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Changes in H reflex and V wave following short-term endurance and strength training

Carolina Vila-Chã,[1,2] Deborah Falla,[3,4] Miguel Velhote Correia,[2] and Dario Farina[3]

[1]*Polytechnic Institute of Bragança, Bragança;* [2]*Universidade do Porto, Faculdade de Engenharia, Porto, Portugal;* [3]*Department of Neurorehabilitation Engineering, Bernstein Center for Computational Neuroscience, University Medical Center Göttingen, Georg-August University; and* [4]*Pain Clinic, Center for Anesthesiology, Emergency and Intensive Care Medicine, University Hospital Göttingen, Göttingen, Germany*

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Vila-Chã C, Falla D, Correia MV, Farina D. Changes in H reflex and V wave following short-term endurance and strength training. *J Appl Physiol* 112: 54–63, 2012. First published October 13, 2011; doi:10.1152/japplphysiol.00802.2011.—This study examined the effects of 3 wk of either endurance or strength training on plasticity of the neural mechanisms involved in the soleus H reflex and V wave. Twenty-five sedentary healthy subjects were randomized into an endurance group (n = 13) or strength group (n = 12). Evoked V-wave, H-reflex, and M-wave recruitment curves, maximal voluntary contraction (MVC), and time-to-task-failure (isometric contraction at 40% MVC) of the plantar flexors were recorded before and after training. Following strength training, MVC of the plantar flexors increased by 14.4 ± 5.2% in the strength group ($P < 0.001$), whereas time-to-task-failure was prolonged in the endurance group (22.7 ± 17.1%; $P < 0.05$). The V wave-to-maximal M wave (V/M_{max}) ratio increased significantly (55.1 ± 28.3%; $P < 0.001$) following strength training, but the maximal H wave-to-maximal M wave (H_{max}/M_{max}) ratio remained unchanged. Conversely, in the endurance group the V/M_{max} ratio was not altered, whereas the H_{max}/M_{max} ratio increased by 30.8 ± 21.7% ($P < 0.05$). The endurance training group also displayed a reduction in the H-reflex excitability threshold while the H-reflex amplitude on the ascending limb of the recruitment curve increased. Strength training only elicited a significant decrease in H-reflex excitability threshold, while H-reflex amplitudes over the ascending limb remained unchanged. These observations indicate that the H-reflex pathway is strongly involved in the enhanced endurance resistance that occurs following endurance training. On the contrary, the improvements in MVC following strength training are likely attributed to increased descending drive and/or modulation in afferents other than Ia afferents.

maximal voluntary contraction; evoked potentials; neural adaptations

THE HUMAN NERVOUS SYSTEM IS highly adaptive in response to training (2). Neural adaptations occur in response to both endurance (34, 39) and strength training (1, 7, 8, 10, 11, 27, 39) and are thought to contribute to enhanced motor performance (11, 34). Although efforts have been made to elucidate the mechanisms underlying these adaptations, the results are not clear (5, 11). The sites and mechanisms underlying neural adaptations to motor training can be investigated by measuring reflex responses in particular the H reflex and V wave (1, 7, 11, 15, 18, 34). Although these evoked responses are affected by common neural mechanisms, during voluntary contractions, the H reflex is more sensitive to altered presynaptic inhibition and motoneuron excitability (11, 19, 29, 31, 36), whereas the V wave is more sensitive to changes in supraspinal input to the motor neuron pool (1, 9, 38). Thus combined measures of the H reflex and V wave may provide a better understanding of the neural adaptations elicited by specific motor training programs.

A number of cross-sectional studies have shown that the H-reflex excitability measured at rest is higher in endurance-trained athletes than in power-trained athletes (6, 25, 28, 32, 37) and lower in power-trained athletes than in sedentary people (6). Another study (30) reported that H-reflex excitability was higher in moderately and well-trained individuals compared with sedentary people but was lowest in a group of ballet dancers. Taken together, these observations suggest that spinal reflex circuits adapt specifically to the training demands. However, results from cross-sectional studies should be interpreted with caution since it is not possible to fully dissociate intrinsic genetic endowment from actual training adaptations (1, 40).

Reflex investigations have been performed in few longitudinal strength training studies. Some studies have reported increases in the V wave, without changes of the H reflex (7, 11–13), while others observed increases in both V-wave and H-reflex responses (1). The different results may be attributed to diverse training protocols and/or methodological approaches (5, 7). The only longitudinal study on the effects of endurance training on the size of the H reflex revealed that 75% of the subjects increased both spinal excitability and maximal aerobic capacity, while for the remaining participants these variables were barely modified or even decreased (34). The heterogeneity of the results was likely due to differences in the subject's fitness level and/or the subject's involvement in other sport activities (34).

Understanding the extent to which the nervous system can adapt to specific motor training programs is of extreme importance in both rehabilitation and exercise training (41). However, based on the current literature it is difficult to compare and interpret training-induced neural adjustments since studies have employed subjects with different physical fitness levels and applied different experimental methodologies, which contributes to the observed discrepancies between studies. To overcome this limitation, we selected to investigate, longitudinally, spinal reflex plasticity in two training groups with similar baseline characteristics, using the same experimental methodology so that the adaptations to motor training could be directly compared. Thus the present study intended to investigate if endurance and strength training induce parallel changes in motor performance and H-reflex and V-wave responses during voluntary contractions of the soleus muscle and, if so,

Address for reprint requests and other correspondence: D. Farina, Dept. of Neurorehabilitation Engineering, Bernstein Center for Computational Neuroscience, Georg-August Univ. of Göttingen, Von-Siebold-Str. 437075 Göttingen, Germany (e-mail: dario.farina@bccn.uni-goettingen.de).

whether there are associations between changes in motor performance (maximal strength and resistance to fatigue) and changes in reflex responses.

METHODS

Subjects

Twenty six healthy volunteers (4 women and 22 men; age: 24.0 ± 2.6 yr; means ± SD) with no history of lower limb disorders participated in the study. None of the subjects were involved in regular strength or endurance training. All participants gave their informed written consent before inclusion in the study. The study was approved by the local ethics committee (N-20090032) and conducted in accordance with the Declaration of Helsinki.

Once the baseline measures were completed, the subjects were matched in pairs based on their age, sex, and fitness level and from each pair one subject was randomly allocated to the endurance and one to the strength training group.

Study Design

The subjects participated in three laboratory sessions, on 3 separate days, and in nine training sessions over a 3-wk training period (3/wk). A short period of training was chosen since neural adaptations to training can be observed within a few sessions of training (7, 39) and a short duration of training would limit the bias of potential peripheral adaptations on neural responses (7). To assess day-to-day variability, two laboratory sessions were completed 1–2 wk before training (PRE-S1and PRE-S2), with at least 3 days between sessions. The subjects performed the last laboratory session (POST) 24 to 48 h after the last training session.

Training Programs

For both endurance and strength training programs, the load intensity increased progressively over the 3-wk period. The load was continuously monitored to keep the intensity at the required level. All training sessions were supervised by an investigator of the study.

Endurance training. Endurance training was performed on a cycle ergometer and the exercise intensity was prescribed based on the percentage of the heart rate reserve (HRR) according to the Karvonen method (20). Each subject maintained the exercise intensity within the required target heart rate range (THRR) by using a pulse meter during the training sessions. During the first week of training, THRR was set between 55 and 65% of the HRR, and each training session lasted 30–40 min. On *weeks 2* and *3*, the duration of the training sessions was 40–50 min and the THRR was 60–75 and 65–75% of the HRR, respectively.

Strength training. The strength training program included three bilateral leg exercises (leg press, seated calf raise, and calf raise on the leg press) and four extra exercises for the main muscle groups of the trunk and upper body [lateral pull down, bench press, and exercise for the trunk flexors and for extensors (abdominal crunch and back extensions)]. To avoid muscle soreness and to get the subjects familiarized with the lateral pull down, bench press, and lower limb exercises, in the first week the load intensity used varied between 60 and 65% of the one-repetition maximum (1RM) and the number of repetitions between 15 and 18 repetitions, performed over 3 sets. On the *week 2*, the load intensity for the lower limb exercises ranged between 65 and 70% of the 1RM and the participants performed 3 sets of 13–15 repetitions and on the last week the load intensity varied between 70–80% of the 1RM, performed over 3 sets of 8–12 repetitions. For the lateral pull down and bench press exercises, the load intensity used in the last 2 wk was 65–70% of the 1RM, performed over 2–3 sets of 15–18 repetitions. The subjects finalized each training session with abdominal crunch and back extensions exercises performed over 2–3 sets of 15–20 repetitions, with no additional load.

Instrumentation

All tests were performed on the right leg while the subjects were comfortably seated in an Isokinetic dynamometer (KinCom Dynamometer, Chattanooga, TN) with their trunk, hips, and right thigh firmly strapped to an adjustable chair. The subjects maintained their hips and knee flexed at 120° and ankle at 110° of plantar flexion. The right foot was firmly attached to a force plate mounted in the dynamometer. The foot plate was adjusted so that the lateral malleolus was aligned with the rotational axis of the dynamometer. Particular care was taken to monitor the posture of the subjects. During reflex testing, all subjects were asked to focus on the task and to not alter their posture.

Surface EMG. Surface EMG signals were recorded from the tibialis anterior (TA) and soleus (SOL) muscles with Ag-AgCl electrodes (Ambu Neuroline 720; Ambu, Ballerup, Denmark; conductive area: 28 mm^2 and interelectrode distance: 20 mm), located as recommended by Hermens et al. (17). Before electrode placement, the skin was shaved, lightly abraded, and cleansed with water. A ground electrode was placed around the right ankle. Surface EMG signals were amplified as bipolar derivations (custom-built EMG amplifier), band-pass filtered (−3 dB bandwidth, 10–2,000 Hz), sampled at 10,000 samples/s, and converted to digital data by a 12-bit A/D converter board.

Stimulation. The H, M, and V waves of the SOL muscle were elicited by stimulation of the common posterior tibial nerve. The electrical stimulus was provided by an isolated stimulator (Noxitest IES 230). A monopolar stimulation of the common posterior tibial nerve of the right leg was elicited by a cathode (custom-built silver ball with 10-mm diameter) located in the popliteal fossa and the anode (PALs platinum rectangular electrode, 75 × 100 mm; Axelgaard Man) proximal to the patella. Before the cathode electrode placement, the optimal position was identified using a handheld cathode ball electrode (10-mm diameter). The position eliciting the greatest response with the minimum stimulus intensity was chosen.

Experimental Procedures

During laboratory sessions, the subject was comfortably seated in the isokinetic dynamometer as described above. The subject's position was saved in the dynamometer device to maintain similar postures over experimental sessions. After placement of the surface electrodes, the subjects performed a warm-up that consisted of multiple submaximal isometric contractions of the plantar flexors [3–4 repetitions at ~50% maximal voluntary contractions (MVC)] and then the following measures were collected.

Strength. The subjects performed three progressive MVCs of the plantar flexors of 5 s of duration, separated by 2-min rest. Subjects were verbally encouraged to produce maximal force, and visual feedback was displayed by a moving bar on a computer monitor. The highest plantar flexor MVC in each experimental session was used to compute the submaximal target force levels.

H- and M-recruitment curve recordings. The motor response (M wave) and H reflex of the SOL muscle were elicited while the subject was performing a low-level tonic contraction of the plantar flexors (10% MVC). Subjects were provided with online feedback of the force exerted, which was displayed on a computer monitor. The testing procedure and recordings started by progressively increasing the current intensity in 5-mA increments until both peak-to-peak amplitude of the M wave and peak of the twitch force reached their maximum size during rest condition. A total of three trials at each current intensity were recorded. Then, at each current intensity, the preceding M-wave peak-to-peak amplitude was compared with the new M-wave peak-to-peak amplitude. Once the preceding M-wave peak-to-peak amplitude and new M-wave peak-to-peak amplitude had reached a plateau over the three trials, the current intensity of the previous stimulation was considered the maximum current intensity. Then, the upper current intensity used was 5 mA higher than necessary to elicit the maximal M wave to ensure that the last two points of the H- and M-recruitment curve represented the plateau of the M-wave amplitude and no further increments of the M wave could be observed. To construct the M- and H-recruitment curves, the upper current intensity was divided into 22 segments that were equally separated on a logarithmic scale (3). For each current intensity, a total of 16 stimuli were delivered at random time intervals between 2 and 3 s. To avoid fatigue and mental distraction of the participants, rest periods of 2 min were given every 88 stimuli. Moreover, the subjects were given the possibility to pause the experiment at any time if they reported fatigue.

Contractile properties. Maximal twitch amplitude, time to peak, and half-relaxation time were measured from the twitch evoked by supramaximal electrical stimulation. After H-M measurements, four single pulses (1-ms square pulse) at supramaximal intensity (150% of the current needed to evoke peak twitch amplitude) were delivered to the tibial nerve every 5–7 s.

V-wave recordings. The subjects were asked to perform 7–10 progressive MVCs of ~5 s duration, with 2 min of rest in between. During the progressive contraction, a supramaximal stimulus (150% of the current needed to evoke maximal M wave; 1-ms square pulse) was applied to the tibial nerve at the instant that the force exceeded 90% of the MVC (1).

Time-to-task-failure. Resistance to fatigue was assessed by performing a sustained contraction at 40% MVC. The subjects were asked to maintain the isometric contraction of the plantar flexors for as long as possible. Task failure was defined as a drop in force greater than 10% of the target force level for >5 s, after strong verbal encouragement to the subject to maintain the target force.

Data Analysis

Evoked potentials. Peak-to-peak amplitude of the H reflex, M wave, and V wave was computed offline from the unrectified EMG signals. To reduce inter-subject variability, H, M, and V waves were normalized to the corresponding maximal M wave (M_{max}) and the maximal M wave (H_{max})/M_{max} and V/ M_{max} ratios were computed. For each recruitment curve, the current intensity at H_{max} and M_{max} was identified. Since the size of the M wave is affected by contraction intensity (33), the M_{max} wave elicited concomitantly either with H reflex or V wave was used for the respective normalization.

The ascending part of recruitment curve was fit by a general least squares model, as described by Klimstra and Zehr (23). From the curve fit analysis, the following parameters were analyzed: current intensity at H-reflex threshold (H_{thresh}); current intensity at 50% of the H_{max} (50%H_{max}) and; the slope of the ascending limb of the recruitment curve at 50% of the H_{max} (H_{slope}) (Fig. 1). Additionally, the relative current intensities coinciding with the H-reflex variables computed from the PRE-S1 recruitment curves were utilized as inputs to the equations describing the PRE-S2 and POST training recruitment curves. According to Darget and Zehr (8), this procedure is more sensitive for detecting training-induced changes since it allows comparison of reflex amplitudes at the same relative current intensities. To differentiate the reflex parameters obtained from the fitted curves and from the standard recruitment curve, the predicted parameters are identified with "@", as earlier defined by Klimstra and Zehr (23). Only the recruitment curves with the r square > 0.90 were used for analysis.

Surface EMG background level. Average rectified value (ARV) of the SOL EMG was estimated from each sweep for an epoch of 500 ms before the stimulation and then averaged. The ARV values were normalized with respect to the ARV computed from the highest MVC and expressed as a percentage. During the MVCs performed with supramaximal stimulation, the EMG was analyzed over a 500-ms period before stimulation and then normalized to the corresponding amplitude of the M_{max}. The level of co-activation was quantified by computing the ratio between the agonist (SOL) and antagonist (TA) EMG ARV and multiplying by 100.

Statistical Analysis

Before statistical comparison, all data were tested for normal distribution by a Kolmogorov-Smirnov test. All pre- to posttraining changes were evaluated using a two-way repeated-measures ANOVA with factors group (endurance and strength) and session (PRE-S1, PRE-S2, and POST). For multiple comparison analysis, post hoc Student-Newman-Keuls test was used when ANOVA was significant. Statistical significance was set at $P < 0.05$ for all comparisons.

Results are reported as means and SD in the text and means and SE in the figures. To investigate associations between the variables

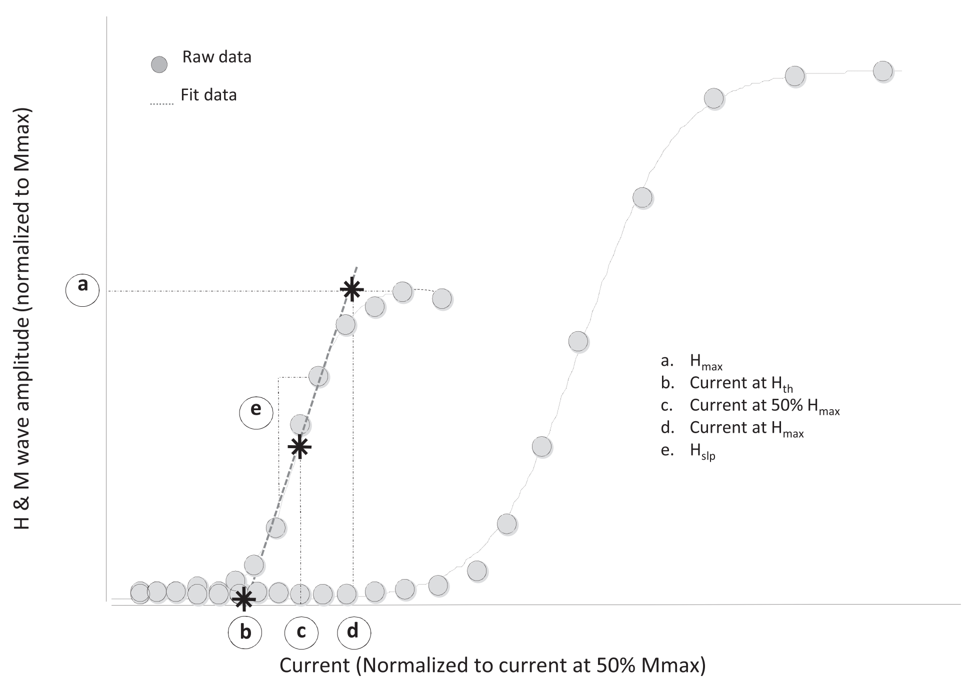

Fig. 1. Representation of the H-reflex parameters investigated in this study. Parameters are taken from the ascending limb of the H-reflex recruitment curve. The following parameters were analyzed: maximum amplitude of the H-reflex (H_{max}; *a*); current intensity at H-reflex threshold (H_{thresh}; *b*); current intensity at 50% of the H_{max} (50%H_{max}; *c*); current intensity at H_{max} (*d*); and the slope of the ascending limb of the recruitment curve at 50% of the H_{max} (H_{slope}; *e*).

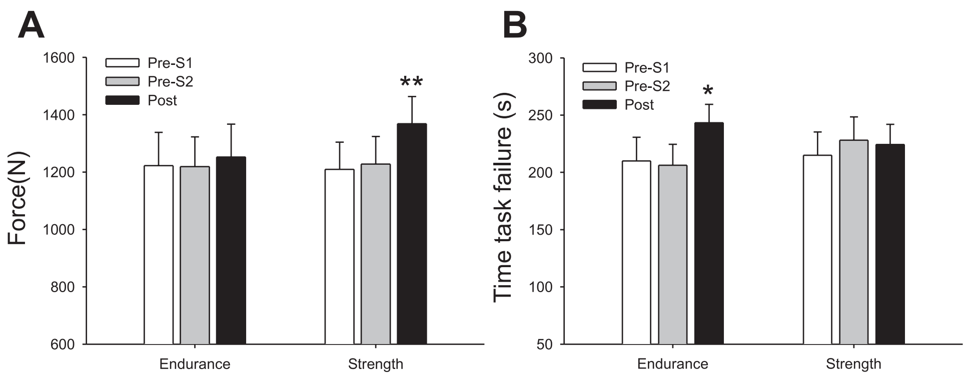

Fig. 2. Changes in motor performance following 3 wk of strength or endurance training. Values are means ± SE. *A*: maximal voluntary contraction (MVC) of the plantar flexors. *B*: time to task failure assessed during isometric contractions at 40% MVC. $*P < 0.05$ and $**P < 0.01$, when comparing after (POST) to before (PRE-S1 and PRE-S2) training.

affected by training a multiple regression was performed with changes in the evoked potentials parameters as the independent variables and maximal strength or time-task-failure as dependent variables. The regressions were performed separately for each training group.

RESULTS

One subject from the strength group did not complete the final laboratory session and was excluded from the analysis. Therefore, the results are presented for 12 subjects in the strength group (age, 23.6 ± 2.2 yr; height, 177.5 ± 8.7 cm; and weight, 73.2 ± 13.5 kg) and 13 subjects in the endurance group (age, 24.4 ± 3.8 yr; height, 176.5 ± 10.5 cm; and weight, 76.5 ± 13.6 kg). No differences were observed between groups for any of the anthropometrical characteristics, motor output, or electrophysiological parameters assessed in the PRE-S1 and PRE-S2 sessions.

Motor Performance

During the first two sessions, neither MVC nor time-to-task-failure was altered in either training group ($P > 0.87$; Fig. 2). Following 3 wk of training the MVC increased by 14.4 ± 5.2% in the strength training group ($P < 0.0001$), whereas no significant change in MVC was observed for the endurance group ($P > 0.68$; Fig. 2). Conversely, the time-to-task-failure increased by 22.7 ± 17.1% following endurance training ($P < 0.05$) and was not affected by strength training ($P > 0.68$; Fig. 2).

Contractile Properties

There were no main effects or interaction between group and session for the contractile parameters analyzed in this study ($P > 0.13$ for all conditions and parameters). Across the three laboratory sessions the averaged value of each group for the maximal twitch amplitude ranged between 117.3 ± 32.5 and 121.3 ± 46.4 N ($P > 0.80$ for all conditions), for the time to peak force ranged between 89.3 ± 6.3 and 92.6 ± 9.1 ms ($P > 0.43$ for all conditions), and for the half-relaxation time varied between 254.8 ± 18.2 and 263.7 ± 21.1 ms ($P > 0.28$ for all conditions).

Evoked Potentials

The peak-to-peak amplitude of the SOL maximal compound action potential (M_{max}) did not change significantly following training ($P > 0.52$ for all conditions; see Table 1) and was not different between the two baseline sessions (PRE-S1and PRE-S2; $P > 0.22$ for all parameters).

V-wave amplitudes during MVC. Figure 3 shows representative V waves for one subject of the endurance group and one of the strength group pre- and posttraining. In these examples, the V wave increased following strength training while it did not change substantially following endurance training. This result was confirmed by the group analysis. There was a significant interaction between session and group for the normalized V-wave amplitude (V/M_{max}) assessed during MVC ($P < 0.01$).

Table 1. *M_{max}, H_{max}, and H_{slope} normalized to current at 50%M_{max} at H_{thresh}, at 50% of H_{max}, and at H_{max}, soleus EMG activity during MVC and soleus EMG background during the low-level tonic contractions*

Parameters	Endurance Group			Strength Group		
	PRE-S1	PRE-S2	POST	PRE-S1	PRE-S2	POST
M_{max}, mV	7.0 ± 2.7	6.5 ± 1.5	7.2 ± 1.9	7.1 ± 4.0	7.2 ± 4.1	6.9 ± 3.6
H_{max}, %M_{max}	43.7 ± 16.2	43.6 ± 14.5	54.3 ± 14.2*	53.7 ± 10.9	50.5 ± 11.7	52.2 ± 12.0
H_{slope}, mV/s	2.3 ± 0.7	2.2 ± 0.9	3.1 ± 1.0*	2.9 ± 1.3	2.8 ± 1.4	2.5 ± 1.1
Current at H_{thresh}, %current at 50%M_{max}	50.5 ± 8.2	49.1 ± 6.9	46.0 ± 7.0†	47.4 ± 5.6	47.6 ± 6.6	45.4 ± 6.9†
Current at 50%H_{max}, %current at 50% M_{max}	61.1 ± 7.9	59.6 ± 7.4	55.4 ± 6.5‡	57.8 ± 6.0	56.4 ± 7.2	55.3 ± 7.7
Current at H_{max}, %current at 50% M_{max}	71.9 ± 8.7	70.3 ± 7.5	65.5 ± 7.1*	68.6 ± 8.6	66.9 ± 8.4	66.1 ± 9.2
Soleus EMG						
MVC, %M_{max}	2.3 ± 0.5%	2.4 ± 0.5%	2.5 ± 0.6%	2.5 ± 0.6%	2.5 ± 0.8%	3.2 ± 1.5%δ
Background, %MVC	24.8 ± 8.4%	26.6 ± 7.3%	28.0 ± 7.8%	24.3 ± 5.7%	25.2 ± 6.2%	27.2 ± 11.3%

Data are means ± SD. M_{max}, maximal M wave; H_{max}, maximal H reflex; H_{slope}, slope of the ascending limb of the recruitment curve at 50% of the H_{max}; H_{thresh}, current intensity at H-reflex threshold; MVC, maximal voluntary contraction. $*P < 0.05$, when comparing after (POST) to before (PRE-S1 and PRE-S2) training. †$P < 0.05$, main effect for session when comparing POST to PRE-S1. ‡$P < 0.01$, when comparing POST to PRE-S1, and $P < 0.05$, when comparing POST to PRE-S2. δ$P < 0.01$ when comparing POST to PRE-S1 and PRE-S2 training.

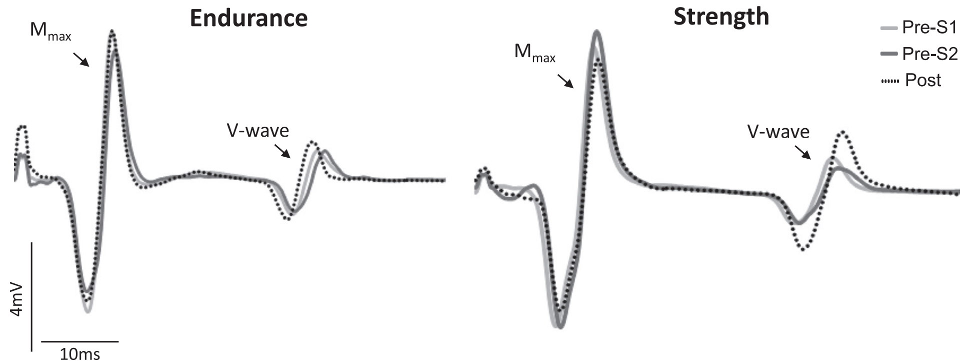

Fig. 3. Evoked V-wave before (PRE-S1 and PRE-S2) and after (POST) training for a representative subject of the endurance and strength training group.

Following strength training the V/M_{max} ratio increased in average by 55.1 ± 28.3% compared with pretraining sessions ($P < 0.001$ when compared POST to PRE-S1 and PRE-S2). For the endurance group, the V/M_{max} ratio did not change significantly over time ($P > 0.34$; Fig. 4).

Low-level tonic contractions and H-reflex parameters. Figure 5 illustrates the M-wave and H-reflex recruitment curve for one subject of the endurance group and one of the strength group, pre- and posttraining. In these examples, the endurance training elicited an increase H-reflex excitability, while in the strength training only slight changes can be observed at H_{thresh}. These observations were confirmed by the group analysis. A significant increment of the SOL H-reflex amplitude was observed following endurance training but not strength training (interaction between group and session: $P < 0.05$; Fig. 5; Table 1).

Since the M_{max} did not change for either training group (Table 1), the endurance group also revealed changes in the H_{max}/M_{max} ratio, which were not observed in the strength training group (interaction between group and session: $P < 0.001$; Fig. 5). Following endurance training, the H_{max}/M_{max} ratio increased by 30.8 ± 21.7%, compared with pretraining sessions ($0.001 < P < 0.05$; Fig. 6).

Similarly, the slope of the ascending limb of the H_{slope} was only affected by the endurance training intervention (interaction between group and session: $P < 0.01$; see Table 1). After 3 wk of endurance training, a significant increment of the H_{slope} was observed compared with both pretraining sessions ($P < 0.05$ compared with both pretraining sessions; see Table 1).

A session effect was obtained for the normalized H_{thresh} ($P < 0.01$; Table 1). Following both endurance and strength training, the H_{thresh} was significantly lower than at the pretraining sessions (−7.7 ± 7.1% and −4.7 ± 6.7%, respectively; $0.01 \leq P < 0.05$ for all conditions; Table 1). An interaction between group and session was observed for the 50%H_{max} and at H_{max} ($P < 0.05$ for both parameters; Table 1).

The normalized current intensity required to evoke 50%H_{max} and the H_{max} was significantly reduced following endurance training (on average −8.6 ± 6.2%) compared with the pretraining sessions (for both parameters: $P < 0.01$ compared with pretraining sessions; see Table 1). Both 50%H_{max} and H_{max} parameters were not affected by strength training ($P > 0.59$ for all conditions).

Figure 7 illustrates the predicted H-reflex amplitudes evoked by the current intensities associated to the H_{thresh}, intensity at 50%H_{max} and at H_{max} observed before training. The predicted values are distinguished by "@".

The $H_{@thresh}$ was significantly affected by both training programs (main effect session: $P < 0.001$; Fig. 7*A*), but no interaction between group and session was observed ($P = 0.26$). Compared with the pretraining session, the $H_{@thresh}$ increased by 182.6 ± 121.4% and by 105.6 ± 88.9% following endurance and strength training, respectively ($0.0001 < P < 0.001$ for all conditions; Fig. 7 A). For the 50%$H_{@max}$ and $H_{@max}$ parameters, an interaction between group and session was observed ($P < 0.05$ for both parameters; Fig. 7, *B* and *C*). After 3 wk of endurance training, the 50%$H_{@max}$ was on average 80.7 ± 42.6% greater than in the pretraining sessions ($0.001 < P < 0.05$; Fig. 6*B*). Further, the $H_{@max}$ observed following endurance training increased by 60.2 ± 34.8% compared with pretraining values ($P < 0.05$; Fig. 7*C*). No

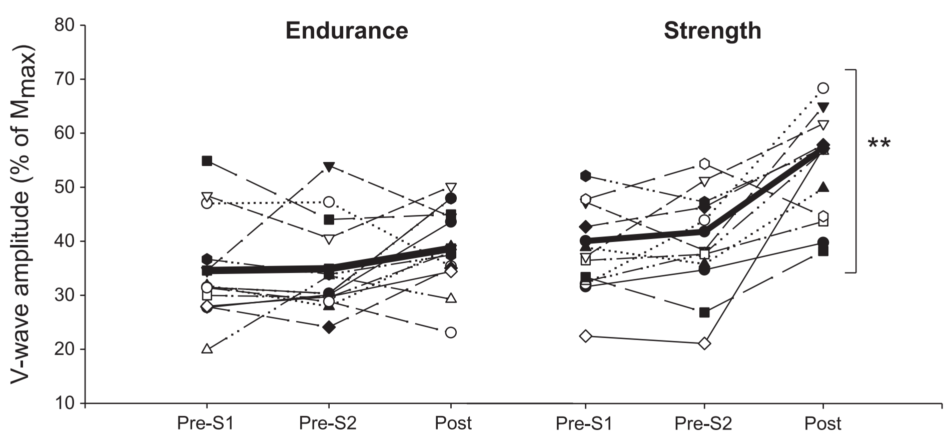

Fig. 4. V-wave peak-to-peak amplitude normalized to maximal M wave (M_{max}) measured during maximal isometric contraction of the plantar flexors before (PRE-S1 and PRE-S2) and after (POST) training. Each line represents 1 subject. Thick black line represents the mean of the group. $^{**}P < 0.001$, when comparing POST to PRE-S1 and PRE-S2 in the strength group.

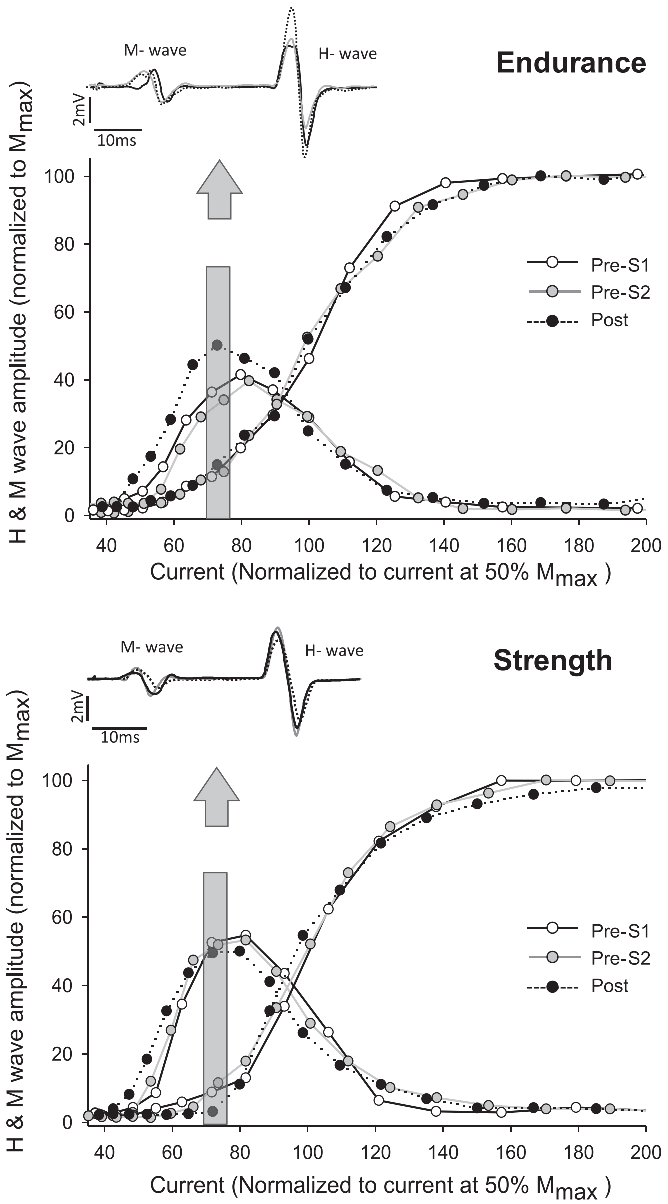

Fig. 5. H and M-wave recruitment curves before (PRE-S1 and PRE-S2) and after (POST) training for a representative subject of the endurance and strength training group. Abscissa represents the stimulation intensity normalized to the current at 50%M_{max}, and ordinate illustrates response amplitude normalized to the corresponding M_{max}. In the left superior corner is represented the average of 8 H and M waves evoked by a current of 70–75% of 50%M_{max}, before [PRE-S1 (black solid line) and PRE-S2 (gray solid line)] and after [POST (black dotted line)].

changes of the 50%$H_{@max}$ and $H_{@max}$ parameters were observed with strength training.

EMG activity and background level. During the MVC, the SOL normalized EMG was only affected by the strength training program (interaction between group and session: $P < 0.05$, Table 1). Following strength training, the SOL normalized EMG was significantly higher compared with baseline ($P < 0.01$; Table 1).

The background EMG level of the SOL muscle during the low-level tonic contractions was not affected by either training program ($P > 0.12$ for all conditions, Table 1). Moreover, the level of coactivation was not affected by training ($P > 0.45$). For the endurance group, the coactivation ratio in the PRE-S1, PRE-S2, and POST sessions was 38.1 ± 10.9, 39.2 ± 13.4, and 35.5 ± 11.6% and for strength training, it was 42.0 ± 11.6, 39.3 ± 9.9, and 38.9 ± 14.6%, respectively.

Associations Between Changes in Strength, Resistance to Fatigue, and Evoked Potential Parameters

For the strength training data, we examined the association between changes in maximal force and V/M_{max} ratio, while for endurance training the association between changes in time-to-task-failure and changes in parameters obtained from the fitted curves ("@"parameters) and from the standard recruitment curve (H_{max}/M_{max}; H_{slope} and H_{thresh}; 50%H_{max}; H_{max}) were examined.

A significant association ($P < 0.01$) was observed between the increase in MVC and increase in V/M_{max} ratio [$\beta = 0.23$; $F(1,3) = 4.25$; adjusted $R^2 = 0.20$] for the strength training group. In the endurance training group, the multiple linear regression showed a significant association between the increase in time-to-task-failure and increase in @$H_{thresh,}$ in @50%H_{max} and in @H_{max} [$\beta = 0.32$, $\beta = 0.05$, and $\beta = 0.26$, respectively; $P < 0.01$; $F(3,3) = 4.7$; adjusted $R^2 = 0.24$]. However, no associations were found between the increase in time-to-task-failure for the endurance group and changes in H_{max}/M_{max}; H_{slope} and H_{thresh}; 50%H_{max}; H_{max}.

DISCUSSION

This study investigated spinal reflex plasticity following 3 wk of either endurance or strength training. For the first time, these changes were concurrently investigated in two training groups with similar characteristics, so that a direct comparison of the neural adaptations was possible. The results show that improvement in time to task failure following endurance training is accompanied by significant changes of the H-reflex recruitment curve whereas no changes in the V/M_{max} ratio are observed. Conversely, following strength training, an increase of the MVC occurs and is accompanied by a significant increase of the V/M_{max} ratio whereas changes in the H-reflex recruitment curve were only observed at H_{thresh}.

Motor Performance

Strength and endurance training result in specific adaptations of motor performance. Following endurance training, the resistance to fatigue increased while the maximal strength of the plantar flexors did not change and strength training improved MVC of the plantar flexors resistance to fatigue remained unchanged.

The results showed that 24% of the improvement in resistance to fatigue could be explained by increased H-reflex excitability, while the increase in V/M_{max} ratio explained 20% of the improvement in MVC. Few other studies have shown positive associations between measures of motor performance and the degree of spinal excitability (11, 34). Ekblom (11) found that 66% of the improvement in maximal isometric force of the plantar flexors following 5 wk of dynamic strength training was explained by increased voluntary activation and V/M_{max} ratios. The only longitudinal study (34) on endurance training and reflex excitability has shown that following 8 wk of training, 75% of the subjects presented positive associations

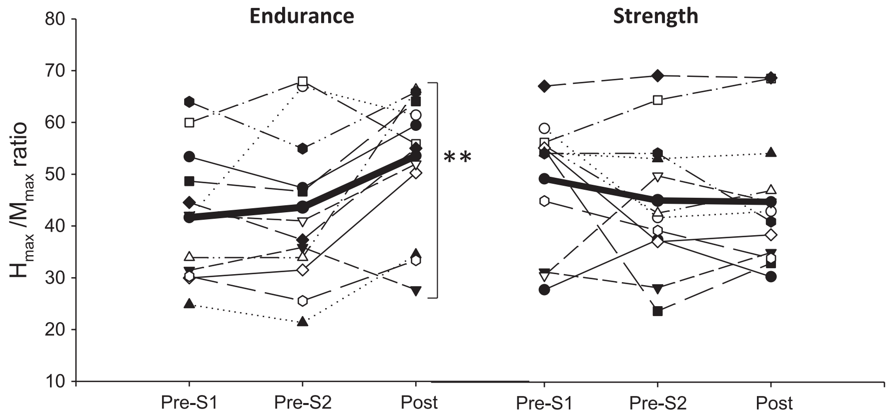

Fig. 6. H_{max}/M_{max} ratios measured during isometric contractions of the plantar flexors at 10% of MVC before (PRE-S1 and PRE-S2) and after (POST) training. Each line represents 1 subject. Thick black line represents the mean of the group. $^{**}P < 0.01$, when comparing POST to PRE-S1 and PRE-S2.

between the H_{max}/M_{max} ratio and maximal aerobic power. In the current study, the low level of association may be due to the different condition of the measures since both endurance and strength training involved dynamic work around several joints while the tasks for motor performance and the neural plasticity tests were performed under isometric conditions. Despite the weak association, the present study indicates that neural plasticity occurred in response to specific motor training and such alterations contributed to the specific motor performance improvements.

Methodological Considerations

H-reflex responses are influenced by several methodological factors, including the size of the afferent volley elicited by the stimulation pulse, background level of muscle activation, muscle contraction intensity, H-reflex normalization, posture, and attention level of the subjects (for review see Refs. 29, 40). Therefore, appropriate interpretation of the H-reflex response requires that particular recording conditions are achieved (24, 40). In the present study, the posture of the subject and the attention level of the subject were carefully controlled.

The H-reflex measures in this study were provided by M- and H-reflex recruitment curves obtained during low-level tonic contraction of the plantar flexors. This procedure has been recommended (5, 29, 40), since it allows the best control over the effect of afferent volley size and attenuates the effect of activity-dependent changes in axonal excitability (4, 5, 29, 40). Moreover, measurement of the H-reflex recruitment curve allows the H reflex to be assessed at different stimulus intensities thereby providing information on the recruitment of motor units of different thresholds (23). Alterations of the contraction intensity and EMG background level of the target muscle can also induce changes in the H-reflex amplitude. Nonetheless, similar contraction intensity across each experimental session was ensured and the background EMG activity during low-level tonic contractions did not differ between experimental sessions in this study.

Effects of Training on V/M_{max} Ratio and EMG Activity

The present study showed that SOL V/M_{max} ratio increased by 55% after 3 wk of strength training but remained unchanged following an equal period of endurance training. Changes in the neural mechanisms underlying the V-wave responses are thus specific to strength training. Enhanced SOL V-wave amplitude following strength training has been reported by other longitudinal studies, showing increments of 55 to 81% compared with the pretraining condition (1, 7, 11, 12, 15). The V-wave results from a supramaximal electrical stimulus applied to the nerve during ongoing muscle contraction, which elicits action potentials in all Ia afferent fibers and motor axons (9, 35, 38). In the motor axons, the action potentials will travel to the muscle, generating the M wave, and antidromically toward the spinal cord. The antidromic potentials collide with orthodromic motor action potentials elicited by the descending voluntary input to the motoneuron pool. This results in cancellation of the two potentials so that the H reflex can pass to the muscle where it is recorded as V wave (1, 38). An increase of the efferent motor output would increase the probability of antidromic collision and thus allow a larger part of the evoked afferent volley to reach the muscle. Consequently, it has been assumed that the increase of V-wave amplitude reflects an increase of supraspinal activation, which enhances descending volitional drive (i.e., recruitment and/or discharge rate of the motor neurons) to the muscle (1, 7, 10). Increased descending drive may also explain the increased SOL normalized EMG during the MVC, which was observed following strength training in this study but not following endurance training. The V-wave amplitude can also be altered by other mechanisms, including changes in motor neuron responsiveness (e.g., changes of intrinsic membrane properties and discharge rate), synaptic transmission efficacy at Ia afferent terminals (e.g., presynaptic inhibition), and/or postsynaptic inhibition (5, 35). Nonetheless, these mechanisms would also contribute in a very similar way to the H reflex (35, 41). In the present study, the strength training program induced a significant increase in V-wave amplitude while alterations of the H reflex were only observed at H_{thresh}. These observations indicate that increased V-wave amplitude mostly reflects changes in the descending neural drive to the muscle.

Effects of Training on H-Reflex Responses

Following endurance training, the normalized current intensity at H_{thresh}, 50%H_{max}, and H_{max} was significantly lower, confirming increased H-reflex excitability. These results were supported by the significant change of the predicted amplitudes (@H_{thresh}, @50%H_{max}, and @H_{max}), which are more sensitive to training-induced changes (8, 23). An increase of the predicted amplitudes indicates that the current intensities at

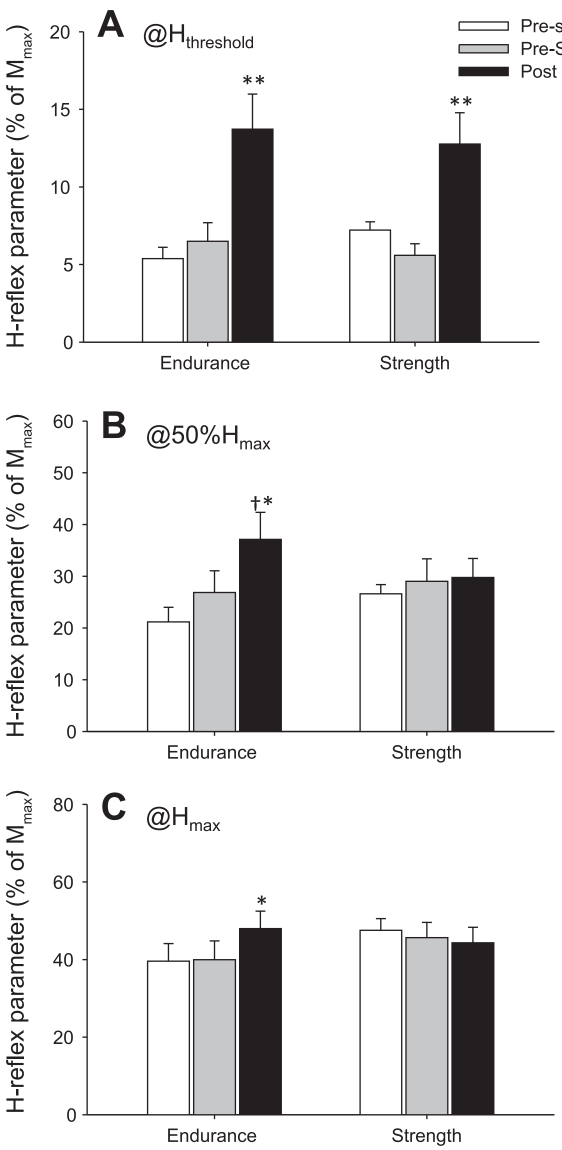

Fig. 7. Predicted H-reflex amplitudes evoked by the current intensity associated to the H_{thresh}, intensity at 50%H_{max} and at H_{max} observed before training. Values are means ± SE. *A*: predicted H-reflex amplitude at H_{thresh}. *B*: predicted H-reflex amplitude at 50%H_{max}. *C*: predicted H-reflex amplitude at H_{max}. @, Predicted parameters. $*P < 0.05$ and $**P < 0.001$, when comparing POST to PRE-S1 and PRE-S2. $^{\dagger}P < 0.001$, when comparing POST to PRE-S1.

H_{thresh}, 50%H_{max}, and H_{max} observed before training enhanced the H reflex after endurance training. The H_{max}/M_{max} ratio and the slope of the ascending limb also increased following endurance training only. Taken together, the above findings reveal that endurance training elicited a leftward shift of the ascending limb of the H-reflex recruitment curve (Fig. 5) and increased H-reflex amplitudes and H-reflex gain (measured as H_{slope}), confirming plastic adaptations in the Ia spinal reflex pathway. Furthermore, this adaptation appeared to contribute for improved resistance to fatigue following training.

These alterations suggest that endurance training lowers the recruitment threshold of motor neurons to Ia afferent input (28, 34) and increases the recruitment gain (i.e., the magnitude of the threshold differences between motor neurons decreases; Refs. 21, 22). Several cross-sectional studies (6, 26, 28, 37) have also shown increased H-reflex excitability in endurance-trained athletes compared with strength and power-trained athletes. These results were partly explained by differences in the muscle fiber type distribution between endurance- and power-trained athletes. Endurance-trained athletes have a higher percentage of slow-twitch fibers (14, 16), and the excitatory postsynaptic potentials are largest in small motor neurons innervating slow-twitch motor units (35), which would explain greater H-reflex responses in endurance-trained athletes (26, 28). However, in the present study the contractile properties were not influenced by training, which indicates that 3 wk of training was probably not sufficient to induce peripheral changes. Thus it is likely that the enhanced H-reflex excitability resulted from a change in the distribution of motor neuron excitability and synaptic inputs across the motor neuron pool (21, 22). In a previous study (39), it was reported that for the same relative load (30% MVC), the motor unit discharge rate of the vasti muscles decreased following endurance training. Based on these results, it seems that to maintain the same relative load the decreased discharge would be compensated by increased number of recruited motor units. It can be speculated that these changes represent a mechanism to reduce fatigue, which would optimize motor performance during prolonged exercise. Lower discharge rates and increased motor unit recruitment would increase the energy efficiency (ATP supply through the aerobic metabolism) and counteract muscle fatigue without affecting force and rate of force development (21). The neural mechanisms that may contribute to these observed changes include decreased presynaptic Ia and reciprocal inhibition and increased motor neuron excitability and supraspinal activation. Based on the V-amplitude measures, it is unlikely that changes in the descending drive occurred following endurance training. Furthermore, the coactivation ratio was not altered by endurance training, suggesting that changes in the H-reflex response were not due to a change in reciprocal inhibition. Thus the training induced alterations of the H reflex were most likely due to adjustments in motor neuron responsiveness and/or in presynaptic inhibition of Ia terminals.

Contrary to endurance training, strength training only elicited a decrease in the normalized current intensity at H_{thresh}, while no changes were observed in other measures of the H reflex. It is well known that the motor neurons are recruited in an orderly fashion by the Ia input from the smallest to the largest, according to the size principle (35). The present results suggest that the net excitability was only altered for the low-threshold motor units while no changes were observed for the higher threshold motor units involved in the maximal H-reflex response. Other studies (8, 27) involving strength training also reported increased H-reflex excitability at very low stimulus intensities (at H_{thresh}, and 5%M_{max}) and no change for the H_{max}/M_{max} ratios. While unchanged H_{max}/M_{max} ratios have been reported in several studies (10, 11, 15), some report increased H-reflex response at stimulus intensities of 20%M_{max} (1, 18) or no change at 10%M_{max} (12). Such conflicting results may partly be due to differences in the methodologies applied to elicit and measure the H reflex (7, 27). In addition, the contraction level used varies across studies, thus the activation of different motor unit populations may contribute to the inconsistency of the results.

Conclusion

The current work showed that following 3 wk of endurance training the excitability in the H-reflex pathway increased but the V-wave amplitude remained unchanged. In contrast, following strength training, the V-wave amplitude increased whereas subtle changes were observed in the H-reflex pathway. Moreover, although weakly, the improvement in time-to-task-failure of the plantar flexors was associated with increased H-reflex excitability while the increase in MVC was associated with increased V-wave amplitude. These results suggest that the elements of the H-reflex pathway are strongly involved in chronic adjustments in response to endurance training, contributing to enhance resistance to fatigue. Conversely, following strength training, it is more likely that increased descending neural drive during MVC and/or modulation in afferents other than Ia afferents contributed to increased motoneuron excitability and MVC of the plantar flexors.

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DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the author(s).

AUTHOR CONTRIBUTIONS

Author contributions: C.V.-C., D. Falla, M.V.C., and D. Farina conception and design of research; C.V.-C. performed experiments; C.V.-C., D. Falla, and D. Farina analyzed data; C.V.-C., D. Falla, M.V.C., and D. Farina interpreted results of experiments; C.V.-C. prepared figures; C.V.-C., D. Falla, M.V.C., and D. Farina drafted manuscript; C.V.-C., D. Falla, M.V.C., and D. Farina edited and revised manuscript; C.V.-C., D. Falla, M.V.C., and D. Farina approved final version of manuscript.

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