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Neural adaptations in quadriceps muscle after 4 weeks of local vibration training in young versus older subjects

Robin Souron, Thibault Besson, Thomas Lapole, and Guillaume Y. Millet

Abstract: This study investigated the effects of a 4-week local vibration training (LVT) on the function of the knee extensors and corticospinal properties in healthy young and older subjects. Seventeen subjects (9 young and 8 older) performed 3 testing sessions: before (PRE₁) and after (PRE₂) a 4-week resting period to control the repeatability of the data as well as after the LVT (POST). Jump performance, maximal voluntary contraction (MVC) and electromyographic (EMG) activity on vastus lateralis and rectus femoris muscles were assessed. Single-pulse transcranial magnetic stimulation (TMS) allowed evaluation of cortical voluntary activation (VA_{TMS}), motor evoked potential (MEP) area, and silent period (SP) duration. All training adaptations were similar between young and older subjects ($p > 0.05$) and the following results reflect the pooled sample of subjects. MVC (+11.9% ± 8.0%, $p < 0.001$) and VA_{TMS} (+3.6% ± 5.2%, $p = 0.004$) were significantly increased at POST compared with PRE₂. Maximal vastus lateralis EMG was significantly increased at POST (+21.9% ± 33.7%, $p = 0.03$). No changes were reported for MEPs on both muscles ($p > 0.05$). SPs recorded during maximal and submaximal contractions decreased in both muscles at POST ($p < 0.05$). Vertical jump performance was increased at POST ($p < 0.05$). LVT seems as effective in young as in older subjects to improve maximal functional capacities through neural modulations occurring at least partly at the supra-spinal level. Local vibration may be used as an efficient alternative training method to improve muscular performance in both healthy young and older subjects.

Key words: local vibration training, transcranial magnetic stimulation, cortical voluntary activation, corticospinal excitability and inhibition, older population.

Résumé : Cette étude examine les effets de 4 semaines d'entraînement par vibration locale (« LVT ») sur les propriétés fonctionnelles et corticospinales des muscles extenseurs du genou de sujets jeunes et âgés en bonne santé. Dix-sept sujets (9 jeunes et 8 personnes âgées) participent à trois séances d'évaluation : avant (« PRE₁ ») et après (« PRE₂ ») 4 semaines de repos pour le contrôle de la répétabilité des données ainsi qu'après LVT (« POST »). On évalue la hauteur de saut, la contraction maximale volontaire (« MVC ») et l'activité myoélectrique (« EMG ») des muscles vastus lateralis et rectus femoris. Une seule impulsion issue de la stimulation magnétique transcrânienne (« TMS ») permet d'évaluer l'activation corticale volontaire (« VA_{TMS} »), l'aire du potentiel évoqué moteur (« MEP ») et la durée de la période de silence (« SP »). Les sujets jeunes et âgés présentent des adaptations à l'entraînement similaires ($p > 0,05$); les résultats suivants regroupent donc tous les sujets. Au moment POST, on note une augmentation significative de MVC (+11,9 ± 8,0 %, $p < 0,001$) et VA_{TMS} (+3,6 ± 5,2 %, $p = 0,004$) comparativement au moment PRE₂. L'activité myoélectrique maximale du vastus lateralis est significativement plus élevée à POST (+21,9 ± 33,7 %, $p = 0,03$). On n'enregistre aucune modification des MEP des deux muscles ($p > 0,05$). Les SP enregistrées au cours des contractions sous-maximales et maximales sont moins longues à POST dans les deux muscles ($p < 0,05$). La hauteur de saut augmente à POST ($p < 0,05$). LVT semble aussi efficace chez les jeunes personnes que chez les plus âgées pour améliorer les capacités fonctionnelles via des modulations nerveuses s'effectuant, du moins partiellement, au niveau supraspinal. On peut utiliser la vibration locale en tant que méthode alternative d'entraînement efficace pour améliorer la performance musculaire chez des personnes jeunes et âgées.

Mots-clés : entraînement par vibration locale, stimulation magnétique transcrânienne, activation corticale volontaire, excitabilité et inhibition corticospinale, population âgée.

Introduction

The idea of using local vibration (LV) as a training method to enhance muscle performance is relatively recent. While the chronic effects of whole-body vibration (WBV) have been well described (Cochrane 2011), the concept of local vibration training (LVT), i.e., the repetition of LV sessions across multiple days with the aim to improve neuromuscular function, is relatively und investigated so far (Souron et al. 2017b). It has been reported that LVT performed on relaxed lower limb muscles was efficient to

improve muscle strength in healthy young subjects (Lapole and Pérot 2010; Iodice et al. 2011; Lapole et al. 2013; Souron et al. 2017c). Neural adaptations were proposed to mainly account for the strength gains after LVT (Lapole and Pérot 2010; Lapole et al. 2013; Souron et al. 2017c), as first evidenced by an increase in electromyographic (EMG) amplitude and an increase in voluntary activation during maximal voluntary contraction (MVC) after 14 consecutive days of LVT on the Achilles tendon in healthy young subjects (Lapole and Pérot 2010).

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Of the receptors that are sensitive to vibration, i.e., cutaneous receptors (Ribot-Ciscar et al. 1996), Golgi tendon organs (Burke et al. 1976), or muscle spindles (Burke 1980; Roll et al. 1989), the latter have been reported to be the most responsive. It has been shown that Ia afferent discharge elicits an excitatory input on alpha motoneurons and may evoke a reflex contraction of the vibrated muscle called the tonic vibration reflex (Eklund and Hagbarth 1965; Hagbarth and Eklund 1966), that is paralleled with a paradoxical decreased spinal loop excitability (Desmedt and Godaux 1978). Decreased spinal excitability has been well-reported after a single session of prolonged LV of quadriceps (Fry and Folland 2014) or soleus (Lapole et al. 2012) muscles. This may trigger spinal adaptations in the long term as suggested by previous findings of increased Hoffmann reflex (H-reflex) amplitude in the soleus muscle after LVT (Lapole and Pérot 2012; Lapole et al. 2013). Supra-spinal modulations have also been reported during LV application since vibration-induced Ia afferent discharge activates the same motor cortical areas as those activated during a voluntary contraction, i.e., both motor and sensorimotor cortex and contralateral supplementary motor area (Naito et al. 1999; Naito and Ehrsson 2001), which may lead to an increased corticospinal excitability (Lapole et al. 2015a, 2015b). Supra-spinal adaptations with training may be investigated using transcranial magnetic stimulation (TMS). For instance, motor evoked potentials (MEPs), i.e., compound muscle action potentials because of TMS, and silent period (SP), i.e., the period of no EMG activity that follows the MEP when elicited during a contraction, may be recorded to provide information about the excitability and inhibition of cortical neurons and/or motoneuron pools of the stimulated muscles (Goodall et al. 2014). Increased cortical excitability has been recently reported after a single session of prolonged LV of quadriceps muscle (Souron et al. 2017a). These results could suggest supra-spinal adaptations in the long term despite our recent report of no changes in MEP amplitude and SP duration after 4 and 8 weeks of LVT applied on the dorsiflexor muscles (Souron et al. 2017c). Moreover, cortical voluntary activation (VA_{TMS}) can be calculated by evoking superimposed twitches (SIT) during voluntary contractions (Todd et al. 2003). A SIT elicited by TMS during MVC highlights a suboptimal drive from the motor cortex (Goodall et al. 2014). Our research group recently reported that VA_{TMS} was significantly increased in healthy young subjects after 4 weeks of LVT applied on the dorsiflexor muscles (Souron et al. 2017c).

Adaptations within the central nervous system may enhance muscle performance after LVT in healthy young subjects (Lapole and Pérot 2012; Lapole et al. 2013; Souron et al. 2017c). It has recently been reported that this form of training may also benefit to older populations (Tankisheva et al. 2015), which is characterized by neuromuscular deconditioning. Indeed, aging results in decreased output from the neuromuscular system, which causes reductions in force-generating capacity of muscles (Dalton et al. 2010; Kirk et al. 2016). Further, alterations in muscle properties, such as loss in muscle mass or changes in fibre-type distribution (see Evans and Lexell (1995) for a review) have been documented with aging. Alterations in neural properties may also arise at both spinal (e.g., loss of spinal motoneurons (Power et al. 2010) or decrease in the efficiency of Ia afferents pathway to activate spinal motoneurons (Aagaard et al. 2010; Baudry and Duchateau 2012)) and supra-spinal levels (e.g., reductions in the availability of several cortical neurotransmitters or reduction in brain volume (Volkow et al. 1998; Mattay et al. 2002)). The alterations in force-generating capacity may lead to an impaired mobility, a loss of autonomy, and an increased risk of fall, which represent the major causes of dependency in older subjects (Hepple and Rice 2016). It has yet to be determined whether LVT may promote chronic neural adaptations that might reduce such age-related neuromuscular deconditioning.

In the present study, we aimed to investigate the effects of a 4-week unilateral LVT program on the functional capacities and

associated corticospinal properties of the knee extensor muscles, known for their important functional role in activities of daily living and their progressive weakness with aging (Hurley et al. 1998). This research is novel because it is the first study to test the neural adaptations due to LVT in (i) knee extensor muscles and (ii) healthy older subjects. All the theory behind chronic adaptations are related to acute deleterious effects and recovery (Burtin et al. 2012; Gathercole et al. 2015). Based on recent results that report neural modulations (i.e., decreased maximal EMG activity) after an acute exposure to LV in both healthy young and older subjects (Souron et al. 2017a), we hypothesized that a repeated exposure to LV would trigger long-term neural adaptations that would accompany the significant augmentation in MVC force. This study also assessed if the magnitude of training adaptations is different between these 2 populations, considering (i) differences in muscle fibre composition, i.e., reduced number and size of type II muscle fibres in older subjects (Grimby et al. 1982; Aniansson et al. 1986), and (ii) the lower muscle spindles sensitivity to muscle stretch in older subjects (Corden and Lippold 1996), which are 2 parameters known to influence the sensitivity to LV stimuli. An understanding of the sites of neural adaptation for the knee extensors in response to LVT, and potential age-related differences, may help to improve training and/or rehabilitation technique, with age-based specificity.

Materials and methods

Subjects

Seventeen healthy subjects volunteered for this study after giving their written informed consent. The current study included 9 young (5 men and 4 women; age, 25 ± 1 years; height, 173 ± 7 cm; weight, 66 ± 5 kg) and 8 older (2 men and 6 women; age, 65 ± 5 years; height, 168 ± 15 cm; weight, 72 ± 10 kg) subjects. The level of weekly physical activity was reported to be between 0 and 4 h per week for each subject. This study conformed to the standards from the latest revision of the *Declaration of Helsinki* and was approved by the local ethics committee of the University of Calgary (Research Ethic Board no. 15.2752). All subjects were free of lower limb injury during the previous 3 months, had no contraindications to TMS as indicated by a questionnaire (Rossi et al. 2011), and no acute or chronic neurological disorders and/or trauma. Subjects were not informed of the investigators' hypotheses, only that the effect of a local vibration training was being tested. They were instructed to abstain from caffeine for a minimum of 12 h before each session.

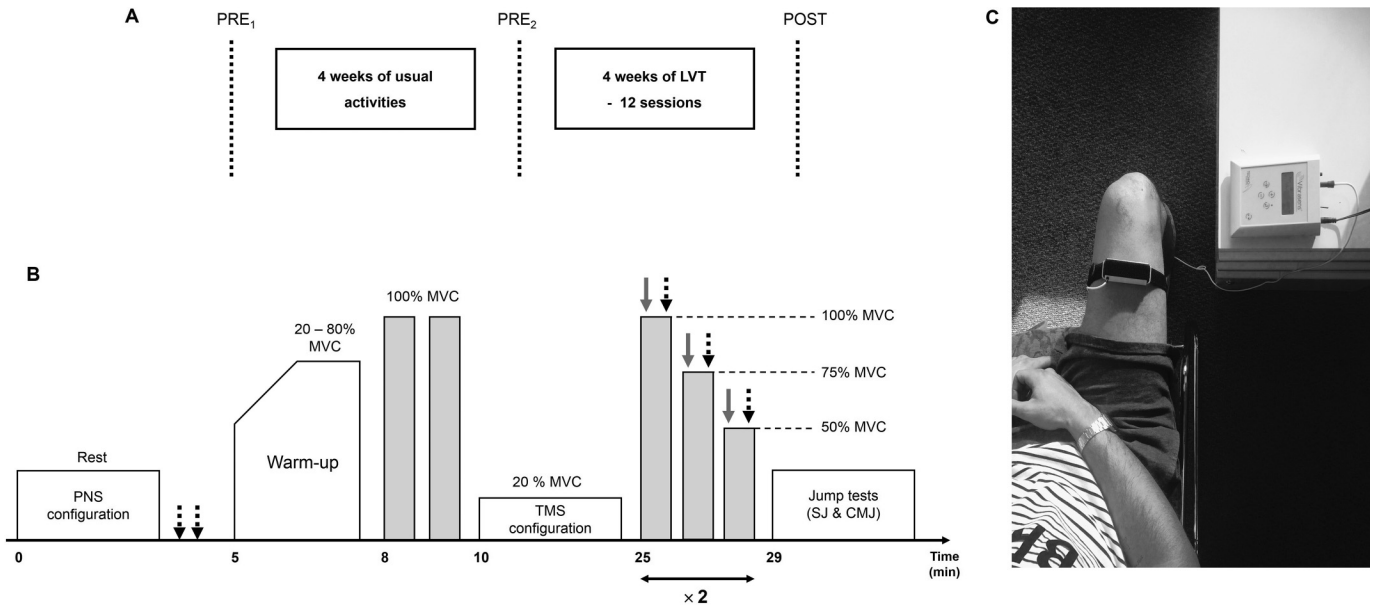
Experimental design

The experimental design is illustrated in Fig. 1A. All the subjects performed the experimental procedures 3 times, at the same time of the day, after they were first familiarized with the electrical and magnetic stimulations and the proper technique for the maximal isometric knee extension. The first testing session (PRE_1) was performed 4 weeks before the second testing session (PRE_2), in which subjects were retested to control the repeatability of data. No specific recommendations were given and the subjects were only asked not to change their usual activities during the 4-week period between PRE_1 and PRE_2 . After PRE_2 , the subjects started to follow the 4-week LVT and then returned for follow-up testing (POST).

LVT

The subjects underwent a 4-week unilateral LVT. After identifying the muscle through palpation, the vibrating device (VB 115; Techno Concept, Mane, France) was applied locally and strapped directly on the right rectus femoris (RF) muscle (i.e., 40% of the muscle length from the upper edge of the patella to the anterior superior iliac spine) using elastic Velcro fasteners (Fig. 1C). The subject was seated on a chair during the entire vibration session, with a knee angle of 90° . The vibrating device was always placed

Fig. 1. (A) Experimental design of the study. (B) Overview of the neuromuscular testing protocol. Dotted black and grey arrows represent peripheral nerve stimulation and transcranial magnetic stimulation, respectively. (C) Local vibratory device and the application site for the training session. CMJ, countermovement jump; LVT, local vibration training; MVC, maximal voluntary contraction; POST, after the 4-week local vibration training; PNS, peripheral nerve stimulation; PRE₁, PRE₂, before and after the control condition, respectively; SJ, squat jump; TMS, transcranial magnetic stimulation.



on the muscle by the same investigator to ensure the same pressure was exerted on the leg, although this was not measured. The 4-week LVT program consisted of three 1-h vibration sessions per week with at least 1 day of rest in between, for a total of 12 vibration sessions. As Ia afferents are sensitive to small vibration amplitude (Roll et al. 1989) and fire synchronously with vibration frequencies up to 80–120 Hz (Roll et al. 1989), vibration characteristics were 100 Hz frequency and 1-mm amplitude in the present study, as already set in previous works led by our research group (Souron et al. 2017c). Because no EMG measurement was performed during LVT sessions, it is impossible to rule out an eventual occurrence of tonic vibratory reflexes during training sessions. The vibration device and parameters used in the present study, however, were the same as in a previous one from our research group (Lapole et al. 2015b) that reported no occurrence of tonic vibratory reflexes during LV application (frequency: 110 Hz; amplitude: 1 mm). The compliance for LVT was excellent since none of the subjects missed a session. The training was also reported to be well tolerated by each subject.

Force and EMG recordings

Knee extensor force of the right limb was measured during voluntary contraction by a calibrated force transducer (Omega Engineering Inc., Stamford, Conn., USA). Subjects were seated upright in a chair with both right knee and hips at 90° of flexion. Movement of the upper body was minimized using 3 belts across the thorax and waist. During all measurements, subjects were provided with real-time feedback of the force trace displayed on a screen, and visual guidelines were added when subjects had to maintain a targeted submaximal level of MVC.

EMG activity of the vastus lateralis (VL), RF, and biceps femoris (BF) was recorded with pairs of self-adhesive surface electrodes (Meditrace 100; Covidien, Mansfield, Mass., USA) placed at the distal end of each muscle of interest in a bipolar configuration with a 30-mm interelectrode distance. The reference was placed on the patella. Low impedance (<5 k Ω) was obtained by shaving, gently abrading the skin, and then cleaning it with isopropyl alcohol. Signals were amplified with an octal bio-amplifier (ML138; ADInstruments, Bella Vista, Australia), bandpass filtered

(5–500 Hz) and analogue-to-digital converted at a sampling rate of 2000 Hz by PowerLab System (16/35, ADInstruments). All data were analyzed offline using Labchart 8 software (ADInstruments).

Peripheral nerve stimulation

Single rectangular pulses with 1-ms duration and 400 V maximal output voltage were delivered via constant-current stimulator (DS7A; Digitimer, Hertfordshire, UK) to the right femoral nerve via a 30-mm-diameter surface cathode (Meditrace 100) manually pressed into the femoral triangle and 50 × 90 mm anode (Durastick Plus; DJO Global, Vista, Calif., USA) in the gluteal fold. To determine the optimal intensity of stimulation for M-wave measurement, single stimuli were delivered incrementally by steps of 5 mA until resting M-wave (M_{max}) and twitch amplitudes plateaued. The optimal intensity was then increased by 30% to confirm supramaximal stimulation. The determination of optimal peripheral nerve stimulation (PNS) position and intensity was performed at the beginning of the neuromuscular testing session to avoid any potentiation or fatigue effects.

TMS

The left motor cortex was stimulated by a magnetic stimulator (Magstim 200²; The Magstim Company Ltd., Whitland, UK) with a 110-mm double-cone-coil (maximum output of 1.4 T). The coil was positioned to induce a postero-anterior current and manually controlled by the same investigator throughout all the testing sessions. A cervical collar was worn during all TMS measures to stabilize the head and neck and a swim cap was worn to ensure consistent coil placement relative to the optimal position. To determine this site, 6 marks were drawn on the cap: the vertex, 1 and 2 cm posterior to the vertex, and 1 cm to the left of these 3 marks along the midline. Optimal coil position was determined as the site eliciting the largest SIT as well as VL and RF MEP amplitudes, with minimal MEP amplitude in the antagonist BF, in response to stimulation at a known suprathreshold stimulator output (50% maximum) cccduring a 10% MVC knee extension. When optimal MEPs and peak force were not recorded at the same coil position, the optimal coil position was chosen according to MEP amplitude, because the evoked peak force may be influenced by

activation of other muscles (Todd et al. 2016). This position was marked on the swim cap and was the same for both RF and VL muscles.

As per our recent recommendation (Temesi et al. 2014), the optimal stimulus intensity was determined from SIT and MEP stimulus-response curves obtained during brief (2–3 s) voluntary contractions at 20% MVC. In brief, intensities of 20%, 30%, 40%, 50%, 60%, 70%, and 80% stimulator output were tested in random order. At each intensity, 4 contractions were performed at 10-s intervals. Rest periods of 10 s separate each intensity. In 1 subject, the SIT and MEP amplitudes did not plateau using these intensities so stimulator outputs of 90% and 100% were added to reach a plateau. The optimal stimulation intensity was considered as the lowest, which showed a plateau for VL and RF MEPs as well as the SIT. The MEP evoked in the antagonist BF was also measured to make sure that its size was low compared with those recorded in VL and RF.

Experimental procedures

The experimental procedures are illustrated in Fig. 1B. All the neuromuscular measurements were performed on the right (i.e., trained) leg only, which was the dominant one for all the subjects. First, the optimal position and intensity for PNS were determined to assess resting M-waves (M_{max}). Then, after a standardized warm-up consisting of 3 brief (~3 s) submaximal isometric voluntary contractions at 20%, 40%, 60%, and 80% MVC, the subjects performed 2 brief (~3 s) MVCs interspaced by 1 min. Optimal coil position and intensity for transcranial magnetic stimulation were then established. Cortical voluntary activation, i.e., VA_{TMS} , was calculated using 2 series of 3 brief (~5 s) contractions (100%, 75%, and 50% MVC), with single TMS and PNS pulses delivered during each contraction. Rest periods of 15 s and 1 min were provided between contractions within a series and between the series, respectively. To permit accurate determination of the SP, subjects were instructed to momentarily (<1 s) contract as strong and quickly as possible immediately after delivery of the single TMS pulse. Finally, 2 squat jumps (SJs) and countermovement jumps (CMJs) were performed (see below) at the end of the session.

Data analysis

As the results for M-wave and MEP peak-to-peak amplitudes and areas were similar, only areas are reported. Evoked EMG data (M-wave, MEP, and SP) are presented as the average values of all responses collected at PRE₁, PRE₂, and POST. A representative trace of EMG recording in response to TMS is displayed in Fig. 2.

PNS

M-Wave areas were measured from electrical nerve stimulations in both VL and RF when they were either relaxed (M_{max_VL} and M_{max_RF}) or maximally contracted (M_{sup_VL} and M_{sup_RF}).

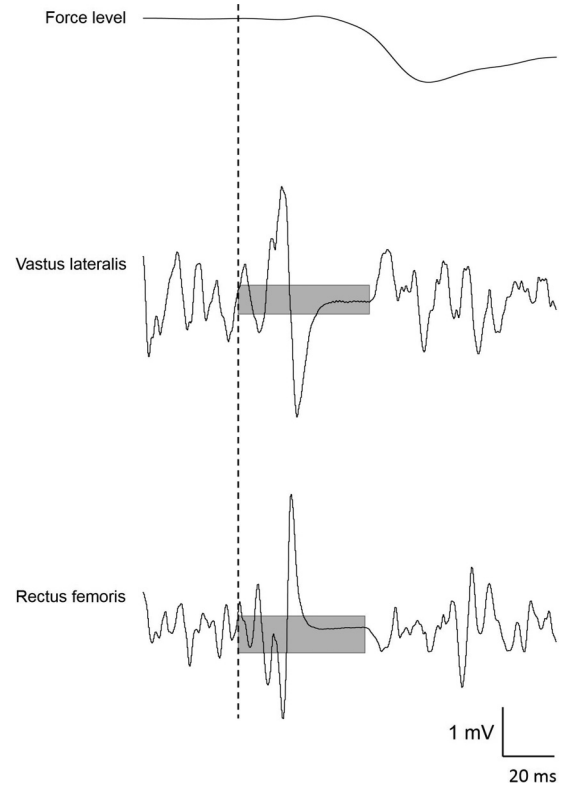
Force and EMG

Maximal force was calculated as the highest peak force recorded from the 4 MVCs. Root mean square (RMS) EMG was calculated for VL (RMS_{VL}) and RF (RMS_{RF}) muscles over a 500-ms period once the force reached a plateau. RMS_{VL} and RMS_{RF} were then normalized to M_{sup} .

TMS

VA_{TMS} was measured by the modified twitch interpolation technique (Todd et al. 2003). Corticospinal excitability increases substantially during the transition from relaxed to contracted muscle states (Ugawa et al. 1995), thus underestimating TMS evoked twitch in the relaxed muscle. Hence, the estimated resting twitch (ERT) was determined as the y intercept of a linear regression of SIT amplitude and absolute voluntary force during the 2 series of contractions at 100%, 75%, and 50% MVC. VA_{TMS} was then assessed with the following equation:

Fig. 2. Example of electromyographic (EMG) recording in response to transcranial magnetic stimulation (TMS) during maximal voluntary contractions for the agonists vastus lateralis and rectus femoris. The dotted vertical line indicates the time of magnetic stimulation. The grey box represents the silent period duration, i.e., the time interval between TMS stimulus and the return of continuous voluntary EMG.



$$VA_{TMS} = (1 - SIT_{MVC}/ERT) \times 100$$

where SIT_{MVC} is the superimposed twitch evoked during MVC. Two series were performed with contractions and series separated by 10 s and 2 min, respectively. Thus, the linear regression was performed with the 3 values from each series (R^2 range: 0.83–0.99). The highest value of VA_{TMS} was kept for further analysis.

MEP areas were measured between set cursors placed at the beginning (i.e., initial deflection from baseline) and the end (i.e., second horizontal crossing) of the evoked potentials (see fig. 1D in Martin et al. (2006)) and normalized to the M-wave measured at the same contraction intensity, i.e., 100%, 75%, and 50% MVC. To assess M-wave during voluntary contractions, PNS was delivered 2–3 s after TMS once the force returned to the appropriate contraction level. To ensure the lowest possible co-activation was elicited, which is mandatory to ensure a correct evaluation of VA_{TMS} (Todd et al. 2016), MEP areas were also recorded on the antagonist BF muscle during MVC. As no M-waves were recorded on the BF, MEPs are presented as absolute values for this muscle. SP durations for VL and RF were determined visually and defined as the duration from the TMS stimulus to the return of continuous voluntary EMG, i.e., when clear EMG bursts could be identified (Taylor et al. 1996).

Jump performance

Two sSJs and 2 CMJs were performed on a jumping mat (27 × 27"; Probotics Inc., Huntsville, Ala., USA) at the end of the testing session. For the SJ, subjects were instructed to start from a semi-squatted position, i.e., knee flexion at 90°, which was maintained

Table 1. Neuromuscular measurements for young and older subjects before control condition (PRE₁), after control condition (PRE₂), and after the 4-week local vibration training program (POST).

	Young subjects			Older subjects			Time	Group	Time × group
	PRE ₁	PRE ₂	POST	PRE ₁	PRE ₂	POST			
MVC (N)	502.6±112.7	501.2±112.9	551.2±132.5	310.4±128.4	311.3±115.6	354.6±123.6	<0.001	0.004	0.90
VA _{TMS} (%)	95.2±2.7	94.9±3.3	97.2±2.5	90.3±8.9	90.3±9.8	94.2±5.7	0.001	0.15	0.55
RMS _{VL} (%M _{sup})	6.5±1.9	6.5±1.9	6.7±1.9	4.4±1.4	4.3±1.1	5.9±1.5	0.04	0.02	0.14
RMS _{RF} (%M _{sup})	7.6±1.9	7.7±2.5	8.3±1.6	4.3±1.6	4.3±1.4	5.0±1.9	0.07	0.001	0.96
MEP _{VL_MVC} (%M _{sup})	49.2±13.1	47.0±14.1	49.1±12.1	50.5±11.1	50.8±8.7	45.7±9.8	0.53	0.85	0.25
MEP _{VL_75} (%M _{sup})	59.7±9.2	57.5±8.0	58.7±14.0	63.9±9.3	61.4±9.8	55.7±10.7	0.22	0.72	0.19
MEP _{VL_50} (%M _{sup})	68.5±13.1	64.7±12.1	66.7±16.0	57.9±21.6	57.3±19.1	53.5±16.0	0.41	0.18	0.49
MEP _{RF_MVC} (%M _{sup})	64.8±12.0	67.4±11.8	75.8±21.6	51.8±19.0	54.8±15.4	57.6±12.7	0.07	0.04	0.67
MEP _{RF_75} (%M _{sup})	84.3±11.9	82.6±10.6	84.3±17.0	61.4±30.2	64.5±18.1	72.4±26.5	0.29	0.04	0.35
MEP _{RF_50} (%M _{sup})	92.1±10.8	88.9±11.1	95.6±14.7	68.0±20.4	69.0±20.0	71.3±27.8	0.48	0.009	0.80
SP _{VL_MVC} (ms)	239±74	236±89	217±79	246±61	254±59	251±58	0.12	0.62	0.76
SP _{VL_75} (ms)	237±72	234±83	214±83	262±62	258±76	243±69	0.05	0.59	0.24
SP _{VL_50} (ms)	245±72	234±78	213±81	254±72	249±67	237±71	0.004	0.65	0.58
SP _{RF_MVC} (ms)	243±69	233±78	215±77	255±78	256±62	257±56	0.07	0.53	0.79
SP _{RF_75} (ms)	239±65	230±77	211±77	251±86	255±79	242±66	0.02	0.59	0.85
SP _{RF_50} (ms)	245±61	241±84	231±63	245±83	237±73	227±67	0.008	0.83	0.65
M _{sup_VL} (mV·s)	0.056±0.021	0.057±0.018	0.060±0.023	0.043±0.018	0.041±0.014	0.044±0.020	0.77	0.08	0.93
M _{sup_RF} (mV·s)	0.041±0.010	0.038±0.008	0.039±0.009	0.030±0.009	0.031±0.009	0.029±0.012	0.65	0.06	0.30
SJ (cm)	28.1±7.5	28.8±8.1	32.9±7.1	16.5±7.1	17.3±7.0	18.9±6.7	<0.001	0.004	0.20
CMJ (cm)	33.9±7.9	33.6±8.0	36.2±8.1	19.9±7.5	20.3±7.9	20.8±7.4	<0.001	0.003	0.09

Note: Data are means ± SD. 50, measurement performed during submaximal voluntary contractions at 50% MVC; 75, measurement performed during submaximal voluntary contractions at 75% MVC; CMJ, counter movement jump; MEP, motor evoked potential; M_{sup}, M-wave recorded during MVC; MVC, maximal voluntary contraction; RF, rectus femoris; RMS, maximal electromyographic root-mean-square; SP, silent period; SJ, squat jump; VA_{TMS}, maximal voluntary activation assessed by transcranial magnetic stimulation; VL, vastus lateralis.

for 2 s before jumping vertically without making any counter-movement. The CMJ started in an erect position and subjects were instructed to make a downward movement to almost 90° knee flexion (visually controlled by the experimenter), before starting to push-off with the lower limbs (Markovic et al. 2004). For SJ and CMJ, subjects were instructed to keep their hands on the hips to control for arm assistance. They were asked to jump continuously, as explosively and as highly as possible. Maximal performance was identified as the highest jump obtained from the 2 trials.

Statistical analysis

Statistical analyses were performed with Statistical software (StatSoft Inc., Tulsa, Okla., USA). All variables were normally distributed (Kolmogorov–Smirnov normality test). For ANOVA analyses, homogeneity of variance was verified by Levene’s test. Two-way repeated-measures ANOVAs were performed on the neuromuscular parameters for both control and training conditions. Factors included in the statistical analysis were the group (young or older) and time (PRE₁ vs PRE₂ vs POST). Post hoc analyses were performed using Bonferroni testing when the ANOVA identified significant differences. Statistical significance was set at $p < 0.05$. All data are presented as mean ± SD. SD is indicated by error bars on the figures.

Results

The mean TMS intensities used for VA_{TMS}, MEPs, and SPs assessment were consistent across the 3 testing sessions (67% ± 12%, 65% ± 11%, and 65 ± 11% for PRE₁, PRE₂, and POST, respectively). Similarly, no differences in TMS intensities were found between young and older subjects for each testing sessions ($p = 0.15$).

No significant differences were found in the control condition, i.e., between PRE₁ and PRE₂, for any neuromuscular parameter ($p > 0.05$, Table 1). Also, no significant group × time interaction was found for any parameter ($p > 0.05$, Table 1).

MVC and voluntary activation

A significant group effect was found for MVC ($F_{[1,15]} = 10.99$; $p = 0.004$), with lower values reported at baseline (−37.9%) in older than young subjects. A significant time effect was reported for

MVC ($F_{[2,30]} = 24.68$; $p < 0.001$), with a significant increase reported after LVT (+11.9 ± 8.0%) (Fig. 3A).

No significant group effect was found for VA_{TMS} ($F_{[1,15]} = 2.24$; $p = 0.15$) but a significant time effect was observed for this parameter ($F_{[2,30]} = 8.21$; $p = 0.001$) with VA_{TMS} being significantly increased by 3.6% ± 5.2% after LVT (Fig. 3B). A significant group effect was reported for the RMS measurement, with lower values reported at baseline in older than young subjects for RMS_{VL} (−34.1%; $F_{[1,15]} = 6.38$; $p = 0.02$) and RMS_{RF} (−44.4%; $F_{[1,15]} = 16.17$; $p = 0.001$). RMS_{VL} was significantly increased after LVT (+21.9% ± 33.7%) as demonstrated by a significant time effect ($F_{[2,30]} = 3.32$; $p = 0.04$), while the changes in RMS_{RF} did not reach the level of significance (+14.1% ± 19.7%, $F_{[2,30]} = 2.85$, $p = 0.054$ for the main time effect) (Fig. 3C).

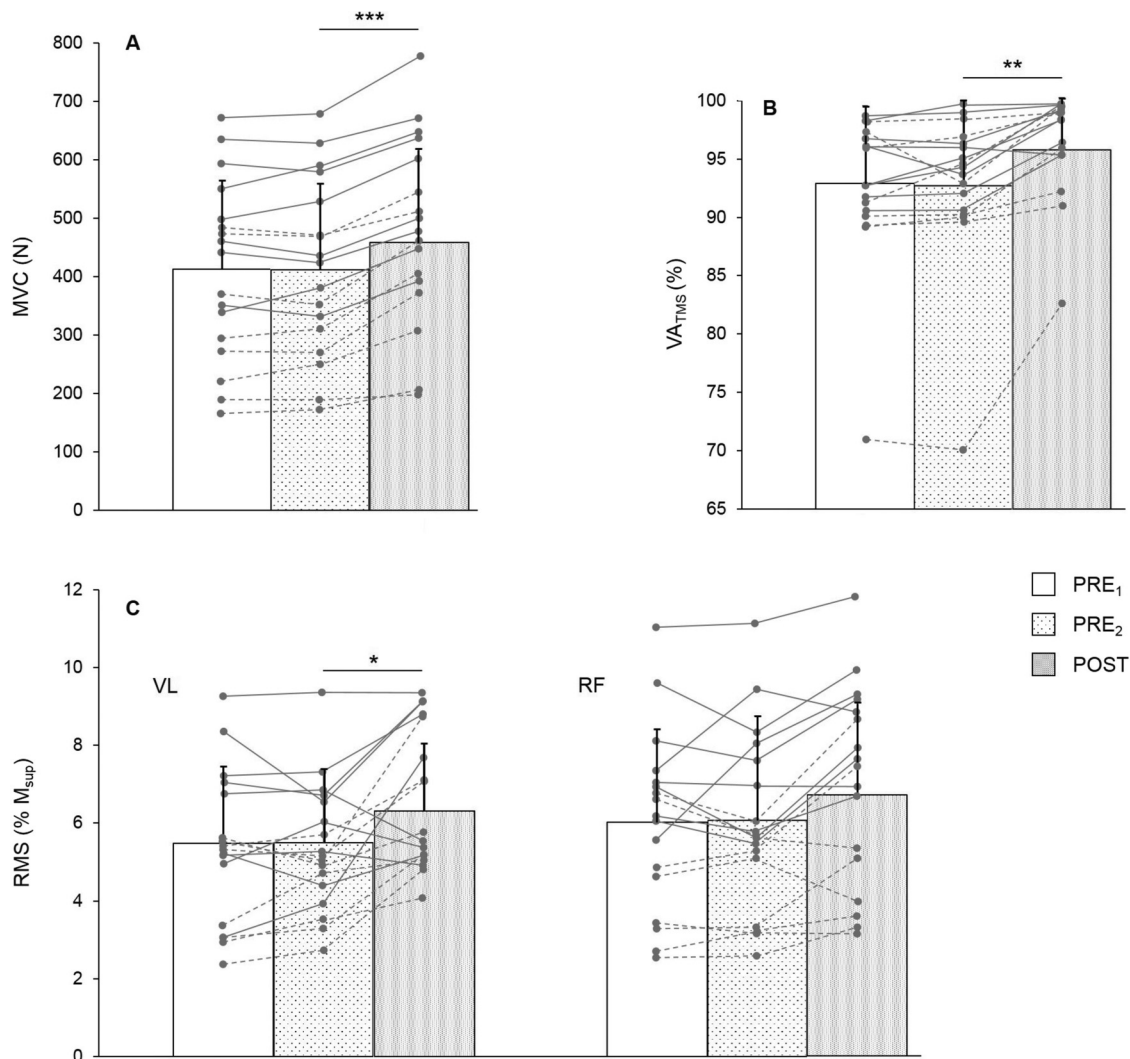
MEPs, SPs, and M-waves

MEPs, SPs, and M-waves are displayed in Table 1.

A significant group effect was found for MEPs recorded on the RF ($p = 0.04$, $p = 0.04$, and $p = 0.009$ for MEPs recorded during 100%, 75%, and 50% MVC, respectively), with lower values reported at baseline in older subjects (−18.6%, −21.3%, and −22.3%, respectively). Time effects were not significant for MEPs on either RF or VL muscles ($F_{[2,30]} = 0.64$ –2.21; $p = 0.06$ –0.56). MEPs recorded on the BF remained consistent across the 3 testing sessions ($F_{[2,30]} = 0.01$; $p = 0.98$).

No significant differences were found in SP durations between young and older subjects as demonstrated by the nonsignificant group effects ($p = 0.53$ –0.83). No changes were reported on SPs recorded during MVC following LVT on VL ($F_{[2,30]} = 2.18$; $p = 0.12$ for the main time effect). SPs during MVCs were not significantly reduced after LVT on RF (−9.2% ± 17.1%, $F_{[2,30]} = 3.18$; $p = 0.07$ for the main time effect). SPs recorded during submaximal voluntary contractions were significantly reduced after LVT ($F_{[2,30]} = 4.25$ –6.38; $p < 0.05$) on both VL (−7.0% ± 12.5% for SPs recorded at 50% MVC) and RF (−6.7% ± 11.5% and −4.1% ± 12.0% for SPs recorded during 75% and 50% MVC, respectively). The changes in SPs recorded on VL during a 75% MVC submaximal voluntary contraction did not reach the level of significance after LVT (−7.2% ± 11.1%, $F_{[2,30]} = 2.71$; $p = 0.051$).

Fig. 3. Knee extensors maximal voluntary contraction (MVC) isometric force (A), maximal cortical voluntary activation assessed with transcranial magnetic stimulation (VA_{TMS} ; B) and electromyographic (EMG) root-mean-square (RMS) normalized to M-wave recorded during MVC (M_{sup}) for vastus lateralis (VL) and rectus femoris (RF; C) muscles before control condition (PRE₁), after control condition (PRE₂), and after the 4-week local vibration training (POST). Values are means \pm SD. Data from individual young (solid lines) and older (dashed lines) subjects are displayed for the 3 testing sessions. Asterisks indicate significantly different from PRE₂ (main effect of time) at *, $p < 0.05$; **, $p < 0.01$; and ***, $p < 0.001$, respectively.



No differences in M_{sup} values were observed between young and older subjects as demonstrated by the nonsignificant group effect ($F_{[1,15]} = 3.36$, $p = 0.08$ and $F_{[1,15]} = 4.22$, $p = 0.06$ for M_{sup} recorded on VL and RF, respectively). M_{sup} was unchanged following LVT for both VL ($F_{[2,30]} = 0.25$; $p = 0.77$) and RF ($F_{[2,30]} = 0.42$; $p = 0.65$) muscles.

Vertical jumps

A significant group effect was found for SJ ($F_{[1,15]} = 11.72$; $p = 0.003$) and CMJ ($F_{[1,15]} = 13.20$; $p = 0.003$), with lower height jumps recorded at baseline in the older subjects (-39.3% and -39.5% for SJ and CMJ, respectively). Maximal jump heights recorded in SJ and CMJ were significantly improved after LVT by $15.2\% \pm 16.2\%$ ($F_{[2,30]} = 11.97$; $p < 0.001$ for the main time effect) and $6.5\% \pm 7.1\%$ ($F_{[2,30]} = 9.52$; $p = 0.008$ for the main time effect), respectively (Fig. 4).

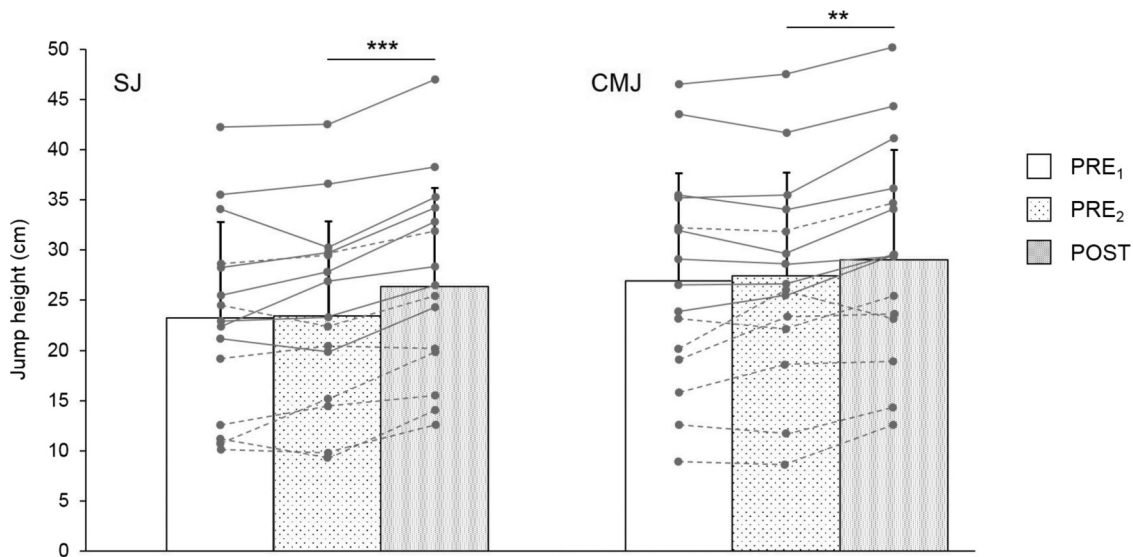
Discussion

The purpose of the present study was to investigate the effects of a 4-week LVT program on knee extensor muscles' functional abilities and corticospinal properties in healthy young and older

subjects. The hypothesis that LVT would be effective in inducing functional and neural adaptations in knee extensor muscles was confirmed since the main findings of the present study are that a 4-week LVT: (i) significantly enhances MVC and vertical jump performance; and (ii) induces modulations within the central nervous system, i.e., maximal VA_{TMS} , maximal EMG RMS activity for the VL, and SP duration for VL and RF muscles for both groups of subjects.

While we recently shown that neuromuscular modulations (i.e., decreased MVC, maximal EMG activity and VA_{TMS} for knee extensor muscles) after an acute exposure to LV were similar between young and older subjects (Souron et al. 2017a), Richardson et al. (2006) reported age differences in the post-LV responses for MVC and quadriceps EMG (i.e., decreased MVC and EMG in young but not older subjects). These authors suggested that an impairment in gamma loop function, owing to a reduced number and size of type II muscle fibres in older subjects, was the likely explanation for the absence of neuromuscular modulations. This hypothesis relies on the fact that the decrease in synaptic input from Ia afferents to alpha motoneurons is thought to predominantly af-

Fig. 4. Performance in squat (SJ) and countermovement (CMJ) jumps before control condition (PRE₁), after control condition (PRE₂), and after the 4 weeks local vibration training program (POST). Values are means \pm SD. Data from individual young (solid lines) and older (dashed lines) subjects are displayed for the 3 testing sessions. Asterisks indicate significantly different from PRE₂ (main effect of time) at **, $p < 0.01$; and ***, $p < 0.001$, respectively.



fect the recruitment of high-threshold motoneurons that supply fast-twitch muscle fibres, i.e., type II (Bongiovanni et al. 1990). A reduced sensitivity of the muscle spindles (and thus a lower Ia afferents discharge in response to vibration stimuli) in older subjects has also been suggested by Richardson et al. (2006). Based on the results reported by this latter study (Richardson et al. 2006), one could have expected differences in the magnitude of training adaptations between these 2 populations, even if this hypothesis remains speculative considering the recent opposite results reported by our research group (Souron et al. 2017a). Although insufficient statistical power due to the small sample size could have prevented detection of age-related differences in the present study (i.e., have caused a type II error), the present study did not show any difference between training adaptations induced in young and older subjects (Table 1).

LVT effects on functional abilities

The increased MVC reported in the present experiment ($+ \sim 10\%$ and $+ \sim 14\%$ for young and older subjects, respectively) after LVT is consistent with previous studies. Indeed, MVC has been found to increase by $\sim 7\%$ – 10% (Lapole and Pérot 2010; Lapole et al. 2013) to $\sim 30\%$ (Iodice et al. 2011) in healthy young subjects, while similar results ($+ \sim 14\%$) were found in healthy older subjects (Tankisheva et al. 2015). Since training parameters used in this later study differed from ours, e.g., 6 months versus 1 month of training and 30–45 versus 100 Hz of vibration frequency, it is difficult to directly compare the current results with those reported by Tankisheva et al. (2015) in older subjects. The present study is novel because it is the first to directly compare the effects of the same LVT program between young and older subjects.

One important and new result of the present study is that a 4-week LVT performed on relaxed muscles was also effective for enhancing vertical jump performance in both healthy young and older subjects. This result may be of clinical interest since a greater leg extensor power may be important to reduce the risk of fall in older subjects (Bassej et al. 1992).

LVT-induced neural modulations

In the present study, significant improvements in MVC and vertical jump performance are likely due to adaptations within the central nervous system, despite the lack of direct correlations between changes in central adaptations and functional parameters

(data not shown). Neural adaptations were first evidenced by the $\sim 4\%$ increase in VA_{TMS} ($+ \sim 3\%$ and $+ \sim 5\%$ for separate young and older subjects, respectively). This agrees with recent results obtained by our research group reporting an increased voluntary activation evaluated by means of the classic, i.e., nerve stimulation, twitch interpolated technique after LVT (Lapole and Pérot 2010). In another study, we also recently demonstrated that an 8-week LVT was sufficient to significantly improve VA_{TMS} ($+ \sim 5\%$) in healthy young subjects, with the increase being significant as soon as after 4 weeks of LVT (Souron et al. 2017c). Neural adaptations were also demonstrated in the present study by the increase in maximal EMG activity for the VL ($p = 0.054$ for the RF). These results appear consistent with a previous study from our group demonstrating a 17% increased maximal EMG activity of the triceps surae after 14 consecutive days of training (Lapole and Pérot 2010). The strong and repeated activation of Ia spindle afferents during LV (Roll and Vedel 1982; Roll et al. 1989) that project their excitatory input toward spinal and supra-spinal levels may likely explain the greater muscle activation (i.e., increased VA_{TMS} and maximal EMG activity) reported in this study.

As previously stated, vibratory stimuli strongly activate the motor areas, which are activated during a voluntary contraction, i.e., both primary motor and sensorimotor cortex and contralateral supplementary motor area (Naito et al. 1999; Naito and Ehrsson 2001). It has also been suggested that acute LV exposure can induce persistent changes in corticospinal excitability (Lapole et al. 2012). Modulations at the cortical level may also be expected after LVT because it was demonstrated that an LV program designed to provide illusory movements during a 5-day immobilization period can prevent the reduced cortical activation of several areas (e.g., sensorimotor cortex, supplementary motor area) when performing voluntary movement (Roll et al. 2012). Then, it is tempting to ascribe part of the LVT-induced neural adaptations to changes at the supra-spinal level. We recently demonstrated unchanged MEP after LVT on tibialis anterior muscle (Souron et al. 2017c). Previous findings also demonstrated that combined WBV with strength training did not further increase corticospinal excitability compared with strength training alone (Weier and Kidgell 2012). Although nonsignificant, an increase in MEP at MVC was found on the RF after LVT in the present study ($+9.3\% \pm 32.5\%$, $p = 0.06$). The interpretation of this result is unclear since it was the only MEP-

related parameter to be affected by LVT. Indeed, MEP on the RF at 50% and 75% MVC and MEP on the VL at all force levels were not changed. It is important to consider that interpreting MEP behaviours at various levels of contractions (i.e., MVC, 75%, and 50% MVC) is challenging. A direct link between the recruitment pattern of motor units and MEPs behaviour has previously been reported (Taylor et al. 1997). Because the MVC was increased in this study, it might have affected motor unit recruitment (spatially, i.e., higher number of recruited motor units, and temporally, i.e., higher discharge rate) at submaximal and maximal levels of contractions. Although these 2 physiological mechanisms are acting in a synergistic way, they may have opposite effect on MEPs behaviour that makes the interpretation of our results difficult. Indeed, a higher spatial recruitment increases the number of functioning motor units that are able to respond to the TMS stimulus and thus lead to a higher excitability, and as a result lead to an increased MEP amplitude. A higher temporal recruitment, however, increases the discharge rate on the recruited corticospinal neurons thus increasing the probability for the TMS pulse to be evoked during the refractory period (Todd et al. 2003). Such a mechanism could mask potential MEP amplitude increases after training. Thus, these changes may have induced discrepancies in MEP responses at maximal or submaximal levels of contractions. Yet, this remains purely speculative and needs to be addressed in future studies. Since long-term facilitation of corticospinal excitability was not induced after LVT in one of our previous work (Souron et al. 2017c) and is still unclear in the present study, it remains to be determined how repeated activation of Ia afferents during LV sessions may have led to a greater VA_{TMS} , even if the link between changes in the neural drive efficiency (through the assessment of VA_{TMS}) and changes in corticospinal excitability (through the assessment of MEPs) is not clear (Gruet et al. 2013). Any changes upstream of the motor cortical output cells (e.g., circuitry of the primary motor cortex, adaptations in the secondary motor cortical areas) may explain the VA_{TMS} augmentation observed after training (Carroll et al. 2011), although changes in spinal/motoneuronal excitability cannot be totally ruled out since it is a single continuous pathway.

Nonetheless, supra-spinal adaptations after LVT are suggested in the present study as evident from the significant decrease in SP duration during submaximal voluntary contractions in both VL and RF ($p = 0.07$ during MVC). Even if the exact mechanisms of the SP remain unclear, the initial part could be mainly due to reduced spinal excitability while the final part could be cortical in origin (Inghilleri et al. 1993; Chen et al. 1999). Then, the final part of SP is thought to result from the activation of inhibitory cortical neurons projecting onto the pyramidal cells in the motor cortex (Inghilleri et al. 1993). Decreased SP duration in the present study suggests that modulations in intracortical inhibitory mechanisms mediated by GABA_B receptors, i.e., the G-protein-coupled receptors (Nakamura et al. 1997), arise within the primary motor cortex and may be an early adaptation to LVT in both young and older subjects. It appears in contrast with the only study that investigated LVT-induced changes in SP duration so far and reporting no significant results neither during maximal and submaximal voluntary contractions of dorsiflexor muscles (Souron et al. 2017c). Strong and repeated sensory feedback from muscle spindles to supra-spinal areas (e.g., motor and sensorimotor cortex, contralateral supplementary motor area (Naito et al. 1999; Naito and Ehrsson 2001)) may have induced long-term modulations in corticospinal inhibition and may have decreased the inhibitory input to the motoneuron pool. This could have partly contributed to the increased MVC (Latella et al. 2012). The SP-related results that provide information about supra-spinal adaptations, however, should be interpreted with caution. Indeed, a recent study that assessed cervico-medullary motor evoked potentials during the SP suggested that the spinal portion of the TMS-evoked silent period is considerably longer than previously stated (Yacyszyn et al.

2016). In that way and based on the current results, it is difficult to completely rule out an eventual spinal contribution to the SP decreases reported in the current study. The techniques of paired-pulse TMS (i.e., assessment of intracortical inhibition and facilitation) should be considered in future studies in parallel to SP measurements since they have been reported as the more appropriate methods to measure changes in intracortical inhibition (Kidgell and Pearce 2010).

Our results may also be explained by increased excitatory inputs from the proprioceptive feedback loop during voluntary contractions in response to the strong activation of Ia afferents by the vibratory stimuli (Lapole and Pérot 2010). Even if it is not possible to directly confirm this hypothesis based on the results recorded in this work, enough evidence has been found to support this idea, especially with the well-reported increased H-reflex amplitude following LVT (Lapole and Pérot 2012; Lapole et al. 2013) that suggest changes in the extent of Ia afferent input that would excite alpha motoneurons (Aagaard et al. 2002). We have also recently shown that an acute exposure to prolonged LV (30 min at 100 Hz frequency) on the same muscle group had the potential to modulate spinal excitability, as demonstrated by the decrease in thoracic MEP areas (Souron et al. 2017a). Consequently, chronic spinal modulations could be expected in the present study. Thus, while the greater muscle activation demonstrated by increased VA_{TMS} and maximal EMG activity may be linked to modulations upstream the motor cortical output cells (see above), it is also likely that changes occurring downstream of the motor cortical output cells are involved. It implies changes in spinal loop excitability between Ia afferents and alpha motoneurons, e.g., modulation in the amount of presynaptic inhibition level (Lapole et al. 2012), as well as changes in corticospinal pathway (i.e., (i) excitability of the corticospinal descending tracts, (ii) efficacy in synaptic transmission between corticospinal descending tracts and alpha motoneurons, and/or (iii) motoneuronal excitability (Giesebrecht et al. 2010)).

Knowing the limitations of the methods classically used to assess training-induced corticospinal adaptations (e.g., TMS, EMG), other methods should be considered to give new insight on neural adaptations, i.e., cervicomedullary and/or thoracic electrical stimulation, and structural changes among supra-spinal structures after LVT (e.g., functional connectivity among the motor-related areas using functional magnetic resonance imaging or positron emission tomography).

Finally, a well-known neural mechanism of enhanced strength following training is a reduced antagonist activity (Carolan and Cafarelli 1992). Based on previous results from our research group (Lapole and Pérot 2010), it is speculated that the level of co-activation was kept constant after LVT in the present work. In our study, however, BF EMG activity was not directly assessed, which may represent a limit to the interpretation of our results.

Practical applications

Our results demonstrate that (i) maximal strength and power can be enhanced by a short-term local vibration intervention in healthy young and aging populations and (ii) this is due to neural adaptations as shown by the higher maximal voluntary activation, the higher maximal EMG activity and the lower SP duration. Training adaptations were not significantly different between young and older subjects despite weaker neuromuscular capacities (e.g., MVC and maximal EMG activity) at baseline in the older participants. Nonetheless, the ability for a short (4 weeks) LVT period to significantly increase functional performance in this study, as already reported by our group on tibialis anterior muscle (Souron et al. 2017c), has important clinical relevance. It suggests that LV can be an effective training method to counteract the neuromuscular deconditioning of knee extensor muscles, which are functionally involved in several activities of daily living such as standing up, sitting down, and gait (Hurley et al. 1998). LVT may

also decrease the risk of fall, one of the major causes of dependency in older populations. Of note is the fact that LVT may be used as an alternative method to the classic methods used to counteract neuromuscular deconditioning (e.g., strength training, WBV training) with the limitation that highly frail individuals may not be able to benefit from this training. Indeed, LVT does not require an active contribution from the subject, can directly target a specific muscle group, and does not have the prohibitive cost of WBV training. In addition, the portability of most LV devices and the capacity to directly target a muscle make it easier for older or clinical populations (e.g., retirement homes, hospital) to implement. Since different populations may benefit from LVT to enhance functional abilities, i.e., healthy young (Souron et al. 2017c) and older (Tankisheva et al. 2015) subjects as well as clinical populations (Pietrangelo et al. 2009), future investigations are now needed to precisely determine the training characteristics (i.e., session duration, number of sessions, number of sessions per week, vibrations parameters, etc.) so that the training can be optimal and tailored to these populations.

Conflict of interest statement

The authors have no conflicts of interest that are directly related to the contents of this article. The authors accept the full responsibility for the conduct study, had full access to all the data, and controlled the decision to publish. The results of the study are presented clearly, honestly, and without fabrication, falsification, or inappropriate data manipulation. The present study does not constitute endorsement by the American College of Sports Medicine.

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References

- Aagaard, P., Simonsen, E.B., Andersen, J.L., Magnusson, P., and Dyhre-Poulsen, P. 2002. Neural adaptation to resistance training: changes in evoked V-wave and H-reflex responses. *J. Appl. Physiol.* **92**: 2309–2318. doi:10.1152/jappphysiol.01185.2001. PMID:12015341.
- Aagaard, P., Suetta, C., Caserotti, P., Magnusson, S.P., and Kjær, M. 2010. Role of the nervous system in sarcopenia and muscle atrophy with aging: strength training as a countermeasure. *Scand. J. Med. Sci. Sports*, **20**: 49–64. doi:10.1111/j.1600-0838.2009.01084.x. PMID:20487503.
- Aniansson, A., Hedberg, M., Henning, G.B., and Grimby, G. 1986. Muscle morphology, enzymatic activity, and muscle strength in elderly men: a follow-up study. *Muscle Nerve*, **9**: 585–591. doi:10.1002/mus.880090702. PMID:3762579.
- Bassey, E.J., Fiatarone, M.A., O'Neill, E.F., Kelly, M., Evans, W.J., and Lipsitz, L.A. 1992. Leg extensor power and functional performance in very old men and women. *Clin. Sci.* **82**: 321–327. doi:10.1042/cs0820321. PMID:1312417.
- Baudry, S., and Duchateau, J. 2012. Age-related influence of vision and proprioception on Ia presynaptic inhibition in soleus muscle during upright stance. *J. Physiol.* **590**: 5541–5554. doi:10.1113/jphysiol.2012.228932. PMID:22946095.
- Bongiovanni, L.G., Hagbarth, K.E., and Stjernberg, L. 1990. Prolonged muscle vibration reducing motor output in maximal voluntary contractions in man. *J. Physiol.* **423**: 15–26. doi:10.1113/jphysiol.1990.sp018008. PMID:2388149.
- Burke, D. 1980. Muscle spindle activity induced by vibration in man: implications for the tonic stretch reflex. Spinal and supraspinal mechanisms of voluntary motor control and locomotion. Karger, Basel.
- Burke, D., Hagbarth, K.-E., Löfstedt, L., and Wallin, B.G. 1976. The responses of human muscle spindle endings to vibration during isometric contraction. *J. Physiol.* **261**: 695–711. doi:10.1113/jphysiol.1976.sp011581. PMID:135841.
- Burtin, C., Saey, D., Saglam, M., Langer, D., Gosselink, R., Janssens, W., et al. 2012. Effectiveness of exercise training in patients with COPD: the role of muscle fatigue. *Eur. Respir. J.* **40**: 338–344. doi:10.1183/09031936.00111811. PMID:22135284.
- Carolan, B., and Cafarelli, E. 1992. Adaptations in coactivation after isometric resistance training. *J. Appl. Physiol.* **73**: 911–917. PMID:1400055.
- Carroll, T.J., Selvanayagam, V.S., Riek, S., and Semmler, J.G. 2011. Neural adaptations to strength training: moving beyond transcranial magnetic stimulation and reflex studies. *Acta Physiol. (Oxf.)*, **202**: 119–140. doi:10.1111/j.1748-1716.2011.02271.x.
- Chen, R., Lozano, A.M., and Ashby, P. 1999. Mechanism of the silent period following transcranial magnetic stimulation. Evidence from epidural recordings. *Exp. Brain Res.* **128**: 539–542. PMID:10541749.
- Cochrane, D. 2011. Vibration exercise: the potential benefits. *Int. J. Sports Med.* **32**: 75–99. doi:10.1055/s-0030-1268010. PMID:21165804.
- Corden, D.M., and Lippold, O.C. 1996. Age-related impaired reflex sensitivity in a human hand muscle. *J. Neurophysiol.* **76**: 2701–2706. PMID:8899639.
- Dalton, B.H., Power, G.A., Vandervoort, A.A., and Rice, C.L. 2010. Power loss is greater in old men than young men during fast plantar flexion contractions. *J. Appl. Physiol.* **109**: 1441–1447. doi:10.1152/jappphysiol.00335.2010. PMID:20829493.
- Desmedt, J.E., and Godaux, E. 1978. Mechanism of the vibration paradox: excitatory and inhibitory effects of tendon vibration on single soleus muscle motor units in man. *J. Physiol.* **285**: 197–207. doi:10.1113/jphysiol.1978.sp012567. PMID:154563.
- Eklund, G., and Hagbarth, K. 1965. Motor effects of vibratory muscle stimuli in man. *Electroencephalogr. Clin. Neurophysiol.* **19**: 619.
- Evans, W.J., and Lexell, J. 1995. Human aging, muscle mass, and fiber type composition. *J. Gerontol. A Biol. Sci. Med. Sci.* **50**: 11–16. doi:10.1093/gerona/50A.Special_Issue.11. PMID:7493202.
- Fry, A., and Folland, J.P. 2014. Prolonged infrapatellar tendon vibration does not influence quadriceps maximal or explosive isometric force production in man. *Eur. J. Appl. Physiol.* **114**: 1757–1766. doi:10.1007/s00421-014-2904-z. PMID:24846679.
- Gathercole, R.J., Stellingwerff, T., and Sporer, B.C. 2015. Effect of acute fatigue and training adaptation on countermovement jump performance in elite snowboard cross athletes. *J. Strength Cond. Res.* **29**: 37–46. doi:10.1519/JSC.0000000000000622. PMID:25029001.
- Giesebrecht, S., Martin, P.G., Gandevia, S.C., and Taylor, J.L. 2010. Facilitation and inhibition of tibialis anterior responses to corticospinal stimulation after maximal voluntary contractions. *J. Neurophysiol.* **103**: 1350–1356. doi:10.1152/jn.00879.2009. PMID:20071624.
- Goodall, S., Howatson, G., Romer, L., and Ross, E. 2014. Transcranial magnetic stimulation in sport science: a commentary. *Eur. J. Sport Sci.* **14**(Suppl. 1): S332–S340. doi:10.1080/17461391.2012.704079. PMID:24444227.
- Grimby, G., Danneskiold-Samsøe, B., Hvid, K., and Saltin, B. 1982. Morphology and enzymatic capacity in arm and leg muscles in 78–81 year old men and women. *Acta Physiol. Scand.* **115**: 125–134. doi:10.1111/j.1748-1716.1982.tb07054.x. PMID:7136797.
- Gruet, M., Temesi, J., Rupp, T., Levy, P., Millet, G.Y., and Verges, S. 2013. Stimulation of the motor cortex and corticospinal tract to assess human muscle fatigue. *Neuroscience*, **231**: 384–399. doi:10.1016/j.neuroscience.2012.10.058. PMID:23131709.
- Hagbarth, K., and Eklund, G. 1966. Motor effects of vibratory muscle stimuli in man. *In* Muscular Afferents and Motor Control. Almqvist & Wiksell. pp. 177–186.
- Hepple, R.T., and Rice, C.L. 2016. Innervation and neuromuscular control in ageing skeletal muscle. *J. Physiol.* **594**: 1965–1978. doi:10.1113/jp270561. PMID:26437581.
- Hurley, M.V., Rees, J., and Newham, D.J. 1998. Quadriceps function, proprioceptive acuity and functional performance in healthy young, middle-aged and elderly subjects. *Age Ageing*, **27**: 55–62. doi:10.1093/ageing/27.1.55. PMID:9504367.
- Inghilleri, M., Berardelli, A., Cruccu, G., and Manfredi, M. 1993. Silent period evoked by transcranial stimulation of the human cortex and cervicomedullary junction. *J. Physiol.* **466**: 521–534. PMID:8410704.
- Iodice, P., Bellomo, R.G., Gialluca, G., Fanò, G., and Saggini, R. 2011. Acute and cumulative effects of focused high-frequency vibrations on the endocrine system and muscle strength. *Eur. J. Appl. Physiol.* **111**: 897–904. doi:10.1007/s00421-010-1677-2. PMID:21063726.
- Kidgell, D.J., and Pearce, A.J. 2010. Corticospinal properties following short-term strength training of an intrinsic hand muscle. *Hum. Mov. Sci.* **29**: 631–641. doi:10.1016/j.humov.2010.01.004. PMID:20400192.
- Kirk, E.A., Copithorne, D.B., Dalton, B.H., and Rice, C.L. 2016. Motor unit firing rates of the gastrocnemii during maximal and sub-maximal isometric contractions in young and old men. *Neuroscience*, **330**: 376–385. doi:10.1016/j.neuroscience.2016.05.059. PMID:27298006.
- Lapole, T., and Pérot, C. 2010. Effects of repeated Achilles tendon vibration on triceps surae force production. *J. Electromyogr. Kinesiol.* **20**: 648–654. doi:10.1016/j.jelekin.2010.02.001. PMID:20223682.
- Lapole, T., and Pérot, C. 2012. Hoffmann reflex is increased after 14 days of daily repeated Achilles tendon vibration for the soleus but not for the gastrocnemii muscles. *Appl. Physiol. Nutr. Metab.* **37**(1): 14–20. doi:10.1139/h11-129. PMID:22148919.
- Lapole, T., Deroussen, F., Perot, C., and Petitjean, M. 2012. Acute effects of Achilles tendon vibration on soleus and tibialis anterior spinal and cortical excitability. *Appl. Physiol. Nutr. Metab.* **37**(4): 657–663. doi:10.1139/h2012-032. PMID:22568876.
- Lapole, T., Canon, F., and Perot, C. 2013. Ipsi- and contralateral H-reflexes and V-waves after unilateral chronic Achilles tendon vibration. *Eur. J. Appl. Physiol.* **113**: 2223–2231. doi:10.1007/s00421-013-2651-6. PMID:23652708.

- Lapole, T., Temesi, J., Arnal, P.J., Gimenez, P., Petitjean, M., and Millet, G.Y. 2015a. Modulation of soleus corticospinal excitability during Achilles tendon vibration. *Exp. Brain Res.* **233**: 2655–2662. doi:10.1007/s00221-015-4336-3. PMID:26048160.
- Lapole, T., Temesi, J., Gimenez, P., Arnal, P.J., Millet, G.Y., and Petitjean, M. 2015b. Achilles tendon vibration-induced changes in plantar flexor corticospinal excitability. *Exp. Brain Res.* **233**: 441–448. doi:10.1007/s00221-014-4125-4. PMID:25370344.
- Latella, C., Kidgell, D.J., and Pearce, A.J. 2012. Reduction in corticospinal inhibition in the trained and untrained limb following unilateral leg strength training. *Eur. J. Appl. Physiol.* **112**: 3097–3107. doi:10.1007/s00421-011-2289-1. PMID:22200796.
- Markovic, G., Dizdar, D., Jukic, I., and Cardinale, M. 2004. Reliability and factorial validity of squat and countermovement jump tests. *J. Strength Cond. Res.* **18**: 551–555. doi:10.1519/00124278-200408000-00028. PMID:15320660.
- Martin, P.G., Gandevia, S.C., and Taylor, J.L. 2006. Output of human motoneuron pools to corticospinal inputs during voluntary contractions. *J. Neurophysiol.* **95**: 3512–3518. doi:10.1152/jn.01230.2005. PMID:16481454.
- Mattay, V.S., Fera, F., Tessitore, A., Hariri, A., Das, S., Callicott, J., and Weinberger, D. 2002. Neurophysiological correlates of age-related changes in human motor function. *Neurology*, **58**: 630–635. doi:10.1212/WNL.58.4.630. PMID:11865144.
- Naito, E., and Ehrsson, H.H. 2001. Kinesthetic illusion of wrist movement activates motor-related areas. *Neuroreport*, **12**: 3805–3809. doi:10.1097/00001756-200112040-00041. PMID:11726799.
- Naito, E., Ehrsson, H.H., Geyer, S., Zilles, K., and Roland, P.E. 1999. Illusory arm movements activate cortical motor areas: a positron emission tomography study. *J. Neurosci.* **19**: 6134–6144. PMID:10407049.
- Nakamura, H., Kitagawa, H., Kawaguchi, Y., and Tsuji, H. 1997. Intracortical facilitation and inhibition after transcranial magnetic stimulation in conscious humans. *J. Physiol.* **498**: 817–823. doi:10.1113/jphysiol.1997.sp021905. PMID:9051592.
- Pietrangolo, T., Mancinelli, R., Toniolo, L., Cancellara, L., Paoli, A., Puglielli, C., et al. 2009. Effects of local vibrations on skeletal muscle trophism in elderly people: mechanical, cellular, and molecular events. *Int. J. Mol. Med.* **24**: 503–512. PMID:19724891.
- Power, G.A., Dalton, B.H., Behm, D.G., Vandervoort, A.A., Doherty, T.J., and Rice, C.L. 2010. Motor unit number estimates in masters runners: use it or lose it? *Med. Sci. Sports Exerc.* **42**: 1644–1650. doi:10.1249/MSS.0b013e3181d6f9e9. PMID:20142771.
- Ribot-Ciscar, E., Roll, J.P., Tardy-Gervet, M.F., and Harlay, F. 1996. Alteration of human cutaneous afferent discharges as the result of long-lasting vibration. *J. Appl. Physiol.* **80**: 1708–1715. PMID:8727558.
- Richardson, M.S., Cramer, J.T., Bembem, D.A., Shehab, R.L., Glover, J., and Bembem, M.G. 2006. Effects of age and ACL reconstruction on quadriceps gamma loop function. *J. Geriatr. Phys. Ther.* **29**: 28–34. PMID:16630374.
- Roll, J.P., and Vedel, J.P. 1982. Kinaesthetic role of muscle afferents in man, studied by tendon vibration and microneurography. *Exp. Brain Res.* **47**: 177–190. PMID:6214420.
- Roll, J.P., Vedel, J.P., and Ribot, E. 1989. Alteration of proprioceptive messages induced by tendon vibration in man: a microneurographic study. *Exp. Brain Res.* **76**: 213–222. PMID:2753103.
- Roll, R., Kavounoudias, A., Albert, F., Legre, R., Gay, A., Fabre, B., and Roll, J.P. 2012. Illusory movements prevent cortical disruption caused by immobilization. *Neuroimage*, **62**: 510–519. doi:10.1016/j.neuroimage.2012.05.016. PMID:22584228.
- Rossi, S., Hallett, M., Rossini, P.M., and Pascual-Leone, A. 2011. Screening questionnaire before TMS: an update. *Clin. Neurophysiol.* **122**: 1686. doi:10.1016/j.clinph.2010.12.037. PMID:21227747.
- Souron, R., Besson, T., McNeil, C.J., Lapole, T., and Millet, G.Y. 2017a. An acute exposure to muscle vibration decreases knee extensors force production and modulates associated central nervous system excitability. *Front. Hum. Neurosci.* **11**: 519. doi:10.3389/fnhum.2017.00519. PMID:29118698.
- Souron, R., Besson, T., Millet, G.Y., and Lapole, T. 2017b. Acute and chronic neuromuscular adaptations to local vibration training. *Eur. J. Appl. Physiol.* **117**(10): 1939–1964. doi:10.1007/s00421-017-3688-8. PMID:28766150.
- Souron, R., Farabet, A., Féasson, L., Belli, A., Millet, G.Y., and Lapole, T. 2017c. Eight weeks of local vibration training increases dorsiflexor muscle cortical voluntary activation. *J. Appl. Physiol.* **122**: 1504–1515. doi:10.1152/jappphysiol.00793.2016. PMID:28385918.
- Tankisheva, E., Bogaerts, A., Boonen, S., Delecluse, C., Jansen, P., and Verschueren, S.M. 2015. Effects of a six-month local vibration training on bone density, muscle strength, muscle mass and physical performance in postmenopausal women. *J. Strength Cond. Res.* **29**: 2613–2622. doi:10.1519/JSC.0000000000000895. PMID:25992656.
- Taylor, J.L., Butler, J.E., Allen, G.M., and Gandevia, S.C. 1996. Changes in motor cortical excitability during human muscle fatigue. *J. Physiol.* **490**(Pt. 2): 519–528. doi:10.1113/jphysiol.1996.sp021163. PMID:8821148.
- Taylor, J., Allen, G.M., Butler, J.E., and Gandevia, S. 1997. Effect of contraction strength on responses in biceps brachii and adductor pollicis to transcranial magnetic stimulation. *Exp. Brain Res.* **117**: 472–478. doi:10.1007/s002210050243. PMID:9438716.
- Temesi, J., Gruet, M., Rupp, T., Verges, S., and Millet, G.Y. 2014. Resting and active motor thresholds versus stimulus-response curves to determine transcranial magnetic stimulation intensity in quadriceps femoris. *J. Neuroeng. Rehabil.* **11**: 40. doi:10.1186/1743-0003-11-40. PMID:24655366.
- Todd, G., Taylor, J.L., and Gandevia, S.C. 2003. Measurement of voluntary activation of fresh and fatigued human muscles using transcranial magnetic stimulation. *J. Physiol.* **551**: 661–671. doi:10.1113/jphysiol.2003.044099. PMID:12909682.
- Todd, G., Taylor, J.L., and Gandevia, S.C. 2016. Measurement of voluntary activation based on transcranial magnetic stimulation over the motor cortex. *J. Appl. Physiol.* **121**: 678–686. doi:10.1152/jappphysiol.00293.2016. PMID:27418687.
- Ugawa, Y., Terao, Y., Hanajima, R., Sakai, K., and Kanazawa, I. 1995. Facilitatory effect of tonic voluntary contraction on responses to motor cortex stimulation. *Electroencephalogr. Clin. Neurophysiol.* **97**: 451–454. doi:10.1016/0924-980X(95)00214-6. PMID:8536598.
- Volkow, N.D., Gur, R.C., Wang, G.-J., Fowler, J.S., Moberg, P.J., Ding, Y.-S., et al. 1998. Association between decline in brain dopamine activity with age and cognitive and motor impairment in healthy individuals. *Am. J. Psychiatry*, **155**: 344–349. PMID:9501743.
- Weier, A.T., and Kidgell, D.J. 2012. Strength training with superimposed whole body vibration does not preferentially modulate cortical plasticity. *Sci. World J.* **2012**: 876328. doi:10.1100/2012/876328. PMID:22654645.
- Yacyshyn, A.F., Woo, E.J., Price, M.C., and McNeil, C.J. 2016. Motoneuron responsiveness to corticospinal tract stimulation during the silent period induced by transcranial magnetic stimulation. *Exp. Brain Res.* **234**: 3457–3463. doi:10.1007/s00221-016-4742-1. PMID:27481287.