated peak torque value not contaminated by M-wave mechanical contribution. *F* and *P* values from one-way ANOVA are also presented (df = 2, 21 for all comparisons). Significantly different from power-type athletes (Newman-Keuls post hoc test): *$P < 0.01$, †$P < 0.05$. ‡$P_{t_{H\text{-}M}}$ values significantly lower than P_{t_H} within respective groups, $P < 0.05$ (Student's paired *t*-test).

Table 2. *Soleus M_{max} and related plantar-flexor twitch contractile properties*

	E	N	P	ANOVA	
				F	*P*
M_{max}, mV	6.24 ± 4.45	5.88 ± 2.80	6.86 ± 3.57	0.135	0.874
P_{t_M}, N·m	10.36 ± 2.19*	13.80 ± 3.15†	19.46 ± 5.13	12.35	0.0003
CT_M, ms	131.7 ± 12.54	137.6 ± 15.73‡	120.4 ± 7.87	3.902	0.036
RD_M, $N \cdot m \cdot ms^{-1}$	0.174 ± 0.064†	0.247 ± 0.104	0.324 ± 0.093	5.632	0.011
RR_M, $N \cdot m \cdot ms^{-1}$	0.095 ± 0.016*	0.141 ± 0.031†	0.208 ± 0.073	11.71	0.0004

Values are means ± SD; $n = 8$ subjects/group. M_{max}, maximal M wave; P_{t_M}, peak twitch associated with M_{max}; CT_M, contraction time of M wave; RD_M, rate of twitch tension development of M wave; RR_M, rate of twitch tension relaxation of M wave. Significantly different from power-type athletes (Newman-Keuls post hoc test): $*P < 0.001$, $†P < 0.01$, $‡P < 0.05$.

subjects and endurance-trained athletes (Table 2). On average, the P_t of the last group was almost one-half that of the first ($P < 0.001$; post hoc test). There was no significant difference between the P_t of nontrained and endurance subjects. The other contractile properties of the twitch produced by M_{max} were also different between power and endurance athletes or nontrained subjects, but not between nontrained subjects and endurance-trained athletes. Maximal rates of twitch tension buildup and relaxation were higher, whereas twitch CT was shorter, in the power-trained group. The post hoc test showed that the maximal rates of tension buildup and relaxation were significantly lower in endurance- compared with power-trained athletes.

When the contractile properties of the twitch associated with the H_{max} wave are considered, some differences were observed among the three groups (Table 1). In particular, a main effect was observed for P_t values and maximal rate of twitch tension buildup and relaxation. Endurance-trained athletes showed the lowest values of P_t, RD, and RR and the longest CT value of all groups. Post hoc test indicated that the differences in the contractile properties (except for CT) were significant between endurance- and power-trained athletes. No difference was observed for any of these variables between nontrained subjects and power-type athletes. However, the H_{max} was often associated with an M potential of nonnegligible size (Table 1). The amplitude of this wave was, on average, ~12, 11, and 14% of the M_{max} in endurance, nontrained, and power subjects, respectively. Although it is likely that the above reported values of RD, RR, and CT can still be considered the expression of real differences in the twitch time course of the three groups, the contribution of the M potential to the P_t amplitude may not be negligible and would affect the P_t of H_{max}.

H_{max}/M_{max} P_t values (mechanical ratio) and H_{max}/M_{max} waves (EMG ratio). By using the $P_{t_{H\text{-}M}}$ values, the ratios of the amplitudes of the true P_t values associated with H_{max} and with M_{max} were then constructed to detect the possible relative difference in the capacity of force production of the three subject groups in response to reflex activation. The mechanical ratio ($P_{t_{H\text{-}M}}/P_{t_M}$) proved to be significantly lower in power-trained than in the other two groups (Fig. 2*B*), indicating that the H_{max} twitch produced a smaller share of the total muscle force in power-trained athletes. To check whether the mechanical ratio could give different information than the EMG ratio (H_{max}/M_{max}), the former was plotted against the latter. By collapsing all data points across all subjects, mechanical and EMG ratios were significantly correlated ($r = 0.59$; $P < 0.01$). However, the line best fitting these data points (Fig. 3) was not coincident with the identity. Identity would be natural in the case in which the fiber-type composition of the motor units subserving the H and M wave were the same, so that the twitches evoked by either wave would be equal for equal-wave amplitudes. For exam-

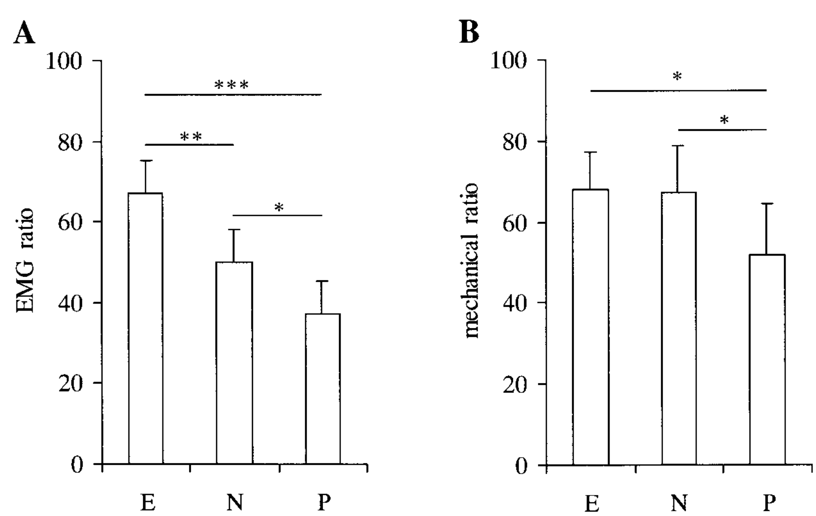

Fig. 2. *A*: electromyographic (EMG) ratio (or H_{max}-to-M_{max} ratio) in endurance-trained athletes (E), nontrained subjects (N), and power-trained athletes (P). *B*: mechanical ratio (the ratio between the peak twitch associated with H_{max} and the peak twitch associated with the maximal M response) among groups. All values are means from 8 subjects. Error bars correspond to SD. Significant differences between the mean ratios of the 3 groups (Newman-Keuls post hoc test): $*P < 0.05$, $**P < 0.01$, and $***P < 0.001$.

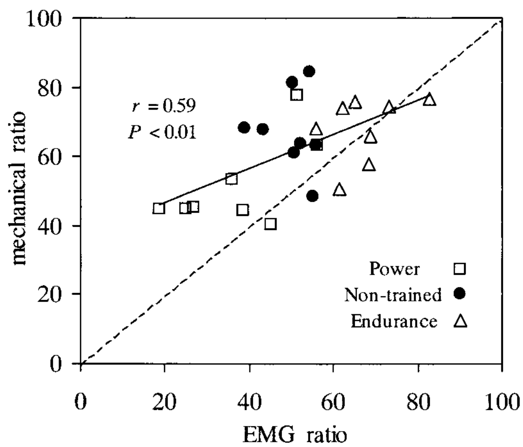

Fig. 3. Mechanical ratio between the peak twitch associated with H_{max} and the peak twitch associated with M_{max} is plotted against the EMG (or H_{max}/M_{max}) ratio for all subjects (the 3 types of subjects are indicated by different symbols). Linear best-fit line (solid line), *r*, and *P* values from Pearson's analysis are also presented. Dashed line corresponds to the identity line, which would fit the hypothetical data where the twitches associated with equal-amplitude H or M waves had the same amplitude.

ple, such behavior would necessarily be observed in the case in which $H_{max}/M_{max} = 1$, i.e., when the whole motor pool would be recruited by either wave. As a matter of fact, the best-fit line tended to converge toward the identity for larger H_{max}/M_{max} (i.e., those of endurance athletes; Fig. 3). Conversely, for smaller H_{max}/M_{max}, the best-fit line lies above the identity line, pointing to a relatively higher contribution of the H twitches with respect to the M twitches (Fig. 3). In other words, there were subjects (power athletes mostly) with small H_{max} waves and thus with poor excitability of the monosynaptic reflex of the soleus pool but with relatively more powerful P_t values.

The ratio between twitch and EMG amplitudes for H_{max} (reflex ratio) and M_{max} (maximal ratio). A quick way of emphasizing this finding is to calculate the ratio between the corrected P_t value and the H wave amplitude ($P_{t_{H\text{-}M}}/H_{max}$, i.e., the "reflex" ratio). This is reported in Fig. 4*A* for each group of subjects (open bars) and is compared with the ratio of the entire motor pool (P_{t_M}/M_{max}, i.e., the "maximal" ratio; solid bars). No significant difference was observed in the endurance group between the reflex and the maximal ratios; the mean values were almost superimposable. On the other hand, paired *t*-test showed a significantly greater ratio for the reflexly evoked twitch in both nontrained and power-trained groups ($P < 0.05$). In general, the ratios of both the reflex response and the entire motor pool were greatest in power-trained and lowest in endurance-trained athletes (although not significantly so). To get rid of the great variability in H_{max} or M_{max} potentials across subjects (see SD in Tables 1 and 2), which caused a great variability in both reflex and maximal ratios (see Fig. 4*A*), the quotient between the two ratios was calculated for each subject and averaged within groups. This is reported in Fig. 4*B*. In this display, the identity line of Fig. 3 becomes the horizontal dashed line crossing the bars at $y = 1$. It is evident that endurance-trained athletes had no particular "mechanical advantage" with respect to the other groups. The nontrained and power-trained subjects, instead, could generate relatively more torque during the reflex than direct muscle activation.

DISCUSSION

We compared the EMG and mechanical characteristics of the soleus motor units activated during H_{max} and direct M response among subjects with different training backgrounds to assess whether plastic changes occur at the spinal cord and muscle unit level to a similar or a different extent. Our results confirm that the efficacy of the reflex transmission between Ia spindle afferent input and soleus α-MN, as witnessed by the H_{max}/M_{max}, was greater in endurance-trained and weaker in power-trained athletes compared with nontrained subjects. This is in line with previous findings (6, 22) and supports the hypothesis that the H_{max}/M_{max} is related to the type of physical training (endurance vs. power type). Therefore, endurance training increases and power training decreases the relative number of MNs activated by the electrically evoked Ia

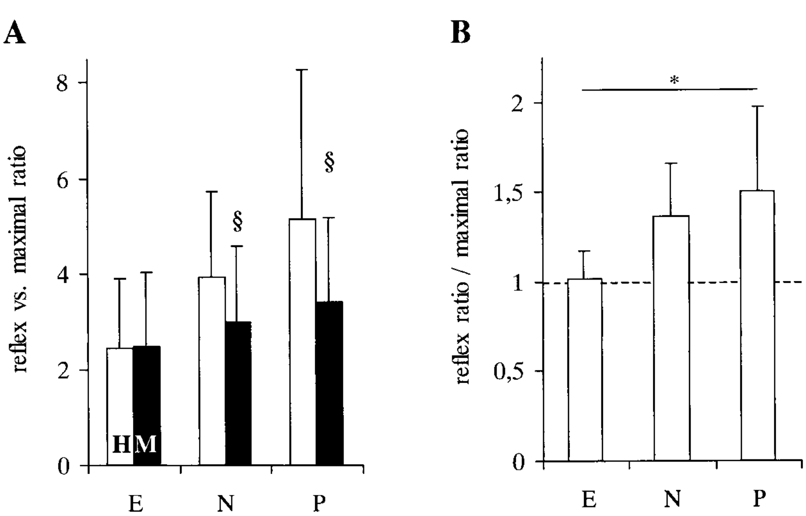

Fig. 4. *A*: ratio between twitch and EMG amplitudes for H_{max} (H; reflex ratio; open bars) and M_{max} (M; maximal ratio; solid bars) in E, N, and P. §Maximal ratio is significantly lower than reflex ratio (Student's paired *t*-test), $P < 0.05$. *B*: quotient between reflex and mechanical ratio. Dashed line is the identity line of Fig. 3 and corresponds to the hypothetical case in which the twitches evoked by the either wave are identical for identical wave amplitudes. *Significant difference between the mean ratios of power- vs. endurance-trained athletes (Newman-Keuls post hoc test), $P < 0.05$. All values are means of 8 subjects. Error bars correspond to SD.

afferent volley. The different motor-unit-type distribution would affect the efficacy of type Ia α-MN synapses (see Ref. 17). Power-trained athletes have been shown to have a predominance of fast-twitch (7) or type IIb muscle fibers (24), and it is known that fast motor units are less easily excited by the Ia afferent volley than are slow motor units (2). Nielsen et al. (19) have posited that, in ballet dancers, the Ia afferents were subjected to a large degree of presynaptic inhibition. Power-trained subjects would, therefore, also exhibit a lesser effect of type Ia excitatory input on slow MNs. On the other hand, soleus H_{max}/M_{max} were regularly found to be higher for endurance-trained subjects, both in the present investigation and in several previous studies (9, 15, 22).

To investigate better the characteristics of the force output of the reflex response and make inferences on the distribution and characteristics of motor unit types in power- and endurance-trained athletes, we studied the P_t values associated with soleus H_{max} in these groups and in nontrained subjects. We found that power-trained athletes exhibited the lowest H_{max} potential (about one-half that of the endurance counterparts) and generated the strongest H_{max} twitches. This result was somewhat surprising because we expected that the subjects having the greater reflex response (i.e., endurance-trained athletes) would develop the greater level of force and vice versa. However, this was in keeping with the value found for the P_t/EMG (i.e., the reflex ratio), which was the lowest in endurance- and the highest in power-trained athletes (see Fig. 4*A*).

Endurance training is known to increase muscle resistance to fatigue by inducing increases in mitochondrial content and volume and oxidative capacity in all muscle fiber types (11, 12) and by increasing the percentage of type I muscle fibers (10). It is well documented that endurance-type athletes possess a higher percentage of slow-twitch or type I fibers in their plantar-flexor muscles compared with their power-type counterparts (7) or untrained individuals (25). In our hands, endurance-trained athletes produced the smallest twitches with the lowest rate of twitch tension buildup and relaxation when stimulated at H_{max} intensity, thus indicating the preferential activation of the slow-twitch units (3, 5, 13, 18). Power-trained athletes showed the greatest peak reflex torque, as previously shown by Koceja and Kamen (14). The same results were obtained by stimulation of the entire pool of soleus motor units at M_{max} intensity. This was expected because the maximal M response activates few additional motor units with respect to the maximal H response and more particularly in the soleus muscle, so that the compound twitch torque obtained by stimulation of all motor units is dominated by the motor units normally activated by the reflex pathway. The present findings extend the conclusion of a recent investigation that focused on the M_{max} twitch characteristics of untrained subjects and endurance- and power-trained athletes (20). These authors associated the different twitch contractile properties observed in the three groups of subjects to the kinetics of the excitation-contraction coupling (including intracellular calcium movements), to the efficiency in the function of the sarcoplasmic reticulum, and to the binding of Ca^{2+} to myosin. It was concluded that long-term training (power or endurance type) resulted in a selective adaptation of the plantar-flexor muscle fibers. It is likely that the same changes occur also for the reflexly activated motor units.

Therefore, the slow-twitch fibers, which are those mostly recruited during submaximal exercise (1) that produce little force with respect to those recruited later during the buildup of force, apparently are not stronger in the athletes undergoing extensive endurance training. This conclusion becomes easily acceptable in view that what matters in these athletes, as much as in any subject and motor task, is the capacity to produce the force adequate to the task. As the force output of the product of the number of motor units by the force produced by each of them, endurance-trained athletes can produce the necessary force by recruitment of more slow-twitch units than can other subjects for comparable levels of force and type of task. What is then remarkable is that the enhanced excitability level of the pool makes this process automatic and effortless: the segmental Ia input, which is naturally boosted during the movement by the drive of the γ-MNs associated with the α-MN activation, adds to the descending command directed to the motor pool, thereby favoring the recruitment of the appropriate level of motor units and force. The notion that a greater monosynaptic excitability is associated with a lower level of force evoked reflexly in endurance-trained athletes becomes thus understandable on the basis of known physiological processes.

The above conclusions are based on the estimated H_{max} P_t. In the majority of our subjects, in fact, the H_{max} was preceded by a submaximal M wave, which affected the resulting mechanical response. We have provided evidence that the occurrence of this event led to significant overestimation of the P_t associated with H_{max} (see Table 1), and we have, therefore, deduced the relative mechanical contribution of the submaximal M wave preceding H_{max}. The equation used to correct for the M-wave contamination was obtained from a mixed population. As a check that it was applicable to the present three different groups of subjects, we calculated the ratio between the twitch and EMG amplitudes for the submaximal M wave preceding H_{max}. This proved to be nonsignificantly different in endurance-trained, nontrained, and power-trained subjects. The M wave preceding the H_{max} is mostly produced by the units innervated by the largest diameter motor axons, which are the most excitable by the electrical nerve stimulation. The mechanical contribution of the small M wave on the resulting P_t was similar across the three groups, thereby allowing the equation obtained from a mixed population to extend to all of our subjects. On the other hand, some caution should be exercised when the time-dependent properties associated with H_{max} twitch (i.e., CT, RD, and RR) are considered, because the possible influence of the M wave could not be corrected by the present method.

In conclusion, the findings of the present study have indicated that *1*) the soleus twitch contractile properties associated with both H_{max} and M_{max} were different between power- and endurance-trained athletes. In both cases, the former subjects produced stronger twitches with a higher rate of twitch tension buildup and relaxation than the latter. *2*) The twitch/EMG of the slow-twitch soleus motor units activated by the H_{max} was greater than the twitch/EMG of the entire pool (the M_{max}) in power-trained athletes. Endurance-trained athletes exhibited, instead, similar twitch/EMG for both H_{max} and M_{max}. By analyzing the relationship between both the mechanical and EMG ratios (H_{max}/M_{max}), it is interesting to notice that endurance-trained athletes, despite their EMG ratio, had no particularly stronger reflex contraction with respect to the other groups, which, in contrast, could reflexly generate more torque for a given EMG ratio. It seems, therefore, that power training increases the force output of the whole ensemble of motor units, herewith including the units that are the most excitable in response to the Ia afferent input, namely, the low-threshold, slow-twitch units. In fact, in the case of power-type training, the slow-twitch fibers are always active during submaximal exercise, whereas the fast-twitch fibers are additionally recruited as exercise approaches maximal intensity.

Finally, this study supports the concept that the type of contraction performed during long-term power or endurance training leads to appropriate matching of the nervous and mechanical properties.

We gratefully acknowledge the cooperation of all our subjects and the excellent technical assistance of Yves Ballay.

REFERENCES

1. **Abernethy PJ, Thayer R, and Taylor AW.** Acute and chronic responses of skeletal muscle to endurance and sprint exercise. *Sports Med* 10: 365–389, 1990.
2. **Almeida-Silveira MI, Pérot C, and Goubel F.** Neuromuscular adaptations in rats trained by muscle stretch-shortening. *Eur J Appl Physiol* 72: 261–266, 1996.
3. **Buchthal F and Schmalbruch H.** Contraction times of twitches evoked by H-reflex. *Acta Physiol Scand* 80: 378–382, 1970.
4. **Burke D, Gandevia SC, and McKeon B.** Monosynaptic and oligosynaptic contributions to human ankle jerk and H-reflex. *J Neurophysiol* 52: 435–448, 1984.
5. **Calancie B and Bawa P.** Motor unit recruitment in humans. In: *The Segmental Motor Systems*, edited by Binder MD and Mendell LM. Oxford, UK: Oxford Univ. Press, 1990, p. 75–95.
6. **Casabona A, Polizzi MC, and Perciavalle V.** Differences in H-reflex between athletes trained for explosive contractions and non-trained subjects. *Eur J Appl Physiol* 61: 26–32, 1990.
7. **Clarkson PM, Kroll W, and McBride TC.** Plantar flexor fatigue and muscle fiber type in power and endurance trained athletes. *Med Sci Sports Exerc* 12: 262–267, 1980.
8. **Dawson B, Fitzsimons M, Green S, Goodman C, Carey M, and Cole K.** Changes in performance, muscle metabolites, enzymes and fibre types after short sprint training. *Eur J Appl Physiol* 78: 163–169, 1998.
9. **Ginet J, Guiheneuc P, Prévot M, and Vecchierini-Blineau F.** Etude comparative du recrutement de la réponse réflexe monosynaptique du soléaire (réflexe H) chez des sujets non entraînés et chez des sportifs. *Med Sport* 49: 55–64, 1975.
10. **Goubel F and Marini JF.** Fibre type transition and stiffness modifications of soleus muscle of trained rats. *Pflügers Arch* 410: 321–325, 1987.
11. **Holloszy JO and Booth FW.** Biochemical adaptations to endurance exercise in muscle. *Annu Rev Physiol* 38: 273–291, 1976.
12. **Howald H, Hoppeler H, Claassen H, Mathieu O, and Straub R.** Influences of endurance training on the ultrastructural composition of the different muscle fiber types in humans. *Pflügers Arch* 403: 369–376, 1985.
13. **Hugon M.** Methodology of the Hoffmann reflex in man. In: *New Developments in Electromyography and Clinical Neurophysiology*, edited by Desmedt JE. Basel: Karger, 1973, vol. 3, p. 277–293.
14. **Koceja DM and Kamen G.** Conditioned patellar tendon reflexes in sprint- and endurance-trained athletes. *Med Sci Sports Exerc* 20: 172–177, 1988.
15. **Le Bars R and Toulouse P.** Le réflexe "H" chez les sprinters et les coureurs de demi-fond: premiers résultats. *Cinésiologie* 13: 283–286, 1974.
16. **Maffiuletti NA, Martin A, Van Hoecke J, and Schieppati M.** The relative contribution to the plantar-flexor torque of the soleus motor units activated by the H reflex and M response in humans. *Neurosci Lett* 288: 127–130, 2000.
17. **Munson JB.** Synaptic inputs to type-identified motor units. In: *The Segmental Motor Systems*, edited by Binder MD and Mendell LM. Oxford, UK: Oxford Univ. Press, 1990, p. 291–307.
18. **Nardone A and Schieppati M.** Shift of activity from slow to fast muscle during voluntary lengthening contractions of the triceps surae muscles in humans. *J Physiol (Lond)* 395: 363–381, 1988.
19. **Nielsen J, Crone C, and Hultborn H.** H-reflexes are smaller in dancers from the Royal Danish Ballet than in well-trained athletes. *Eur J Appl Physiol* 66: 116–121, 1993.
20. **Pääsuke M, Ereline J, and Gapeyeva H.** Twitch contractile properties of plantar flexor muscles in power and endurance trained athletes. *Eur J Appl Physiol* 80: 448–451, 1999.
21. **Pérot C, Goubel F, and Mora I.** Quantification of T and H responses before and after a period of endurance training. *Eur J Appl Physiol* 63: 368–375, 1991.
22. **Rochcongar P, Dassonville J, and Le Bars R.** Modification of the Hoffmann reflex in function of athletic training. *Eur J Appl Physiol* 40: 165–170, 1979.
23. **Schieppati M.** The Hoffmann reflex: a means of assessing spinal reflex excitability and its descending control in man. *Prog Neurobiol* 28: 345–376, 1987.
24. **Staron RS, Hikida RS, Hagerman FC, Dudley GA, and Murray TF.** Human skeletal muscle fiber type adaptability to various workloads. *J Histochem Cytochem* 32: 146–152, 1984.
25. **Trappe SW, Costill DL, Fink WJ, and Pearson DR.** Skeletal muscle characteristics among distance runners: a 20-yr follow-up study. *J Appl Physiol* 78: 823–829, 1995.