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## Evoked H-Reflex and V-Wave Responses During Maximal Isometric, Concentric, and Eccentric Muscle Contraction

Julien Duclay and Alain Martin

*Institut National de la Santé et de la Recherche Médicale/Equipe de Recherche Mixte, Faculté des Sciences du Sport, Université de Bourgogne, Dijon, France*

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**Duclay, Julien and Alain Martin.** Evoked H-reflex and V-wave responses during maximal isometric, concentric, and eccentric muscle contraction. *J Neurophysiol* 94: 3555–3562, 2005. First published July 27, 2005; doi:10.1152/jn.00348.2005. This study was designed to investigate the modulations of H-reflex and V-wave responses during passive and maximal active dynamic actions. Experiments were performed on 16 healthy males [age:  $24 \pm 4$  (SD) yr]. Maximal H-reflexes ( $H_{\max}$ ) and M-waves ( $M_{\max R}$ ) were evoked at the same muscle length during passive isometric, shortening and lengthening actions and during maximal voluntary isometric, concentric, and eccentric plantar-flexion. In all contraction types, supra-maximal stimulus intensity was used to evoke the superimposed maximal M wave ( $M_{\max A}$ ) and V wave ( $V$ ) of the soleus muscle. At rest, the  $H_{\max}/M_{\max R}$  ratio was significantly reduced during lengthening with respect to isometric and shortening actions ( $P < 0.05$ ). For each action type, the ratio between H reflex superimposed to the contraction ( $H_{\text{sup}}$ ) and  $M_{\max A}$  was not different from  $H_{\max}/M_{\max R}$  ratio. When plantar flexors were maximally voluntary activated, the  $H_{\text{sup}}/M_{\max A}$  ratio was still lower during eccentric contraction as compared with isometric and concentric efforts ( $0.33 \pm 0.03$  vs.  $0.47 \pm 0.02$  and  $0.50 \pm 0.03$ ,  $P < 0.001$ ), whereas  $V/M_{\max A}$  ratios were similar for all contraction types (isometric  $0.26 \pm 0.02$ ; concentric  $0.23 \pm 0.03$ , and eccentric  $0.24 \pm 0.02$ ;  $P > 0.05$ ). The  $V/M_{\max A}$  ratio was significantly lower than  $H_{\text{sup}}/M_{\max A}$  during isometric and concentric MVC ( $P < 0.001$ ). No difference was observed between  $V/M_{\max A}$  and  $H_{\text{sup}}/M_{\max A}$  ratios during eccentric efforts. The H-reflex modulations, present during lengthening actions, were mainly attributed to presynaptic inhibition of Ia afferents and to homosynaptic postactivation depression. Results on V wave and H reflex suggest that during eccentric MVC, the spinal loop is specifically modulated by the supra-spinal centers and/or neural mechanisms at spinal level.

### INTRODUCTION

The Hoffmann reflex (H reflex) is used to assess motor units activated by the afferent pathway (Maffiuletti et al. 2001; Schieppati 1987). During voluntary contraction, the combined H reflex and first volitional wave (V wave), which is an electrophysiological variant of the H reflex (Upton et al. 1971), can be used as a tool to evaluate the modulation of the spinal loop. These reflexes reflect the efficiency of the transmission in Ia afferent- $\alpha$  motoneuron synapses, i.e., the presynaptic inhibition (principally H reflex) (Hultborn et al. 1987; Voigt and Sinkjaer 1998; Zehr 2002) and the level of efferent and descending neural drive (mostly V wave) (Aagaard et al. 2002; Upton et al. 1971) while these evoked potentials are both influenced by reciprocal inhibition (Crone and Nielsen 1994)

and recurrent Renshaw inhibitions (Hultborn and Pierrot-Desseilligny 1979; Loscher et al. 1996).

The modulations of the spinal loop during dynamic tasks have been observed during both passive and active actions. Observing passive ankle joint movement, Pinniger et al. (2001) reported a decrease in soleus H-reflex amplitude during passive lengthening actions and an increase during passive shortening actions, related to the tonic discharge of muscle spindle afferents that might affect transmission within the Ia pathway.

During active muscle contraction, although the amplitudes of evoked potentials are potentiated when stimulation is superimposed during a voluntary contraction (Butler et al. 1993; Hicks et al. 1989; Ruegg et al. 1990), the ratio between the maximal H reflex and the maximal M wave (H/M ratio) was similar at rest and during isometric maximal voluntary contraction (MVC) (Pensini and Martin 2004). During active shortening and lengthening actions, modulations of the H/M ratio seem to be different from those obtained during isometric trials. Nordlund et al. (2002) found that lengthening H/M ratio was increased in active sub-maximal conditions with respect to passive conditions. These findings were attributed to neural mechanisms at spinal level (presynaptic inhibition and post-activation depression phenomenon). When soleus (SOL) shortens, the existence of modulations in the H/M ratio between active and passive actions is less clear. Nordlund et al. (2002) found that shortening H/M ratio did not change between active and passive conditions. In contrast, Romano and Schieppati (1987) demonstrated that H/M ratio was increased when SOL was actively shortening. These contradictory results may be explained by different contraction intensities (10, 20, and 30% MVC vs. against a constant load of 100 N), different angular velocities of the joint ( $5^\circ/\text{s}$  vs. 12, 25, and  $50^\circ/\text{s}$ ) and different methodologies used to record H reflex during contraction ( $H_{\max}$  stimulus intensity vs. sub-maximal H-reflex stimulus intensity). In previous studies, the effects of dynamic actions on the SOL H reflex were investigated during sub-maximal contractions with low levels of activation. However, it had not previously been identified how the H reflex is modulated by maximal dynamic efforts. Because Nordlund et al. (2002) showed that the H/M ratios were lower during sub-maximal eccentric contraction as compared with sub-maximal concentric contraction, we hypothesized that the H/M ratio would be modulated in the same way by the MVC.

During MVC, the study of V wave could be used to reflect the magnitude of efferent  $\alpha$ -motoneuron output during volun-

Address for reprint requests and other correspondence: J. Duclay, INSERM/ERM 207 Motricité-Plasticité, Faculté des Sciences du Sport, BP 27 877-21 078 Dijon Cedex, France (E-mail: julien.duclay@u-bourgogne.fr).

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tary muscle activation (Aagaard et al. 2002). The V wave consists of a volley of H-reflex impulses that are allowed to reach the muscle due to the removal of antidromic action potential impulses (generated by  $\alpha$ -motor axon stimulation) by collision with descending neural drive (generated by the voluntary motor effort) (Upton et al. 1971). In the literature, V wave is mainly analyzed during isometric contractions (Aagaard et al. 2002; Butler et al. 1993; Pensini and Martin 2004; Sale et al. 1983). However, neural control of muscle action is highly dependent on the mechanical requirements of a task (Abbruzzese et al. 1994; Nordlund et al. 2004; Westing et al. 1991). To date, no studies had compared the effect of contraction type on V wave. Therefore the aim of the study was to investigate how H reflex and V wave are modulated during isometric and dynamic MVC. Because it is well established, at low contraction intensity, that H reflex is reduced during lengthening, we hypothesized that V wave could be modulated in the same way as V wave is an electrophysiological variant of the H reflex recorded during contraction.

## METHODS

### Subjects.

Experiments were performed on 16 healthy males (age:  $24 \pm 4$  yr; height:  $178 \pm 6$  cm; mass:  $70 \pm 6$  kg, means  $\pm$  SD) with no history of neurological injuries or diseases. Subjects were normally active, were all volunteers, and had signed an informed consent prior to involvement in the investigation. The conditions of the study were approved by the University of Burgundy Committee on Human Research and in conformity with the declaration of Helsinki.

### Experimental setup

**MECHANICAL DATA.** Subjects were seated with the trunk inclined  $30^\circ$  with reference to the vertical and the knee joint flexed at  $120^\circ$  ( $180^\circ =$  full extension). The flexed position at the knee joint was chosen to reduce the mechanical contribution of the gastrocnemii to the plantar flexor torque (Cresswell et al. 1995). Measurements were made on the right foot, which was attached to an isokinetic dynamometer (Biodex, Shirley, NY) that enabled instantaneous recording of muscle torque at constant angular velocity ( $60^\circ/\text{s}$ ). The axis of rotation of the dynamometer was aligned with the anatomical ankle flexion-extension axis. Gravity correction was obtained by measuring the torque exerted on the dynamometer lever arm by the weight of the limb. Once measured, the effect of gravity was automatically incorporated by the Biodex Advantage Software program in the output provided. Subjects were securely stabilized by two crossover shoulder harnesses and a belt across the abdomen. Furthermore, particular care was taken in monitoring the posture of the subject and avoiding head rotations during the test to maintain constant cortico-vestibular influences on the excitability of the motor pool and limit afferent feedback from other peripheral receptors, i.e., Golgi tendon organs, cutaneous and joint afferences (Schieppati 1987; Zehr 2002). To avoid alterations in H reflex due to changes in muscle length (Gerilovsky et al. 1989), stimulation was always delivered at  $0^\circ$  (corresponding to an ankle angle of  $90^\circ$ ) in both isometric and isokinetic conditions. The range of motion was  $60^\circ$ , from  $-30^\circ$  (plantar-flexion) to  $+30^\circ$  (dorsiflexion) ankle flexion.

**STIMULATION.** H reflex, V wave, and M wave were evoked in SOL by percutaneous stimulation of the posterior tibial nerve with a single rectangular pulse (1-ms) delivered by a Digitimer stimulator (model DS7, Hertfordshire, UK). The self-adhesive cathode (8-mm diam,

Ag-AgCL) was placed in the popliteal fossa and the anode ( $5 \times 10$  cm, Medicompex SA, Ecublens, Switzerland) was placed over the patella. The stimulation site, giving the greatest amplitude of the evoked potentials, was first located by a hand-held cathode ball electrode (0.5-cm diam). Once determined, the stimulation electrode was firmly fixed to this site with straps and top rubber.

**ELECTROMYOGRAPHY.** After careful preparation of the skin (shaving, abrading, and cleaning with alcohol) to obtain low-impedance ( $<5$  k $\Omega$ ), pairs of silver-chloride surface electrodes of 8-mm diam (2-cm interelectrode distance) were placed along the mid-dorsal line of the leg,  $\sim 5$ -cm distal from where the two heads of the gastrocnemius join the Achilles tendon for the SOL. To avoid the innervation zone and therefore to obtain the optimal amplitude of the EMG response (Merletti et al. 2001), the SOL site was determined in pilot testing by eliciting, for a given intensity, the greatest M-wave amplitude via tibial nerve stimulation. Because the electrophysiological responses induced by tibial nerve stimulation are generated by the plantar flexors and possibly contaminated by concomitant activation of the tibialis anterior (TA), the EMG activity of the antagonist muscle was also recorded. For this muscle, the electrodes were positioned at 1/3 on the line of the fibula and the tip of the medial malleolus (Hermens et al. 2000). The reference electrode was attached in a central position on the same leg. Electromyographic (EMG) signals were amplified with a bandwidth frequency ranging from 15 Hz to 5 kHz (common mode rejection ratio = 90 dB; impedance = 100 M $\Omega$ , gain = 1,000). The EMG and mechanical signals (torque and position) were digitized on-line (sampling frequency: 2 kHz) and stored for analysis with commercially available software (Tida, Heka Elektronik, Lambrecht/Pfalz, Germany).

### Experimental protocol.

The complete protocol was completed during one session of 2.5 h with each subject performing between 24 and 36 efforts.

**ISOMETRIC REFLEX MODULATIONS.** Passive isometric recruitment curve was first performed to carefully search for the stimulus intensity necessary to obtain the maximal SOL H reflex ( $H_{\text{max}}$ ). Four stimuli were delivered at each intensity level, interspaced by 10 s between each pulse. Intensity was increased by 2 mA from the H-reflex threshold until a maximal SOL M-wave response was obtained. The  $H_{\text{max}}$  stimulation intensity ranged from 10 to 34 mA. Four stimuli at supra-maximal intensity (1.5 times the maximum M-wave stimulus intensity) were delivered and the mean value of the four recorded M-waves was considered as the  $M_{\text{maxR}}$  value. The supra-maximal intensity ranged from 50 to 112 mA. Then subjects were asked to perform four maximal voluntary isometric plantar-flexions for 3 s separated by 1-min rest periods. The visual feedback of the exerted torque was provided on-line on a personal computer screen. This allowed subjects to perform reproducible trials. During each MVC, stimulus intensity, used to record  $H_{\text{max}}$  at rest, was applied 1.5 s after the beginning of the contraction (corresponding to the instant of peak torque), to record superimposed H reflex ( $H_{\text{sup}}$ ) and M wave at  $H_{\text{sup}}$  ( $M_{\text{hsup}}$ ; H superimposed tests). In the present study, therefore it is possible that  $H_{\text{sup}}$  may not reflect the maximal H-reflex amplitude during MVC. Nevertheless, as suggested by Zehr (2002), H reflexes should be evoked with a sufficient level of stimulation to provide a corresponding M wave to help ensure stimulus constancy. At the superimposed stimulus intensities used in the present protocol, the direct M response was a small fraction of the maximal M wave (ranged from 17 to 21%), which does not lay on the descending part of the recruitment curve. In this region of the curve, M wave is sensitive to changes in stimulus conditions and may reliably measure the efficiency of the stimulus intensity (Fig. 1). Furthermore, similar M-wave amplitude should be maintained between conditions (action type and muscle activity) and used for comparison across these

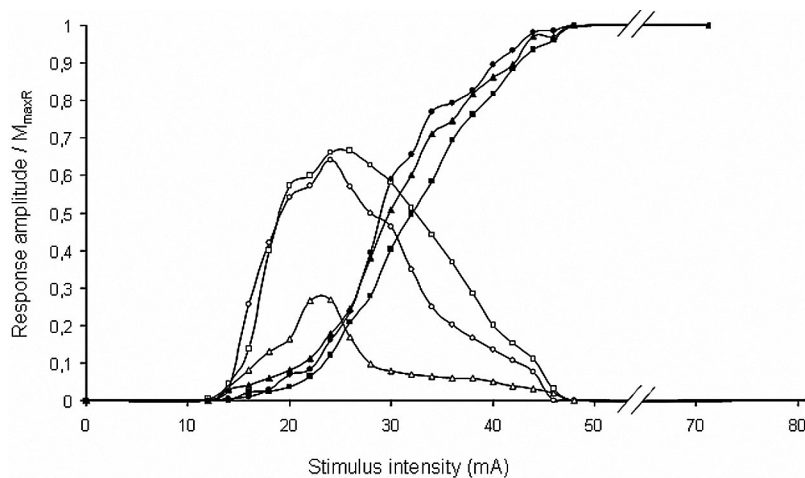


FIG. 1. Passive isometric ( $\square$ ,  $\blacksquare$ ), shortening ( $\circ$ ,  $\bullet$ ), and lengthening ( $\triangle$ ,  $\blacktriangle$ ) recruitment curves of M wave and H reflex, normalized with corresponding maximal M wave, at angular velocity of  $60^\circ/\text{s}$ , for soleus of 1 subject, whose data best represent group data. M waves/ $M_{\text{maxR}}$  are plotted as  $\blacksquare$ ,  $\bullet$ ,  $\blacktriangle$  and H reflexes/ $M_{\text{maxR}}$  as  $\square$ ,  $\circ$ ,  $\triangle$ .

different conditions. After a rest period of 5 min, subjects were instructed to perform four MVC with the same contraction protocol. Superimposed supra-maximal intensity allowed us to obtain two electromyographic responses: the V wave (V) and the superimposed maximal M wave ( $M_{\text{maxA}}$ ). For each subject, the coefficient of variation across trials was calculated. If the V-wave or  $H_{\text{sup}}$  amplitudes varied excessively (coefficient of variation  $>5\%$ ), four additional MVC were performed. Finally, two maximal voluntary isometric dorsiflexions were performed to evaluate the magnitude of antagonist TA coactivation.

**DYNAMIC REFLEX MODULATIONS.** The order of concentric and eccentric sessions was counterbalanced among subjects. During dynamic actions, alterations in the spatial relationship between the stimulating electrode and the tibial nerve may influence the  $H_{\text{max}}$  intensity. Therefore to adjust  $H_{\text{max}}$  stimulus intensity, passive shortening or lengthening recruitment curves were firstly obtained with an increment in stimulus intensity similar to those used in the isometric trial. The  $H_{\text{max}}$  stimulation intensity ranged from 12 to 30 mA during both shortening and lengthening conditions. The ankle was maintained at the starting position ( $-30^\circ$  for shortening and  $+30^\circ$  for lengthening) for 10 s and was subsequently moved at  $60^\circ/\text{s}$ . Electrical stimulation of the tibial nerve was triggered as the ankle passed the  $0^\circ$  position (isometric angular position). A rest period of 4 s was then observed at the ending position. Finally, the ankle was moved at  $60^\circ/\text{s}$  to the starting position. Eight seconds before each motion, subjects performed a sub-maximal isometric plantar-flexion (during  $\sim 1$  s) to obtain similar thixotropic effects (resulting from the previous change in muscle length) between conditions (Proske et al. 1993).

During dynamic contraction sessions, the ankle was maintained at rest for 29 s in the starting position. To limit thixotropic effects, subjects were asked to develop isometric torque as preactivation contraction for 1 s. Maximal dynamic plantar-flexion at  $60^\circ/\text{s}$  followed this preactivation. Electrical stimulation of the tibial nerve was triggered as the ankle passed the  $0^\circ$  position. After a rest period of 30 s at the ending position, the ankle was moved at  $60^\circ/\text{s}$  to the starting position. As previously mentioned, the visual feedback of the exerted moment was provided.

This protocol was repeated four times with  $H_{\text{max}}$  stimulus intensity and four times with supra-maximal stimulus intensity. For every action type, the order of the M-V and the  $H_{\text{max}}$  superimposed tests was randomized, and a rest period of 5 min was observed between tests. As during isometric contractions, four additional MVC were performed if the V-wave or  $H_{\text{sup}}$  amplitudes were not sufficiently reproducible (coefficient of variation  $>5\%$ ). Finally, two maximal shortening and lengthening dorsiflexions were executed to evaluate coactivation in the tibialis anterior.

### Data analysis

**MAXIMAL MUSCLE STRENGTH.** Maximal constant angular torques (CAT) at  $0^\circ$  were obtained prior to the superimposed stimulation under isometric, concentric, and eccentric plantar flexions. For isometric and dynamic muscular actions, mean over four trials, was considered to determine MVC.

**EMG ACTIVITY.** SOL RMS over a 200-ms period prior to stimulation was normalized to the corresponding amplitude of  $M_{\text{maxR}}$  (RMS/ $M_{\text{maxR}}$ ) during passives actions (background level of EMG) and to the corresponding amplitude of maximal superimposed M wave (RMS/ $M_{\text{maxA}}$ ) during MVC (SOL EMG activity). TA EMG was determined as being mean over four recorded TA RMS over a 200-ms period prior to the stimulation at rest (background level of TA EMG) and during MVCs (coactivation). During isometric action, the TA RMS was expressed as a fraction of TA RMS determined during maximal voluntary isometric dorsiflexion. During dynamic actions, TA RMS obtained during concentric plantar flexion was normalized to TA RMS determined during maximal voluntary eccentric dorsiflexion and TA RMS recorded during eccentric plantar flexion was normalized to TA RMS calculated during maximal voluntary concentric dorsiflexion (Hagood et al. 1990).

**EVOKED POTENTIALS.** The means over four recordings were calculated to determine the following parameters: peak-to-peak amplitude of H reflex ( $H_{\text{max}}$  and  $H_{\text{sup}}$ ), V wave, sub-maximal M evoked at H reflex ( $M_{\text{hmax}}$  and  $M_{\text{hsup}}$ ) and maximal M wave ( $M_{\text{maxR}}$  and  $M_{\text{maxA}}$ ). The  $H_{\text{max}}/M_{\text{maxR}}$ ,  $H_{\text{sup}}/M_{\text{maxA}}$ , and  $V/M_{\text{maxA}}$  ratios were calculated to assess the proportion of motor units (MUs) activated by the Ia afferents. As potentials may be potentiated by the contraction, the  $M_{\text{hsup}}/M_{\text{maxA}}$  ratio was determined and compared with  $M_{\text{hmax}}/M_{\text{maxR}}$  ratio to ensure that the same proportion of  $\alpha$ -motoneurons was activated by the stimulation. The potentiation of the H reflex was evaluated with the ratio between  $H_{\text{sup}}/M_{\text{maxA}}$  and  $H_{\text{max}}/M_{\text{maxR}}$ . During shortening and lengthening, position was recorded to be sure that stimulation was delivered at the corresponding isometric angle.

**STATISTICAL ANALYSIS.** All data are presented as means  $\pm$  SE. The normality of the data were tested using the Shapiro-Wilks  $W$  test. Repeated-measures ANOVA examined the effects of activation (passive as compared with active trials) and action type (isometric as compared with shortening and lengthening) and their interactions, on H reflex, M wave, and M at H. A second two-way ANOVA with repeated measures examined the effects of condition (rest with  $H_{\text{max}}$  stimulus intensity, MVC with  $H_{\text{max}}$  stimulus intensity, and MVC with supramaximal stimulus intensity) and action type (isometric as compared with concentric and eccentric) and their interactions, on  $H_{\text{max}}/M_{\text{maxR}}$ ,  $H_{\text{sup}}/M_{\text{maxA}}$ ,  $V/M_{\text{maxA}}$ , and SOL and TA EMG activities.

TABLE 1. Effect of action type and muscle EMG activity on amplitudes of soleus evoked potentials

Variables	Isometric	Concentric	Eccentric
<i>Passive</i>			
$H_{\max}$ , mV	3.11 ± 0.28	2.85 ± 0.33	1.43 ± 0.25***
$M_{\text{hmax}}/M_{\text{maxR}}$	0.14 ± 0.08	0.16 ± 0.02	0.16 ± 0.02
$M_{\text{maxR}}$ , mV	5.70 ± 0.38	5.30 ± 0.44	5.24 ± 0.45
<i>Active</i>			
$H_{\text{sup}}$ , mV	4.15 ± 0.28 <sup>§§</sup>	4.18 ± 0.32 <sup>§§§</sup>	2.82 ± 0.30 <sup>***,§§§</sup>
$M_{\text{hsup}}/M_{\text{maxA}}$	0.17 ± 0.06	0.21 ± 0.09	0.21 ± 0.06
$M_{\text{maxA}}$ , mV	8.68 ± 0.53 <sup>§§§</sup>	8.27 ± 0.52 <sup>§§§</sup>	8.65 ± 2.15 <sup>§§§</sup>
V-wave, mV	2.27 ± 0.22	1.84 ± 0.32	2.09 ± 0.23

Data are means ± SE,  $n = 16$  \*\*\*  $P < 0.001$ : eccentric vs. isometric and concentric. <sup>§§</sup>  $P < 0.01$  passive vs. active. <sup>§§§</sup>  $P < 0.001$ : passive vs. active.

Another repeated-measures ANOVA examined the effects of action type (isometric as compared with shortening and lengthening) on the CAT and  $(H_{\max}/M_{\text{maxR}})/(H_{\text{sup}}/M_{\text{maxA}})$ .

When a major effect or an interaction was found, a post hoc analysis was made using the Scheffe test. ANOVAs and post hoc test were performed using Statistica (Statsoft, version 6.0, Statistica, Tulsa, OK). Significance was accepted at  $P < 0.05$ .

## RESULTS

### Passive reflex modulation.

Passive isometric, shortening, and lengthening recruitment curves, normalized with corresponding maximal M wave, for one representative subject are shown in Fig. 1. For this subject, the  $H_{\max}$  stimulus intensities were 24 mA during isometric action and 26 mA during shortening and lengthening actions. At these intensities,  $M_{\text{hmax}}$ , which represent on average 18.2% of  $M_{\text{maxR}}$ , is not different between action types and is sensitive to changes in stimulus intensity.

Across the range of stimulus intensities, the H-reflex recruitment curve is depressed in amplitude during lengthening ac-

tions with respect to isometric and corresponding shortening actions, whereas  $M_{\text{maxR}}$  amplitudes are similar (Table 1).  $H_{\max}$  stimulus intensities were similar for each action type (isometric: 21.5 ± 1.75 mA, shortening: 21.75 ± 1.57 mA, and lengthening: 22 ± 1.69 mA;  $P > 0.05$ ). Recording of  $H_{\max}$ ,  $M_{\text{hmax}}$ , and  $M_{\text{maxR}}$  from an individual subject, whose data best reflect the group mean, are presented in Fig. 2. For each action type, the M wave recorded at  $H_{\max}$  ( $M_{\text{hmax}}$ ) was normalized to the  $M_{\text{maxR}}$ . No significant difference was found between these ratios according to action type (mean  $M_{\text{hmax}}/M_{\text{maxR}}$  ranged from 0.14 ± 0.08 to 0.16 ± 0.02;  $P > 0.05$ ), suggesting that stimulus conditions were stable (Fig. 2). The background level of SOL EMG was similar among action types ( $P > 0.05$ ). Background level of TA EMG was on average 1.2 ± 0.2% ( $P > 0.05$ ) and remained unchanged whatever the action type.

Mean H-reflex amplitudes were significantly depressed in amplitude during lengthening actions as compared with isometric and shortening actions (Table 1;  $P < 0.001$ ). Consequently, the  $H_{\max}/M_{\text{maxR}}$  ratio was significantly reduced during lengthening ( $P < 0.05$ ; Fig. 3).

### H-reflex and V-wave modulations during MVC.

Concentric CAT values (72.94 ± 6.6 N · m) were significantly lower than isometric and eccentric CAT values (102.67 ± 6.57 and 105.07 ± 5.78 N · m, respectively;  $P < 0.001$ ). No significant difference was observed between isometric and eccentric CAT values ( $P > 0.05$ ). For each action type, the CAT value was the same between the H superimposed test and the M-V test (isometric: 102.30 ± 6.13 vs. 103.05 ± 7.33 N · m, concentric: 74.44 ± 7.44 vs. 71.44 ± 5.86 N · m, and eccentric: 102.59 ± 5.31 vs. 107.55 ± 6.6 N · m;  $P > 0.05$ ). There was no action type effect on SOL RMS/ $M_{\text{maxA}}$  (isometric: 0.023 ± 0.001; concentric: 0.023 ± 0.002; eccentric: 0.022 ± 0.001;  $P > 0.05$ ). The amount of antagonist muscle coactivation (tibialis anterior) was 10.62 ±

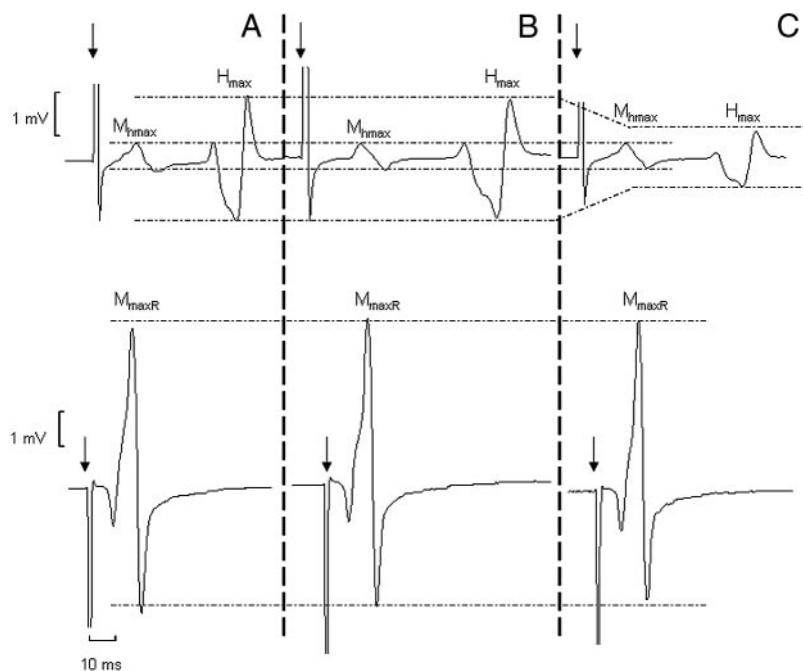


FIG. 2. Maximal H reflex, sub-maximal M wave ( $M_{\text{hmax}}$ ), and compound action potential ( $M_{\text{maxR}}$ ) during passive actions: electrical responses recorded in 1 subject. Examples of SOL  $M_{\text{hmax}}$ ,  $H_{\max}$  (top traces), and  $M_{\text{maxR}}$  (bottom traces) recorded during isometric (A), shortening (B), and lengthening (C) actions at angular velocity of 60°/s. ↓, stimulus delivery. The initial spikes represent the stimulus artifact. - - -, the peak-to-peak amplitudes of the  $H_{\max}$ ,  $M_{\text{hmax}}$ , and  $M_{\text{maxR}}$  responses evoked during passive trials and have been inserted to facilitate comparisons.

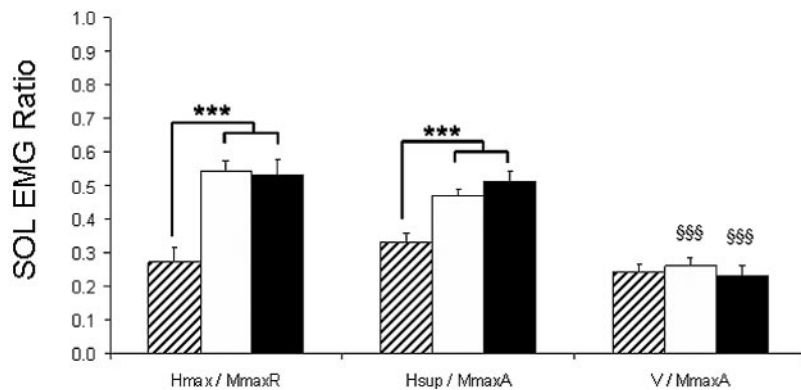


FIG. 3. Effects of action type on soleus  $H_{max}/M_{maxR}$ ,  $H_{sup}/M_{maxA}$ , and  $V/M_{maxA}$  ratios. The means  $\pm$  SE ( $n = 16$ ) of SOL  $H_{max}/M_{maxR}$ ,  $H_{sup}/M_{maxA}$ , and  $V/M_{maxA}$  ratios during eccentric (▨), isometric (□), and concentric (■) actions. \*\*\* $P < 0.001$ . Significant difference in eccentric as compared with concentric and isometric efforts. \$\$\$ $P < 0.001$ . Significant difference in  $V/M_{maxA}$  as compared with  $H_{sup}/M_{maxA}$  ratio.

0.69,  $11.12 \pm 1.27$ , and  $10.29 \pm 1.26\%$  during isometric, concentric, and eccentric contractions, respectively. No significant difference was observed between contraction modes ( $P > 0.05$ ).

Examples of H reflex and M-wave evoked during isometric, concentric, and eccentric contractions are shown in Fig. 4. As can be seen in Fig. 4, the amplitudes of  $M_{hsup}$  were stable across all contraction types ( $P > 0.05$ ). In contrast,  $H_{sup}$  amplitude was significantly depressed during eccentric contraction ( $P < 0.001$ ). The  $M_{hsup}/M_{maxA}$  ratios were similar for all action types (isometric:  $0.17 \pm 0.06$ , concentric:  $0.21 \pm 0.09$ , and eccentric  $0.21 \pm 0.08$ ;  $P > 0.05$ ) and was not different from  $M_{hmax}/M_{maxR}$ , suggesting that stimulus conditions were stable whatever the test used ( $P > 0.05$ ; Table 1).

The potentiation of the H reflex, evaluated by the ratio between  $H_{sup}/M_{maxA}$  and  $H_{max}/M_{maxR}$ , was higher ( $P < 0.001$ ) during eccentric contraction ( $1.79 \pm 0.34$ ) as compared with isometric ( $0.94 \pm 0.26$ ) and concentric ( $1.12 \pm 0.57$ ) actions.  $H_{sup}/M_{maxA}$  tended to be higher than  $H_{max}/M_{maxR}$  during ec-

centric ( $0.33 \pm 0.03$  vs.  $0.27 \pm 0.04$ ) actions and lower than  $H_{max}/M_{maxR}$  during isometric ( $0.48 \pm 0.01$  vs.  $0.54 \pm 0.03$ ) and concentric ( $0.50 \pm 0.03$  vs.  $0.53 \pm 0.05$ ) efforts. Nevertheless, no significant difference was observed, for any action type, between  $H_{sup}/M_{maxA}$  (active trials) and  $H_{max}/M_{maxR}$  (passive trials;  $P > 0.05$ ; Fig. 3). Consequently, the  $H_{sup}/M_{maxA}$  ratio was still significantly lower ( $P < 0.05$ ) during eccentric actions as compared with isometric and concentric actions ( $0.33 \pm 0.03$  vs.  $0.48 \pm 0.01$  and  $0.50 \pm 0.03$ , respectively). No difference was observed between  $H_{sup}/M_{maxA}$  ratios during isometric and concentric plantar flexions ( $P > 0.05$ ).

V wave and  $M_{maxA}$ , recorded during isometric, concentric, and eccentric action, for an individual subject whose data best reflect the group mean are presented in Fig. 4. Whatever the action type,  $M_{maxA}$  was significantly higher ( $P < 0.001$ ) than  $M_{maxR}$  recorded with the same stimulation intensity at rest (Table 1). Unlike  $H_{max}/M_{maxR}$  and  $H_{sup}/M_{maxA}$ ,  $V/M_{maxA}$  ratio did not change with the action type (isometric:  $0.26 \pm 0.02$ ; concentric:  $0.23 \pm 0.03$ , and eccentric:  $0.24 \pm 0.02$ ;  $P > 0.05$ ).

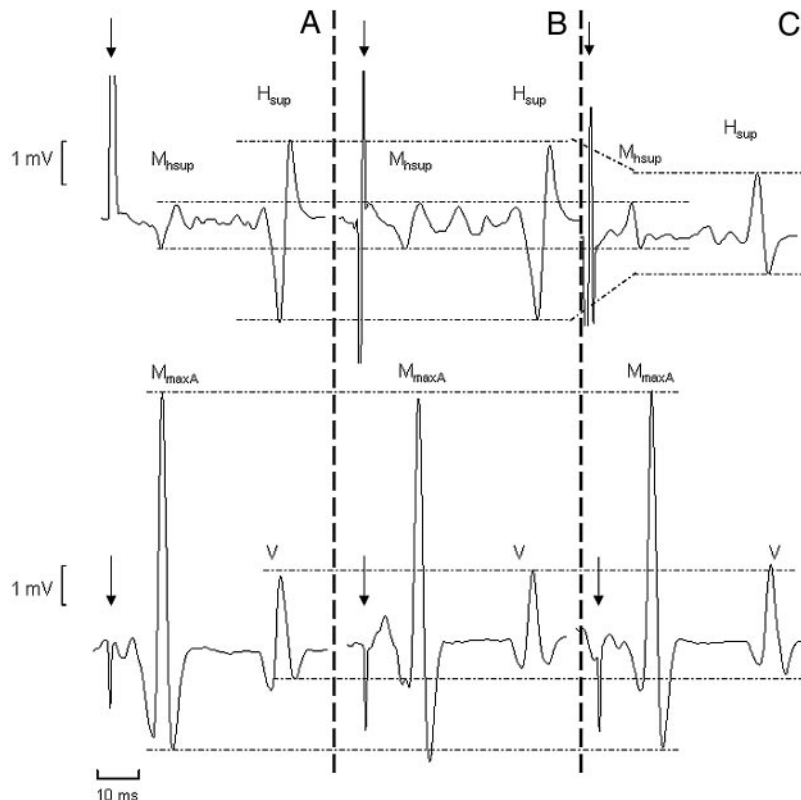


FIG. 4. Super-imposed H reflex ( $H_{sup}$ ) and V wave: electrical responses recorded during isometric (A), concentric (B), and eccentric (C) contractions. The stimulation intensity necessary to obtain  $H_{max}$  at rest were superimposed to contraction to record  $M_{hsup}$  and  $H_{sup}$  (top). When supra-maximal stimuli were superimposed to MVC, SOL  $M_{maxA}$  and V wave were recorded (bottom).  $\downarrow$ , stimulus delivery.  $- \cdot - \cdot -$ , peak-to-peak amplitudes of the  $H_{sup}$ , V, and  $M_{maxA}$  responses evoked during active trials and have been inserted to facilitate comparisons.

$V/M_{\max A}$  ratios were significantly lower ( $P < 0.001$ ) than  $H_{\text{sup}}/M_{\max A}$  during isometric and concentric MVC (Fig. 3). In contrast, there was no significant difference between  $H_{\text{sup}}/M_{\max A}$  and  $V/M_{\max A}$  during eccentric actions (Fig. 3;  $P > 0.05$ ).

## DISCUSSION

The aims of the study were to investigate how H reflex and V wave are modulated during isometric and maximal dynamic contractions. The main finding was that the  $V/M_{\max A}$  ratio does not differ according to action type although the H reflex is depressed during passive and active lengthening as compared with isometric and concentric actions. Within action types, the SOL  $H_{\max}/M_{\max R}$  ratios were not different from SOL  $H_{\text{sup}}/M_{\max A}$  ratios.

### *Methodological considerations.*

Methodological requirements should be maintained for accurate interpretation of H reflex in exercise study (Zehr 2002). Results could be influenced by recording conditions. In the passive dynamic actions, a modification in the quantity of contractile equipment under the electrodes can modify the reflex amplitude. For this reason, all potentials evoked in the present study were recorded for a given angle of the ankle to avoid any effect of muscular length on reflex amplitude (Girilovsky et al. 1989). Factors, which are known to be indexes of the stability of recording conditions, include the constancy of M wave recorded at  $H_{\max}$  and the constancy of the maximal amplitude of the M wave, whatever the solicitation type. As previously observed by Pinniger et al. (2001); data from the present study indicated that neither  $M_{\max R}$  nor  $M_{\max A}$  amplitudes did not differ between action types. Therefore the variations of the amplitude of the H reflex cannot be attributed to a modification of the position of the stimulation electrode with respect to the tibial nerve. Usually, the M wave elicited concomitantly with the H reflex has been used to control stimulation intensity (reference M wave) (Schieppati 1987). In the present study, reference M waves represent on average 16% of  $M_{\max R}$  during passive trial and 18% of  $M_{\max A}$  during MVC. It is important to note that the ratio between the M wave associated to the H reflex, and the corresponding maximal M wave was not altered by the MVC and the action type. The same proportion of motor axons is therefore directly recruited in each trial by the stimulation. We can thus suppose that the same proportion of  $\alpha$ -motoneurons was activated by the stimulation during isometric, lengthening, and shortening actions. H-reflex modulations observed here could not be attributed to recording conditions and are then explained by neural mechanisms at both spinal and/or supra-spinal level.

### *Effects of action type and MVC on H reflex.*

During passive lengthening,  $H_{\max}/M_{\max R}$  ratio was significantly depressed and was 50% of concentric value. Data from the present study were similar to those obtained by Pinniger et al. (2001) and Nordlund et al. (2002) (47 and 38%, respectively). In agreement with these previous studies dealing with H reflex during dynamic actions, H-reflex modulations, present during passive lengthening actions, may be mainly attributed to presynaptic inhibition of Ia afferents (Rudomin and Schmidt

1999) and to the homosynaptic post activation depression phenomenon (HPAD) (Hultborn et al. 1987). Concerning the HPAD phenomenon, it was reported by Burke et al. (1978) that muscle spindles fire rapidly during passive muscle lengthening, whereas they fall silent during passive shortening. As a result, the HPAD, which depends on preceding activity in the Ia afferents, should be more involved during passive lengthening action as compared with passive shortening action. Furthermore, it is interesting to note that the effects of the action type on the H reflex during passive actions, observed previously at low angular velocity by Pinniger et al. (2001) and Nordlund et al. (2002), seem to be present also at high angular velocity adopted in the present study.

During MVCs, for each type of contraction, results showed that the CAT obtained during the H and the M-V superimposed tests were similar, suggesting that the type of test (H superimposed test vs. M-V superimposed test) was not influenced by the force output. During voluntary contractions, the peak-to-peak amplitudes of the evoked potential were increased. M wave is potentiated to the same extent whatever the contraction type. Fitch and McComas (1985) suggested that the enlargement of the M wave resulted from greater synchronization of muscle fiber action potentials. For Hicks et al. (1989) on the other hand, the potentiation was associated with higher amplitude of the action potentials related to more effectiveness of the  $\text{Na}^+ - \text{K}^+$  pump and to a different threshold of excitability from that at rest. Thus it seems more appropriate to normalize the superimposed responses with respect to the maximal M wave recorded under similar conditions.

From passive to active actions, it is interesting to note that the H reflex tends to be potentiated during concentric contraction (potentiation was 1.12), whereas no effect was obtained during isometric MVC (potentiation was 0.96). However, no statistical difference was obtained between  $H_{\max}/M_{\max R}$  and  $H_{\text{sup}}/M_{\max A}$ . Similar findings have been reported with lower levels of activation during shortening action by Nordlund et al. (2002) and during isometric action by Pensini and Martin (2004). Despite the increase in excitability of the motoneuron pool during active action with respect to passive action, the lack of change between  $H_{\max}/M_{\max R}$  and  $H_{\text{sup}}/M_{\max A}$  during isometric and concentric actions could be partially caused by presynaptic inhibitory mechanisms (Nordlund et al. 2002; Pensini and Martin 2004).

Despite a greater H-reflex potentiation during lengthening, no difference was observed between  $H_{\max}/M_{\max R}$  and  $H_{\text{sup}}/M_{\max A}$ . Mean  $H_{\max}/M_{\max R}$  ratios were nevertheless higher than mean  $H_{\text{sup}}/M_{\max A}$  ratios during isometric and concentric actions, whereas the opposite was observed for eccentric actions. A significantly greater  $H_{\text{sup}}/M_{\max A}$  ratio recorded during eccentric contractions, with respect to passive lengthening has already been obtained by Nordlund et al. (2002). Compared with Nordlund et al. (2002), the higher angular velocity and the greater level of effort adopted here, have probably increased the amount of coactivation in the tibialis anterior (on average 11%) (Ebenbichler et al. 1998; Kellis and Baltzopoulos 1997) and affected the reciprocal inhibition and thus limited the facilitation of the H reflex induced by the contraction.

The lower  $H_{\text{sup}}/M_{\max A}$  ratio, obtained during eccentric contractions with respect to isometric and concentric actions, in theory could have been caused by increased amounts of reciprocal inhibition. However, the amount of coactivation was



similar for all action types. Similar findings have been reported for sub-maximal voluntary contractions by Pinniger et al. (2003). Consequently, it could be suggested that reciprocal inhibition of the SOL Ia afferents might be similar between all action types.

During eccentric contractions, sensory Ib afferents from Golgi organs may modulate the level of force to protect the musculoskeletal system from injuries (Aagaard et al. 2000). Ib afferents activation, via Ia inhibitory interneurons, could then partially explain this decrease. Furthermore, spindle afferent discharges likely increased during the fast lengthening contractions (Burke et al. 1978). Therefore the decrease of eccentric  $H_{\text{sup}}/M_{\text{maxA}}$  ratio may also be related to homosynaptic postactivation depression (Hultborn et al. 1996).

According to previous studies investigating H reflex during sub-maximal contractions and our data, collected during MVCs, it seems that contraction intensities do not influence the effect of action type on the H/M ratio.

#### *Effect of action types on V wave*

Because  $H_{\text{sup}}/M_{\text{maxA}}$  ratio was lower during lengthening, as compared with isometric and concentric actions, it was hypothesized that the  $V/M_{\text{maxA}}$  ratio would be modulated in the same way. Because V wave is an electrophysiological variant of the H reflex, recorded during contractions, we were however surprised to notice that  $V/M_{\text{maxA}}$  ratio was similar whatever the contraction type. Reflex inhibitions, present during lengthening, were therefore compensated by neural mechanisms that may influence V-wave amplitude. During a voluntary contraction, the antidromic volley may be abolished in some of the motor axons by collisions with volitional impulses; these axons would be "cleared" for transmission of H-reflex impulses down to the muscle (Upton et al. 1971). V wave would be therefore modulated by the antidromic collision and the motoneurons excitability (Aagaard et al. 2002).

During maximal voluntary concentric and eccentric contractions, transcranial magnetic stimulation (TMS) has been utilized by Loscher and Nordlund (2002) to assess cortico-spinal transmission efficacy and voluntary activation. These authors suggested that the corticospinal excitability was not different between maximal concentric and eccentric elbow flexor contractions because the motor-evoked potentials elicited by TMS did not differ according to the contraction type. However, TMS was able to induce greater additional elbow flexor torque during eccentric MVC (4.37% of the underlying voluntary torque) as compared with concentric MVC (2.13% of the underlying voluntary torque). These findings imply that either the motor cortex or part of the motor pathway down to the contractile apparatus is not working optimally during eccentric action as compared with concentric action despite maximal voluntary effort. Therefore a lesser degree of voluntary activation, during eccentric MVC, would reduce the amount of antidromic collision and thus limit V-wave amplitude during eccentric action with respect to isometric and concentric efforts. Nevertheless, this hypothesis does not seem to be supported by the results on V wave obtained in the present study. The lack of change in the  $V/M_{\text{maxA}}$  ratio could be related to the fact that the difference in voluntary activation between concentric and eccentric contractions was only of a small magnitude (Loscher and Nordlund 2002). In the present study,

because  $SOL\ RMS/M_{\text{maxA}}$  did not differ according to the action type, the amount of antidromic collision was theoretically the same. The  $V/M_{\text{maxA}}$  ratio seems related to the pool of motor units able to take advantage of the antidromic collision, which is function of the transmission of efferent impulses, i.e., their number and frequency, in  $\alpha$ -motoneuron axons during voluntary muscle activation. For sub-maximal contractions, the hypothesis has already been formulated that eccentric contractions, compared with isometric and concentric actions, appear to require unique activation strategies by the nervous system (recruitment order, discharge rate and recruitment threshold of motor units) (Enoka 1996). A recent study by Fang et al. (2004) showed that the area of the brain involved in the control process is larger for eccentric than concentric muscle activities; this may indicate an involvement of more functional regions and a larger number of neurons in the brain. Specific volitional impulses (frequency and recruitment) would then occur during eccentric actions.

On the other hand, V wave is also sensitive to motoneuron excitability. Then, data from the present study could also be explained by neural mechanisms at spinal level. To compare H-reflex and V-wave modulations, we have to take into account that these two types of evoked responses could recruit different portions of the spinal motoneuron pool due to the large difference in stimulation intensity. As a result, V-wave response will recruit both large as well as small motoneurons, whereas the H-reflex primarily relies on the pool of smaller motoneurons (Aagaard et al. 2002). In accordance with this assumption, a more pronounced degree of Ia afferent presynaptic inhibition of type I motoneurons (which are mainly excited by the H reflex volley) as compared with large-sized type II motoneurons (which could be involved by the V-wave stimulation protocol) would be suggested to explain, at least in part, the lack of decrease in  $V/M_{\text{maxA}}$  during eccentric contraction.

In conclusion, this study shows that the efficacy of the Ia afferent is reduced during passive lengthening and eccentric MVCs. Presynaptic Ia inhibitions were suggested to explain these H-reflex modulations. During MVCs,  $H_{\text{sup}}$ ,  $M_{\text{maxA}}$ , and V wave were recorded to assess motoneurons excitability and its modulation by inhibition mechanisms and the descending neural drive. During eccentric efforts, the  $V/M_{\text{maxA}}$  ratio was not modulated like  $H_{\text{sup}}/M_{\text{maxA}}$  in comparison with isometric and concentric contractions. Findings on V wave and H reflex seem to suggest that during eccentric contractions, the spinal loop is specifically modulated by the supra-spinal centers and/or neural mechanisms at spinal level.

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