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Robin Souron

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THESE DE DOCTORAT

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Robin SOURON

ADAPTATIONS FONCTIONNELLES ET NERVEUSES A L'ENTRAÎNEMENT PAR VIBRATION LOCALE : DU SUJET SAIN A LA REEDUCATION

Devant le jury composé de :

Pr Serge **COLSON** (Rapporteur)

Dr Stéphane **BAUDRY** (Rapporteur)

Université Nice Sophia Antipolis

Université Libre de Bruxelles (Belgique)

Dr Jeanne **DEKERLE** (Examinatrice)

Dr Christophe **HAUTIER** (Examineur)

Université de Brighton (Royaume-Uni)

Université Claude Bernard Lyon 1

Dr Thomas **LAPOLE** (Directeur de thèse)

Pr Guillaume **MILLET** (Co-directeur de thèse)

Pr Alain **BELLI** (Co-directeur de thèse)

Université Jean Monnet, Saint-Etienne

Université de Calgary (Canada)

Université Jean Monnet, Saint-Etienne

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Souron, R., Besson, T., McNeil, C.J., Lapole, T., Millet, GY. (2017). An acute exposure to muscle vibration decreases knee extensors force production and modulates associated central nervous system excitability. *Frontiers in Human Neuroscience*. 11:519. doi: 10.3389/fnhum.2017.00519.

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Souron, R., Besson, T., Lapole, T., Millet, GY. (2017). Effects of 4-weeks of local vibration training on knee extension force production and cortical voluntary activation in elderly and young populations. European College of Sport Sciences. Juillet, Essen (Allemagne).

Souron, R., Farabet, A., Belli, A., Millet, GY., Lapole, T. (2015). Reproductibilité intra- et inter-session du niveau d'activation cortical du muscle tibial antérieur. Congrès International de l'Association des Chercheurs en Activité Physique et Sportive. Octobre, Nantes.

Souron, R., Farabet, A., Belli, A., Millet, GY., Lapole, T. (2015). Reproducibility of cortical voluntary activation level in tibialis anterior muscle. European College of Sport Sciences. Juin, Malmö (Suède).

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Souron, R., Farabet, A., Belli, A., Féasson, L., Millet, GY., Lapole, T. (2015). Adaptations nerveuses cortico-spinales suite à un entraînement de 8 semaines par vibrations localisées du muscle tibial antérieur. Congrès de la Société Française de Myologie. Novembre, Lyon.

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Liste des principales abréviations utilisées dans ce manuscrit

CMJ	Saut vertical avec contre-mouvement (<i>Counter-Movement Jump</i>)
EMG	Electromyographie
ERT	Estimation de l'amplitude de la secousse évoquée sur le muscle relâché (<i>Estimated Resting Twitch</i>)
FNM	Fuseau neuromusculaire
I₅₀	Intensité de stimulation évoquant un MEP égal à 50% du MEP max
k	Pente de la relation entre l'intensité de la TMS et l'amplitude du MEP dans la modélisation de Boltzmann
LCA	Ligament croisé antérieur
MEP	Potentiel évoqué moteur (<i>Motor Evoked Potential</i>)
Mn α	Motoneurone alpha
MVC	Contraction maximale volontaire (<i>Maximal Voluntary Contraction</i>)
NMES	Stimulation électrique neuromusculaire (<i>Neuromuscular Electrical Stimulation</i>)
P	MEP maximal défini par la modélisation de Boltzmann
PA	Potentiel d'action
RF	<i>Rectus femoris</i>
RFD	Taux de montée en force (<i>Rate of Force Development</i>)
RMS	Root mean square
SJ	Saut vertical sans contre-mouvement (<i>Squat Jump</i>)
SIT	Secousse surimposée (<i>Superimposed Twitch</i>)
SP	Période de silence (<i>Silent Period</i>)
TA	Tibial antérieur
TMEP	Potentiel évoqué moteur thoracique (<i>Thoracic Motor Evoked Potential</i>)
TMS	Stimulation magnétique transcrânienne (<i>Transcranial Magnetic Stimulation</i>)
VA	Niveau d'activation volontaire mesuré par stimulation électrique périphérique (<i>Voluntary Activation</i>)
VA_{TMS}	Niveau d'activation volontaire cortical mesuré par TMS
VL	<i>Vastus lateralis</i>
VM	<i>Vastus medialis</i>
WBV	Vibration corps entier (<i>Whole body vibration</i>)

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INTRODUCTION GENERALE

Le phénomène de déconditionnement neuromusculaire, et notamment la recherche de méthodes permettant de lutter contre ses effets néfastes sur le fonctionnement du corps humain, est depuis longtemps un sujet qui préoccupe la communauté scientifique. En effet, de nombreuses situations, comme par exemple un acte chirurgical, e.g. reconstruction du ligament croisé antérieur (LCA), ou encore une immobilisation prolongée liée à une pathologie par exemple, conduisent à une diminution des capacités physiques, aussi bien influencée par des phénomènes nerveux, e.g. diminution de l'intensité de la commande nerveuse (Gondin et al., 2004; Pietrosimone et al., 2015), que musculaires, e.g. diminution de la masse musculaire (Williams et al., 2005; Dirks et al., 2014). Ainsi, de nombreuses techniques ont été proposées pour lutter contre ce déconditionnement neuromusculaire et ont montré des effets bénéfiques sur la fonction neuromusculaire de patients immobilisés ou opérés. C'est par exemple le cas de l'entraînement en force (van Grinsven et al., 2010; Lepley & Palmieri-Smith, 2013) ou de la stimulation neuromusculaire électrique (*neuromuscular electrical stimulation*, NMES) (Dirks et al., 2014; Hauger et al., 2017). Ces techniques présentent néanmoins certaines limites. Par exemple, l'activation de récepteurs nociceptifs via l'utilisation de la stimulation neuromusculaire électrique peut entraîner une sensation de douleur et donc limiter son utilisation pour certains patients (Sheffler & Chae, 2007). L'entraînement en force, même à charges légères, présente la limite de ne pas pouvoir être utilisé pendant ou immédiatement après une période d'immobilisation prolongée ou une opération par certains patients présentant une importante fragilité musculaire.

La vibration corps entier (*whole body vibration*, WBV) est une autre technique de reconditionnement plus récemment proposée, les premières utilisations connues étant dans les années 2000 (Torvinen et al., 2002a; Torvinen et al., 2002b). Le sujet doit maintenir une posture stable sur une plateforme vibrante tandis que les vibrations sont transmises depuis les pieds aux muscles cibles alors pré-contractés. Cette technique a été proposée comme une technique de lutte contre le déconditionnement neuromusculaire lié par exemple à une immobilisation prolongée (Belavy et al., 2011; Buehring et al., 2011) ou encore une opération chirurgicale de ligamentoplastie du genou (Fu et al., 2013; Pistone et al., 2016). Bien que bénéfique pour augmenter les capacités musculaires de diverses populations, e.g. jeune, âgée, clinique (voir Rittweger, (2010) et Cochrane, (2011) pour des revues détaillées), cette technique présente également certaines limites. En effet, la WBV ne peut être appliquée à tous,

notamment aux sujets se trouvant dans l'incapacité de maintenir une posture isométrique stable ou de réaliser un exercice dynamique, e.g. squat, sur la plateforme vibrante. En outre, en plus d'être coûteuse et non-portable, cette technique ne permet pas de cibler un muscle de manière précise, les vibrations étant transmises à l'ensemble du corps à partir des pieds.

La vibration locale peut alors être envisagée comme une alternative permettant de s'affranchir des limites que présentent ces diverses techniques de reconditionnement neuromusculaire. Cette technique consiste à appliquer de petits dispositifs vibratoires portables directement sur le muscle ou le tendon, e.g. Lapole & Pérot, (2010). Contrairement à la WBV, la vibration locale permet d'appliquer le stimulus vibratoire sans aucune participation active de la part du sujet, e.g. lorsque le sujet se trouve en position assise ou allongée. De plus, la vibration appliquée localement sur le muscle présente l'avantage de n'évoquer aucune sensation de douleur (Pantaleo et al., 1986), des effets antalgiques étant même couramment reportés (Lundeberg et al., 1984; Lau & Nosaka, 2011). La vibration locale est en fait déjà connue depuis de nombreuses années, notamment dans le champ scientifique des neurosciences pour activer différents récepteurs sensoriels. Les fuseaux neuromusculaires (FNMs) sont notamment sensibles à la vibration, principalement leurs terminaisons primaires (afférences Ia) (Burke et al., 1976a; Burke et al., 1976b; Burke, 1980; Roll et al., 1989). L'activation des afférences Ia en réponse à la vibration entraîne un influx exciteur sur le motoneurone alpha ($Mn \alpha$) via une boucle spinale réflexe (Lance, 1973) et peut induire, en fonction des paramètres vibratoires utilisés, une activité réflexe de faible amplitude du muscle vibré, i.e. le réflexe tonique vibratoire (Eklund & Hagbarth, 1965; De Gail et al., 1966; Hagbarth & Eklund, 1966). Les afférences Ia projettent leurs influx excitateurs aussi bien au niveau spinal que cortical (Mima et al., 1999). Ainsi, la projection et l'intégration des messages nerveux vers diverses zones corticales, e.g. cortex moteur primaire, cortex sensori-moteur, aire motrice supplémentaire, cortex pré-moteur et pariétal (Naito et al., 1999; Naito & Ehrsson, 2001; Radovanovic et al., 2002; Roll et al., 2012), va parfois permettre d'induire une illusion de mouvement par évocation de messages proprioceptifs proches de ceux induits par le mouvement réel (Hagbarth & Eklund, 1966; Eklund, 1972; Goodwin et al., 1972; Roll et al., 1980). Ceci a d'ailleurs donné naissance au concept de rééducation sensori-motrice par assistance proprioceptive vibratoire, dont le but est de maintenir des sensations kinesthésiques pendant ou après une période

d'immobilisation afin d'en minimiser les troubles, e.g. amplitude de mouvement réduite (Neiger et al., 1986).

Suite à une exposition aigüe et prolongée à la vibration locale, plusieurs travaux ont démontré une diminution de la performance musculaire (Shinohara et al., 2005; Ushiyama et al., 2005; Konishi et al., 2009), suggérant de possibles bénéfices sur le long terme lorsqu'utilisé de façon chronique. En effet, il a été montré un lien étroit entre les modulations neuromusculaires induites par une session d'entraînement unique et les adaptations neuromusculaires intervenant à la suite d'un programme d'entraînement visant la répétition sur plusieurs semaines de ces sessions d'entraînement (Gathercole et al., 2015). Plusieurs études ont mis en évidence les possibilités d'amélioration des capacités de production de force suite à un programme d'entraînement par vibration locale (Lapole & Pérot, 2010; Lapole et al., 2013; Tankisheva et al., 2015). Néanmoins, il existe toujours un manque de connaissances sur les mécanismes exacts (notamment au niveau central) expliquant les modifications de performance neuromusculaire à la suite aussi bien d'une application aigüe que d'une utilisation chronique de la vibration locale.

L'objectif de mon doctorat d'université était alors de caractériser les effets aigus (i.e. une séance unique) et chroniques (i.e. plusieurs séances répétées sur plusieurs semaines) de la vibration locale sur les propriétés fonctionnelles et neurophysiologiques de différents groupes musculaires et sur des populations différentes. Ainsi, une population saine et jeune était premièrement évaluée et servait de « modèle » pour informer des adaptations centrales induites par une application aigüe et chronique de la vibration locale. Une population saine et âgée était ensuite évaluée afin d'investiguer i) les effets de la vibration locale dans un contexte de déconditionnement neuromusculaire et ii) les éventuelles différences pouvant exister avec des sujets jeunes. Pour ces deux populations, ce travail de thèse s'attachait particulièrement à apporter de nouvelles évidences sur les adaptations nerveuses induites par une application aigüe ou chronique de la vibration locale, en utilisant de nouvelles méthodes d'investigation de la voie cortico-spinale, en particulier la stimulation magnétique transcrânienne (*transcranial magnetic stimulation*, TMS) et la stimulation électrique thoracique. La finalité de ce travail de thèse était d'offrir une perspective d'application clinique à la vibration locale, en proposant un programme d'intervention chronique visant à améliorer les conditions de rééducation chez des

patients victimes d'une rupture du LCA et opérés selon une technique de ligamentoplastie.

Dans le cadre de cette thèse, un travail de veille bibliographique a été réalisé et a donné lieu à une revue de littérature publiée dans un journal scientifique (*European Journal of Applied Physiology*). Cette publication servira de support pour le cadre théorique de ce manuscrit et permettra de dresser un état de l'art sur les mécanismes d'action et les effets aussi bien aigus que chroniques de la vibration locale sur la fonction neuromusculaire. Après avoir formulé les objectifs et hypothèses qui découlent de cette analyse approfondie de la littérature scientifique, une partie spécifique s'attachera à présenter le matériel et la méthodologie générale utilisés dans les travaux expérimentaux de ce doctorat. Les contributions expérimentales de ce travail de thèse seront ensuite exposées par l'intermédiaire de quatre études publiées ou actuellement en révision. Un résumé en français de chaque article sera disponible afin de rendre ce manuscrit de thèse accessible au grand public. Une discussion générale permettra de synthétiser et d'interpréter les résultats obtenus lors des différentes études de thèse notamment en les mettant en perspective avec d'autres méthodes permettant de moduler la fonction neuromusculaire sur le court et/ou le long terme (entraînement en force, WBV ou NMES), et précèdera une partie finale de conclusion générale qui résumera et mettra en perspective les résultats obtenus.

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RESUME :

Depuis la fin des années 1980, les stimuli vibratoires sont connus pour leurs effets favorisant le reconditionnement musculaire via des adaptations principalement d'origine nerveuse. Cela a principalement été démontré par l'utilisation de la vibration corps entier, maintenant largement utilisée comme une méthode d'entraînement à part entière permettant d'améliorer la force musculaire et/ou les habiletés fonctionnelles. Cependant, cette technique peut présenter certaines limites, notamment dans un cadre d'application clinique où les patients sont incapables de maintenir une posture statique et/ou active sur la plateforme vibrante. Afin de s'affranchir des limites inhérentes à l'utilisation de la vibration corps entier, une technique de vibration locale a été plus récemment explorée, consistant en l'utilisation de petits dispositifs portatifs vibratoires directement appliqués sur le muscle et/ou le tendon. Le principal avantage de cette technique est qu'elle ne requiert aucune participation active de la part du sujet. Si certaines études ont déjà étudié les effets aigus et/ou chroniques d'une application de vibration locale sur la performance musculaire, e.g. capacité de production de force, aucun consensus sur les adaptations nerveuses qui sous-tendent ces gains de force musculaire ne semblent actuellement avoir émergé. Le premier objectif de ce travail de veille bibliographique était de fournir une revue générale de la littérature sur les effets aigus et chroniques de la vibration locale sur la fonction neuromusculaire, afin de mieux envisager cette technique comme une méthode d'entraînement alternative innovante et efficace. Le second objectif était d'apporter des évidences scientifiques pour l'utilisation de la vibration locale dans un contexte clinique, i.e. prévention du déconditionnement musculaire, rééducation ou réentraînement.



INVITED REVIEW

Acute and chronic neuromuscular adaptations to local vibration training

Robin Souron¹ · Thibault Besson¹ · Guillaume Y. Millet² · Thomas Lapole¹Received: 20 February 2017 / Accepted: 22 July 2017 / Published online: 1 August 2017
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Abstract Vibratory stimuli are thought to have the potential to promote neural and/or muscular (re)conditioning. This has been well described for whole-body vibration (WBV), which is commonly used as a training method to improve strength and/or functional abilities. Yet, this technique may present some limitations, especially in clinical settings where patients are unable to maintain an active position during the vibration exposure. Thus, a local vibration (LV) technique, which consists of applying portable vibrators directly over the tendon or muscle belly without active contribution from the participant, may present an alternative to WBV. The purpose of this narrative review is (1) to provide a comprehensive overview of the literature related to the acute and chronic neuromuscular changes associated with LV, and (2) to show that LV training may be an innovative and efficient alternative method to the ‘classic’ training programs, including in the context of muscle deconditioning prevention or rehabilitation. An acute LV application (one bout of 20–60 min) may be considered as a significant neuromuscular workload, as demonstrated by an impairment of force generating capacity and LV-induced neural changes. Accordingly, it has been reported that a training period of LV is efficient in improving muscular performance over a wide range of training (duration, number of session) and vibration (frequency, amplitude, site of application) parameters. The

functional improvements are principally triggered by adaptations within the central nervous system. A model illustrating the current research on LV-induced adaptations is provided.

Keywords Local vibration · Training · Neuromuscular fatigue · Neuromuscular adaptations · Rehabilitation

Abbreviations

ACL	Anterior cruciate ligament
CSP	Cortical silent period
EMG	Electromyography
ICF	Intracortical facilitation
LICI	Long-interval cortical inhibition
LV	Local vibration
LVT	Local vibration training
MEP	Motor evoked potential
MRI	Magnetic resonance imaging
MVC	Maximal voluntary contraction
PET	Positron emission tomography
rMV	Repeated muscle vibration
SICI	Short-interval cortical inhibition
TMS	Transcranial magnetic stimulation
TVR	Tonic vibration reflex
WBV	Whole body vibration

Introduction

Since pioneering work that aimed to develop athlete’s maximal strength (Nazarov and Spivak 1987), mechanical vibratory stimuli have been considered as a training or rehabilitation modality. Whole-body vibration (WBV) training, where the participant must stand or squat on a vibrating platform while vibration is transmitted through the feet to the targeted pre-contracted muscles,

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✉ Thomas Lapole
thomas.lapole@univ-st-etienne.fr

¹ Univ Lyon, UJM Saint-Etienne, Laboratoire Interuniversitaire de Biologie de la Motricité, EA 7424, 42023 Saint-Etienne, France

² Human Performance Laboratory, Faculty of Kinesiology, University of Calgary, Calgary, Canada

is particularly well documented (for review, see Cochrane 2011; Rittweger 2010). For instance, WBV has been shown to increase maximal strength over 4- to 24-week training programs in healthy participants (Roelants et al. 2004; Schlumberger et al. 2001; Verschueren et al. 2004), although other studies failed to demonstrate similar findings (de Ruiter et al. 2003; Delecluse et al. 2005). Despite its advantages and promising perspectives in the clinical and rehabilitation fields (Aaboe et al. 2009; Moezy et al. 2008; Pamukoff et al. 2016; Pedro et al. 2014), WBV programs may not be suitable to everyone. Indeed, some participants are unable to bear weight due to (1) long-term immobilization (lower limb trauma), (2) immobilization by a cast, or (3) being in the early rehabilitation period after surgery (anterior cruciate ligament reconstruction). These individuals may not be able to benefit from WBV because they cannot squat or stand on the vibrating platform.

For those individuals, local vibration (LV) could be an alternative form of vibration training. LV requires the use of a small and portable device that applies vibration directly over the muscle or the tendon (Lapole and Pérot 2010). The main interest of LV compared to WBV is that it does not necessarily require any active contribution from the participant (i.e. it can be used while the person is seated or lying down). LV is not an entirely novel concept and in fact, it has actually been used for a long time in the field of neuroscience. Indeed, LV applied to the tendon can induce a number of physiological effects such as a tonic vibration reflex or muscle movement illusion depending on the experimental conditions (see “[Neurophysiological responses associated with local vibration](#)”). These are not the only physiological changes associated with LV and instead, several other neuromuscular adaptations occur at spinal and supra-spinal levels during and after LV. The purpose of this narrative review is to provide a comprehensive overview of the literature related to the acute and chronic neuromuscular changes associated with LV. We will review evidence that shows that acute LV application may be considered as a significant neuromuscular workload, as indicated by LV-induced fatigue (reduction of maximal voluntary strength) (see “[Local vibration as a stimulus for neuromuscular adaptation](#)”). Next, we will outline the immediate and long-lasting LV-induced alterations in neuromuscular properties that are dependent on the LV characteristics (e.g. the duration of application, LV frequency, contracted vs. relaxed muscle). In line with the acute neuromuscular adaptations, we will provide evidence that chronic use of LV may improve strength by inducing several neuromuscular adaptations at different levels of the corticospinal pathway, suggesting that it could be used as an innovative and efficient alternative method to other forms of training (resistance training, WBV training) (see “[Chronic effects of local vibration training](#)”). Finally, we will discuss the perspectives of using LV in the context of muscle

deconditioning prevention or rehabilitation (see “[Local vibration training and clinical applications](#)”).

Articles were searched through the PubMed database (up to March 2017) using the keywords “muscle vibration”, “tendon vibration” or “local vibration”. Articles were then checked for pertinent content and included in the current review when investigating acute (single session) or chronic (repeated sessions) effects of local vibration on neuromuscular function and functional capacities of healthy or clinical participants. Further articles were considered after scanning the reference lists of the included articles. Only articles published in English were included.

Neurophysiological responses associated with local vibration

What receptors are sensitive to local vibration?

Several receptors are known to be sensitive to vibratory stimuli. First, cutaneous receptors such as Pacini, Meissner, Ruffini or Merkel receptors are all responsive to LV at varying frequencies (Hunt 1961; Ribot-Ciscar et al. 1996; Roll and Vedel 1982). Golgi tendon organs are also responsive to LV through Ib afferents (Burke 1980; Burke et al. 1976a, b; Hayward et al. 1986). Yet, it has been well reported that muscle spindles, which encode information about the dynamic characteristics of movement (Cordo et al. 1993), are the most responsive receptors to LV. Hunt (1961) was the first to report the sensitivity of muscle spindles to LV in the cat, and follow-up research has confirmed that these findings are applicable to other animal species (Bianconi and Van der Meulen 1963; Matthews 1966). Muscle spindles are innervated by primary (i.e. Ia) and secondary (i.e. II) afferents with the Ia afferents being the most responsive, as shown in animal (Matthews 1964) and human experiments (Burke 1980; Burke et al. 1976a, b; Roll et al. 1989). The level of Ia afferent response to LV is mainly dependent on the LV amplitude and frequency. Indeed, it has been reported that small LV amplitudes (i.e. 0.2–0.5 mm) preferentially recruit Ia afferents (Roll and Vedel 1982), whereas Ib and II afferents predominantly respond to larger amplitudes (Roll et al. 1989). While group II afferents can be recruited with input frequencies between 20 and 60 Hz, the rate of discharge of Ia afferents is proportional to LV frequency in a one-to-one manner for all frequencies up to 120 Hz (Burke et al. 1976a; Roll et al. 1989). For higher frequencies (>150 Hz), the discharge of Ia afferents has been shown to be disharmonious or even unpredictable (i.e. the discharge rate loses one-to-one synchrony with LV frequency) (Burke et al. 1976a; Martin and Park 1997; Roll and Vedel 1982; Roll et al. 1989).

The response of Ia afferents is not rigid and instead is dependent on the state of the muscle, i.e. stretched, relaxed,

or contracted (Brown et al. 1967; Burke 1980; Burke et al. 1976b). Ia afferents are more responsive to LV when the muscle is stretched and during voluntary isometric contractions (Burke 1980; Burke et al. 1976a), probably due to the presence of alpha–gamma co-activation (Vallbo 1974) and/or superior transmission through the musculo-tendinous structures (Burke et al. 1976a), respectively. It should be noted, however, that during WBV where vibration is transmitted through the feet via a platform, vibration transmission can be conversely impaired due to the dampening of mechanical energy by soft tissues (Abercromby et al. 2007; Wakeling et al. 2002).

The tonic vibration reflex

As the discharge of Ia afferents elicits an excitatory input on alpha motoneurons, a reflex contraction of the vibrated muscle has been widely described as the tonic vibration reflex (TVR), which has been observed during LV (De Gail et al. 1966; Eklund and Hagbarth 1965; Hagbarth and Eklund 1966; Nakajima et al. 2009; Park and Martin 1993) and WBV (Zaidell et al. 2013). The TVR reflects an excitatory state mediated by polysynaptic pathways converging onto monosynaptic excitatory inputs (Matthews 1966; Romaguere et al. 1991). The TVR is also known to be associated with relaxation of the antagonist due to reciprocal inhibition (Hagbarth and Eklund 1966). Theoretically, TVR occurs in almost all muscles for frequencies in the range of 20–200 Hz (Eklund and Hagbarth 1966), but has not systematically been observed. For instance, several studies employing LV frequencies in the 20–200 Hz range were subthreshold for the evocation of a TVR when a low LV amplitude (≤ 1.5 mm) was used (Lapole et al. 2015b; Rosenkranz et al. 2003; Rosenkranz and Rothwell 2003; Siggelkow et al. 1999; Ushiyama et al. 2005). This contrasts the early work of Eklund and Hagbarth (1966) who demonstrated that TVR was present for amplitudes of 0.6 mm, but was greater using a 1.8-mm LV amplitude. More recent studies have confirmed the work of Eklund and Hagbarth (1966) and reported that TVR can be obtained with a low LV amplitude (≤ 1 mm) (Martin and Park 1997; Nakajima et al. 2009). Hence, the TVR appears to be a complex response depending not only on the combination of optimal LV frequency and amplitude but also on other experimental parameters such as the muscle, the vibration site (muscle vs. tendon), the initial muscle length, the state of contraction (relaxed vs. contracted) or the visual control (i.e. closed vs. open eyes) (Eklund and Hagbarth 1966; Roll et al. 1980). Moreover, it has been reported that the TVR can be voluntarily suppressed under the influence of descending pathways altering the transmission in the polysynaptic component of the reflex rather than the monosynaptic one (Burke et al. 1976a; Lance 1973). Thus, the optimal experimental parameters to induce TVR are still unclear. Furthermore, it may be difficult

to determine the occurrence of the TVR due to common presence of artefacts in electromyography (EMG) data resulting from electrode/cable motion and nearby electrical noise that may influence the measurements (Abercromby et al. 2007; Fratini et al. 2009). Therefore, WBV studies that investigated EMG amplitude during vibration exposure have attenuated artefacts in raw EMG amplitude with spectral smoothing procedures (Lienhard et al. 2015; Zaidell et al. 2013). While such a methodological approach has, to our knowledge, not been used in the context of LV, this could be utilized to isolate LV effects from movement artefact.

Local vibration-induced cortical activation and proprioceptive illusions

Due to cortical projections of muscle afferents (Mima et al. 1999), LV may induce proprioceptive illusions (Goodwin et al. 1972; Naito and Ehrsson 2001; Roll and Vedel 1982; Roll et al. 2012). For instance, Goodwin et al. (1972) reported that LV applied to either biceps or triceps tendons (100 Hz; 0.5 mm) induced a systematic misjudgment of the elbow angle. These proprioceptive illusions were mainly attributed to the activation of Ia afferents (Goodwin et al. 1972; Roll and Vedel 1982), but the role of other receptors cannot be totally ruled out (Pacinian corpuscles, Golgi tendon organs). Indeed, higher neural centres at the cortical level may have interpreted the Ia afferent discharge as if they were due to excitation of the spindles by actual muscle stretching (Goodwin et al. 1972). These proprioceptive illusions have been related to the presence of evoked potentials (i.e. cortical activation) on the primary somatosensory cortex of the contralateral vibrated arm, with greater LV-induced evoked potentials observed when the LV frequency was 80 Hz compared to 40 and 160 Hz (Munte et al. 1996). Positron emission tomography (PET) studies further demonstrated that LV-induced proprioceptive illusions activate the same motor cortical areas as the ones activated during voluntary contraction, i.e. contralateral sensorimotor, premotor, and parietal cortices, as well as bilateral supplementary and cingulate motor areas (Naito and Ehrsson 2001; Naito et al. 1999; Radovanovic et al. 2002). Using magnetic resonance imaging (MRI), Romaguère et al. (2003) reported similar findings when movement illusions were induced by LV. These authors also observed no or minimal activation of motor-related areas when no illusory movement was perceived.

Local vibration as a stimulus for neuromuscular adaptation

While transient muscle or tendon vibration strongly activates Ia afferents that project their excitatory synaptic inputs to the

spinal cord and cortical areas (see above), it may be questioned whether prolonged (i.e. 20–60 min) LV exposure may be sufficient to induce neuromuscular fatigue and thus, be a potential stimulus for neuromuscular adaptations. Accordingly, many LV studies have investigated acute changes in force output during or following a single LV exposure. It is worth noting that few studies have also considered the potential effect of acute LV proposed for shorter periods as a warm-up intervention (Cochrane 2016b; Pamukoff et al. 2014), in a similar way as it is classically performed for WBV (for a review, see Cochrane 2013). Despite some positive results, likely explained by peripheral ergogenic effects (increased muscle temperature, post-activation potentiation) (Cochrane 2016a), others failed to show any improvement in muscular performance (Cochrane 2016b; Cochrane and Hawke 2007; Pamukoff et al. 2016). Given the lack of consensus in this scientific framework, it is difficult to draw conclusions about the effects of LV as a warm-up modality, and further studies are needed on this topic.

Acute effects of local vibration on neuromuscular output

Local vibration-induced motor performance impairment

Studies that investigated acute changes in neuromuscular output following a single session of prolonged (20–30 min) LV exposure have been summarized in Table 1, which provides detailed information on experimental (participants characteristics, tested muscles) and LV (frequency, amplitude, vibration site) characteristics. 10 out of 16 reviewed LV studies demonstrated a short-term decrease in force-generation capacity of the vibrated muscle group. Indeed, force production decrement (mean 10.2%; range 4.3–19%) was reported following prolonged LV for knee extensor (Jackson and Turner 2003; Konishi et al. 2002, 2009; Kouzaki et al. 2000; Richardson et al. 2006; Saito et al. 2016a), plantar flexor (Herda et al. 2009; Ushiyama et al. 2005; Yoshitake et al. 2004) and first dorsal interosseus muscles (Shinohara et al. 2005). A force decrement has also been demonstrated on the contralateral non-vibrated limb (Jackson and Turner 2003). Conversely, other studies failed to demonstrate maximal force production impairment on plantar flexor (Cattagni et al. 2016; Ekblom and Thorstensson 2011), dorsiflexor (Farabet et al. 2016) and knee extensor muscles (Fry and Folland 2014; Saito et al. 2016b), while one study reported a 8.1% increase in knee extensors maximal voluntary contraction (MVC) after prolonged LV (Iodice et al. 2011). The LV parameters in the latter study, however, were not clear enough to make comparison with the other reviewed studies. Although it is difficult to identify which differences in study design cause the discrepancies in the main findings, we suggest that differences in the combination of vibratory

parameters (i.e. time of application, frequency, amplitude, site of application, muscle investigated) offer the most likely explanation (see Table 1). Although there are inconsistencies in the effects of LV, there is evidence that LV-induced neuromuscular alterations may result in fatigue in contracting muscles exposed to LV. For instance, LV has been demonstrated to decrease the endurance time of sustained submaximal voluntary contractions (Rothmuller and Cafarelli 1995) and to induce a faster force decline during sustained MVC (Bongiovanni et al. 1990; Färkkilä et al. 1980; Samuelson et al. 1989). In the following section, we will discuss the possible causes of LV-induced fatigue.

Aetiology of local vibration-induced neuromuscular fatigue

As for neuromuscular fatigue induced by 'classic' exercise, LV-induced fatigue may in theory arise from central and/or peripheral changes. Since the TVR described above is a tonic contraction of small amplitude, a deficit occurring downstream of the neuromuscular junction (i.e. peripheral fatigue) is unlikely. Moreover, LV-induced fatigue may be observed without evocation of a TVR (Ushiyama et al. 2005). Unfortunately, there is a lack of information about the presence of TVR during the vibratory exposure, aside from the study of Kouzaki et al. (2000) where the presence of rectus femoris muscle electromyographic (EMG) responses to LV is reported (although not synchronous with LV frequency; see Fig. 2). Although studies that addressed the question of muscular effects of LV are very scarce, it has been consistently reported that electrically elicited twitch amplitude (Fry and Folland 2014; Herda et al. 2009; Saito et al. 2016a, b; Ushiyama et al. 2005) and twitch characteristics (i.e. contraction time and half relaxation time) (Ushiyama et al. 2005) are unchanged after a 20–30-min prolonged LV period, using LV frequencies in the range 70–100 Hz and amplitudes in the range 1–1.5 mm (Table 1). This finding suggests that LV-induced decreased MVC are not due to alterations in muscle properties. Maximal muscle response waves (M-wave) were not affected after LV either, suggesting the absence of neuromuscular propagation failure (Cattagni et al. 2016; Ekblom and Thorstensson 2011; Farabet et al. 2016; Fry and Folland 2014; Saito et al. 2016a, b; Ushiyama et al. 2005). Hence, a reduction in the neural command probably fully explains the decrement in force-generation capacity after prolonged LV. This is supported by a decrease in maximal EMG amplitude on soleus (Herda et al. 2009), gastrocnemii (Ushiyama et al. 2005; Yoshitake et al. 2004), knee extensor (Jackson and Turner 2003; Konishi et al. 2002, 2009; Kouzaki et al. 2000; Richardson et al. 2006) and first dorsal interosseus (Shinohara et al. 2005) muscles, after 20–30 min of LV with frequencies between 30–100 Hz and amplitudes between 1.5–3 mm. Conversely, other studies failed to demonstrate any variation in EMG

Table 1 Acute effects of prolonged local vibration on force-generation capacities

Study	Tested subjects	Mean ± SD age (years)	Control condition	Vibration site	Duration (min)	Fr (Hz)	A (mm)	Main outcomes
Kouzaki et al. (2000)	8 HE (7 M, 1F)	25 ± 2	COD	RF (proximal portion)	30	30	2–3	MVC: ↓ ≈10% RFD: ↓ ≈25% EMG: RF ↓ ≈15%, VL and VM →
Konishi et al. (2002)	10 ACL (5 M, 5 F)	22 ± 5	No	Infrapatellar tendon	20	50	1.5	MVC: → (+0.4%) EMG: VL → (-4.1%), VM → (-3.1%), RF → (-2.2%)
	12 HE (8 M, 4 F)	25 ± 4						MVC: ↓ 9.0% EMG: VL ↓ 18.1%, VM ↓ 14.3%, RF ↓ 15.8%
Jackson and Turner (2003)	10 HE M	26 ± 2	COD	RF	30	30	1.5–2.0	MVC: ↓ 6.9% RFD: ↓ 33.3% EMG: RF ↓ 30%, VL → (+15%) Similar contralateral effect for MVC and RFD
						120		MVC: ↓ 4.3% RFD: ↓ 20.9% EMG: RF and VL → Similar contralateral effect for MVC and RFD
Yoshitake et al. (2004)	8 HE M	27 ± 4	CG	Achilles tendon	30	100	1.5	MVC: ↓ 19% EMG: GM ↓ 32%, GL ↓ 12%, SOL → (-12%)
Ushiyama et al. (2005)	13 HE M	22–49	COD	Achilles tendon	30	100	1.5	MVC: ↓ 16.6% EMG: GM ↓ 12.7%, GL ↓ 11.4%, SOL → (-3.4%)
Shinohara et al. (2005)	20 HE	22 ± 3	CG	FDI muscle belly	30	75	NR	MVC: ↓ 15% EMG: FDI ↓ 14%
Richardson et al. (2006)	14 HE	23 ± 1	No	Infrapatellar tendon	20	50	1.5	MVC: ↓ 7.2% EMG: VL ↓ 11.1%, VM ↓ 15.2%, RF ↓ 8.9%
	14 ACL	22 ± 1						MVC: → (+4.7%) EMG: VL → , VM → (+5.0%), RF → (+5.4%)
	7 EL HE	66 ± 1						MVC: → (-0.3%) EMG: VL → (+9.1%), VM and RF →
Herda et al. (2009)	15 HE M	24 ± 3	COD	Achilles tendon	20	70	NR	MVC: ↓ ≈5% EMG: SOL ↓ ≈22%, MG ↓ ≈7% VA _{PNS} : →

Table 1 (continued)

Study	Tested subjects	Mean ± SD age (years)	Control condition	Vibration site	Duration (min)	Fr (Hz)	A (mm)	Main outcomes
Konishi et al. (2009)	8 HE M	18 ± 0	No	Infrapatellar tendon	20	50	1.5	CON and ECC: ↓ 15.5% and ↓ 17.4% EMG CONC: VL ↓ 12.6%, VM ↓ 5.4%, RF → (−5.6%) EMG ECC: VL ↓ 16.6%, VM ↓ 19.2%, RF → (−17.0%)
Eklblom and Thorstensson (2011)	8 HE F	23 ± 2	COD	Achilles tendon	30	100	NR	CON: → (− ≈8.5%) ECC: → (− ≈7.0%) EMG: SOL and GM →
Iodice et al. (2011)	18 HE	21 ± 4	CG	VI, RF, VL, VM, GMA, BF, TA, G	30	300	2	Bilateral knee extension MVC: ↑ 8.1%
Fry and Folland (2014)	18 HE M	20 ± 2	COD	Infrapatellar tendon	30	80	1.5	MVC: → EMG VL, VM and RF →
Cattagni et al. (2016)	10 HE M	22 ± 4	COD	Achilles tendon	30	40	0.2	MVC: → (−2.5%) VA _{PNS} : → (+1.3%) EMG: SOL and GM →
						100		MVC: → (−8.4%) VA _{PNS} : → (−3.3%) EMG: SOL and GM →
Farabet et al. (2016)	13 HE (9 M, 4 F)	23 ± 4	COD	TA muscle belly	30	100	1	MVC: → (+1.7%) EMG: TA → (+3.8%) VA _{TMS} : TA → (+0.6%)
Saito et al. (2016a)	9 HE M	25 ± 4	COD	Patellar tendon (mid-portion)	30	80	1	MVC: ↓ 7.2% EMG: VM ↓ 11.0%, VI → (−6.0%), VL → (−0.4%), RF → (+1.0%)
Saito et al. (2016b)	9 HE M	25 ± 4	COD	VI (superficial region)	30	80	1	MVC: → (−3.6%) EMG: VI → (−1.7%), VL → (−3.3%), VM → (+4.8%), RF → (−0.8%)

A vibration amplitude, *ACL* subjects who had undergone anterior cruciate ligament surgery in the last 6 months, *BF* biceps femoris, *COD* cross-over design, *CON* maximal voluntary concentric contraction, *CG* control group, *ECC* maximal voluntary eccentric contraction, *EMG* electromyography, *F* female, *FDI* first dorsal interosseus, *Fr* vibration frequency, *G* gastrocnemius, *GL* gastrocnemius lateralis, *GM* gastrocnemius medialis, *GMA* gluteus maximus, *HE* healthy population, *M* male, *MVC* isometric maximal voluntary contraction, *NR* not reported, *RF* rectus femoris, *RFD* rate of force development, *SOL* soleus, *TA* tibialis anterior, *VA_{PNS}* voluntary activation assessed via peripheral nerve stimulation, *VA_{TMS}* voluntary activation assessed via transcranial magnetic stimulation, *VI* vastus intermedius, *VL* vastus lateralis, *VM* vastus medialis, ≈ mean changes estimated from values displayed on a graph, → not statistically significant, ↑ statistically significant increase, ↓ statistically significant decrease

amplitude on soleus (Cattagni et al. 2016), knee extensor (Fry and Folland 2014) or tibialis anterior (Farabet et al. 2016) muscles in line with unchanged muscular performance (Table 1). Since LV-induced excitatory Ia afferents project

to both the spinal cord and higher cortical structures, the decreased MVC observed after LV exposure may be related to an alteration in neural drive occurring at a spinal and/or supra-spinal level.

Acute effects of local vibration on spinal cord excitability

The role of Ia afferents on force production capacities

It is well known that Ia afferents facilitate neural activation during voluntary contraction (Gandevia 1998). Indeed, when LV is superimposed during brief submaximal contractions, an enhancement in contraction force level and EMG amplitude activity is reported due to the supplemental Ia excitatory input onto alpha motoneurons (Kihlberg et al. 1995; McCloskey et al. 1974; Mosier et al. 2016). Similarly, increased MVC (Curry and Clelland 1981; Humphries et al. 2004; Samuelson et al. 1989) and power (Issurin and Tenenbaum 1999; Liebermann and Issurin 1997) has been reported during the first seconds of superimposed LV using 20 (Samuelson et al. 1989), 44 (Issurin and Tenenbaum 1999), 50 (Humphries et al. 2004) and 120-Hz LV frequencies (Curry and Clelland 1981). Such LV-induced increases of muscle performance may only be observed when central activation is incomplete. Accordingly, similar findings have been reported when the contracted muscles were in a fatigued state, or after peroneal nerve block by partial anaesthetic, which induces reduced activity of gamma motoneurons (Bongiovanni and Hagbarth 1990). Yet, when LV exposure is prolonged, there is a LV-induced central drive impairment due to decreased alpha motoneuronal activity through attenuation of Ia afferent inputs onto alpha motoneurons (Bongiovanni and Hagbarth 1990; Bongiovanni et al. 1990) (see below). Indeed, most studies that reported a force decrement after prolonged LV suggested an altered spinal loop excitability as the proposed mechanism (Herda et al. 2009; Jackson and Turner 2003; Konishi et al. 2009; Kouzaki et al. 2000; Richardson et al. 2006; Ushiyama et al. 2005). This is confirmed by the studies of Konishi et al. (2002) and Richardson et al. (2006) showing force decrement on knee extensor muscles in healthy young participants after prolonged LV (−9.0 and −7.2%, respectively). Conversely, the same vibratory stimulus failed to elicit similar results in young participants who had undergone ACL reconstruction, as well as in healthy elderly participants (Richardson et al. 2006), i.e. two populations who are known to present with impairments in gamma-loop function.

Local vibration-induced decreased spinal loop excitability

Spinal loop excitability is commonly assessed through the Hoffmann reflex (H-reflex), considered to be the electrical analogue of the stretch reflex but bypassing muscle spindles (McNeil et al. 2013; Schieppati 1987; Zehr 2002). H-reflex amplitude is known to depend not only on motoneuronal excitability (Schieppati 1987), but also on the synaptic efficiency of the Ia–alpha pathway, which depends on

the level of presynaptic inhibition exerted on Ia afferents (Mazevet et al. 2003; Misiaszek 2003). Following prolonged LV, H-reflex amplitude was reported to decrease by 10–15 (Lapole et al. 2012a), 11 (Lapole et al. 2012b), 33 (Ekblom and Thorstensson 2011), 36 (Ushiyama et al. 2005) and 45% (Heckman et al. 1984) for the soleus. H-reflex reductions were also reported for gastrocnemius medialis (−34%) and lateralis (−39%) (Ushiyama et al. 2005), while this was depressed by 60% for the vastus medialis (Fry and Folland 2014) and 21% for the tibialis anterior (Farabet et al. 2016) (Table 2). Similar results were reported after LV applied during short periods on the soleus muscle (i.e. between 30 s and 2 min) (Abbruzzese et al. 2001; Van Boxtel 1986). A reduction in H-reflex amplitude also occurred after a single session of LV, suggesting similar vibration-induced effects as those observed with WBV (Armstrong et al. 2008; Krause et al. 2016). Based on unchanged F-waves that reflect backfiring of a small number of motoneurons which are reactivated by antidromic impulses following supramaximal stimulation of a peripheral nerve (McNeil et al. 2013), previous studies have suggested an unchanged motoneuronal excitability following prolonged LV (Christova et al. 2011; Lapole et al. 2012b). As a result, attenuation of Ia afferent inputs onto alpha motoneurons probably results from presynaptic inhibition of Ia afferents (Hultborn et al. 1987a, b) (see below), an increased firing threshold of Ia afferents (Hayward et al. 1986), or neurotransmitter depletion at the Ia afferent terminal level (Curtis and Eccles 1960). This latter mechanism has been suggested to mainly impair force production capacity but not H-reflex amplitude (Bongiovanni et al. 1990). Reduced Ia afferent excitability has been recently rejected as a contributor to the observed LV-induced vastus medialis H-reflex decrease, as indicated by an unchanged current required to elicit maximal H-reflex amplitude (Fry and Folland 2014). As a result, and although transmitter depletion cannot be ruled out, it is likely that the post-LV decrease in H-reflex amplitude is due to increased presynaptic inhibition of Ia afferents (Lapole et al. 2012b). Local vibration-induced increases in presynaptic inhibition have been extensively described in the early works regarding neuromuscular responses to LV. Indeed, while increased muscle spindle discharge during LV leads to a reflex activation of alpha motoneurons, it is associated with a depression of the H-reflex during the LV application (Abbruzzese et al. 1997; Ashby and Verrier 1975; Brooke and McIlroy 1990; De Gail et al. 1966; Hagbarth 1973; Hagbarth and Eklund 1966; Lance et al. 1966; Van Boxtel 1986), a phenomenon called the vibration paradox (Desmedt 1983; Desmedt and Godaux 1978). This phenomenon was mainly attributed to an increased presynaptic inhibition of the discharging Ia afferents through GABAergic interneurons under supraspinal control (Delwaide 1973; Gillies et al. 1969; Hultborn et al. 1987a). Thus, in response to the high activation of Ia

Table 2 Acute effects of prolonged local vibration on spinal and corticospinal excitability

Study	Tested subjects	Mean ± SD age (years)	Control condition	Vibration site	Duration (min)	Fr (Hz)	A (mm)	Main outcomes
Heckman et al. (1984)	4 HE	NR	No	Achilles tendon		20 100	<3	H-reflex: SOL ↓ ≈45%
Hayward et al. (1986)	5 HE	21–35	No	Triceps surae		20 100	2	H-reflex: SOL ↓ ≈52–93%
Steyvers et al. (2003a)	16 HE (10 M, 6F)	20–27	COD	Distal tendons of the wrist flexor muscles	30 (25 s on/5 s off)	80	0.5	MEP: FCR → (– ≈35%) POST, ↑ ≈40% POST-30 min MEP: ECR ↑ from POST-10 min to POST-30 min
Rosenkranz and Rothwell (2004)	6 HE (5 M, 1 F)	26–32	No	FDI and APB muscle bellies	15 (2 s on/2 s off)	80	0.2–0.5	MEP: APB, FDI and ADM → SICI: APB, FDI and ADM → LICI: APB, FDI and ADM → Changes in sensorimotor organization
Smith and Brouwer (2005)	10 HE (6 M, 4F)	26 ± 3	No	ECR muscle belly	15 (30 s on/15 s off)	100	0.5	MEP: ECR ↑ 33%, FCR →
	10 HE (4 M, 6F)	28 ± 6			30 (30 s on/15 s off)			MEP: ECR and FCR →
Ushiyama et al. (2005)	13 HE M	22–49	COD	Achilles tendon		30 100	1.5	H-reflex: GM ↓ 34.0%, GL ↓ 38.6%, SOL ↓ 36.1%
Rosenkranz and Rothwell (2006a)	6 HE (4 M, 2F)	30–48	COD	FDI and APB muscle bellies	15 (2 s on/2 s off)	80	0.2–0.5	MEP: APB, FDI and ADM → SICI: APB, FDI and ADM → Changes in sensorimotor organization
Christova et al. (2011)	12 HE (3 M, 9 F)	26 ± 4	COD	Whole hand		20 10	±2	MEP: FDI and APB → SICI: FDI and APB → ICF: FDI and APB →
						25		MEP: FDI and APB ↑ up to POST-2 h SICI: FDI and APB ↓ up to POST-2 h ICF: FDI and APB ↑ up to POST-2 h
Ekblom and Thorstensson (2011)	8 HE F	23 ± 2	COD	Achilles tendon		30 100	NR	H-reflex: SOL ↓ 32.6%
Lapole et al. (2012a)	11 HE	27 ± 3	CG	Achilles tendon		60 50	1	H-reflex: SOL ↓ ≈10% (sitting), SOL ↓ ≈15% (standing)

Table 2 (continued)

Study	Tested subjects	Mean \pm SD age (years)	Control condition	Vibration site	Duration (min)	Fr (Hz)	A (mm)	Main outcomes
Lapole et al. (2012b)	12 HE	21 \pm 3	No	Achilles tendon	60	50	0.2	H-reflex: SOL \downarrow \approx 11% POST MEP: SOL \uparrow \approx 30% POST-1 h, TA \uparrow \approx 46% POST-1 h
Fry and Folland (2014)	18 HE M	20 \pm 2	COD	Infrapatellar tendon	30	80	1.5	H-reflex: VM \downarrow 60.2%
Lapole and Tindel (2015)	10 HE (8 M, 2F)	27 \pm 9	No	APB muscle belly	15	80	0.8–1	MEP: APB \rightarrow (+22.3%) \uparrow sensorimotor integration for four subjects identified as responders
Farabet et al. (2016)	13 HE (9 M, 4 F)	23 \pm 4	COD	TA muscle belly	30	100	1	H-reflex: TA \downarrow 21.0% MEP _{MVC} : TA \rightarrow (+19.7%) CSP _{MVC} : TA \rightarrow (+7.3%)

A vibration amplitude, APB abductor pollicis brevis, COD cross-over design, CG control group, CSP_{MVC} cortical silent period during maximal voluntary contraction, ECR extensor carpi radialis, F female, FCR flexor carpi radialis, FDI first dorsal interosseus, Fr vibration frequency, GL gastrocnemius lateralis, GM gastrocnemius medialis, HE healthy population, ICF intracortical facilitation, LICI long-interval cortical inhibition, M male, MEP motor evoked potential, MEP_{MVC} motor evoked potential during maximal voluntary contraction, NR not reported, SICI short-interval cortical inhibition, SOL soleus, TA tibialis anterior, VM vastus medialis, \approx mean changes estimated from values displayed on a graph, \rightarrow not statistically significant, \uparrow statistically significant increase, \downarrow statistically significant decrease

afferents by the vibratory stimuli (Burke et al. 1976a, b; Roll et al. 1989), it was hypothesized that H-reflex depression observed following prolonged LV may result from similar mechanisms as those reported during the vibration paradox (Farabet et al. 2016; Lapole et al. 2012b). Such LV-induced depression of the H-reflex may persist for up to 35 min (Hayward et al. 1986; Heckman et al. 1984; Ushiyama et al. 2005), and return to baseline values 1-h after the end of exposure (Lapole et al. 2012b).

Motor unit recruitment failure in response to decreased Ia afferent efficacy

Using recordings of motor unit firing rates, the decrease in synaptic input from Ia afferents to alpha motoneurons has been suggested to predominantly affect the recruitment of high-threshold motoneurons that supply fast-twitch muscle fibres (Bongiovanni et al. 1990). This can explain why some studies (Ushiyama et al. 2005; Yoshitake et al. 2004) reported a decreased EMG amplitude in medial (–32 and –13%, respectively) and lateral (–12 and –11%, respectively) heads of the gastrocnemius after 30 min of 100-Hz Achilles tendon vibration, with no concomitant change in the soleus muscle (which is known to have more slow-twitch fibres compared to the gastrocnemii). Similarly, LV-induced

decreased EMG amplitude was reported to be more pronounced in the rectus femoris, i.e. the muscle with the higher percentage of fast-twitch fibres among quadriceps muscles (Johnson et al. 1973), than vastus lateralis (Jackson and Turner 2003) and vastus medialis muscles (Kouzaki et al. 2000) after a 30-min prolonged LV period at 30 Hz. Furthermore, a decreased rate of force development in the knee extensors after prolonged LV has been suggested to result from a failure in the capacity to completely recruit high-threshold motoneurons at the onset of the contraction (Jackson and Turner 2003; Kouzaki et al. 2000).

Local vibration-induced decreased spinal loop excitability is well acknowledged and suggested to explain the MVC decrease observed after LV, but only one study has reported decreased H-reflex accompanied by an impairment in force following a 30-min prolonged LV period (frequency 100 Hz; amplitude 1.5 mm) (Ushiyama et al. 2005) while others studies have reported decreased H-reflex without impaired MVC (Ekblom and Thorstensson 2011; Farabet et al. 2016). The reasons why force production capacities are unchanged while the spinal excitability is reduced remains unclear, but differences in investigated muscles (dorsiflexor and knee extensor muscles for Farabet et al. 2016 and Fry and Folland 2014, respectively), and type of contractions (dynamic contractions for Ekblom and Thorstensson 2011) (see Table 2) may

have caused these conflicting results. Alternatively, Ekblom and Thorstensson (2011) hypothesized that decreased activity of Ia afferents could have been counteracted by supra-spinal inputs (i.e. greater descending neural drive through increased motor cortex excitability). This hypothesis will be examined in the next section addressing the acute effects of LV on corticospinal excitability through the use of transcranial magnetic stimulation (TMS).

Acute effects of local vibration on corticospinal excitability

While proprioceptive inputs are essential at the spinal level (Gandevia 1998), they also play a major role in motor control at the cortical level (Wiesendanger and Miles 1982) and it is thought that afferent inputs can modulate motor cortex excitability. The hypothesis that vibratory stimuli may influence the cortical level is supported by studies showing that LV can induce cortical activation of both sensory and motor areas (see above).

Corticospinal excitability modulation during the application of local vibration

Numerous upper limb studies (i.e. various hand and wrist muscles) have demonstrated an increase in corticospinal excitability within the first seconds of LV application. This has been evidenced by (1) an increased motor evoked potential (MEP) peak-to-peak amplitude or area and (2) a decreased resting motor threshold (i.e. the lowest TMS intensity at which a MEP can be elicited in a relaxed muscle (i.e. no background muscle activity) (Claus et al. 1988; Kossev et al. 1999, 2001; Rosenkranz and Rothwell 2003, 2006a; Siggelkow et al. 1999; Steyvers et al. 2003b). This occurs despite the vibration paradox, i.e. a decreased spinal loop excitability during LV (Desmedt 1983; Desmedt and Godaux 1978). More recently, our research group extended these findings to lower limb muscles and demonstrated both decreased resting motor threshold and increased MEP amplitude in the plantar flexors during brief low-amplitude (1 mm) LV exposure (Lapole et al. 2015b). Interestingly, the magnitude of LV-induced MEP amplitude increase was much greater for the soleus (increased by $\approx 275\%$ with 50-Hz LV frequency and $\approx 200\%$ with 80 and 110-Hz frequencies) than gastrocnemius medialis muscle (increased by $\approx 150\%$ at all 50, 80 and 110-Hz frequencies), possibly due to the higher density of muscle spindles in the soleus (Proske 1997), making this muscle group more sensitive to LV. The only study that investigated corticospinal excitability during WBV demonstrated a 56% increase in tibialis anterior MEP amplitude (Mileva et al. 2009). The LV-induced increase in MEP amplitude was reported to be frequency dependent for upper limb muscles (Siggelkow et al. 1999; Steyvers

et al. 2003b). Significant increases in extensor carpi radialis MEP amplitude were reported during 80-Hz LV (increased by 100%) and 120-Hz LV exposure (increased by 50%) while no significant changes were observed with 160 Hz (Siggelkow et al. 1999). Similarly, it has been shown that 75-Hz LV resulted in a more pronounced increase in flexor carpi radialis MEP amplitude compared to 120-Hz LV (50 and 30%, respectively), while a 20-Hz frequency, however, had no effect on MEP amplitude (Steyvers et al. 2003b). The fact that the increase in MEP amplitude depends on LV frequency has mainly been attributed to the one-to-one response of Ia afferents with LV frequencies up to 120 Hz (Burke et al. 1976a; Roll et al. 1989). Since 20-Hz LV is known to induce a suboptimal Ia afferent firing rate (Roll et al. 1989), insufficient central temporal summation of Ia afferent discharge has been suggested to account for the lack of MEP amplitude change (Steyvers et al. 2003b). Similarly, a high LV frequency (i.e. 160 Hz) was ineffective in facilitating MEPs (Siggelkow et al. 1999). This latter finding was hypothesized to result from (1) an overstimulation of Ia afferents (Siggelkow et al. 1999), leading to a possible decrease in their firing rate (Roll et al. 1989) or (2) inhibitory polysynaptic mechanisms mediated by dynamic mechanoreceptors (Siggelkow et al. 1999). In plantar flexor muscles, MEP amplitude was not dependant on the LV frequency as the MEP amplitude increase was the same for input frequencies of 50, 80 and 110 Hz (Lapole et al. 2015b), perhaps because all of these tested frequencies are in the range of optimal firing rates of Ia afferents in response to LV (Burke et al. 1976a; Roll et al. 1989). Hence, the LV-induced increase in MEP amplitude is thought to be directly mediated by the induced discharge of muscle spindle Ia afferents.

Increased corticospinal excitability in the vibrated muscle has concomitantly been reported with modulations for antagonist and contralateral non-vibrated muscles. For instance, while corticospinal excitability in vibrated (upper body) muscles was increased, a reduced excitability was found in the antagonist muscles when LV at 80 (Kossev et al. 2001; Rosenkranz et al. 2003; Rosenkranz and Rothwell 2003, 2006b; Siggelkow et al. 1999), 120 (Siggelkow et al. 1999) and 160 Hz (Siggelkow et al. 1999) were used. This effect is further supported by the increased cortical silent period in the antagonist muscle (Binder et al. 2009), suggesting an enhanced intracortical inhibition via activation of GABAergic inhibitory cortical neurons projecting onto the pyramidal cells in the motor cortex (Inghilleri et al. 1993; Werhahn et al. 1999). Altogether, this highlights the well-known reciprocal inhibitory influences of Ia afferents, mediated by both spinal (Day et al. 1984; Gillies et al. 1969) and supra-spinal inputs (Bertolasi et al. 1998). The role of inhibitory mechanisms originating in vibrotactile afferents or other dynamic mechanoreceptors (cutaneous or joint receptors) has also been suggested (Siggelkow et al. 1999).

This decrease in corticospinal excitability in antagonist muscles was, however, not found in plantar flexor muscles and discrepancies between upper and lower limb muscles remain to be elucidated (Lapole et al. 2015b).

An increase in contralateral agonist MEP area and a decrease in contralateral antagonist MEP area has also been found during 80-Hz LV (Kossev et al. 2001). It was suggested that the facilitatory action of LV may be mediated via transcallosal pathways that in turn cause inhibition of cortical outputs to the contralateral antagonist (Kossev et al. 2001). Conversely, Swayne et al. (2006) reported a decrease in MEP amplitude in the contralateral homologous muscle during 80-Hz LV, suggesting effects occurring in the cortex ipsilateral to the vibrated muscle and mediated via transcallosal fibres. We recently found no effects of LV in contralateral muscles, specifically the plantar flexors muscle (Lapole et al. 2015b). As for antagonist inhibition, the discrepancy between upper and lower limb studies is still unclear.

Since MEP amplitude depends on the synaptic relays of the corticospinal projections at both the cortical and spinal levels (Devanne et al. 1997), the interpretation of LV-induced increased MEP amplitude should be made with caution. The contribution of cortical, spinal or peripheral mechanisms to the increased MEP amplitude is difficult to identify. M- and F-waves, which assess sarcolemmal and motoneuronal excitability, respectively, remain unchanged during 120-Hz LV (Rollnik et al. 2001). Further, MEP amplitude during LV is increased in response to TMS but not transcranial electrical stimulation, suggesting a cortical contribution to this increase in MEP amplitude (Kossev et al. 1999). Overall, the literature suggests that the mechanisms are cortical in origin. The exclusion of spinal contributions to increases in MEP amplitude may be further supported by the unaffected postsynaptic excitability of soleus motoneurons reported during 25-Hz LV (Abbruzzese et al. 1997).

Changes in intracortical excitability and inhibition during local vibration

Paired-pulse TMS (Kujirai et al. 1993) has been used to further understand the effects of LV on cortical excitability. By conditioning a supra-threshold TMS test pulse by a preceding subthreshold pulse, the excitability of intracortical circuits can be assessed. Time-dependent modulation of the test MEP by the conditioning stimulus can be observed when using short (≈ 1 to 6 ms) and long inter-stimulus intervals (≈ 50 to 150 ms) to elicit short-interval cortical inhibition (SICI) and long-interval cortical inhibition (LICI), respectively. If an inter-stimulus interval of 10–15 ms is used, intracortical facilitation (ICF) can be assessed (Benwell et al. 2007; Kujirai et al. 1993). SICI and LICI are known to reflect activity in cortical GABAergic circuits (GABA_A and GABA_B receptors for SICI and LICI, respectively),

which indirectly affect the excitability of pyramidal neurons (Hanajima et al. 1998; Rosenkranz and Rothwell 2003; Ziemann et al. 1996). Conversely, ICF may reflect the activation of excitatory interneurons (Ziemann et al. 1996). In upper limb studies, LV-induced increased MEP amplitude could be explained by a lower inhibition as demonstrated by decreased SICI (Rosenkranz et al. 2003; Rosenkranz and Rothwell 2003, 2006b). Furthermore, an augmentation of LICI occurs during 80-Hz LV application (Rosenkranz and Rothwell 2003). Even if some spinal mechanisms have been proposed to explain the difference between SICI (i.e. decrease) and LICI (i.e. increase), it is likely that LV differently impacts these populations of cortical inhibitory interneurons projecting to cortical zones (Rosenkranz and Rothwell 2003). The results concerning ICF are equivocal with either a small increase or no change observed with 80-Hz LV (Rosenkranz et al. 2003; Rosenkranz and Rothwell 2003). On the soleus muscle, our research group observed unchanged SICI and decreased ICF with LV (frequency 50 Hz; amplitude 1 mm) (Lapole et al. 2015a), a finding in agreement with the study of Mileva et al. (2009) during WBV, and highlighting, once again, the potential differences in LV-induced neural modulations between upper and lower limb muscles. Future studies should consider the use of corticospinal tract electrical stimulation (McNeil et al. 2013) in conjunction with TMS to enable the determination of differential effects of LV on cortical vs. motoneuronal excitability.

The aftereffects of prolonged local vibration on corticospinal excitability

The studies that investigated acute changes in corticospinal excitability after prolonged exposure to LV are summarized in Table 2, which provides detailed information on experimental (subjects characteristics, tested muscles) and LV (frequency, amplitude, vibration site) characteristics. While there is a consensus for increased corticospinal excitability during the application of LV (see above), the findings are equivocal with regard to acute changes after a single session of prolonged LV. While the only WBV study that addressed this question reported increased MEP amplitude after a single session (Krause et al. 2016), resting corticospinal excitability was found to increase (Christova et al. 2011; Lapole et al. 2012b; Smith and Brouwer 2005; Steyvers et al. 2003a), decrease (Farabet et al. 2016; Steyvers et al. 2003a), or even remain unchanged (Lapole et al. 2012b; Lapole and Tindel 2015; Rosenkranz and Rothwell 2004, 2006a; Smith and Brouwer 2005) after prolonged LV. Differences in the investigated muscles, LV parameters and experimental design may all account for these discrepancies (see Table 2 for detailed results). As an example, an increase in MEP amplitude was found after 15 but not 30 min of 100-Hz LV

(Smith and Brouwer 2005). Interestingly, three studies that addressed LV aftereffects on antagonist muscles all demonstrated increased corticospinal excitability (Forner-Cordero et al. 2008; Lapole et al. 2012b; Steyvers et al. 2003a). This may result from reciprocal inhibitory influences of Ia afferents on corticospinal output of the antagonist muscle (Bertolasi et al. 1998). Some studies have addressed whether intracortical circuits are modulated after LV using paired-pulse protocols. Christova et al. (2011) reported decreased SICI and increased ICF for up to 2 h after 20 min of LV. Conversely, it has been reported that 15 min of LV had no effect on SICI (Rosenkranz and Rothwell 2004, 2006a). Differences in vibration frequencies (25 vs. 80 Hz, respectively), vibration amplitudes (2 vs. 0.2–0.5 mm, respectively) and type of vibration (whole hand vs. muscle vibration, respectively) may all account for these discrepancies.

Overall, it remains difficult to interpret this part of the scientific literature because both spinal and supra-spinal levels may be involved in the observed MEP changes (Devanne et al. 1997). As discussed above, cervicomedullary and/or thoracic electrical stimulations (McNeil et al. 2013) used in conjunction with TMS will enable the determination of differential effects of LV on both cortical and motoneuronal excitability in the future. Nonetheless, the existing body of evidence supports the notion that the sensorimotor cortex has a dynamic functional organization and that changes in afferent input may modulate corticospinal excitability. This would rely on topographically and functionally specific reciprocal connections between primary sensorimotor cortex and primary motor cortex (Rocco and Brumberg 2007). These sensorimotor pathways have been investigated by conditioning a TMS test pulse with electrical stimulation of a peripheral nerve (Devanne et al. 2009; Tokimura et al. 2000). Using this technique, changes in sensorimotor integration (i.e. changes in excitability of cortical circuits interposed between the ascending afferent volley and descending corticospinal pathways) after LV occurred for half of the participants while no changes were observed for the others (Lapole and Tindel 2015). The explanation for such dichotomy has been hypothesized to result from the influence of the level of attention that participants gave to the sensory stimulations. For instance, the reorganization of the somatotopic representation of the body within the somatosensory cortex following prolonged sensory stimulation may be achieved only if attention is paid to the changed inputs (Mogilner et al. 1993; Ziemus et al. 2000), even when LV is used (Rosenkranz and Rothwell 2004). Moreover, the reorganization of the somatotopic representation after LV exposure was even greater when attention was paid to the exact site of stimulation (Rosenkranz and Rothwell 2006b).

In summary, prolonged LV exposure may induce decrement in motor performance (i.e. fatigue) and depression of spinal loop excitability. When repeated, this may trigger

training adaptations such as increases in strength (Kraemer and Ratamess 2004). Long-term supra-spinal adaptations to LV may also become apparent with repeated exposures, given the acute modulation of corticospinal excitability with a single exposure.

Chronic effects of local vibration training

While current research on the chronic effects of WBV is well studied (Cochrane 2011; Rittweger 2010), 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 under-investigated. Another limitation of this body of literature is that studies that have addressed this question used a variety of training protocols (i.e. different training duration, LV frequency, number of sessions, etc.) with minimal consistency across studies. Further, these LV sessions have been delivered either on relaxed or contracted muscles, further limiting the comparison between studies (see Table 3 for detailed information on training (duration, number of sessions) and LV (frequency, amplitude, vibration site) characteristics).

Effects of local vibration training on force-generation capacities

As illustrated by Table 3, LVT performed on relaxed muscles has been reported to increase isometric MVC on plantar flexors by 6.9 (Lapole and Pérot 2010) and 9.7% (Lapole et al. 2013), dorsiflexors by 12.0% (Souron et al. 2017) and knee extensors by 13.8 (Tankisheva et al. 2015) and 32.5% (Iodice et al. 2011). Increased performance during dynamic MVC (i.e. +41.0%) was also reported after LVT for knee extensors by Iodice et al. (2011), but not Tankisheva et al. (2015). In the studies presented above, strength gains were achieved with training duration of 2 (Lapole et al. 2013; Lapole and Pérot 2010), 4 (Iodice et al. 2011), 8 (Souron et al. 2017) and 26 weeks (Tankisheva et al. 2015). Souron et al. (2017) further reported that LVT-induced strength gains were not significantly greater after 8 weeks (+12.0%) than 4 weeks (+7.5%), and that gains persisted 2 weeks after the end of LVT (+10.8%). Although most studies have investigated the effect of several weeks of LVT applied on relaxed muscles, other researchers have investigated LVT with shorter training duration [i.e. 3 consecutive days, the so-called 'repeated muscle vibration' (rMV)], with LV being applied either on relaxed or contracted muscles (Aprile et al. 2016; Brunetti et al. 2006, 2014; Caliendo et al. 2012; Fattorini et al. 2006; Filippi et al. 2009; Marconi et al. 2008, 2011; Rabini et al. 2015). However, the feasibility of such rMV designs, when performed during voluntary contractions, is questionable. Indeed, the authors described a single

Table 3 Chronic effect of local vibration training

Study	Tested subjects	Mean ± SD age (years)	Control condition	Vibration site	Training design	Fr (Hz)	A (mm)	Main outcomes
Young population								
Fattorini et al. (2006)	7 HE (5 M, 2 F)	31 ± 2	CG	Distal part of the quadriceps (UL)	3 consecutive days (30 min/day)	100	0.005–0.15	MVC: → (+≈10%) RFD: → Fatigue resistance: → H-reflex: FCR → MEP: FCR and EDC → SICI: FCR and EDC → ICF: FCR and EDC →
Marconi et al. (2008)	5 HE	35 ± 10	CG	FCR muscle belly (UL)	3 consecutive days (30 min/day)	100	0.05–0.1	MVC: ↑ 6.9% EMG: TS ↑ 9.3% Activation deficit: ↓ 44.4% No changes in twitch parameters
Lapole and Pérot (2010)	29 HE	21 ± 2	COD	Achilles tendon (UL)	14 consecutive days (1 h/day)	50	0.2	Bilateral knee extension MVC: ↑ 32.5% Isokinetic MVC: ↑ 41.0% H-reflex: SOL ↑ 34.2%, GM → (+1.6%), GL → (-1.8%)
Iodice et al. (2011)	18 HE	21 ± 4	No	VI, RE, VL, VM, GMA, BF, TA, G (UL)	4 weeks (3 × 30 min/week)	300	2	MVC: ↑ 9.7% H-reflex: SOL ↑ 30.1% V-wave: SOL ↑ 43.3% Cross-education effect for MVC (↑ 10.4%) and V-wave (↑ 41.6%)
Lapole and Pérot (2012)	16 HE	21 ± 2	CG	Achilles tendon (UL)	14 consecutive days (1 h/day)	50	0.2	No changes in number and quality of contractions performed in 30 s on a visually guided reaching task
Lapole et al. (2013)	11 HE	22 ± 3	COD	Achilles tendon (UL)	14 consecutive days (1 h/day)	50	1	Increased number and quality of contractions performed in 30 s on a visually guided reaching task
Aprile et al. (2016)	48 HE (12 M, 36 F)	25–50	CG	Deltoid, BB and pectoralis muscles (UL)	3 consecutive days (30 min/day)	100	±150 mbar	

Table 3 (continued)

Study	Tested subjects	Mean ± SD age (years)	Control condition	Vibration site	Training design	Fr (Hz)	A (mm)	Main outcomes
Souron et al. 2017	22 HE (8 M, 14 F)	20 ± 1	CG	TA muscle belly (UL)	8 weeks (3 × 1 h/week)	100	1	MVC: ↑ 12.0% VA _{TMS} : ↑ 4.9% MEP _{MVC} : TA → (-19.8%) CSP _{MVC} : TA → (-7.2%) Cross-education effect for MVC (↑10.1%) and VA _{TMS} (↑6.2%)
Elderly population								
Fillippi et al. (2009)	20 HE F	64 ± 3	CG	Distal part of the quadriceps (BL)	3 consecutive days (30 min/day)	100	0.2–0.5	Jump height: → Leg power: → Balance: →
Tankisheva et al. (2015)	17 HE F	66–84	CG	Quadriceps (middle portion) and around the hip (UL)	26 weeks (5 × 2–8 min/30–45 min/week)	NR	NR	MVC: ↑ 13.8% No changes in isokinetic and isotonic maximal voluntary contractions Walk test: → (-1.2%) Muscle mass: → (-0.7%)
Clinical population								
Brunetti et al. (2006)	15 ACL M	25 ± 3	CG	Distal part of the quadriceps during 50% MVC contraction (UL)	3 consecutive days (30 min/day)	100	<20 μm	MVC: ↑ Balance: ↑
Pietrangelo et al. (2009)	9 sarcopenia patients (4 M, 5 F)	73 ± 6	No	Distal part of the quadriceps (BL)	12 weeks (1 × 15 min/week for weeks 1–8; 3 × 15 min/week for weeks 9–12)	300	NR	Bilateral MVC: ↑ ≈63% Myofibre transition from IIX to I Muscle mass: → CSA: → (+15.5%)
Marconi et al. (2011)	15 stroke patients (9 M, 6 F)	63 ± 7	CG	FCR and BB muscle bellies during 10–20% MVC voluntary contraction (UL)	3 consecutive days (30 min/day)	100	0.2–0.5	MEP: FCR, BB and EDC ↑ SICI: FCR and BB ↑ and EDC ↓ ICF: → Spasticity (MAS scale): ↓ Prevention of the immobilization-induced reduced EMG and V-wave No changes in H-reflex and F-wave
Zhao et al. (2011)	30 HE IMM (17 M, 13 F)	18–46	CG	SOL muscle belly (UL)	12 consecutive days (48 min daily)	100	0.3	Prevention of immobilization-induced reduced cortical activation (SIM1, PMd, SMA) during voluntary movement
Roll et al. (2012)	16 HE IMM	22–35	CG	Tendons of the wrist extensor and flexor muscles (UL)	5 days (illusory movement, 2 × 30 min/day)	100	NR	Prevention of immobilization-induced reduced cortical activation (SIM1, PMd, SMA) during voluntary movement

Table 3 (continued)

Study	Tested subjects	Mean ± SD age (years)	Control condition	Vibration site	Training design	Fr (Hz)	A (mm)	Main outcomes
Caliandro et al. (2012)	28 stroke patients (20 M, 8 F)	57 ± 12	CG	Pectoralis minor and BB during voluntary contraction (UL)	3 consecutive days (30 min/day)	100	0.2–0.5	Functional ability (WMFT FAS): ↑ Spasticity (MAS scale): → Leg power: ↑ Balance: ↑ Counteract the progressive bone demineralization induced by osteoporosis
Brunetti et al. (2014)	20 postmenopausal osteoporotic F		CG	Quadriceps during voluntary contraction (UL)	3 consecutive days (30 min/day)	100	0.3–0.5	Significant improvement in functional capacity (WOMAC, SPPB and POMA)
Rabini et al. (2015)	25 M and F with knee osteoarthritis	60 or older	CG	Quadriceps during voluntary contraction (BL)	3 consecutive days (30 min/day)	100	0.2–0.5	

A vibration amplitude, *BL* bilateral local vibration application, *COD* cross-over design, *CG* control group, *CSA* cross-sectional area, *CSP* cortical silent period, *CSP_{MVC}* cortical silent period during voluntary contraction, *EDC* extensor digitorum communis, *EMG* electromyography, *F* female, *FCR* flexor carpi radialis, *Fr* vibration frequency, *GL* gastrocnemius lateralis, *GM* gastrocnemius medialis, *HE* healthy population, *ICF* intracortical facilitation, *IMM* subjects who undergone an immobilization period, *M* male, *MAS* Modified Ashworth Scale, *MEP* motor evoked potential, *MEP_{MVC}* motor evoked potential during voluntary contraction, *MVC* isometric maximal voluntary contraction, *NR* not reported, *PMD* dorsal premotor cortex, *POMA* Performance-Oriented Mobility Assessment, *RFD* rate of force development, *S/MI* primary sensorimotor area, *SICI* short-interval cortical inhibition, *SMA* supplementary motor area, *SOL* soleus, *SPPB* short physical performance battery, *TA* tibialis anterior, *TB* triceps brachii, *TS* triceps surae, *UL* unilateral local vibration application, *VATMS* cortical voluntary activation assessed via transcranial magnetic stimulation, *WOMAC* Western Ontario and McMaster Universities Osteoarthritis Index, *WMFT FAS* Functional Ability Scale of the Wolf Motor Function Test, → not statistically significant, ↑ statistically significant increase, ↓ statistically significant decrease

session as 3 bouts of 10 min (with 1-min rest between bouts) with the participants maintaining around 10–20% MVC sub-maximal contractions (Brunetti et al. 2012; Fattorini et al. 2006; Marconi et al. 2008; Filippi et al. 2009). From our experience, this is likely to be extremely difficult to perform for most participants, even at 10% MVC (Arnal et al. 2016). Moreover, it is not clear from these studies how force contraction was monitored during the intervention. After rMV performed on relaxed upper limb muscles, Aprile et al. (2016) recently demonstrated increased motor performance in a robot-based evaluation consisting of visually guided reaching task (increased number of repetition in 30 s), with rMV-induced improvements still present in follow-up measurements performed 10 days later. Conversely, Fattorini et al. (2006) failed to demonstrate an increased MVC 2 weeks after rMV performed either on relaxed or contracted quadriceps muscle. However, this particular study did not assess muscle performance immediately after the end of rMV and had a small sample size ($n = 7$ per group), which may have caused the small effect of a +5 or +10% increased MVC to be significant when LV was performed under voluntary contraction and under relaxed conditions, respectively. In contrast, there was an increased rate of force development (up to 36% at 30 ms after the onset of the contraction) of the vibrated leg and increased resistance to fatigue during a bilateral task, as evidenced by an increased number of repetitions of isotonic contractions (+40.3%) after rMV performed in combination with voluntary contraction, but not when rMV was performed in the relaxed state (Fattorini et al. 2006). Similarly, increased vertical jump performance in elderly participants was reported 1 (+55%), 30 (+70%) and 90 (+90%) days after rMV combined with voluntary contraction of knee extensor muscles, but not when performed on relaxed muscles (Filippi et al. 2009). Recently, this has been confirmed in female volleyball players, with increased jump heights reported 1 (+16 and +9% for squat and counter movement jump, respectively), 30 (+19 and +11% for squat and counter movement jump, respectively) and 240 (+26 and +13% for squat and counter movement jump, respectively) days after rMV combined with voluntary contractions of knee extensors (Brunetti et al. 2012), although only six participants were included in each group in this study.

It appears that regardless of the LVT design, it may induce persistent and long-lasting effects on force production capacities. With short training duration (i.e. rMV), with the exception of the study of Aprile et al. (2016), improvements were only observed when LV was applied on contracted muscles since LV alone or contraction alone did not induce the same improvements (Brunetti et al. 2012; Fattorini et al. 2006; Filippi et al. 2009). In contrast, others demonstrated that superimposing LV during dynamic strength training did not increase the chronic effects of strength training alone on elbow flexors MVC (Drummond et al. 2014) or vertical

jump and running speed (Couto et al. 2012). It is interesting to note that in these last two studies, unilateral LVT induced similar strength gains on the vibrated (+9.7 and +12.0%, respectively) and non-vibrated sides (+10.4 and +10.0%, respectively). With regard to strength training studies, this agrees with the findings of Lagerquist et al. (2006), although it is important to emphasize that most studies reported higher strength increase in the trained but not the untrained leg after voluntary strength training (Munn et al. 2004). This may be explained by the fact that ‘classic’ strength training triggers a combination of hypertrophy and neural adaptations for the trained leg while only neural adaptations are present in the contralateral side (Carroll et al. 2006). It is likely that only neural adaptations account for the increase in muscle strength after LVT for both the non-vibrated limbs (see below).

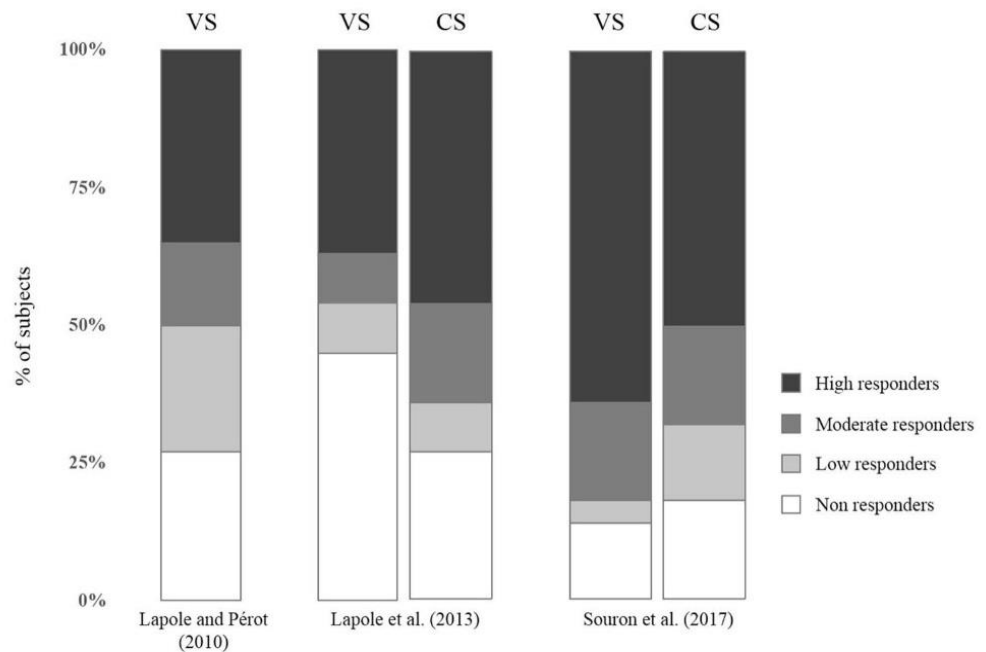
Is local vibration applicable for all population?

As discussed above, it is worth noting that LVT has been shown to induce strength gains in the vibrated muscles for healthy young males and females, as well as elderly females (see Table 3). Clinical populations may also benefit from LVT (see below). This suggests that LVT may be feasible and tolerable in many different populations. There seems to be a high inter-individual variability, however, in the LVT-induced strength gains. Indeed, our team reported coefficient of variations for the LVT-induced pre–post-changes from 78 to 182% (Lapole et al. 2013; Souron et al. 2017; Lapole and Pérot 2010). Figure 1 presents the percentage of responders and non-responders to LVT that we extracted from our studies. It shows that 20–40% of the participants may not benefit from LVT. If the reasons for such disparity appear unclear and require further investigations, it may be linked to the characteristics of the tested populations (initial training level and/or initial strength values). This is in agreement with the concept of trainability known with strength training (Hubal et al. 2005) suggesting that everyone will be impacted differently by a given training stimulus.

Muscle adaptations due to LVT

Direct and indirect data suggest that hypertrophy does not occur after LVT. For instance, Tankisheva et al. (2015) reported no changes in muscle mass for the trained leg assessed by tomography after 26 weeks (5×2 –8 min of 30–45-Hz LV) of LVT on resting knee extensor muscles. Lapole and Pérot (2010) reported unchanged twitch responses and neuromuscular efficiency during voluntary (i.e. as assessed through the slope of EMG–force relationship) and evoked contractions after 14 consecutive days of LV (frequency 50 Hz; amplitude 0.2 mm) applied over the Achilles tendon. The lack of hypertrophy after LVT was

Fig. 1 Percentage of responders and non-responders to local vibration training. Data from our previous studies were re-analysed to characterize the participants as non (less than 2%), low (+2 to +5%), moderate (+5 to +10%) and high (more than +10%) responders based on individual pre–post-changes. CS contralateral side, VS vibrated side



expected since TVR is not always present, and when it is, its amplitude is moderate. Moreover, LVT periods in the reviewed studies were generally too short to induce an increase in muscle mass, as muscle adaptations reported during strength training periods are typically much longer (Sale 1988). This contrasts with some (Bogaerts et al. 2007; Machado et al. 2010) but not all (Verschueren et al. 2004) WBV training studies that reported increased muscle mass attributed to dynamic contractions performed on the vibrating platform. Nonetheless, an increase in growth hormone and a decrease in cortisol level have been reported after a 30-min bout of 300-Hz LV, suggesting that LVT may potentially have a trophic action in the long term (Iodice et al. 2011). Although this tends to agree with WBV studies (Bosco et al. 2000), this may be questioned with regard to the relatively small muscle mass activated by LV when compared to the much larger muscle mass involved during WBV. Hence, the potential for LV to induce a systemic hormonal response remains to be clarified.

Neural adaptations due to LVT

As for the WBV chronic effects (Goodwill and Kidgell 2012; Ness and Field-Fote 2009), neural adaptations were proposed to mainly account for the strength gains after LVT (Brunetti et al. 2012; Fattorini et al. 2006; Filippi et al. 2009; Iodice et al. 2011; Lapole et al. 2013; Lapole and Pérot 2010; Tankisheva et al. 2015; Aprile et al. 2016), although this has been rarely investigated (Lapole et al. 2013; Lapole and Pérot 2010). Adaptations at the central nervous system level were first shown after 14 consecutive days of LV on the triceps surae by a 9.3% increased normalized EMG (i.e.

EMG/M-wave amplitude) during MVC after LVT, while no changes in co-activation were reported (Lapole and Pérot 2010). V-wave, an electrophysiological variant of the H-reflex obtained when a supramaximal electrical stimulus is applied to the nerve during MVC, has also been shown to increase after 14 consecutive days of LV (frequency 50 Hz; amplitude 1 mm) applied over the Achilles tendon in the vibrated (+43.3%) as well as the contralateral non-vibrated leg (+41.6%) (Lapole et al. 2013). However, Souron et al. (2017) reported no parallel changes in normalized EMG amplitude after 8 weeks of LVT (frequency 100 Hz; amplitude 1 mm). Comparison between these last two studies should be made with caution because of the well-known limitations in EMG amplitude to detect small changes in motor unit activity (Farina et al. 2010). Souron et al. (2017), however, reported an increase in dorsiflexor muscles voluntary activation level assessed via TMS in both the vibrated (+4.9%) and non-vibrated (+6.2%) legs after LVT. This is in agreement with previous finding of a 44.4% reduction of activation deficit evaluated by means of the classic (i.e. nerve stimulation) twitch interpolated technique after LVT (Lapole and Pérot 2010). Altogether, these findings suggest an improved spatial and/or temporal motor unit recruitment after LVT.

As for the acute effects of a single session of LV on spinal cord and corticospinal excitabilities (see above), the LVT-induced neural adaptations may come from both an increased spinal reflex excitability and/or an enhanced volitional drive from the primary motor cortex. Since Ia afferent inputs increase force production during isometric contractions (Gandevia 2001; Hagbarth et al. 1986), it has been hypothesized that LVT-induced increased neural drive may

be the result of increased excitatory inputs from the proprioceptive feedback loop during voluntary contractions (Lapole and Pérot 2010). Indeed, an increased soleus H-reflex amplitude has been found after LVT, both in the relaxed state, i.e. +34.2% (Lapole and Pérot 2012) and during MVC, i.e. +30.1% (Lapole et al. 2013); the latter result, however, was not observed in the contralateral non-vibrated leg (Lapole et al. 2013). In contrast, our team recently demonstrated no changes in tibialis anterior H-reflex recorded during sub-maximal voluntary contraction at 20% MVC after 8 weeks of LVT (Souron et al. 2017). Nonetheless, increased H-reflex amplitude after LVT may be explained by an increase in the amount of Ia afferent input that excites alpha motoneurons (Aagaard et al. 2002; Misiaszek 2003). Since presynaptic inhibitory mechanisms largely contribute to the decrease in H-reflex amplitude reported after an acute LV exposure (Heckman et al. 1984; Lapole et al. 2012b; Ushiyama et al. 2005), it has been speculated that some supra-spinal mechanisms may in turn have modulated the level of presynaptic inhibition exerted at the spinal level after LVT, which may contribute to the increase in muscle activation (Lapole et al. 2013; Lapole and Pérot 2012). Besides the effects of LVT on spinal loop excitability, LVT does not seem to modulate corticospinal excitability in the long term, which contrasts with acute studies (see “Acute effects of local vibration on spinal cord excitability”). Indeed, Souron et al. (2017) reported no changes in tibialis anterior MEP amplitude assessed during MVC after LVT. This is consistent with recent results reporting that superimposed WBV to strength training did not further augment the increase in corticospinal excitability induced by strength training alone (Weier and Kidgell 2012). Similar results were reported for resting MEP amplitude following rMV applied on the relaxed flexor carpi radialis muscle (Marconi et al. 2008). These authors, however, reported decreased MEP amplitude and increased SICI up to 2 but not 3 weeks after the end of rMV when vibration was combined with voluntary contraction (see Table 3). Unfortunately, this last study did not assess motor performance so that the functional significance of such long-lasting neural adaptations remains to be determined.

Can local vibration training become an efficient alternative to whole-body vibration training?

To propose vibration as a training method, its feasibility should be considered. Some studies have reported no adverse effects of LV and the training has been reported to be well tolerated (Aprile et al. 2016; Tankisheva et al. 2015), which is in agreement with our experience (Lapole et al. 2013; Lapole and Pérot 2010, 2012). The smaller vibration amplitude used in LV compared to WBV and, more importantly, the fact that LVT can be used on relaxed muscles may justify the high level of compliance reported in some LVT

studies. For instance, a 96.5% compliance was observed by Tankisheva et al. (2015) for a 26-week intervention and 100% for an 8-week program in our study (Souron et al. 2017). Self-reported compliance was also observed to be maximal in our studies when LVT was performed at the participants' home (Lapole et al. 2013; Lapole and Pérot 2010, 2012). Furthermore, LVT has been tested on a variety of designs, populations and muscles (see Table 3). Altogether, these observations suggest that LVT may be considered as a feasible training program.

While a large number of studies have reported improvements in muscle performance after WBV training in healthy participants (Cochrane 2011; Rittweger 2010), similar results have been reported after LVT in young (Fattorini et al. 2006; Lapole et al. 2013; Lapole and Pérot 2010; Iodice et al. 2011; Aprile et al. 2016) and elderly (Filippi et al. 2009; Tankisheva et al. 2015) participants. LVT can improve motor performance over a broad range of muscle groups [knee extensors (Tankisheva et al. 2015), plantar flexors (Lapole et al. 2013; Lapole and Pérot 2010), dorsiflexors (Souron et al. 2017)], by simply positioning the LV device directly on the appropriate area (the muscle belly). It may be hypothesized that muscles that are rich in slow-twitch fibres would be more sensitive to LVT (Lapole and Pérot 2012) due to their greater density in muscle spindles (McCloskey 1978; Proske et al. 2000).

The strength gains reported in the present review after LVT for healthy participants (from 6.9 to 32.5% with a mean +15.2% in the reviewed studies displayed in Table 3) are quite similar to the ones reported after WBV training for the studies reviewed (Rittweger 2010) (from 6 to 24% with a mean +11.3%) despite differences in training characteristics, i.e. training duration between 2–26 and 6–34 weeks, vibration frequencies between 30–300 and 20–45 Hz and vibration amplitudes between 0.2–2 and 1–6 mm for LV and WBV, respectively. Both LV and WBV training improve strength mainly via neural adaptations, although increased muscle mass may play a role in WBV training (Cochrane 2011; Rittweger 2010). Indeed, although an exhaustive review on WBV training was beyond the scope of the present paper, we have reviewed evidence to show that both acute and chronic adaptations are similar between LV and WBV, despite discrepancies between the two methods, amplitude and frequency, duration of the exposure and state of the muscle during vibration. Hence, it can be suggested that LVT may be an efficient alternative to WBV training even if it may be difficult to precisely determine the optimal characteristics for future LVT programs. Indeed, LVT has been reported to be efficient in improving muscular performance when applied on the tendon (Lapole et al. 2013; Lapole and Pérot 2010) or the muscle belly (Iodice et al. 2011; Pietrangelo et al. 2009; Souron et al. 2017; Tankisheva et al. 2015), and with a wide range of vibration parameters,

i.e. frequencies (between 30 and 300 Hz) and amplitudes (between 0.2 and 2 mm) (Table 3). Before considering the implementation of LVT as an ergogenic aid, further studies are needed to confirm the benefits in indices of performance (jump height, sprint performance), as existing literature has mainly focussed on isometric MVC.

Local vibration training and clinical applications

Perspectives for using local vibration training in clinical settings

In addition to using LV in neurorehabilitation to decrease spasticity (for a review see Murillo et al. 2014), LVT may be used in clinical settings to improve motor performance, as illustrated in Table 3. The main advantages of LVT are its portability and its simplicity, i.e. critical factors in clinical settings when patients have weight-bearing restrictions. LVT can improve neuromuscular performance without any active contribution from the patient, it requires very light equipment and has few technical constraints so that it can be used while simply seated or lying down on a hospital bed. This makes this technique highly promising in the perspective of preventing or counteracting muscle weaknesses due to hypo-activity. This applies to patients undergoing long-term immobilization (lower limbs trauma) or being immobilized in a cast. Indeed, it is well known that in the early stages of immobilization, the neural drive is reduced and can contribute to motor performance impairment (Duchateau 1995; Gondin et al. 2004; Lundbye-Jensen and Nielsen 2008). LVT may also be used during rehabilitation programs such as in the early period after surgery. For instance, anterior cruciate ligament reconstruction generally induces an arthrogenic neural deficit that highly contributes to the quadriceps muscle weakness observed up to several months after the surgery (Hart et al. 2010; Rice and McNair 2010).

Neuromuscular adaptations following local vibration training in clinical settings

The feasibility and benefits of LVT in clinical settings is supported by the findings of Pietrangelo et al. (2009), demonstrating that a 12-week 300-Hz LVT has the potential to increase knee extension MVC in elderly patients with sarcopenia (+63%). The limitation of this study was, however, that it was performed without any control group, meaning that the results should be interpreted with caution. Follow-up measurements further demonstrated that force measured 16 weeks after the end of LVT were similar to the values recorded immediately post-LVT. Interestingly, the improvements after LVT were much greater compared to healthy elderly (+13.8%) (Tankisheva et al. 2015) and young

participants (+12.0%) (Souron et al. 2017). Pietrangelo et al. (2009) reported no changes in muscle mass (assessed by thigh circumferences) with LVT, but there was an increase in the percentage of type IIx muscle fibres and a decrease in type I myosin heavy chains. These changes, however, were not accompanied by an increase in muscle fibre-specific tension or fibre thickness and, therefore, cannot explain the increased isometric force, suggesting neural adaptations. In contrast, 14 consecutive days of LV applied on unloaded hindlimb of rats, prevented the I to IIx myofibre transition induced by immobilization (Falempin and In-Albon 1999). In this study, 14 consecutive days of LV was also effective in preventing soleus muscle atrophy where muscle mass was decreased by 41% vs. only 17% with LVT. Despite non-conclusive results from Pietrangelo et al. (2009) on elderly patients with sarcopenia, the possibility exists that LVT may prevent muscle atrophy during disease or immobilization, or potentiate the recovery of muscle mass after surgery, especially considering the increased sensitivity of diseased or atrophied muscles to training stimulus (Lapole and Pérot 2010).

The use of rMV during voluntary contraction on three consecutive days also demonstrated beneficial effects on motor performance in clinical settings. Indeed, rMV was reported to increase physical function in patients with knee osteoarthritis (Rabini et al. 2015) as well as short- and long-term increase in leg power (+35 and +40%, respectively) during vertical jump in postmenopausal osteoporotic females (Brunetti et al. 2014). While an increased bone density was reported 1 year after the intervention in this latter study, it is not known if bone density increased in the short term, which questions the possibility of fracture through an imbalance between changes in muscle strength vs. bone density. In addition, rMV was reported to induce positive effects on force-generation capacities in patients after anterior cruciate ligament reconstruction with a total recovery in leg extensor muscle torque from 120 days after surgery while it was still significantly reduced for the control group (Brunetti et al. 2006). Recently, positive effects of rMV to decrease spasticity in stroke patients have also been reported (Caliandro et al. 2012; Marconi et al. 2011). rMV performed in addition with voluntary contraction, however, may be questioned, especially since in the latter study it may have been difficult to implement the rMV during 50% MVC contractions (3 × 10 min). Other clinical studies reported beneficial effects of 12 sessions of LVT for the prevention of reduced maximal neural drive induced by 2 weeks of calf muscle plaster-cast immobilization (Zhao et al. 2011). Using functional MRI, it was further demonstrated that a LV program designed to provide illusory movements during a 5-day immobilization period can prevent the reduced cortical activation of several areas (sensorimotor cortex, supplementary motor area) when performing voluntary movement

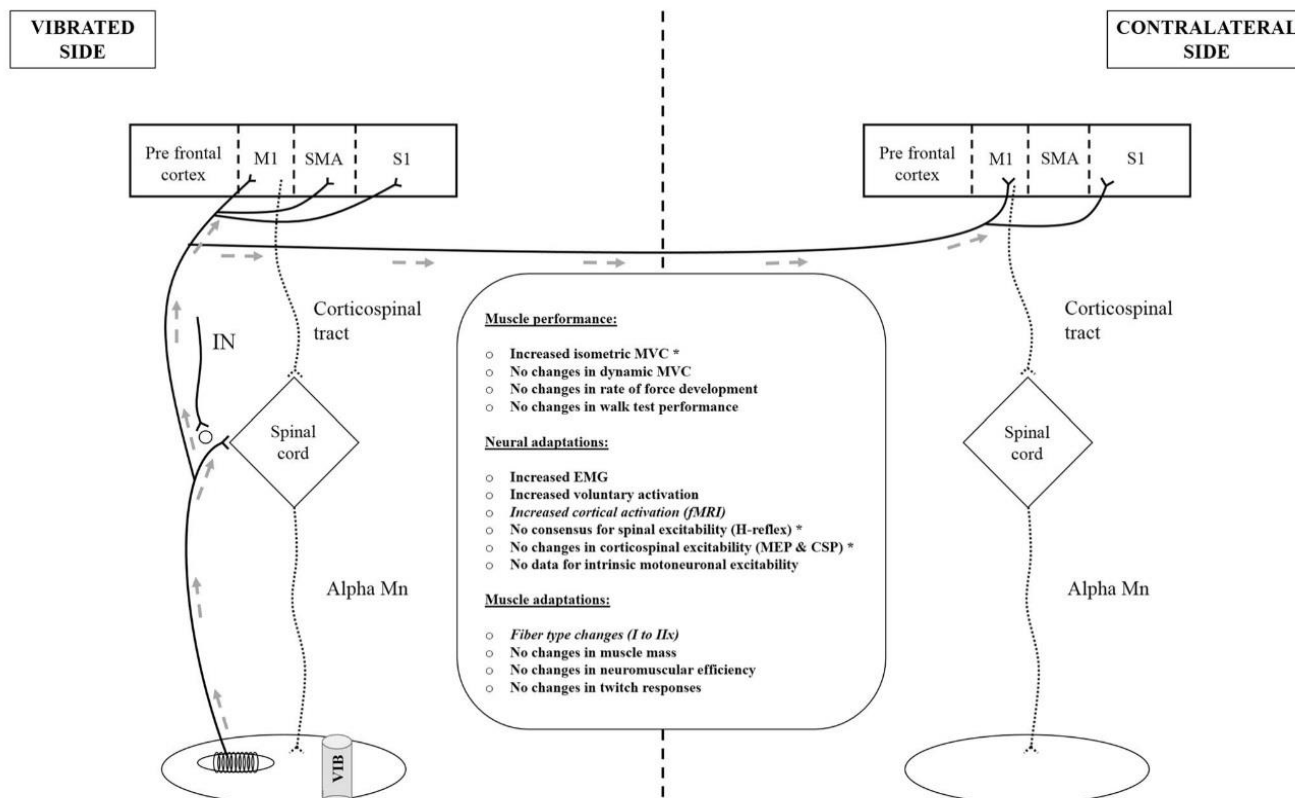


Fig. 2 Summary of the current findings of local vibration training-induced adaptations. The activation and projection of Ia afferents from muscle spindle [spiral elements represented within the muscle (oval element)] toward spinal and cortical levels are represented by dotted grey arrows. *Italic writing in the box highlights results obtained for clinical participants. Asterisk in the box highlights results*

obtained on both vibrated and contralateral sides. *CSP* cortical silent period, *fMRI* functional magnetic resonance imaging, *IN* interneurons, *M1* primary motor cortex, *MEP* motor evoked potential, *Mn* motoneuron, *MVC* maximal voluntary contraction, *S1* sensorimotor cortex, *SMA* supplementary motor area, *VIB* local vibratory device

(Roll et al. 2012). Whether or not the adaptations reported in these two studies may lead to functional improvement remains to be determined.

While promising results have been reported in WBV (Huang et al. 2017; Pistone et al. 2016; Wang et al. 2016) and neuromuscular electrical stimulation (de Oliveira Melo et al. 2016; Fitzgerald et al. 2003; Glinsky et al. 2007) studies, it has also been suggested that LVT may be beneficial for various clinical populations (participants with knee osteoarthritis, anterior cruciate ligament reconstruction or central nervous system disorders) (see Table 3). However, further studies are needed to confirm the benefits in either muscular or neural components in a variety of clinical populations, especially by further considering muscle performance and functional test measurements.

Conclusion

For more than four decades, vibratory stimuli have been considered as a training or rehabilitation modality. While

WBV is particularly well documented, LV techniques have been more recently developed to overcome some limitations related to the use of WBV, i.e. prohibitive cost, non-portability of the system, inability to directly target a specific muscle group or inability for some subjects to maintain an active position during the vibration application on the platform.

There is clear evidence that vibration is a strong stimulus to modulate the central nervous system through the activation of Ia afferents that project on both the spinal cord and supra-spinal structures. When LV is acutely applied (one bout of 20–30 min), a decrease in force-generation capacities has been reported, principally triggered by adaptations within the central nervous system (i.e. spinal loop excitability depression). Thus, LV stimuli have the potential to act as a significant neuromuscular workload by inducing some fatigue which, when repeated, could trigger long-term neural adaptations leading to improved functional performance. Indeed, the present review confirms that LVT can increase motor performance through a wide range of training (duration, number of session) and vibration (frequency, amplitude, site of application) parameters. While there seems to

be a consensus about the neural nature of the induced adaptations, the precise mechanisms of these adaptations at both the spinal and supra-spinal levels remain to be clarified. In an attempt to summarize the current research findings of LVT-induced adaptations, we propose a model in Fig. 2.

LVT has been mainly used with healthy participants, although some preliminary results revealed in clinical populations suggest that its use for prevention or rehabilitation settings may be developed in the future. Further studies are needed to test the effects of LVT in various diseases and ageing populations. It is currently difficult to suggest definitive practical recommendations because of inconsistencies in the experimental settings. Thus, more work is needed to help establish research-based guidelines for LVT programs.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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OBJECTIFS DE LA THESE

Les nombreuses réponses neurophysiologiques pouvant être observées pendant la vibration, e.g. réflexe tonique vibratoire, illusion proprioceptive de mouvement (**figure 1**), ont amené à penser l'utilisation de cette technique comme un potentiel stimulus permettant d'induire des adaptations neuromusculaires sur le court

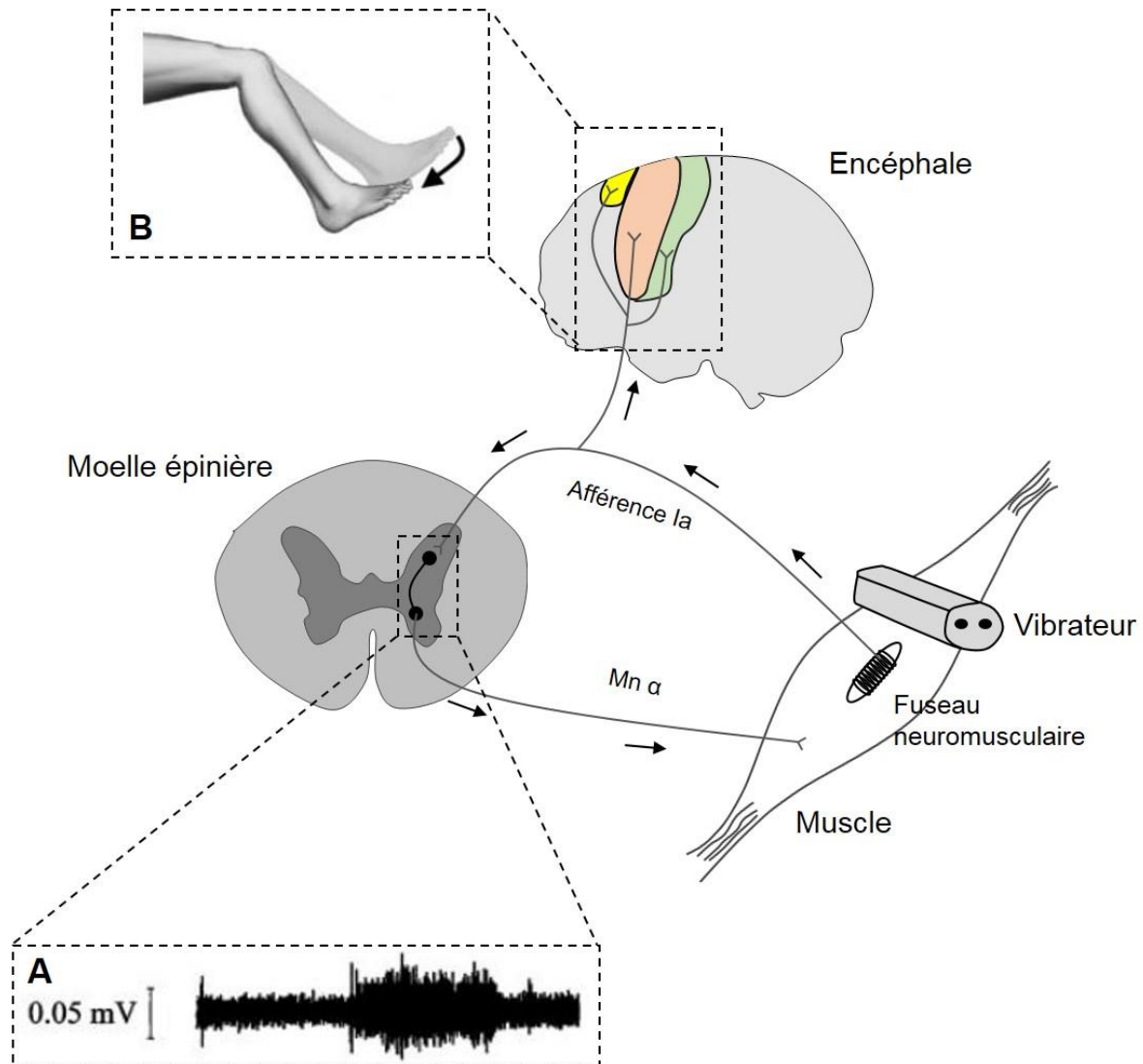


Figure 1. Représentation schématique de l'action de la vibration locale au niveau spinal et cortical. L'activation des afférences primaires des fuseaux neuromusculaires (Ia) par la vibration entraîne un influx excitateur sur le motoneurone alpha (Mn α), pouvant parfois (dépendant des paramètres de vibration utilisés) induire une contraction musculaire réflexe de faible amplitude du muscle vibré, i.e. le réflexe tonique vibratoire. La présence ou non de ce phénomène en réponse à la vibration peut être vérifiée grâce à l'analyse électromyographique du muscle vibré et relâché soumis aux stimuli vibratoires (panel A). Les afférences Ia projettent également leur influx excitateur au niveau cortical, notamment au niveau du cortex sensorimoteur (vert), de l'aire motrice supplémentaire (jaune), et du cortex moteur primaire (orange) et peuvent induire des illusions de mouvement, phénomène pouvant servir de base à la rééducation sensori-motrice par assistance proprioceptive vibratoire (panel B).

La diminution de force classiquement reportée après une exposition prolongée à la vibration locale (20-30 minutes) témoigne de l'efficacité de ce stimulus à moduler certains niveaux de la chaîne de la commande neuromusculaire. Puisqu'aucune altération musculaire n'a été reportée après une séance unique de vibration locale (Ushiyama et al., 2005; Herda et al., 2009; Fry & Folland, 2014; Saito et al., 2016b; a), il semble que des altérations intervenant au niveau central soient la cause principale de la diminution de force post-vibration.

Alors que l'utilisation de la WBV comme une technique d'entraînement permettant d'améliorer la fonction neuromusculaire semble s'être démocratisée (voir les articles de Cochrane, (2011) et Rittweger, (2010) pour des revues détaillées), il existe encore actuellement un manque de connaissance sur les effets d'un entraînement par vibration locale. Même si des gains de force semblent intervenir de manière quasi-systématique après ce type d'entraînement (Brunetti et al., 2006; Pietrangelo et al., 2009; Lapole & Pérot, 2010; Iodice et al., 2011; Lapole et al., 2013; Tankisheva et al., 2015), il n'existe actuellement aucun consensus sur les adaptations neuromusculaires qui sous-tendent cette augmentation de la performance musculaire. De plus, certaines études montrant une augmentation des capacités musculaires après une application chronique de la vibration locale (Brunetti et al., 2006; Lapole & Pérot, 2010; Lapole et al., 2013) s'éloignent des recommandations standards généralement proposées dans une perspective d'entraînement et/ou de rééducation (plusieurs séances d'entraînement par semaine réparties sur plusieurs semaines), rendant l'interprétation des résultats difficile.

Mes travaux de thèse visaient dans un premier temps à déterminer les effets d'une application aiguë de la vibration locale sur la fonction neuromusculaire, et plus particulièrement sur la composante centrale de cette dernière (par l'utilisation notamment de la TMS et de la stimulation électrique thoracique). Dans un 2^{ème} temps, et ceci représentait l'objectif majeur de ce doctorat, nous avons caractérisé les effets à long terme de la vibration locale lorsqu'elle était utilisée comme technique d'entraînement. Les travaux ont débuté au sein du Laboratoire de Physiologie de l'Exercice (LPE), désormais Laboratoire Interuniversitaire de Biologie de la Motricité (LIBM), à Saint-Etienne, où nous avons ciblé les muscles fléchisseurs dorsaux de la cheville de jeunes adultes sains (études #1 et #2). Nous avons préalablement testé la reproductibilité de plusieurs paramètres d'évaluation de la fonction neuromusculaire

pour ce groupe musculaire afin d'en valider leur utilisation pour les études suivantes (cf. annexe 1 à la page 192 de ce manuscrit).

Ensuite, au cours d'une mobilité de 7 mois (janvier-août 2016) au sein du « Human Performance Laboratory » (HPL) de l'Université de Calgary (Canada), nous avons ciblé les muscles extenseurs du genou (études #3 et #4) et nous avons comparé les résultats obtenus chez de jeunes adultes sains et une population saine âgée. Ces différents travaux nous ont alors conduit à la mise en place d'une troisième partie à visée clinique, dont le but consistait à évaluer l'efficacité d'une rééducation par vibration locale sur des patients opérés d'une ligamentoplastie du LCA du genou (étude #5 présentée en annexe 2).

Nous avons émis l'hypothèse générale selon laquelle une séance d'exposition à la vibration prolongée induirait une diminution aiguë des capacités de production de force (études #1 et #3), concomitante d'adaptations nerveuses d'origine cortico-spinales. Nous avons ensuite émis l'hypothèse générale que sous l'influence de ces adaptations aiguës, la capacité de production de force pourrait être augmentée à la suite d'un entraînement par vibration locale chez le sujet sain (études #2 et #4) et que ces gains de force seraient influencés par des adaptations d'origines spinales et/ou supra-spinales. Dans l'étude #5, nous avons enfin émis l'hypothèse que ces adaptations chroniques à l'entraînement par vibration locale pourraient permettre de limiter le phénomène de sidération couramment observé après une ligamentoplastie du genou, et donc de limiter la perte de force musculaire post-opératoire ainsi que les limitations fonctionnelles engendrées.

METHODOLOGIE GENERALE

1. Justification des groupes musculaires investigués

Les muscles fléchisseurs dorsaux de la cheville, et plus particulièrement le muscle tibial antérieur (TA), étaient évalués dans les études #1 et #2 de ce travail de thèse. Le choix de ce groupe musculaire a notamment été guidé par l'importance des projections cortico-spinales qu'il présente (Perez et al., 2004), ce critère étant primordial pour envisager des études mobilisant l'utilisation de la TMS et également pour évaluer le niveau d'activation cortical (Goodall et al., 2009), marqueur important pour l'évaluation de la voie cortico-spinale lors des quatre premières études de ce travail de thèse. De plus, le TA étant un muscle lent (Johnson et al., 1973), il est intéressant d'observer si les effets de la vibration qui ont été reportés pour un muscle différent mais de typologie similaire, i.e. soléaire (Ushiyama et al., 2005; Lapole & Pérot, 2010; Lapole et al., 2013), sont retrouvés sur le muscle TA.

Dans les études #3 et #4, les muscles extenseurs du genou étaient évalués. Le choix de ce groupe musculaire a été réalisé en raison i) de son importance fonctionnelle dans les activités de la vie quotidienne, e.g. marche (Hurley et al., 1998), et ii) du phénomène de dégénérescence neuromusculaire progressive dont il souffre avec l'âge (Hurley et al., 1998). Il était également intéressant d'étudier la réponse d'un groupe musculaire à typologie davantage mixte (Johnson et al., 1973) aux stimuli vibratoires et le comparer à celle d'un muscle lent (TA), au regard de la probable proportion différente en FNMs dans ces deux groupes musculaires (Barker, 1974).

2. Vibration locale

La vibration se définit classiquement par un mouvement mécanique oscillatoire, qui se caractérise par deux paramètres. La fréquence, qui est le taux de répétition des cycles oscillatoires, est mesurée en Hertz. L'amplitude (ou magnitude) de l'oscillation, qui permet généralement de mesurer un déplacement, est mesurée en millimètres (Griffin, 1990). Lors de ce travail de thèse, le même dispositif vibratoire a été utilisé pour l'ensemble des études (VB 115, Techno Concept, Mane, France). Le choix des paramètres vibratoires a été fait en accord avec la littérature existante, qui démontre que les afférences la sont sensibles à de faibles amplitudes de vibration (Roll & Vedel, 1982) et déchargent de manière synchronisée pour des fréquences allant jusqu'à 80–120 Hz (Roll & Vedel, 1982; Roll et al., 1989). Le **tableau 1** présente de manière précise les paramètres vibratoires utilisés dans les différentes études de ce travail de

thèse, tandis que la **figure 2** fournit une représentation précise des sites d'application du dispositif vibratoire dans les différentes études de cette thèse.

Tableau 1. Paramètres de vibration et sites d'application du dispositif vibratoire pour l'ensemble des études.

	Fréquence (Hz)	Amplitude (mm)	Site d'application	Durée d'application (min)	Nombre total de séances	Durée de l'entraînement (semaines)
Etude #1	100	1	TA	30	1	NA
Etude #2	100	1	TA	60	24	8
Etude #3	100	1	RF	30	1	NA
Etude #4	100	1	RF	60	12	4

TA : muscle tibial antérieur ; RF : muscle droit fémoral (rectus femoris) ; NA : non applicable.

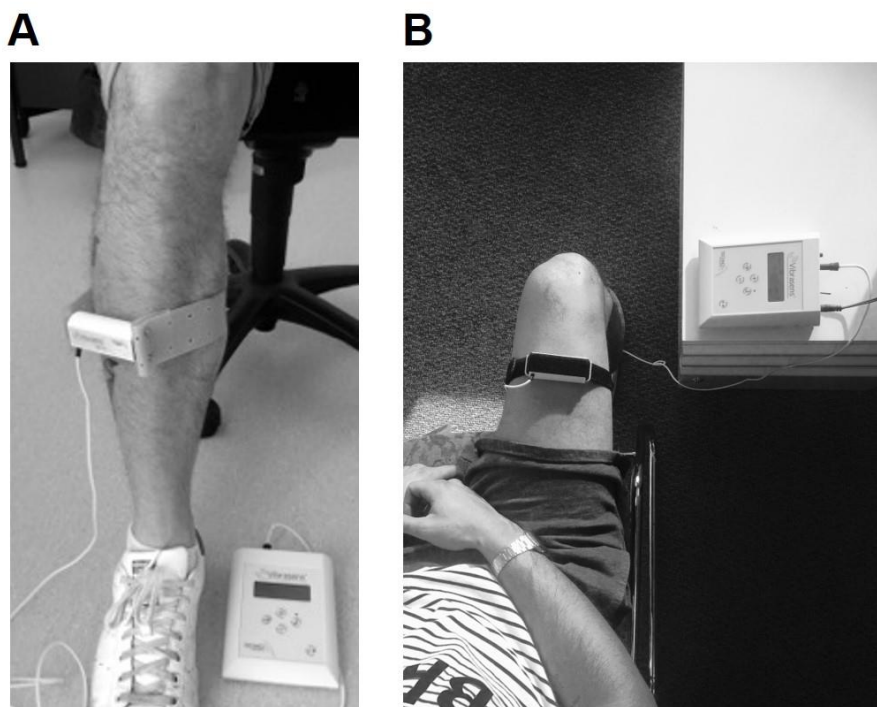


Figure 2. Sites d'application du dispositif de vibration locale. Pour les études #1 et #2, le vibreur était appliqué localement et directement attaché sur la partie la plus large du muscle tibial antérieur à environ 50% de la longueur musculaire totale, i.e. éloigné des insertions tendineuses (panel A). Pour les études #3 et #4, le vibreur était appliqué localement et directement attaché sur le muscle droit fémoral à environ 40% de la longueur musculaire entre le bord supérieur de la rotule et l'épine iliaque antéro supérieure (panel B).

3. Outils de mesure

3.1. Mesures de force

Le couple de force produit par les fléchisseurs dorsaux de la cheville (études #1 et #2) était mesuré par une pédale instrumentalisée et calibrée (CS1060 300 Nm, FGP Sensors, Les Clayes Sous Bois, France). Comme représenté sur la **figure 3**, les sujets étaient assis sur le siège de l'ergomètre et les angles articulaires étaient fixés à 120 et 90° respectivement pour le genou et la cheville. L'utilisation de deux ceintures attachées au niveau du thorax permettait de minimiser les mouvements du haut du corps.



Figure 3. Positionnement du sujet lors des mesures de couple de force maximal des fléchisseurs dorsaux de la cheville (études #1 et #2). L'avant pied était fixé à la pédale instrumentalisée par une bande velcro, et des cales en bois étaient ajoutées ou retirées afin d'ajuster la hauteur du pied à la longueur de la pédale.

La force produite par les extenseurs du genou (études #3 et #4) était mesurée par un capteur de force (Omega Engineering Inc., Stamford, CT) fixé à l'ergomètre (cadre Kin-Com) (**figure 4**). Les sujets étaient assis sur le siège de l'ergomètre et les angles articulaires étaient fixés à 90° pour la hanche et le genou. L'utilisation de trois ceintures attachées au niveau du thorax et de la taille permettait de minimiser les mouvements du haut du corps.

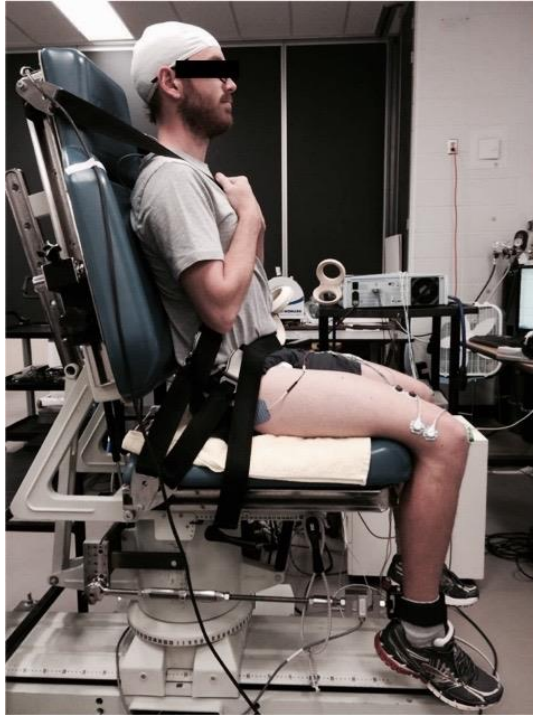


Figure 4. Positionnement du sujet lors des mesures de force maximale des extenseurs du genou (études #3 et #4). La cheville était fixée au capteur de force par une attache Velcro permettant la mesure des forces isométriques.

Pour l'ensemble des études, le sujet disposait d'un feedback visuel de la force produite en temps réel, i.e. affichée sur un écran positionné en face de lui, et des lignes guides étaient ajoutées lorsqu'il était demandé au sujet de maintenir un plateau de force à des niveaux sous-maximaux.

3.2. Electromyographie de surface

Dans l'ensemble des études, les signaux électromyographiques de surface (sEMG) ont été recueillis à partir d'électrodes (Meditrace 100, Covidien, Mansfield, MA) positionnées en configuration bipolaire (intervalle inter-électrodes : 30 mm). Les signaux EMG ont été amplifiés (ML138, ADInstruments ; gain = $\times 500$), filtrés (bande passante : 5-500 Hz) et échantillonnés à une fréquence de 2000 Hz (PowerLab system, 16/30—ML880/P, ADInstruments, Bella Vista, Australia). Préalablement à la pose des électrodes, la peau a été préparée, i.e. rasée, poncée et nettoyée avec une solution hydro-alcoolique, pour réduire l'impédance et favoriser le recueil du signal. L'électrode de référence était placée sur la malléole latérale (études #1 et #2) ou la rotule (études #3, #4 et #5). Dans les études #1 et #2, les électrodes EMG étaient positionnées sur le corps musculaire du TA, i.e. à 1/3 de la distance entre la tête de la

fibula et la pointe de la malléole médiale, et du muscle soléaire, i.e. 2 cm en dessous de l'insertion du muscle gastrocnémien sur le tendon d'Achille. Dans les études #3 et #4, les électrodes EMG étaient placées sur la partie distale des muscles droit fémoral (*rectus femoris*, RF), vaste latéral (*vastus lateralis*, VL) et biceps fémoral.

3.3. Neurostimulation percutanée

Un stimulateur électrique (DS7A, Digitimer, Welwyn Garden City, Hertfordshire, UK) permettait de délivrer des impulsions électriques rectangulaires (400 V max, durée d'impulsion : 500 μ s (études #1 et #2) et 1 ms (études #3 et #4)) sur le nerf à travers la peau. Dans les études #1 et #2, le nerf fibulaire commun était stimulé via une électrode de stimulation bipolaire (Bipolar Felt Pad Stimulating Electrode Part Number E.SB020/4mm, Digitimer) placée à hauteur de la tête de la fibula (**figure 5, panel A**). Dans les études #3 et #4, la cathode (diamètre : 30 mm, Meditrace 100) était placée sous le creux inguinal, au-dessus du nerf fémoral, et l'anode (30 \times 90 mm, Durastick Plus; DJO Global, Vista, CA) était positionnée sur la partie latérale du sillon sous-fessier (**figure 5, panel B**). La position optimale de stimulation était identifiée et marquée comme la zone produisant la plus grande réponse mécanique, i.e. force, et EMG, i.e. onde M, en réponse à des stimulations électriques d'intensité sous-maximale.

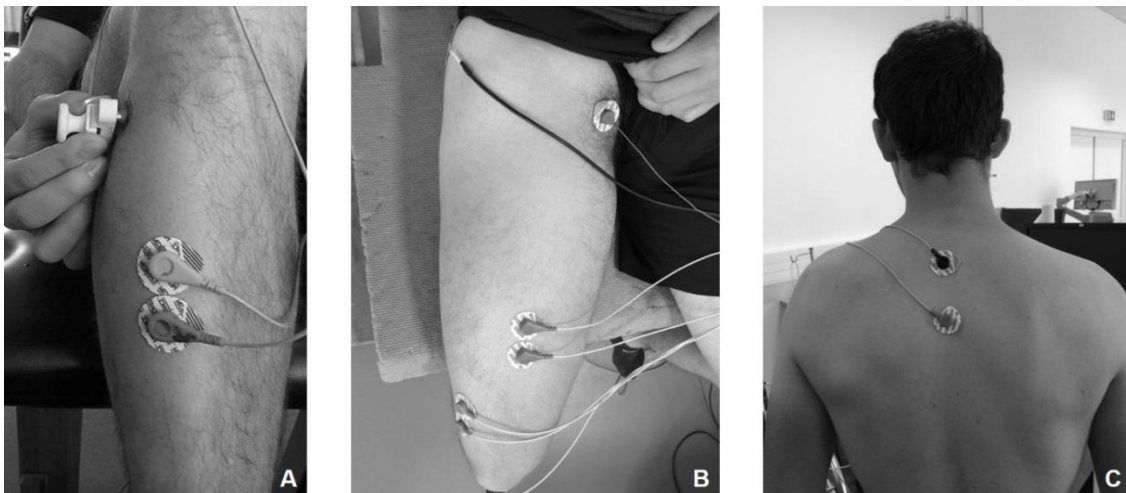


Figure 5. Positionnement des électrodes de stimulation. Dans les études #1 et #2, le nerf fibulaire commun était stimulé pour obtenir des signaux EMG sur le muscle tibial antérieur (panel A). Dans les études #3 et #4, le nerf fémoral était stimulé pour obtenir des signaux EMG sur les muscles vaste latéral et droit fémoral (panel B). Dans l'étude #3, le faisceau pyramidal était directement stimulé via des électrodes situées i) entre les processus épineux des vertèbres thoraciques T3 et T4 et ii) 5-10 cm au-dessus de cette première électrode (panel C, voir ci-après).

La technique de neurostimulation percutanée nous permettait d'évaluer principalement trois paramètres, i.e. l'onde M et le réflexe H (**figure 6**) ainsi que le niveau d'activation volontaire (*voluntary activation*, VA ; voir à la page 209 en annexe 2 de ce manuscrit).

Pour l'analyse de l'onde M, qui donne un indice sur le niveau d'excitabilité sarcolemmale et la propagation du potentiel d'action le long de cette structure (Racinais et al., 2013), l'intensité optimale de stimulation était obtenue en incrémentant l'intensité par palier de 5 mA jusqu'à ce que les réponses mécaniques et EMG associées atteignent un plateau. Pour s'assurer de la supra-maximalité de la stimulation électrique, l'intensité optimale préalablement déterminée était augmentée de 30% dans les études #3 et #4 (Bachasson et al., 2016) et de 50% dans les études #1 et #2 (Jubeau et al., 2014).

Le réflexe H représente un index sur l'efficacité de la transmission spinale entre les afférences Ia et les neurones moteurs (Palmieri et al., 2004), pouvant être influencé par divers paramètres physiologiques, e.g. inhibition pré-synaptique au niveau des afférences Ia (Zehr, 2002), interneurons inhibiteurs Ib, inhibition récurrente des cellules de Renshaw (Pierrot-Deseilligny & Mazevet, 2000). L'intensité de stimulation pour l'analyse du réflexe H était choisie comme l'intensité permettant d'évoquer des ondes M égales à 20% de l'amplitude maximale enregistrée au préalable. Cela permettait de s'assurer que la mesure du réflexe était réalisée dans les mêmes conditions de stimulation (Aagaard et al., 2002b). Pour l'étude aiguë (étude #2), l'intensité choisie en pré-intervention était la même en post-intervention. Pour l'étude chronique (étude #3), l'intensité était déterminée avant chaque session de test.

3.4. Stimulation électrique thoracique

La stimulation directe du faisceau pyramidal permet de s'affranchir des phénomènes d'inhibition pré-synaptique qui influencent le réflexe H et donc de donner une meilleure estimation du niveau d'excitabilité motoneuronale (Nielsen & Petersen, 1994; Giesebrecht et al., 2010). La stimulation du faisceau pyramidal est possible en utilisant un stimulus magnétique ou électrique. Parce qu'il n'est pas possible de placer de façon optimale la bobine de stimulation magnétique au niveau de la colonne thoracique quand le sujet est assis sur l'ergomètre (cf. **figure 4**), et parce que les signaux sont généralement plus élevés lors d'une stimulation électrique (Taylor & Gandevia, 2004),

le faisceau pyramidal était stimulé électriquement. Ainsi, il est possible d'activer directement la voie cortico-spinale en stimulant au niveau i) de la décussation pyramidale (jonction cervico-médullaire) pour obtenir un potentiel évoqué moteur cervico-médullaire (CMEP ; Taylor & Gandevia, (2004)) ou ii) de la colonne thoracique pour obtenir un potentiel évoqué moteur thoracique (*thoracic motor evoked potential*, TMEP) (**figure 6**). Dans la mesure où l'activation des membres inférieurs est plus importante en réponse à une stimulation au niveau thoracique (Taylor & Gandevia, 2004), c'est cette dernière technique qui a été utilisée dans le cadre de ce travail de thèse. Des électrodes de stimulation (Meditrace 100) étaient situées i) entre les processus épineux des vertèbres thoraciques T3 et T4 (cathode) et ii) 5-10 cm au-dessus de cette première électrode (anode) (**figure 5, panel C**). Parce que l'excitabilité motoneuronale est plus élevée sur un muscle contracté que sur un muscle relâché, permettant ainsi d'enregistrer de plus larges TMEPs (Taylor, 2006; Martin et al., 2008), l'intensité optimale de stimulation était déterminée durant des contractions volontaires isométriques sous-maximales correspondant à 50% de MVC. L'intensité des stimulations électriques (400 V max, durée : 1 ms) était incrémentée par palier de 5 mA afin de produire un TMEP égal à environ 20-30% de l'onde M enregistrée au préalable pour un même niveau de force (Aboodarda et al., 2015). Pour valider l'intensité optimale de stimulation, il fallait qu'un minimum de 3 essais sur 5 atteignent cette valeur cible de pourcentage d'onde M (Aboodarda et al., 2015), chaque essai étant séparé d'une période de récupération de 10 s pour minimiser l'apparition de fatigue.

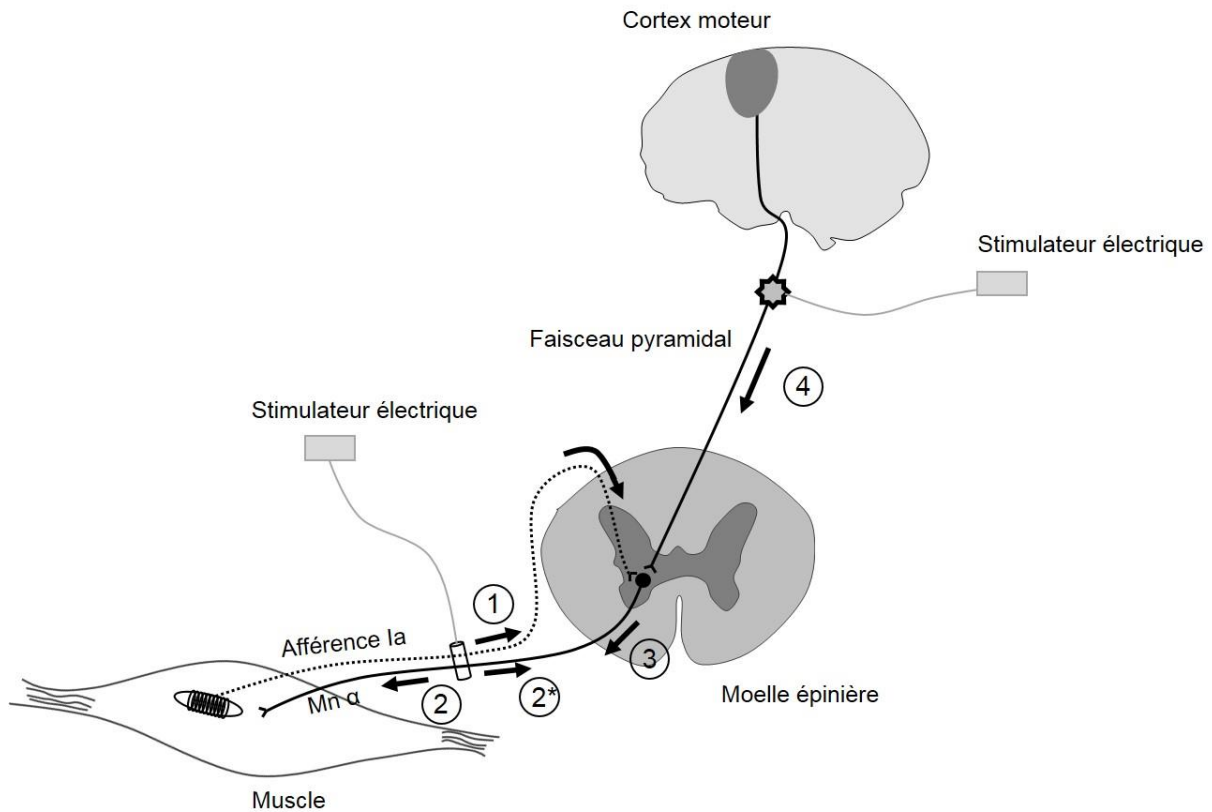


Figure 6. Méthodologie nécessaire à l'obtention de l'onde M, du réflexe H et des potentiels évoqués moteurs thoraciques (TMEPs). Pour l'enregistrement du réflexe H, une stimulation nerveuse électrique de faible intensité entraîne une décharge des afférences Ia (1). Les potentiels d'action (PA) se propagent jusqu'aux motoneurones alpha ($Mn \alpha$) avant d'être transmis au muscle (3), permettant d'enregistrer le réflexe H. Si l'intensité de la stimulation est augmentée, les $Mn \alpha$ sont directement excités et les PA se dirigeront à la fois vers le muscle, i.e. réponse orthodromique qui donne lieu à l'onde M (2), et la moelle épinière, i.e. réponse antidromique qui entre en collision avec les PA du réflexe H causant sa diminution et pouvant aller jusqu'à sa suppression (2*).

Pour l'enregistrement des TMEPs, une stimulation nerveuse électrique de haute intensité est délivrée au niveau thoracique (⚡), créant un PA qui se propage le long du faisceau pyramidal (4) pour atteindre le $Mn \alpha$ et induire un nouveau PA qui sera conduit en direction du muscle (3). Figure adaptée de Aagaard et al., (2002b).

3.5. Stimulation magnétique transcrânienne

La technique de TMS est une technique de stimulation non invasive du cortex cérébral développée dans les années 80 (Barker et al., 1985). Le courant magnétique délivré par la bobine de stimulation située en contact avec le cuir chevelu induit un courant électrique de faible intensité qui dépolarise les axones des interneurones qui font synapse avec les neurones pyramidaux (cortico-spinaux) du cortex moteur primaire lorsque la bobine est positionnée au regard de ce dernier. Pour des stimulations à plus haute intensité, les axones des neurones cortico-spinaux peuvent également être

directement dépolarisés (Di Lazzaro et al., 2004; Rossini et al., 2015). Une fois générés, les potentiels d'actions (PA) traversent le tronc cérébral pour venir exciter les Mn α du muscle controlatéral à la région cérébrale stimulée (Rossini et al., 2015). Des PAs sont alors générés au niveau des Mn α et un PA musculaire est généré au niveau de la jonction neuromusculaire. L'activation musculaire qui en résulte permet alors d'enregistrer sur le signal EMG un potentiel évoqué moteur (*motor evoked potential*, MEP) pour peu que la stimulation soit d'intensité suffisante. Le MEP fournit alors des informations sur l'excitabilité des neurones corticaux et/ou du pool motoneuronal des muscles stimulés (voir Rossini et al., (2015) pour une revue détaillée). Le MEP est généralement suivi d'une période de silence sur le signal EMG (*silent period*, SP) (**figure 7**). Si les mécanismes physiologiques exacts de la SP font toujours débat, il est acquis que sa phase initiale (~0-50 ms) est due à une diminution de l'excitabilité spinale tandis que la phase finale, i.e. à partir de ~50-100 ms selon les auteurs (Inghilleri et al., 1993; Chen et al., 1999; Rossini et al., 2015), est liée à des mécanismes d'inhibition intra-corticaux (Chen et al., 1999), principalement médiés par la neurotransmission GABAergique (Werhahn et al., 1999; Terao et al., 2000).

La capacité de la TMS à stimuler les neurones pyramidaux permet donc d'investiguer l'excitabilité des circuits intra-corticaux et cortico-spinaux, grâce à l'enregistrement de divers paramètres de MEPs et SPs.

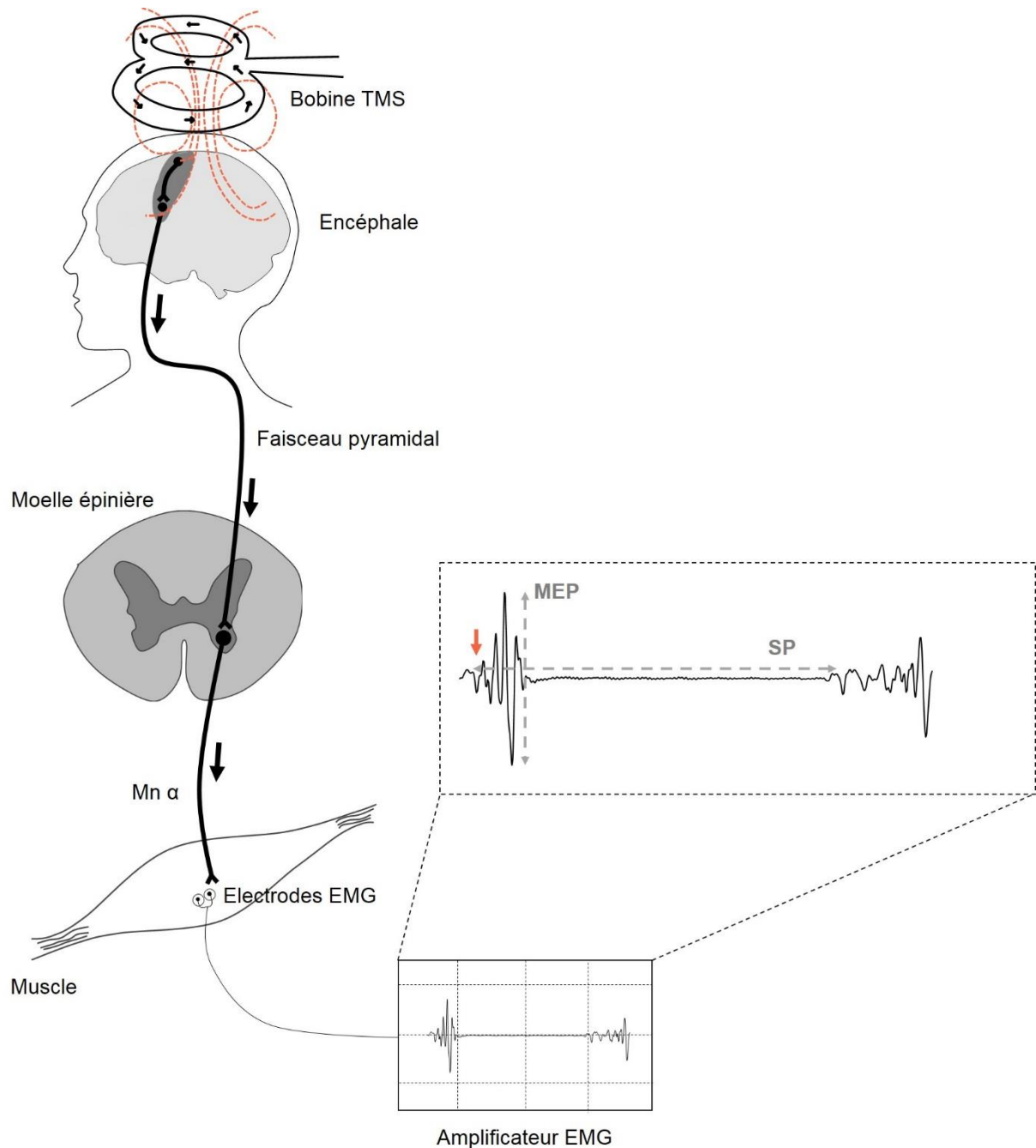


Figure 7. Stimulation magnétique transcrânienne. Une bobine est directement appliquée au niveau du cortex moteur (zone foncée à l'intérieur de l'encéphale) permettant d'induire un courant magnétique (traits pointillés orange) qui dépolairise directement ou indirectement (via des interneurons) les neurones du cortex moteur primaire. La volée excitatrice induite par la stimulation va se propager le long du faisceau pyramidal pour dépolairiser les motoneurons α (Mn α) au niveau spinal et ainsi créer un PA qui se propagera vers le muscle ciblé. En plaçant des électrodes électromyographiques (EMG) sur le muscle, il est possible d'enregistrer un potentiel évoqué moteur (MEP) et une période de silence (SP) pour renseigner respectivement sur l'excitabilité des circuits cortico-spinaux et intra-corticaux. L'amplitude ou l'aire du MEP peuvent être analysées (cf. **figure 10**), et la SP est caractérisée comme la durée entre l'instant du stimulus magnétique (flèche orange) et la reprise d'une activité EMG continue.

Pour l'ensemble des études nécessitant l'utilisation de la TMS, un stimulateur magnétique (Magstim 2002, The Magstim Company Ltd, Whitland, UK) permettait de délivrer des stimulations (durée : 1 ms) au niveau du cortex moteur controlatéral à la jambe testée via une bobine à double cône de 110 mm de diamètre. La bobine était manuellement contrôlée par le même expérimentateur tout au long des expérimentations. La position optimale de la bobine de stimulation était déterminée à partir de différentes positions marquées sur un bonnet positionné sur la tête du sujet. Pour chaque position, des mesures de forces (ou secousses) surimposées (*superimposed twitch*, SIT) à la contraction volontaire, i.e. 10% de la contraction maximale volontaire (*maximal voluntary contraction*, MVC) enregistrée au préalable, et les MEPs étaient enregistrées à la suite d'une stimulation magnétique sous-maximale, i.e. 50% de l'intensité maximale du stimulateur (**figure 8**).

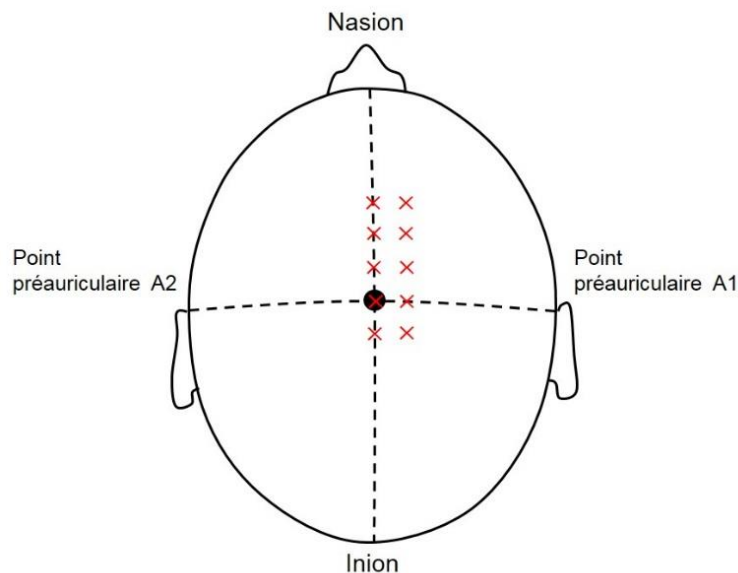


Figure 8. Détermination de la position optimale pour la bobine de stimulation (schéma représentatif pour l'étude du membre inférieur gauche). Après avoir identifié le vertex, i.e. point de croisement entre l'axe nasion-inion et l'axe A1-A2 (rond noir sur la figure), les sites de stimulation (croix rouge sur la figure) étaient marqués sur le bonnet i) tous les centimètres à partir de 1 cm antérieur jusqu'à 3 cm postérieur au vertex (études #1 et #2) ou ii) à partir du vertex jusqu'à 2 cm postérieur à ce dernier (études #3 et #4). Une stimulation à une intensité de 50% de l'intensité maximale du stimulateur était délivrée pour chacune de ces positions, et l'amplitude de la secousse surimposée et du potentiel évoqué moteur était enregistrée pour le muscle agoniste. La position optimale de stimulation était alors choisie comme celle permettant d'obtenir les plus hauts signaux. La réponse EMG du muscle antagoniste était également prise en compte dans la détermination de la position optimale de la bobine TMS, afin de s'assurer d'un faible niveau de co-activation.

L'intensité optimale de stimulation était déterminée via une courbe de recrutement mettant en relation l'intensité de la stimulation magnétique avec l'amplitude de la SIT et de la valeur absolue du MEP enregistré sur le(s) muscle(s) agoniste(s) et antagoniste (Temesi et al., 2014) lors d'une contraction à 20% de MVC. Sept intensités de stimulation étaient testées, i.e. de 20 à 80% de l'intensité maximale du stimulateur. Pour chaque intensité, quatre contractions étaient réalisées, soit 28 stimulations au total. Si la SIT et le MEP n'atteignaient pas un plateau en utilisant ces intensités, ces dernières étaient augmentées à 90% et si besoin 100% de l'intensité maximale du stimulateur. L'intensité optimale de stimulation était alors choisie lorsque la SIT et le MEP du muscle agoniste atteignaient un plateau (**figure 9**). Le MEP du muscle antagoniste était également contrôlé pour s'assurer d'un faible niveau de co-activation, phénomène pouvant potentiellement influencer les paramètres enregistrés (Temesi et al., 2014; Todd et al., 2016). Si des amplitudes égales de MEPs et de SITs étaient observées pour deux intensités de stimulation différentes, l'intensité optimale était choisie en considérant les MEPs les plus faibles enregistrés sur le muscle antagoniste (**figure 9**).

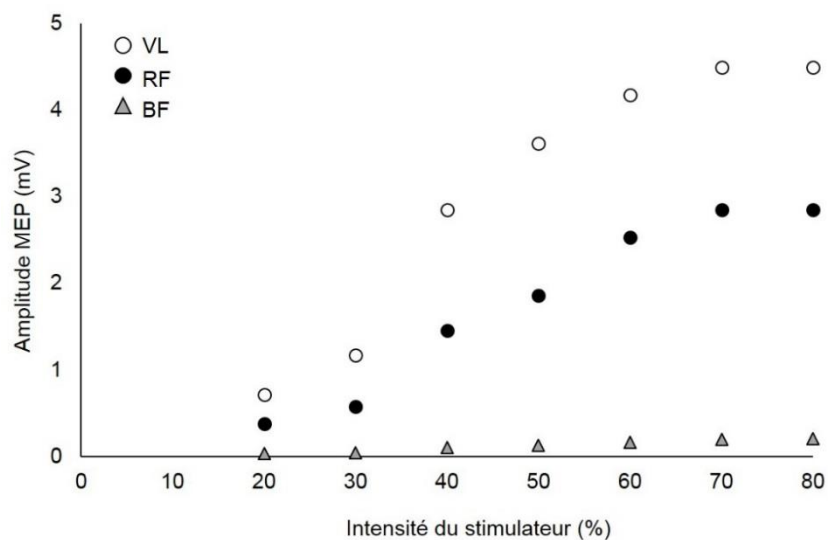


Figure 9. Détermination de l'intensité optimale de stimulation magnétique via une courbe de recrutement (schéma représentatif de l'étude #3 pour le muscle vaste latéral (VL), droit fémoral (RF) et biceps fémoral (BF)). L'intensité optimale de stimulation était choisie quand les potentiels évoqués moteurs (MEP) des muscles agonistes (VL et RF) atteignaient un plateau et quand ceux du muscle antagoniste (BF) étaient faibles (pour ce sujet, l'intensité retenue était de 70% de l'intensité maximale du stimulateur). Une courbe de recrutement identique mettait en relation l'intensité du stimulateur avec l'amplitude de la secousse surimposée.

4. Traitement des données

L'ensemble des données a été analysé à partir de la version 7 (études #1, #2, et #5) ou 8 (études #3 et #4) du logiciel Labchart (ADInstruments, Bella Vista, Australia).

4.1. Mesures de force

La MVC des muscles fléchisseurs dorsaux de la cheville et extenseurs du genou était calculée comme la valeur maximale enregistrée avant stimulation lors des différentes MVCs réalisées.

L'intensité de l'activité électrique musculaire enregistrée par EMG lors des MVCs a été calculée à partir de la valeur Root Mean Square (RMS) enregistrée sur une période de 500 ms après que la force a atteint un plateau. Pour s'affranchir de variations physiologiques musculaires (e.g. orientation des fibres musculaires, volume musculaire, distance à la plaque motrice, excitabilité sarcolemmale) et de phénomènes de variabilité inter-individuelle (e.g. placement des électrodes), le signal RMS était normalisé par l'amplitude maximale de l'onde M.

4.2. Neurostimulation percutanée

L'amplitude de la secousse musculaire électriquement évoquée sur le muscle relâché était évaluée dans l'étude #3 comme la moyenne des 2 secousses enregistrées. Un changement d'amplitude est généralement principalement associé à des modifications intervenant au niveau du couplage excitation-contraction (i.e. ensemble des mécanismes impliqués depuis la transmission neuromusculaire jusqu'à la production de force au niveau articulaire) (Cheng & Rice, 2005; Fitts, 2008).

L'amplitude et les aires des signaux EMGs évoqués par neurostimulation percutanée, i.e. onde M, réflexe H et TMEP, ont été enregistrées sur le muscle relâché ou contracté en condition isométrique maximale et sous-maximale (**figure 10**).

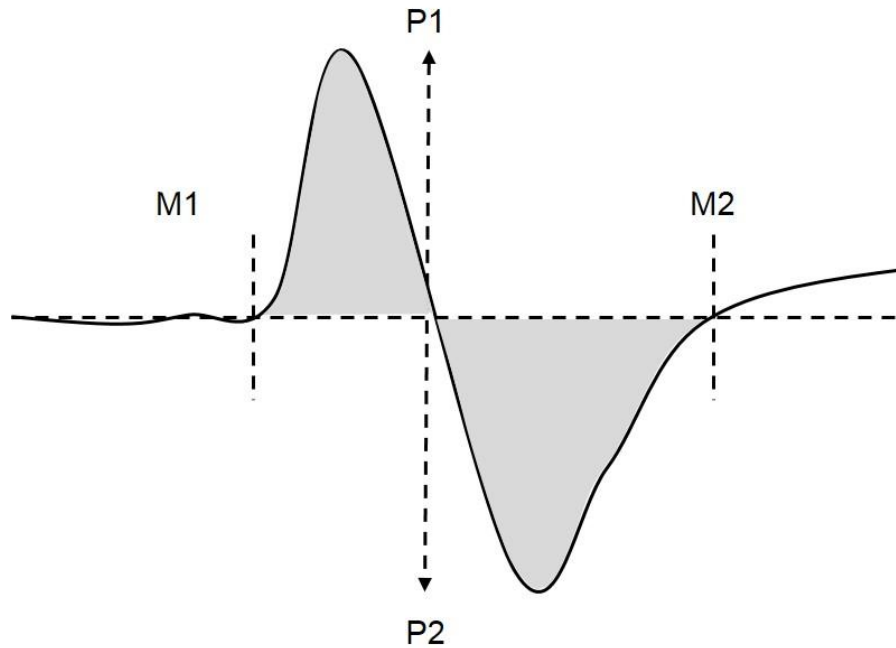


Figure 10. Détermination de l'amplitude et de l'aire des signaux EMG évoqués par neurostimulation percutanée (exemple représentatif pour une onde M obtenue sur le muscle relâché). L'amplitude du potentiel évoqué était calculée entre le pic 1 (P1) et le pic 2 (P2), et l'aire (partie grisée) était calculée entre le marqueur 1 (M1), i.e. la déflexion initiale du signal de la ligne de base, et le marqueur 2 (M2), i.e. le moment du second croisement horizontal. La même méthode d'analyse était utilisée pour l'évaluation du réflexe H et du TMEP.

4.3. Stimulation magnétique transcrânienne

4.3.1. Niveau d'activation cortical

Le niveau d'activation volontaire cortical mesuré par TMS (VA_{TMS}) était calculé en utilisant la technique de secousse surimposée modifiée proposée par Todd et al., (2003). Cette technique consiste à appliquer un stimulus magnétique au niveau du cortex moteur pendant le maintien d'une contraction maximale volontaire. Dans la mesure où l'excitabilité cortico-spinale augmente substantiellement avec l'activité musculaire (Ugawa et al., 1995), il n'est pas possible d'utiliser une secousse évoquée sur le muscle relâché. L'amplitude de la secousse évoquée sur le muscle relâché, nécessaire au calcul du VA_{TMS} (voir ci-dessous), était donc estimée par extrapolation de la relation linéaire entre i) l'amplitude de la SIT quand la TMS était délivrée à des niveaux de force maximaux et sous-maximaux, i.e. 75 et 50% de MVC, et ii) la force volontaire (**figure 11**).

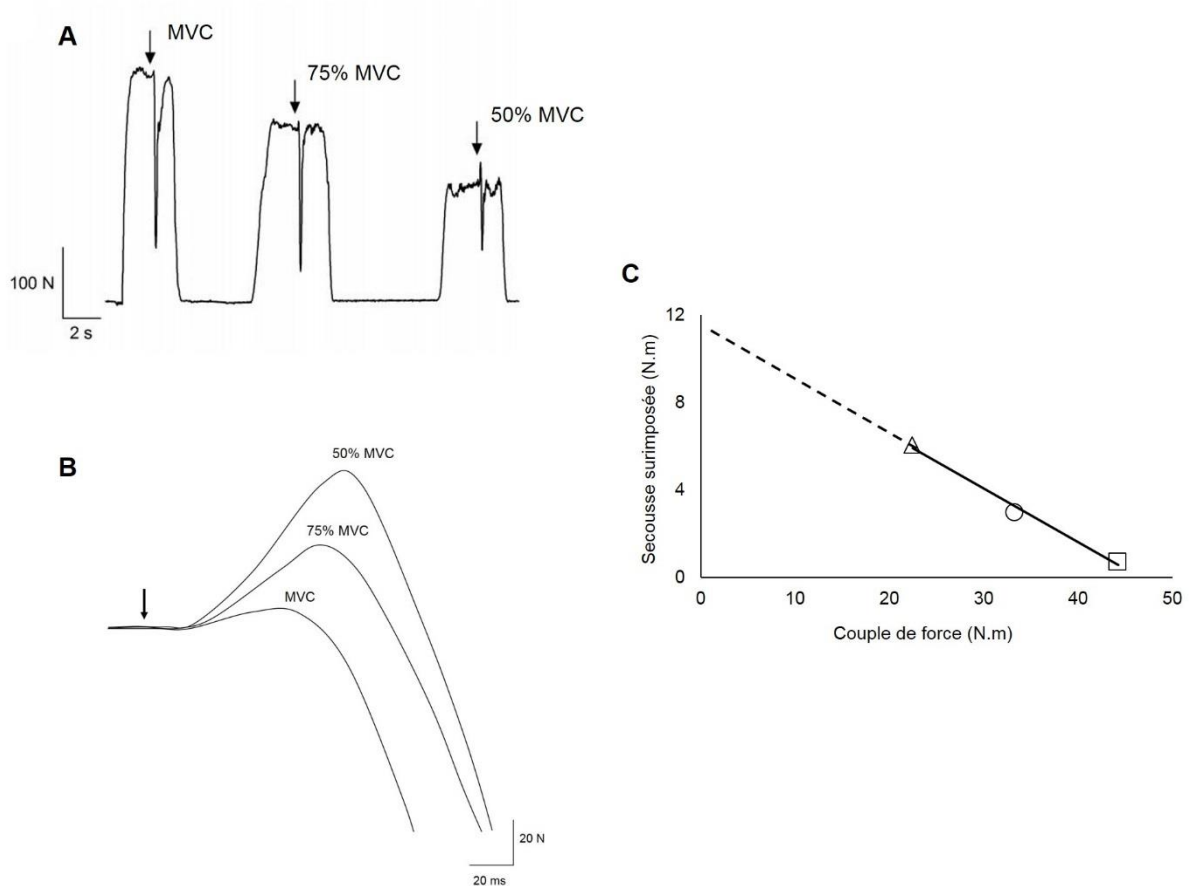


Figure 11. Méthodologie nécessaire à l'évaluation du niveau d'activation cortical. Il était demandé au sujet de réaliser une contraction maximale volontaire (MVC) et deux contractions sous-maximales volontaires à 75 (75% MVC) et 50% (50% MVC) de la MVC préalablement enregistrée (panel A, adapté de Goodall et al., (2014)). Une stimulation magnétique transcrânienne était délivrée durant le maintien de la contraction et l'amplitude de la secousse surimposée (SIT) à chaque niveau de contraction était par la suite calculée (panel B), et permettait d'estimer l'amplitude de la secousse musculaire sur le muscle relâché par extrapolation de la relation linéaire entre i) l'amplitude de la SIT quand la TMS était délivrée à des niveaux de force maximaux (carré) et sous-maximaux à 75 (rond) et 50% (triangle) de MVC, et ii) la force volontaire (panel C).

Le niveau d'activation cortical était alors évalué selon l'équation suivante :

$$VA_{TMS} = [1 - (SIT/ERT)] \times 100$$

SIT étant l'amplitude de la secousse surimposée enregistrée pendant la contraction maximale volontaire, et ERT l'estimation de l'amplitude de la secousse évoquée sur le muscle relâché.

Deux (études #3 et #4) ou trois (études #1 et #2) séries étaient réalisées, et la valeur maximale de VA_{TMS} était gardée pour les futures analyses.

4.3.2. Potentiel évoqué moteur et période de silence

L'amplitude et les aires des MEPs évoqués à différents niveaux de contractions étaient calculées (voir **figure 10**). Afin de s'affranchir d'éventuelles modifications pouvant intervenir au niveau périphérique, le MEP était normalisé à l'onde M.

La durée de la SP (en ms) était calculée entre le moment où le stimulus magnétique était délivré jusqu'au retour d'une activité EMG continue (**voir figure 7**).

4.3.3. Modélisation de Boltzmann

La modélisation de Boltzmann, réalisée sur la courbe de recrutement décrite précédemment (**figure 9**), permet de fournir des informations additionnelles sur le niveau d'excitabilité cortico-spinale (Capaday, 1997; Devanne et al., 1997). Cette modélisation se traduit par l'équation suivante :

$$A_{MEP} = \frac{P}{1 + \exp\left[\frac{150-I}{k}\right]}$$

Elle permet de déterminer la relation entre l'amplitude du MEP (A_{MEP}) et l'intensité de la TMS (I , en pourcentage de l'intensité maximale du stimulateur). Trois paramètres peuvent alors être extraits : i) le MEP maximal défini par la fonction (P , en % de l'onde M maximale), ii) l'intensité de stimulation qui permet d'évoquer un MEP égal à 50% du MEP maximal (I_{50} , en pourcentage de l'intensité maximale du stimulateur) et iii) la pente de la relation (k) (**figure 12**).

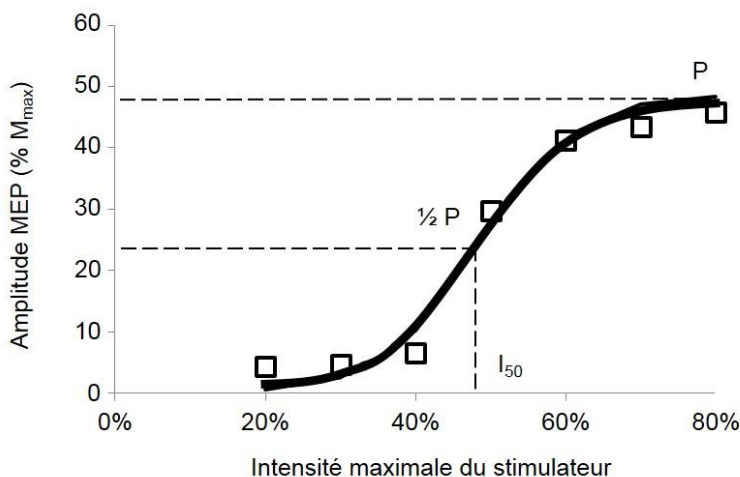


Figure 12. Modélisation de Boltzmann. La modélisation mathématique de Boltzmann (ligne noire continue) est appliquée sur la courbe de recrutement qui met en relation l'amplitude du MEP normalisée à l'onde M avec l'intensité de stimulation (exprimée en pourcentage de l'intensité maximale du stimulateur). Les lignes pointillées indiquent I_{50} , i.e. l'intensité qui permettrait d'obtenir un MEP égal à 50% du MEP maximal ($\frac{1}{2} P$), et P , i.e. le MEP maximal défini par la fonction.

4.4. Tests fonctionnels

La hauteur de saut vertical lors d'un exercice de squat jump (SJ) et de contre-mouvement jump (CMJ) était mesurée lors de l'étude #4. Deux SJs et deux CMJs étaient réalisés sur un tapis de saut (68,5 × 68,5 cm, Probotics Inc., Huntsville, AL). Pour le SJ, il était demandé au sujet de partir d'une position semi-fléchie (flexion de genou à environ 90°) qui était maintenue environ 2 secondes. Par la suite, les sujets devaient sauter verticalement le plus haut possible sans réaliser de contre-mouvement. Pour les CMJs, les sujets partaient d'une position debout et devaient réaliser un contre-mouvement (jusqu'à environ 90° de flexion de genou) avant l'exécution de la détente verticale maximale. Pour les deux modalités de saut, les sujets avaient comme consigne de garder les mains sur les hanches afin de s'affranchir d'une éventuelle aide des bras qui aurait pu influencer les résultats, et d'atterrir avec les pointes de pieds tendues. La performance maximale était identifiée comme le plus haut saut réalisé lors des deux essais.

ETUDES REALISEES PENDANT LA THESE

ETUDE #1

CHANGEMENT DES PROPRIETES CORTICO-SPINALES DU MUSCLE TIBIAL ANTERIEUR APRES UNE EXPOSITION AIGUE ET PROLONGEE A LA VIBRATION MUSCULAIRE

Publication associée :

Farabet A., **Souron R.**, Millet GY., Lapole T. (2016)

*CHANGES IN TIBIALIS ANTERIOR CORTICOSPINAL PROPERTIES AFTER
ACUTE PROLONGED MUSCLE VIBRATION*

European Journal of Applied Physiology, 116(6):1197-205. doi: 10.1007/s00421-016-3378-y.

RESUME :

Objectif : La vibration locale appliquée de manière prolongée peut détériorer la performance musculaire, e.g. la force maximale. Alors qu'il a été montré que des modulations spinales permettent d'expliquer cette diminution de force, l'hypothèse de modulations d'origine supra-spinale a également été avancée. Le but de cette étude visait à évaluer les effets d'une application prolongée de la vibration locale sur les capacités de production de force des muscles fléchisseurs dorsaux de la cheville et d'identifier d'éventuelles modulations spinales et/ou supra-spinales. **Méthodes :** Treize sujets ont été testés i) avant et après une exposition prolongée de 30 min à la vibration locale et ii) avant et après une période de repos de 30 min. La force maximale volontaire isométrique (MVC) en flexion dorsale était mesurée. La stimulation magnétique transcrânienne était surimposée pendant les MVCs afin d'évaluer le niveau d'activation volontaire cortical (VA_{TMS}). Les potentiels évoqués moteurs (MEPs) et les périodes de silence (SPs) étaient également analysés. Enfin, l'excitabilité spinale était évaluée via le réflexe de Hoffman (réflexe H). **Résultats :** La vibration locale appliquée de manière prolongée n'impactait pas de manière significative la MVC ($p = 0,80$), le VA_{TMS} ($p = 1$) et les SPs ($p = 0,87$). Une tendance à la diminution des MEPs était observée ($p = 0,11$), et le réflexe H était significativement diminué après les 30 minutes de vibration ($p = 0,008$). **Conclusion :** Malgré une altération de l'excitabilité spinale, i.e. réflexe H, et une tendance à l'altération de l'excitabilité cortico-spinale, i.e. MEP, la force maximale volontaire en dorsiflexion plantaire n'était pas affectée par la vibration locale prolongée. Ces résultats confirment les effets de la vibration locale sur le système nerveux central (spinal), sans pour autant altérer la capacité de production de force maximale.

Changes in tibialis anterior corticospinal properties after acute prolonged muscle vibration

Adrien Farabet¹ · Robin Souron¹ · Guillaume Y. Millet² · Thomas Lapole¹

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Abstract

Purpose Prolonged local vibration is known to impair muscle performance. While involved mechanisms were previously evidenced at the spinal level, changes at the cortical level were also hypothesized. The aims of the present study were to investigate the effects of 30 min of 100-Hz tibialis anterior muscle vibration on force production capacities and to further identify the respective changes in spinal loop properties, descending voluntary drive and corticospinal properties.

Methods Thirteen subjects were tested before and after a vibration condition, and before and after a resting control condition. Maximal voluntary contraction (MVC) in dorsiflexion was measured. Transcranial magnetic stimulation was superimposed during MVCs to assess cortical voluntary activation (VA_{TMS}), motor-evoked potential amplitude (MEP) and cortical silent period length (CSP). MEP and CSP were also measured during 50 and 75 % MVC contractions. Spinal excitability was investigated by mean of H-reflex.

Results There were no vibration effects on MVC ($p = 0.805$), maximal EMG activity ($p = 0.653$), VA_{TMS} ($p = 1$), and CSP ($p = 0.877$). Vibration tended to decrease MEP amplitude ($p = 0.117$). H-reflex amplitude was depressed following vibration ($p = 0.008$).

Conclusions Dorsiflexion maximal force production capacities were unaffected by 30 min of tibialis anterior muscle vibration, despite spinal loop and corticospinal excitabilities being reduced. These findings suggest that acute prolonged vibration has the potential to modulate corticospinal excitability of lower limb muscles without a concomitant functional consequence.

Keywords Vibration · Transcranial magnetic stimulation · Cortical voluntary activation · H-reflex

Abbreviations

CSP	Cortical silent period
CSP ₅₀	CSP recorded during 50 % MVC contraction
CSP _{MVC}	CSP recorded during MVC
ERT	Estimated resting twitch
MEP	Motor-evoked potential
MEP ₅₀	MEP recorded during 50 % MVC contraction
MEP _{MVC}	MEP recorded during MVC
M_{max}	Peak to peak amplitude of the maximal M-wave
MVC	Maximal voluntary contraction
RMS	Root mean square of electromyography
rMT	Resting motor threshold
SIT	Superimposed twitch
SIT _{MVC}	Superimposed twitch during MVC
TA	Tibialis anterior muscle
TMS	Transcranial magnetic stimulation
VA_{TMS}	Cortical voluntary activation

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✉ Thomas Lapole
thomas.lapole@univ-st-etienne.fr

¹ Univ Lyon, UJM-Saint-Etienne, Laboratoire Interuniversitaire de Biologie de la Motricité, EA 7424, F-42023 SAINT-ETIENNE, France

² Human Performance Laboratory, Faculty of Kinesiology, University of Calgary, Calgary, Canada

Introduction

Prolonged local vibration (i.e. applied directly to a muscle or a tendon) is known to induce a short-term decrease in force-generation capacity of the corresponding muscle.

This has been reported following 20–30 min of local vibration of knee extensors (Jackson and Turner 2003; Konishi et al. 2009; Kouzaki et al. 2000), plantar flexors (Herda et al. 2009; Ushiyama et al. 2005) or first dorsal interosseus muscle (Shinohara et al. 2005). Reduced motor performance was suggested to be due to impaired ability of the central nervous system to activate motoneurons.

Changes in the motor drive may come from spinal and/or supraspinal factors (Gandevia 2001; McNeil et al. 2011). At the spinal level, the main mechanism involved in the vibration-induced central drive impairment is thought to be a decreased alpha motoneurons activity through attenuation of Ia afferent efficacy (Bongiovanni et al. 1990), Ia fibers being largely solicited by vibrations (Eklund and Hagbarth 1966). Indeed, most studies that reported a vibration-induced force decrement suggested an altered spinal loop excitability as the main hypothesis (Jackson and Turner 2003; Kouzaki et al. 2000; Konishi et al. 2009; Ushiyama et al. 2005; Herda et al. 2009). Spinal loop excitability is commonly assessed through the Hoffmann reflex (H-reflex) (McNeil et al. 2013; Zehr 2002). Its amplitude is known to depend directly on the motoneuron excitability (Schieppati 1987), but also on the level of presynaptic inhibition exerted on Ia afferents (Misiąszek 2003). Accordingly, soleus H-reflex amplitude was reported to decrease following 30 (Ekblom and Thorstensson 2011; Ushiyama et al. 2005) and 60 min (Lapole et al. 2012b) of Achilles tendon vibration. Similar results were recently reported for the vastus medialis muscle following 30 min of infrapatellar tendon vibration (Fry and Folland 2014). From these studies, only the study of Ushiyama et al. (2005) reported decreased H-reflex with concomitant motor performance impairment. Altered spinal excitability due to prolonged local vibration is not the only mechanism that could reduce motor voluntary drive following vibration: a decrease in motor cortex excitability was also suggested to be a potential mechanism (Jackson and Turner 2003; Ushiyama et al. 2005). Corticospinal excitability may be tested through the analysis of motor-evoked potentials (MEPs) recorded in response to stimulation applied over the motor cortex (Mills 1999). Steyvers et al. (2003) reported an attenuation of the motor cortex excitability of the flexor carpi radialis muscle during the first minutes after prolonged vibration. Such an attenuation of the corticospinal excitability may potentially be a factor in vibration-induced motor performance decrement (Ushiyama et al. 2005) but this remains to be tested.

TMS may also be used to evoke superimposed twitches during contractions, in a similar way as the classical interpolated twitch technique (Merton 1954). While the latter method cannot distinguish adaptations at the spinal and

cortical levels, TMS can be used to assess cortical voluntary activation level (VA_{TMS}), i.e. to highlight the presence of suboptimal drive from the motor cortex to the involved muscles during maximal voluntary contraction (MVC) (Goodall et al. 2014). Tibialis anterior muscle (TA) is known to have the strongest corticospinal projections among all leg muscles (Perez et al. 2004; Brouwer and Ashby 1992). Thus, to study the role of motor cortex in the vibration-induced MVC impairment in this muscle is of major interest. Moreover, when applied during a voluntary contraction, TMS may also inform about intracortical inhibition through the assessment of cortical silent period (CSP) (Terao and Ugawa 2002). CSP results from the activation of inhibitory cortical neurons projecting onto the pyramidal cells in the motor cortex (Inghilleri et al. 1993), and is thought to be mainly influenced by GABA (gamma aminobutyric acid) neurotransmission (Werhahn et al. 1999).

Therefore, the aim of the present study was to investigate the effects of prolonged vibration of the TA muscle on force production capacities, and to further identify the respective changes in spinal loop properties (i.e. H-reflex), descending voluntary drive (i.e. VA_{TMS}) and corticospinal properties (MEP and CSP). It was hypothesized that prolonged TA vibration would impair motor performance through reduced spinal loop excitability and decreased cortical voluntary activation.

Methods

Subjects

Thirteen young and healthy subjects (9 males; age: 23 ± 4 years; height: 177 ± 8 cm; body mass: 69 ± 10 kg) participated in this study. Written informed consent was obtained from all subjects prior to their participation and this study conformed to the standards from latest revision of the Declaration of Helsinki and was approved by the local ethics committee. All participants were free of lower-limb injury during the previous 3 months, contraindications to TMS, acute and chronic neurological disorders and trauma. They were instructed to abstain from caffeine for a minimum of 12 h before each session.

Design of the study

Subjects were tested twice in random condition (crossover design) on two separate days with a 1-week interval. Prior to the first testing session, subjects were familiarized to the whole experimental protocol. The subjects were then randomly divided into two groups: one group performed the

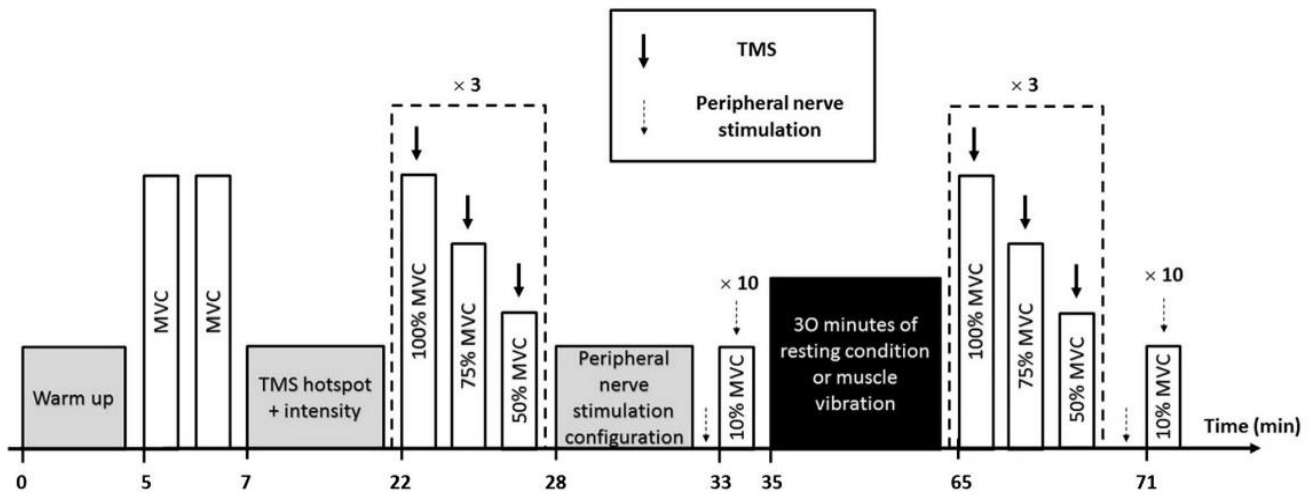


Fig. 1 Illustration of the experimental protocol



Fig. 2 Illustration of the vibratory device strapped on the tibialis anterior muscle belly

first test with the control condition and the other started with the vibration condition. This was inverted for the second session. Both sessions took place at the same time of the day, to avoid circadian variations. A testing session consisted in neuromuscular measurements performed before (PRE) and immediately after (POST) a 30-min resting period (control condition) or 30 min of muscle vibration (vibration condition) (Fig. 1). The application of vibration (1 mm amplitude and 100 Hz frequency) was performed with local vibrator (VB 115, Techno Concept, Mane, France) strapped on the tibialis anterior muscle belly (Fig. 2).

Torque and electromyographic recordings

Dorsiflexion torque was measured during voluntary contractions by a calibrated instrumented pedal (CS1060 300 Nm, FGP Sensors, Les Clayes Sous Bois, France). Subjects were seated upright in a custom-built chair with pelvis, knee and ankle angulations of 90, 120 and 90°, respectively. Electromyographic activity (EMG) of the right TA and soleus was recorded with pairs of self-adhesive surface electrodes (Meditrace 100, Covidien, Mansfield, USA) in bipolar configuration with a 30 mm interelectrode distance and the reference on the internal malleolus. Soleus electrodes were placed 2 cm below the insertion of the gastrocnemii on the Achilles tendon and TA electrodes were placed on the muscle belly according to SENIAM recommendations (Hermens et al. 2000). Low impedance (<5 k Ω) between electrodes was obtained by shaving, gently abrading the skin and then cleaning it with isopropyl alcohol. Signals were analogue-to-digitially converted at a sampling rate of 2000 Hz by PowerLab system (16/30—ML880/P, ADInstruments, Bella Vista, Australia) and octal bio-amplifier (ML138, ADInstruments; common mode rejection ratio = 85 dB, gain = 500) with bandpass filter (5–500 Hz) and analyzed offline using Labchart 7 software (ADInstruments).

Transcranial magnetic stimulation

Single TMS pulses of 1-ms duration were manually delivered to elicit MEPs and superimposed twitches (SITs) during voluntary isometric dorsiflexion. The motor cortex contralateral to the right TA 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). Subjects wore a cervical collar during all

TMS measures to stabilize the head and neck. The coil was positioned over the leg area of the motor cortex along the nasal-inion axis to induce a posteroanterior current. After a standardized warm-up, subjects performed two maximal dorsiflexion (MVCs) lasting approximately 3 s, with a 30-s resting period between trials. Optimal coil position was then determined as the site eliciting the largest SIT and TA MEP amplitude with minimal soleus MEP amplitude in response to stimulation at 50 % maximal stimulator output during brief voluntary dorsiflexion at 10 % MVC. This position was marked on a swim cap secured to the scalp. Before the delivery of each stimulus, the coil position was verified with regard to the marks on the swim cap. Stimulus intensity for VA_{TMS} measurement was determined at PRE from an input–output curve determined during brief voluntary dorsiflexion at 20 % MVC. The same intensity was used at POST. Input–output curve was drawn from the average of four consecutive contractions performed at 15-s intervals at each of the following randomly-ordered stimulus intensities: 20, 30, 40, 50, 60, 70 and 80 % of maximal stimulator output. Optimal stimulus intensity was then defined as the lowest stimulus intensity eliciting maximal TA MEP and SIT amplitude (i.e. 65.4 ± 7.8 and 65.4 ± 8.8 % of maximal stimulator output for control and vibration conditions, respectively). If a plateau was not confirmed from these intensities, higher TMS intensities were used (i.e., 90 and 100 % of maximal stimulator output). Such method has been recently reported to be appropriate for determining TMS intensity in the quadriceps (Temesi et al. 2014a). During voluntary contractions, TMS was delivered once the subject had stabilized the force on the target level. Subjects were instructed to re-contract as strong and as fast as possible immediately after TMS delivery to permit accurate measurement of the CSP.

Neuromuscular measurements

Corticospinal properties

VA_{TMS} during maximal effort was measured by a modified version of the interpolated twitch technique. Measurement consisted of three series of three contractions performed at 100, 75 and 50 % MVC with real-time visual feedback (Fig. 3) (3 to 5 s of contraction, 30 s between contractions and 1 min between sets). In each series, contraction at 100 % MVC was always performed first while 50 and 75 % MVC contractions were randomized. TMS was delivered at each target force to record the evoked SITs. 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, estimated resting twitch (ERT) was determined by a linear regression of the relation between SIT amplitude evoked when TMS was delivered at 100,

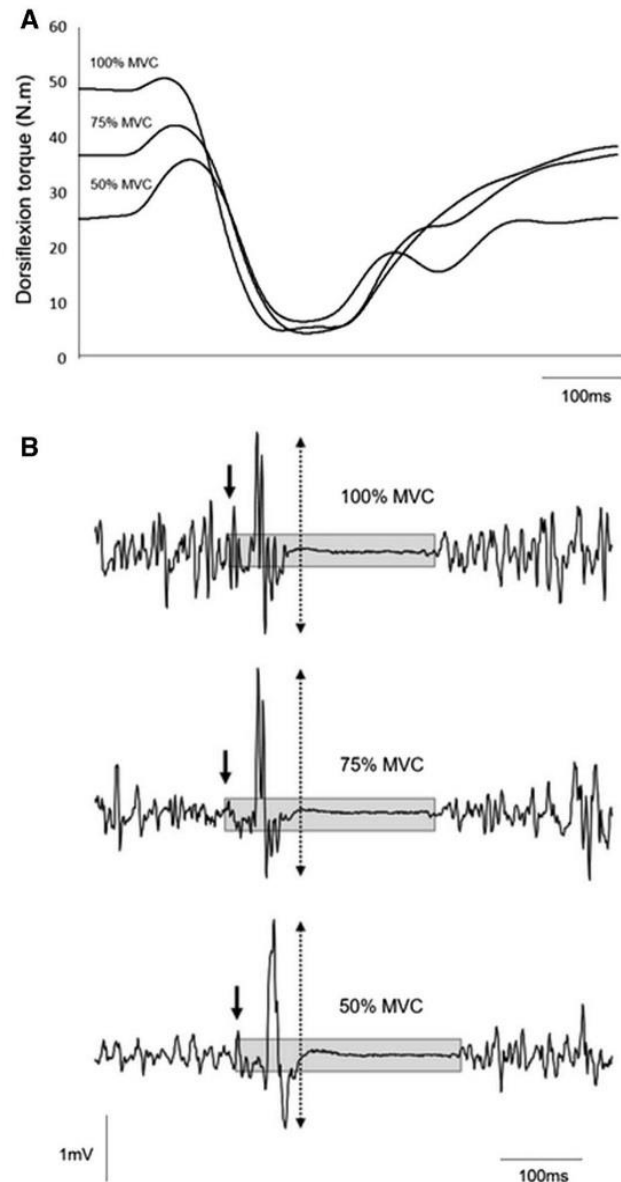


Fig. 3 Example of torque (a) and electromyographic (b) recordings in response to TMS for a representative subject at 100, 75 and 50 % MVC. Bold arrows indicate the time point of TMS. Dashed arrows and grey rectangles show how MEP amplitudes and CSP duration were calculated, respectively

75 and 50 % MVC and voluntary force (Todd et al. 2003). This relation was extrapolated and the y-intercept was interpreted as the ERT amplitude. VA_{TMS} during MVCs was calculated as follows:

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

where SIT_{MVC} is the superimposed twitch evoked during MVC. Mean R^2 of the linear regression was 0.93 ± 0.10 and 0.90 ± 0.10 before and after control condition, respectively; and 0.93 ± 0.08 and 0.97 ± 0.05 before and after

vibration, respectively. MVC was determined as the highest torque value achieved during maximal effort. TA EMG root mean square (RMS_{MVC}) was calculated as the mean over a 500-ms period after maximal force had reached a plateau. EMG-RMS was then normalized to the maximal peak-to-peak amplitude of the M-wave (M_{max} ; see below) obtained at each time point. MEPs and CSPs elicited by TMS during contractions were also calculated and averaged over the three sets. Peak-to-peak amplitude of MEPs were measured and normalized to M_{max} (MEP_{MVC} , MEP_{75} and MEP_{50} , respectively) obtained at each time point. The duration of the CSPs were determined visually and defined as the duration from the TMS stimulus to the return of continuous voluntary EMG (CSP_{MVC} , CSP_{75} and CSP_{50} , respectively) (Sidhu et al. 2009).

Spinal excitability

Single electrical stimuli of 0.5-ms duration were delivered to the right peroneal nerve via constant-current stimulator (DS7A, Digitimer, Welwyn Garden City, Hertfordshire, UK) and bipolar bar stimulating electrode with 30 mm anode–cathode spacing (Bipolar Felt Pad Stimulating Electrode Part number E.SB020/4 mm, Digitimer) placed next to the fibular head. The optimal site of stimulation was determined as the location eliciting the greatest TA M-wave for a given stimulus intensity. This site was marked with semi-permanent ink. Single electrical stimuli were delivered incrementally (5-mA step) at rest until maximal TA M-wave plateaued (M_{max}). The amplitude of the H-reflex was then recorded during low contraction intensity of 10 % MVC to ensure easily identifiable TA H-reflex with background EMG (Tallent et al. 2012). In H-reflex recordings, it is essential to ensure that effective stimulus intensity remains constant (Aagaard et al. 2002; Lapole et al. 2013). Thus, H-reflex measurements were performed

with a stimulation intensity producing concomitant TA M-waves equal to 15–20 % of M_{max} (Tallent et al. 2012). Once the appropriate target stimulus intensity was found, 10 H-reflexes were recorded, measured peak-to-peak, and expressed relative to M_{max} . Ten seconds intervals separated the stimulations. Only recordings that met the criteria of a concomitant M-wave 15–20 % of TA M_{max} were averaged (i.e., 8.2 ± 1.1 and 7.8 ± 0.9 recordings kept before and after control condition, respectively; 7.6 ± 1.4 and 8.1 ± 1 recordings before and after vibration, respectively).

Statistics

Statistical analyses were performed using Statistica software (StatSoft Inc., Tulsa, Oklahoma, USA). All variables were normally distributed (Kolmogorov–Smirnov normality test). For ANOVA analyses, homogeneity of variance was verified by Levene’s test. A two-way (condition \times time) repeated measures ANOVA was performed on M_{max} , MVC, RMS_{MVC}/M_{max} , SIT_{MVC} and VA_{TMS} . A three-way (conditions \times time \times force levels) repeated measures ANOVA was performed on MEP and CSP. When the ANOVA identified significant interaction effects (condition \times time), post hoc Student–Newman–Keuls testing was performed. Data are presented as mean \pm SD. Statistical significance was set at $p < 0.05$.

Results

P values from all ANOVA analyses are presented in Table 1. Vibration did not influence MVC or TA maximal EMG activity. Similarly, no interaction effect was reported for SIT_{MVC} , VA_{TMS} and CSP. Figure 4 presents the results for MEP amplitude during 50, 75 and 100 % MVC contractions. Although there was a significant condition \times time

Table 1 p values from all ANOVA analyses

	Condition	Time	Condition \times time	Force level	Condition \times force level	Time \times force level	Condition \times time \times force level
M_{max}	0.692	0.168	0.255				
H-reflex	0.133	0.237	0.006				
MVC	0.770	0.344	0.805				
RMS_{MVC}/M_{max}	0.950	0.894	0.653				
SIT_{MVC}	0.225	0.810	0.967				
VA_{TMS}	0.094	0.372	1.000				
MEP	0.005	0.041	0.040	0.017	0.721	0.417	0.891
CSP	0.427	0.122	0.877	0.905	0.916	0.187	0.897

M_{max} the amplitude of the maximal M-wave evoked in the relaxed muscle, *H-reflex* amplitude of the H-reflex expressed as a percentage of maximal M-wave amplitude, *MVC* Maximal voluntary contraction in dorsiflexion, RMS_{MVC}/M_{max} Tibialis anterior maximal EMG activity expressed as a percentage of maximal M-wave amplitude, SIT_{MVC} superimposed twitch during MVC, VA_{TMS} Cortical voluntary activation, *MEP* Motor-evoked potential, *CSP* Cortical silent period

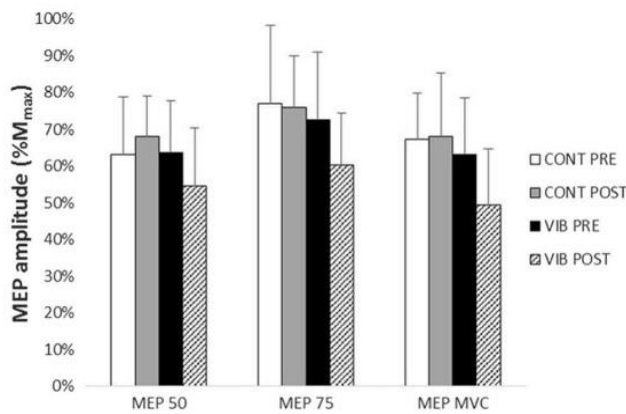


Fig. 4 MEP amplitude recorded during dorsiflexion at 50, 75 and 100 % MVC (MEP_{50} , MEP_{75} and MEP_{MVC} , respectively) for PRE/POST vibration and control conditions. MEP amplitude is expressed as a percentage of M_{max} , the amplitude of the maximal M-wave evoked in the relaxed muscle

interaction for MEP, Post-hoc testing only demonstrated a trend for decreased MEP amplitude after vibration ($p = 0.117$; -13.7 ± 20.3 , -14.8 ± 22.0 , and -19.7 ± 26.1 % for MEP_{50} , MEP_{75} and MEP_{MVC} , respectively). There was a significant condition \times time effect for H-reflex with decreased H-reflex amplitude following vibration (-21.0 ± 23.0 %; $p = 0.008$) while no changes were apparent in the control condition ($p = 0.387$) (Fig. 5). M_{max} remained stable over time and conditions (Table 2).

Discussion

This is the first study investigating the effects of vibration on maximal force production capacities and its effects at both the spinal and cortical levels. Although there was significant TA H-reflex and a trend toward MEP amplitude decrease after 30 min of 100-Hz vibration applied over the TA muscle, there were no effects on motor performance as indicated by unchanged MVC and VA_{TMS} .

The vibration exposure performed in the present study was effective in altering Ia afferent efficacy, as suggested by the 21 ± 23 % decrease in H-reflex amplitude. This is in agreement with the previously reported decreased soleus H-reflex amplitude following 30 (Ekblom and Thorstensson 2011; Ushiyama et al. 2005) and 60 min (Lapole et al. 2012b) of Achilles tendon vibration, as it is with decreased vastus medialis H-reflex following 30 min of infrapatellar tendon vibration (Fry and Folland 2014). H-reflex amplitude depends on both motoneuron excitability (Schieppati 1987) and the level of presynaptic inhibition exerted on Ia afferents (Misiąszek 2003). Since previous studies reported unchanged motoneuron excitability following prolonged vibration, as indicated by unchanged F-waves (Lapole

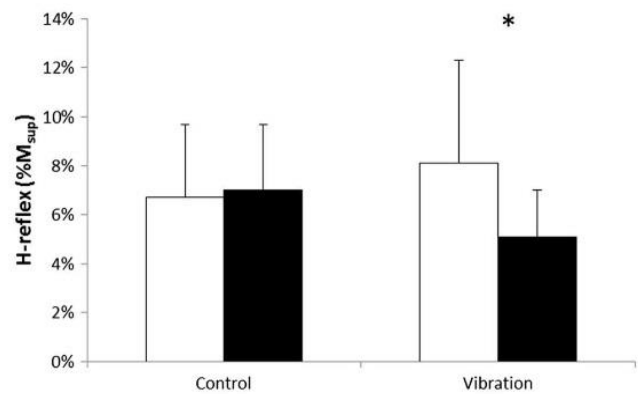


Fig. 5 Mean amplitude of the H-reflex PRE (open bars) and POST (filled bars) in vibration and control conditions. H-reflex amplitude is expressed as a percentage of M_{max} , the amplitude of the maximal M-wave evoked in the relaxed muscle. Significant difference between PRE and POST values: $*p < 0.05$

et al. 2012b; Christova et al. 2011), changes in the level of presynaptic inhibition exerted on Ia afferents may more likely have resulted in the attenuation of Ia afferent efficacy (Misiąszek 2003). This attenuation has been previously considered to result from several mechanisms including presynaptic inhibition of Ia afferents (Hultborn et al. 1987), an increased firing threshold of Ia afferents (Hayward et al. 1986), and transmitter depletion at the Ia afferents terminals (Curtis and Eccles 1960). This latter mechanism has been suggested to mainly impair force production capacity (Bongiovanni et al. 1990) but not H-reflex although this has not been evidenced (Fry and Folland 2014). Reduced excitability of the Ia afferents has been recently rejected to contribute to the observed vibration-induced vastus medialis H-reflex decrease, as indicated by the constancy of the current at which maximal H-reflex was elicited (Fry and Folland 2014). As a result, and although transmitter depletion cannot be totally ruled out, it is likely that increased presynaptic inhibition of Ia afferents largely contributed to the post-vibration decrease in H-reflex amplitude (Lapole et al. 2012a), in response to the high activation of these Ia afferents by the vibratory process (Roll et al. 1989; Burke et al. 1976). In other words, H-reflex depression following prolonged vibration may essentially result from similar mechanisms as during the vibration paradox, i.e. with presynaptic inhibitory interneurons under supra-spinal control inhibiting Ia afferents (Gillies et al. 1969; Delwaide 1973).

Despite decreased spinal loop excitability after prolonged TA vibration, the present study failed to demonstrate any motor performance impairment (i.e., unchanged MVC, VA_{TMS} and maximal EMG activity). This contrasts with several studies that reported force production decrement and altered EMG activity following 20–30 min of local vibration of knee extensors (Jackson and Turner 2003; Konishi et al. 2009; Kouzaki et al. 2000), plantar

Table 2 Neuromuscular measurements PRE and POST vibration and control conditions

	Control		Vibration	
	Pre	Post	Pre	Post
M_{max} (mV)	4.8 ± 1.4	4.7 ± 1.3	5.1 ± 1.2	4.8 ± 1.0
MVC (Nm)	54.0 ± 13.1	54.4 ± 13.3	53.4 ± 12.7	54.3 ± 13.0
RMS_{MVC}/M_{max} (%)	10.7 ± 3.4	10.5 ± 2.1	10.3 ± 3.0	10.7 ± 3.6
SIT_{MVC} (Nm)	0.94 ± 1.05	0.92 ± 1.10	0.66 ± 0.74	0.62 ± 0.49
VA_{TMS} (%)	95.4 ± 5.6	95.9 ± 5.3	96.9 ± 3.8	97.5 ± 2.9
CSP_{50} (ms)	254.7 ± 52.4	260.9 ± 67.5	251.6 ± 49.6	252.8 ± 58.6
CSP_{75} (ms)	261.4 ± 64.5	264.5 ± 60.3	259.6 ± 54.5	264.6 ± 63.0
CSP_{MVC} (ms)	249.1 ± 52.5	267.3 ± 54.0	225.7 ± 63.5	233.0 ± 70.5

M_{max} the amplitude of the maximal M-wave evoked in the relaxed muscle, MVC Maximal voluntary contraction in dorsiflexion, RMS_{MVC}/M_{max} Tibialis anterior maximal EMG activity expressed as a percentage of maximal M-wave amplitude, SIT_{MVC} superimposed twitch during MVC, VA_{TMS} Cortical voluntary activation, CSP_{50} Cortical silent period recorded during 50 % MVC dorsiflexion, CSP_{MVC} Cortical silent period recorded during MVC

flexor muscles (Herda et al. 2009; Ushiyama et al. 2005) or first dorsal interosseus muscle (Shinohara et al. 2005). However, our results are in agreement with other studies on plantar flexor (Ekblom and Thorstensson 2011) and knee extensor muscles (Fry and Folland 2014). The causes of discrepancies between studies remain unclear. The lack of observed MVC impairment in the present study despite decreased spinal excitability may be explained by the fact that there is no evidence that the adaptations observed during a low intensity contraction reflect the functional adaptations during MVC (Taylor and Gandevia 2008). Nevertheless, it has been previously reported that the soleus muscle maximal H-reflex was similar at rest and during MVC (Pensini and Martin 2004). H-reflex recording may also not reflect the efficacy of the entire γ -loop (Fry and Folland 2014), stretch reflexes being paradoxically reported to increase after vibration despite decreased H-reflex (Van Boxtel 1986). However, in the study of Van Boxtel (1986), the vibration exposure only lasted 2 min and different results may be expected following prolonged vibration (i.e. 20-30 min). Hence, unchanged TA force production capacities despite reduced spinal loop excitability remain to be further investigated.

The main originality of the present study was to investigate the effects of prolonged vibration on corticospinal properties by using transcranial magnetic stimulation in TA muscle. Indeed, since decreased MEP amplitude has been reported immediately after vibration exposure (Steyvers et al. 2003), vibration-induced altered voluntary drive was suggested as a potential mechanism explaining MVC impairment after vibration (Jackson and Turner 2003; Ushiyama et al. 2005). Consistent with MVC and TA-EMG activity results, VA_{TMS} remained unaffected by prolonged vibration. Hence, the hypothesis of impaired voluntary drive from the motor cortex following vibration exposure

as it has been reported in fatigue conditions (Temesi et al. 2014b; Gruet et al. 2013) has not been validated. Despite the lack of VA_{TMS} change, MEP amplitude, a marker of corticospinal excitability (Mills 1999), tended to decrease after vibration. This would be in agreement with findings of Steyvers et al. (2003) who reported an immediate attenuation of resting flexor carpi radialis muscle MEP amplitude following 30 min of tendon vibration. While a reduced synchrony of motor units action potentials evoked by TMS could potentially explain the decreased MEP amplitude, this hypothesis could be rejected since MEP duration did not change (data not shown). Hence, decreased MEP amplitude may be explained here by a lower number of activated motor units by TMS. Since MEP amplitude depends on the synaptic relays of the corticospinal projections at both the cortical and spinal levels, spinal mechanisms (i.e. reduced motoneuronal excitability) can contribute to the vibration-induced MEP depression (Devanne et al. 1997), which is consistent with the reported decreased H-reflex. In the future, the use of cervicomedullary stimulation (McNeil et al. 2013) in conjunction with TMS would enable the determination of differential effects of vibration on both cortical and motoneuronal excitability. The functional significance of decreased corticospinal excitability remains unclear since motor performance was unaffected.

While MEP amplitude tended to be altered by vibration, no effects were found in CSP. To our knowledge, only one study investigated vibration effect on CSP. Binder et al. (2009) reported during extensor carpi radialis muscle vibration an increased CSP in the antagonist flexor carpi radialis, suggesting enhanced intracortical inhibition in the non-vibrated antagonist muscle, a parameter which was not measured in our study. Still, our results suggest that acute prolonged muscle vibration did not alter GABA neurotransmission (Werhahn et al. 1999) of inhibitory cortical

neurons projecting onto the pyramidal cells in the motor cortex (Inghilleri et al. 1993).

In conclusion, while TA spinal loop and corticospinal excitabilities were reduced by 30 min of muscle vibration, force production capacities and maximal voluntary activation were unaffected. Although the functional link between the recorded parameters and motor performance remain to be elucidated, these findings suggest that acute prolonged vibration has the potential to modulate corticospinal excitability of lower limb muscles.

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Synthèse de l'étude #1 :

Malgré l'absence de perte de force qui apparaît en désaccord avec certains travaux (Jackson & Turner, 2003; Ushiyama et al., 2005), les résultats de cette étude confirment que la vibration locale appliquée de manière aigüe et prolongée est un stimulus efficace permettant des modulations nerveuses sur le court terme (Lapole et al., 2012a,b; Fry & Folland, 2014) comme démontré par la diminution de l'excitabilité spinale (réflexe H) associée à une tendance à la modulation de l'excitabilité cortico-spinale (MEPs). Il peut alors être suggéré que ce type de stimulus a la capacité d'induire de potentielles adaptations nerveuses sur le long terme. C'est ce que nous avons investigué lors de l'étude #2 pour les muscles fléchisseurs dorsaux de la cheville.

ETUDE #2

AUGMENTATION DU NIVEAU D'ACTIVATION CORTICAL DES MUSCLES FLECHISSEURS DORSAUX DE LA CHEVILLE APRES 8 SEMAINES D'ENTRAÎNEMENT PAR VIBRATION LOCALE

Publication associée :

Souron R., Farabet A., Féasson L., Belli A., Millet GY., Lapole T. (2017)
*EIGHT WEEKS OF LOCAL VIBRATION TRAINING INCREASES DORSIFLEXOR
MUSCLES CORTICAL VOLUNTARY ACTIVATION*

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RESUME :

Objectif : Cette étude évaluait les effets d'un programme d'entraînement de 8 semaines par vibration locale sur les propriétés fonctionnelles et cortico-spinales des muscles dorsiflexeurs de la cheville, et plus particulièrement le muscle tibial antérieur (TA). **Méthodes :** Quarante-quatre sujets étaient répartis de manière randomisée dans un groupe entraînement (VIB, n = 22) ou contrôle (CON, n = 22). Les sujets du groupe VIB réalisaient 24 sessions d'entraînement par vibration locale appliquée sur le TA de la jambe droite (1 h par session, 3 sessions par semaine). Les deux jambes étaient testées pour chaque groupe avant l'entraînement, après 4 et 8 semaines d'entraînement ainsi que deux semaines après la fin de l'entraînement. La force maximale volontaire isométrique (MVC) était mesurée et la stimulation magnétique transcrânienne était utilisée pour évaluer le niveau d'activation cortical (VA_{TMS}), les potentiels évoqués moteurs (MEPs), les périodes de silence (SPs) et les paramètres extraits des courbes de recrutement en se servant de la modélisation mathématique de Boltzmann. **Résultats :** La MVC était significativement augmentée après 4 semaines d'entraînement pour le groupe VIB sur la jambe droite (+ 7,4%, $p = 0,001$) et gauche (+ 6,2%, $p < 0,01$), et restait statistiquement augmentée à la fin des 8 semaines d'entraînement (respectivement + 12,0%, $p < 0,001$ et + 10,1%, $p < 0,001$ pour la jambe droite et gauche). Le VA_{TMS} était significativement augmenté pour la jambe droite et gauche après 4 (respectivement + 4,4%, $p < 0,01$ et + 4,7%, $p < 0,01$) et 8 (respectivement + 4,9%, $p = 0,001$ et + 6,2%, $p = 0,001$) semaines d'entraînement. Ces deux paramètres restaient améliorés pour les deux jambes 2 semaines après la fin de l'entraînement. Les MEPs et SPs enregistrés pendant la MVC ainsi que les paramètres extraits des courbes de recrutement n'étaient pas modifiés par l'entraînement. **Conclusion :** Malgré l'absence de modifications d'excitabilité et/ou d'inhibition cortico-spinale observée, un entraînement par vibration locale semble être une méthode efficace pour augmenter la force maximale volontaire via des adaptations nerveuses, comme suggéré par l'augmentation du niveau d'activation volontaire mesuré par stimulation magnétique transcrânienne. Ces résultats permettent alors d'envisager l'utilisation de la vibration locale comme technique d'entraînement pour des populations spécifiques, e.g. cliniques ou âgées.

RESEARCH ARTICLE

Eight weeks of local vibration training increases dorsiflexor muscle cortical voluntary activation

Robin Souron,¹ Adrien Farabet,¹ Léonard Féasson,^{1,2} Alain Belli,¹  Guillaume Y. Millet,³ and Thomas Lapole¹

¹Laboratoire Interuniversitaire de Biologie de la Motricité, Université de Lyon, Université Jean Monnet Saint-Etienne, Saint-Etienne, France; ²Myology Unit, Referent Center of Rare Neuromuscular Diseases, Centre Hospitalier Universitaire Saint-Etienne, France; and ³Human Performance Laboratory, Faculty of Kinesiology, University of Calgary, Calgary, Alberta, Canada

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Souron R, Farabet A, Féasson L, Belli A, Millet GY, Lapole T. Eight weeks of local vibration training increases dorsiflexor muscle cortical voluntary activation. *J Appl Physiol* 122: 1504–1515, 2017. First published April 6, 2017; doi:10.1152/jappphysiol.00793.2016.—The aim of this study was to evaluate the effects of an 8-wk local vibration training (LVT) program on functional and corticospinal properties of dorsiflexor muscles. Forty-four young subjects were allocated to a training (VIB, $n = 22$) or control (CON, $n = 22$) group. The VIB group performed twenty-four 1-h sessions (3 sessions/wk) of 100-Hz vibration applied to the right tibialis anterior. Both legs were tested in each group before training (PRE), after 4 (MID) and 8 (POST) wk of training, and 2 wk after training (POST_{2w}). Maximal voluntary contraction (MVC) torque was assessed, and transcranial magnetic stimulation (TMS) was used to evaluate cortical voluntary activation (VA_{TMS}), motor evoked potential (MEP), cortical silent period (CSP), and input-output curve parameters. MVC was significantly increased for VIB at MID for right and left legs [+7.4% ($P = 0.001$) and +6.2% ($P < 0.01$), respectively] and remained significantly greater than PRE at POST [+12.0% ($P < 0.001$) and +10.1% ($P < 0.001$), respectively]. VA_{TMS} was significantly increased for right and left legs at MID [+4.4% ($P < 0.01$) and +4.7% ($P < 0.01$), respectively] and at POST [+4.9% ($P = 0.001$) and +6.2% ($P = 0.001$), respectively]. These parameters remained enhanced in both legs at POST_{2w}. MEP and CSP recorded during MVC and input-output curve parameters did not change at any time point for either leg. Despite no changes in excitability or inhibition being observed, LVT seems to be a promising method to improve strength through an increase of maximal voluntary activation, i.e., neural adaptations. Local vibration may thus be further considered for clinical or aging populations.

NEW & NOTEWORTHY The effects of a local vibration training program on cortical voluntary activation measured with transcranial magnetic stimulation were assessed for the first time in dorsiflexors, a functionally important muscle group. We observed that training increased maximal voluntary strength likely because of the strong and repeated activation of Ia spindle afferents during vibration training that led to changes in the cortico-motoneuronal pathway, as demonstrated by the increase in cortical voluntary activation.

local vibration; transcranial magnetic stimulation; cortical voluntary activation; corticospinal excitability and inhibition; Boltzmann modeling

THE IDEA OF USING VIBRATION as a training intervention in healthy and/or clinical populations is relatively recent. Issurin et al. (28) were the first to show significant enhancement of strength with a chronic vibration intervention. Since then, whole body vibration (WBV) training has been largely used as an alternative method to improve physical capacities (55). However, despite its potential effects in the field of rehabilitation (4), WBV may not be suitable for clinical and/or aging populations because some fragile/weak subjects may not be able to maintain an active contraction (e.g., squat) on the vibratory platform. To overcome WBV limitations, small local and portable vibratory devices have been recently proposed (36). This method consists of applying vibration directly on the muscle belly or the tendon, without any active muscular contribution.

It has been shown that local vibration training (LVT) significantly increases strength in plantar flexor muscles after 14 days of daily exposure (34, 36) as well as in knee extensor muscles after 12 (53) and 24 (66) wk. Evidence based on muscle mass (66) and neuromuscular efficiency assessed in both electrically evoked and voluntary conditions (36) highlighted the absence of muscle adaptations (e.g., hypertrophy) after LVT, suggesting that the strength gains observed were related to neural adaptations. Accordingly, increased EMG activity during MVC has been reported after LVT as well as a reduction of activation deficit evaluated by means of the interpolated twitch technique (36).

Among the receptors that are sensitive to vibration, Ia afferents of muscle spindles are the most responsive (5). Because Ia afferent discharge elicits an excitatory input on alpha motoneurons, a reflex contraction of the vibrated muscle has been widely described, the so-called tonic vibration reflex (13). It is associated with changes in spinal loop excitability (11) that may induce adaptations in the long term. We accordingly observed an increase of soleus (SOL) spinal excitability [i.e., increased Hoffmann reflex (H reflex) amplitude] after 14 consecutive days of LVT applied on the Achilles tendon (34, 37). Since vibration-induced Ia afferent discharge led to an activation of the same motor cortical areas as those activated

Address for reprint requests and other correspondence: T. Lapole, Laboratoire Interuniversitaire de Biologie de la Motricité, Bâtiment IRMIS, 10 rue de la Marandière, 42270 Saint Priest en Jarez, France (e-mail: thomas.lapole@univ-st-etienne.fr).

during a voluntary contraction (i.e., both motor and sensorimotor cortex and contralateral supplementary motor area) (49, 50, 59), one could assume that LVT may also lead to some supraspinal adaptations (e.g., increased corticospinal excitability, decreased intracortical inhibition), as already reported after strength (e.g., Refs. 10, 24) or neuromuscular electrical stimulation (see Ref. 26) training. Thus, the use of transcranial magnetic stimulation (TMS) should be considered to give new and more precise insight in the origin of neural adaptations after LVT.

TMS is a reliable and painless alternative to assess corticospinal adaptations through activation of both the initial axonal segments of pyramidal tract neurons (i.e., D waves) and pre-synaptic neurons projecting onto the primary motor cortex (i.e., I waves) (3). TMS may provide information about the excitability of cortical neurons and/or motoneuron pools of the stimulated muscles when measuring motor evoked potentials (MEPs), which are compound electrical potentials recorded with surface electromyography (EMG). When applied during a voluntary contraction, TMS may also assess cortical silent periods (CSPs), which are the silent EMG periods recorded after a TMS stimulus, providing information on GABA_B-mediated intracortical inhibition (70). Although the exact mechanisms of the CSP remain unclear, the initial part could be mainly due to reduced spinal excitability while the final part could be cortical in origin (9). Strength training is known to change both MEP amplitude (24) and CSP duration (10), yet this remains to be examined after LVT.

TMS has also been used to assess cortical voluntary activation (VA_{TMS}) by evoking superimposed twitches (SIT) during voluntary contraction, similar to the classic interpolated twitch technique (46). A SIT elicited by TMS during maximal voluntary contraction (MVC) has been suggested to highlight a suboptimal drive from the motor cortex (20), although the VA_{TMS} change can be due to modulation at any level of the corticospinal network (i.e., through reduced spinal and/or motoneuronal excitability). Despite VA_{TMS} being widely used to explore the effect of fatiguing exercise (e.g., Ref. 69), it has been rarely investigated in the context of training. To our knowledge, only two studies have investigated the effect of strength training on VA_{TMS} , and they showed either no change (41) or significant contralateral changes (42) after the training period. Again, the effects of vibration training on VA_{TMS} have yet to be determined. The assessment of VA_{TMS} cannot be performed on all muscles because some criteria must be met, mainly that the muscles must have strong cortico-motoneuronal projections (21). Thus, in addition to its important functional role, contributing to almost half of the voluntary torque produced in ankle dorsiflexion (44), the tibialis anterior (TA) is an interesting muscle since it is known to have the strongest corticospinal projections among all lower limb muscles (52).

Therefore, the aim of the present study was to determine the effects of an 8-wk unilateral LVT program on dorsiflexor muscle VA_{TMS} and TA corticospinal functional properties (e.g., MEP amplitude, CSP duration, H-reflex amplitude). Since cross-education was previously reported after LVT (34), measurements were also performed on the contralateral untrained side.

MATERIALS AND METHODS

Subjects

Forty-four young, healthy subjects (20 men and 24 women; age 20 ± 1 yr, height 171 ± 11 cm, weight 64 ± 13 kg) participated in this study. The level of weekly physical activity was reported to be between 0 and 5 h per week for each subject. Written informed consent was obtained from all subjects before their participation. This study conformed to standards from the latest revision of the Declaration of Helsinki and was approved by the local research ethic committee and registered on ClinicalTrial.gov (NCT02668224). All subjects were free of lower limb injury during the previous 3 mo and had no contraindications to TMS (60) and in particular no acute or chronic neurological disorders and trauma. They were instructed to abstain from caffeine for a minimum of 12 h before each session.

Design of Study

Subjects were randomly assigned to either the control (CON; $n = 22$, 12 men and 10 women) or the vibration (VIB, $n = 22$, 8 men and 14 women) group (Fig. 1A). The first visit aimed to familiarize the subject with the correct development of the left and right dorsiflexion maximal isometric torque as well as magnetic and electrical stimulations. Thereafter, all the subjects performed the experimental procedures during four testing sessions conducted approximately at the same time of the day (see below). All the neuromuscular measurements were performed on the right (i.e., trained) and then the left (i.e., untrained) leg (Fig. 1B).

The experimental design is illustrated in Fig. 1A. After a pretraining test session (PRE), the subjects followed an 8-wk LVT program, for a total of 24 vibration sessions. Subjects were tested after 4 (MID) and 8 (POST) wk of training as well as 2 wk after the end of the training period (POST_{2w}). No specific recommendations were given to the subjects of the CON group, who were asked not to change their usual activities for the duration of the study.

After muscle palpation, the vibrating device (VB 115; Techno Concept, Mane, France) was applied locally and strapped directly on the largest part of the resting TA muscle of the right leg with elastic Velcro fasteners. The right leg was the dominant leg for 20 of 22 subjects in VIB and 19 of 22 subjects in CON; this corresponded to the strongest leg for 14 and 12 subjects for VIB and CON, respectively. This corresponded to a position at around 50% of muscle length and far from the tendon insertions (Fig. 1C). The subject was seated on a chair during the entire vibration session, with a knee angle of 90° . The vibration device was always placed on the muscle by the same investigator to ensure the same pressure on the leg. The LVT program consisted of three 1-h vibration sessions per week with at least 1 day of rest between consecutive sessions. Since small vibration amplitudes are effective for stimulating Ia afferents (57), and considering that Ia afferents can fire synchronously with vibration frequencies up to 80–120 Hz (56, 57), vibration characteristics were set to 100 Hz with 1-mm amplitude in the present study.

Torque and Electromyographic Recordings

Dorsiflexion torque was measured during voluntary contractions by a calibrated instrumented pedal (CS1060 300 Nm; FGP Sensors, Les Clayes Sous Bois, France). Subjects were seated upright in a custom-built chair with hip, knee, and ankle angles of 90° , 120° , and 90° , respectively (full extension = 180°). The foot was securely attached to the pedal with a custom-made hook and loop fastener. During all measurements, subjects were provided with real-time feedback of the force trace displayed on a screen, and guidelines were added when subjects had to maintain a targeted submaximal level of MVC. EMG signals were recorded from TA and SOL muscles with pairs of self-adhesive surface electrodes (Meditrace 100; Covidien, Mansfield, MA) in bipolar configuration with a 30-mm interelectrode distance.

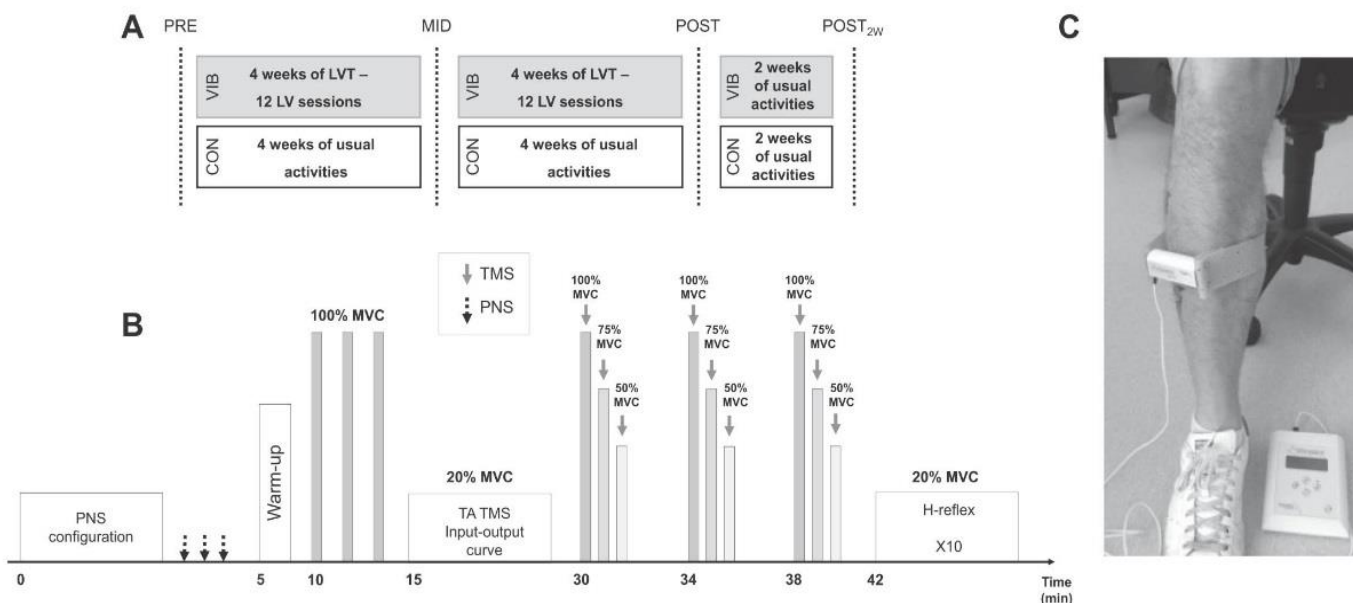


Fig. 1. *A* and *B*: overview of the experimental design of the study (*A*) and the neuromuscular testing protocol (*B*). *C*: vibratory device strapped onto the tibialis anterior muscle belly. Neuromuscular tests were performed before (PRE), during (MID), immediately after (POST), and 2 wk after (POST_{2w}) the local vibration training (LVT) period for control (CON) and vibration (VIB) groups. First, the optimal position and intensity of stimulation were determined for peripheral nerve stimulation (PNS) to determine M_{max} (1st 3 black arrows). Then, the subjects performed 3 maximal voluntary contractions (MVCs) interspaced by 1 min. Optimal coil position and intensity for transcranial magnetic stimulation (TMS) were then performed. Cortical voluntary activation (i.e., VA_{TMS}) was then calculated using 3 series of 3 maximal (100% MVC) and submaximal (75% and 50% MVC) voluntary contractions with superimposed TMS single pulse during each contraction. Finally, the H reflex (i.e., H_{20}) was determined. The neuromuscular measurements were done on both right and left legs, except for H_{20} , which was recorded on the right leg only.”

SOL electrodes were placed 2 cm below the insertion of the gastrocnemii on the Achilles tendon. TA electrodes were placed on the muscle belly parallel to the longitudinal axis of the muscle at one-third of the distance between the head of the fibula and the tip of the medial malleolus, according to SENIAM recommendations. The ground electrode was positioned on the patella. Low impedance (<5 k Ω) between electrodes was obtained by shaving and gently abrading the skin and then cleaning it with isopropyl alcohol. Signals were amplified with an octal bio-amplifier (ML138; ADInstruments, Bella Vista, Australia; common mode rejection ratio = 85 dB, gain = 500), band-pass filtered (5–500 Hz), and analog-to-digital converted at a sampling rate of 2,000 Hz by a PowerLab system (16/30—ML880/P; ADInstruments). All data were analyzed off-line with Labchart 7 software (ADInstruments).

Peripheral Nerve Stimulation

Single rectangular electrical pulses with 0.5-ms duration and 400 V maximal output voltage were delivered to the right and left peroneal nerves via a constant-current stimulator (DS7A; Digitimer, Welwyn Garden City, UK) and a bipolar bar stimulating electrode with 30-mm anode-cathode spacing (Bipolar Felt Pad Stimulating Electrode part no. E.SB020/4mm; Digitimer) placed next to the fibular head. The best stimulation site was defined as the location eliciting the greatest TA M-wave amplitude for a given stimulus intensity. This site was marked with semipermanent ink.

To determine the optimal intensity of stimulation for M-wave measurement, the intensity was increased by 5 mA until the resting TA M wave plateaued. The optimal stimulating intensity was then increased by 50% (supramaximal intensity) to allow M-wave assessment on the relaxed muscle (see below). For H-reflex recordings, measurements were performed with a stimulation intensity producing concomitant TA M waves equal to ~20% of the maximal M wave recorded on relaxed muscles (M_{max}) (65) to ensure that effective stimulus intensity remained constant (2, 34). The determination of optimal peripheral nerve stimulation position and intensity was per-

formed at the beginning of the neuromuscular testing session to avoid any potentiation or fatigue effect.

Transcranial Magnetic Stimulation

Single TMS pulses (1-ms duration) were manually delivered to elicit MEPs and SIT during voluntary isometric dorsiflexion. The motor cortex contralateral to the tested leg was stimulated by a magnetic stimulator (Magstim 200²; Magstim, Whitland, UK) with a 110-mm double-cone coil (maximum output of 1.4 T). The coil was manually controlled by the same investigator throughout all the testing sessions. Subjects wore a cervical collar during all TMS measures to stabilize the head and neck. The coil was positioned over the leg area of the motor cortex along the nasal-inion axis to induce a postero-anterior current. It was demarcated on a swim cap every centimeter from 1 cm anterior to 3 cm posterior to the vertex along the nasal-inion line and also to 2 cm over the left motor cortex area. One stimulation was delivered at each of these specified anatomical positions. Optimal coil position was determined as the site eliciting the largest SIT and maximal TA MEP amplitude with minimal SOL MEP amplitude in response to stimulation at 50% maximal stimulator output during a 10% MVC dorsiflexion. In ~20% of the subjects, optimal MEP and peak torque were not recorded at the same coil position. In that case, the optimal coil position was chosen according to MEP amplitude, since the evoked peak torque may be influenced by activation of other muscles (71). This position was marked on a swim cap secured to the scalp. Before the delivery of each stimulus, the coil position was verified with regard to the marks on the swim cap.

Stimulus intensity was determined from an input-output curve determined from SIT and MEP responses evoked during brief voluntary contractions at 20% MVC. Four consecutive 2- to 3-s contractions were performed at 10-s intervals at each of the following randomly ordered stimulus intensities: 20%, 30%, 40%, 50%, 60%, 70%, and 80% maximal stimulator output; a TMS pulse was delivered during each of these contractions (i.e., 28 stimulations were initially delivered). If SIT and TA MEP amplitudes did not plateau with these

intensities, higher TMS intensities (i.e., 90% and 100% maximal stimulator output) were investigated. The optimal stimulation intensity obtained from the input-output curve was chosen when TA MEP and SIT plateaued. The MEP evoked in the antagonist SOL was also measured to ensure the lowest possible value (Fig. 2). Such methods have been recently reported to be appropriate for determining TMS intensity in the quadriceps (68). The size of the TA MEPs was measured as the peak-to-peak amplitude of the nonrectified EMG response and expressed relative to M_{\max} (see below) and then averaged and plotted against the stimulus intensity (Fig. 3A). TMS was delivered during voluntary contractions once the subject had stabilized the force on the target level. Subjects were instructed to recontract as strongly and as quickly as possible immediately after delivery of the single TMS pulse to permit accurate determination of the CSP.

Data Analysis

Peripheral nerve stimulation. M-wave peak-to-peak amplitudes were measured from electrical nerve stimulations in relaxed muscle (M_{\max}). M_{\max} was then calculated as the mean peak-to-peak amplitude from three separated stimulations (Fig. 1B). The mean intensity used from all groups, sessions, and legs was 64.7 ± 15.4 mA (range: 30–100 mA).

Torque. Maximal torque was calculated as the highest peak torque recorded from three MVCs lasting ~3 s, interspaced by 1 min of rest to avoid fatigue. Subjects were provided with real-time feedback of the force displayed on a screen and were instructed to contract as strongly as possible during a 3-s contraction.

Corticospinal properties. Boltzmann modeling was performed from the input-output curve to apply a nonlinear regression analysis (Fig. 3A) (10, 12):

$$A_{\text{MEP}} = \frac{P}{1 + \exp\left[\frac{I_{50} - I}{k}\right]}$$

This function allowed the determination of the relation between MEP amplitude (A_{MEP}) and the TMS intensity (I , as % of resting motor threshold). Three parameters were extracted from this relation: the maximum MEP defined by the function (P , in % M_{\max}), the stimulus intensity at which the MEP size was 50% of the maximal MEP (I_{50} , in % of stimulator output), and the slope parameter (k) that is inversely proportional to the maximal function steepness (12).

Cortical voluntary activation (VA_{TMS}) during maximal effort was measured by the modified twitch interpolation technique (72). Stimulus intensity used for the investigation of cortical voluntary activa-

tion was defined as the lowest stimulus intensity eliciting maximal SIT and TA MEP amplitude and minimal SOL MEP amplitude from the input-output curve performed for corticospinal excitability measurement. Corticospinal excitability increases substantially during the transition from relaxed to contracted muscle states (74), thus underestimating TMS-evoked twitch in the relaxed muscle. Hence, estimated resting twitch (ERT) was determined by linear regression of the relation between SIT amplitude evoked when TMS was delivered at 100%, 75%, and 50% MVC and voluntary force (Fig. 3B) (72). This relation was extrapolated, and the y -intercept was interpreted as the ERT amplitude (Fig. 3C). VA_{TMS} was assessed with the equation

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

where SIT_{MVC} is the superimposed twitch evoked during MVC. Three series were performed with contractions and series separated by 30 s and 2 min, respectively. Thus, the linear regression was performed with the three values from each series. ERT was excluded and VA_{TMS} was not calculated when the linear regression was not linear within a series ($r^2 < 0.9$) (27). The highest value of VA_{TMS} was kept for further analysis.

MEP and CSP elicited by TMS during 100%, 75%, and 50% MVC contractions were also calculated and averaged over the three series (Fig. 3D). Peak-to-peak MEP amplitudes were measured and normalized to M_{\max} (MEP_{MVC} , MEP_{75} , and MEP_{50} , respectively). To ensure that the lowest possible coactivation was elicited, MEP amplitude was also recorded on the SOL muscle (MEP_{SOL}) during MVC. Since no SOL M_{\max} were recorded in the experimental protocol, MEP_{SOL} are presented as absolute values. The duration of the CSPs was 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) (67) (CSP_{MVC} , CSP_{75} , and CSP_{50} , respectively).

Spinal Excitability

The amplitude of the H reflex was recorded during low tonic voluntary contractions at 20% MVC (i.e., H_{20}) to ensure easily identifiable TA reflex (65) (Fig. 4). Note that this was only done for the right leg (i.e., the vibrated leg) since no contralateral effect was previously observed for H-reflex amplitude following LVT (34). Ten H reflexes that met criteria of a concomitant M wave ~20% of TA M_{\max} were recorded, averaged, and expressed relative to M_{\max} . Ten-second intervals separated each stimulation.

Statistical Analysis

Data are presented as means \pm SD. The sample size was calculated at the outset for a statistical power of 0.80 and an α risk of 0.05. Since the main criterion of our study was the increase in MVC after LVT for the vibrated leg, the calculation was based on a target vibration-induced gain of $10 \pm 11.7\%$ for VIB (34) and no differences for CON. With these targets, including a minimum of 20 subjects per group was necessary to reach the desired power of 0.80 on a two-way repeated-measures ANOVA, i.e., group (CON or VIB) \times time (PRE, MID, POST, POST_{2w}), performed on MVC. This was achieved by including 22 subjects in each group to anticipate possible drop-out. Statistical tests were performed with Statistica software (StatSoft, Tulsa, OK). All variables were normally distributed (Kolmogorov-Smirnov normality test). For ANOVA analyses, homogeneity of variance was verified by Levene's test. Since factors other than force and time may be considered with regard to the present experimental protocol, the statistical design was not based on a two-way repeated-measures ANOVA but included the time, leg, and force level (when applicable) as within-subject variables and group and sex as between-subject variables in multiple-way repeated-measures ANOVA. A three-way repeated-measures ANOVA was performed on H_{20} [group (CON or VIB) \times time (PRE, MID, POST, POST_{2w}) \times sex (male or female)]. A four-way repeated-measures ANOVA was performed on

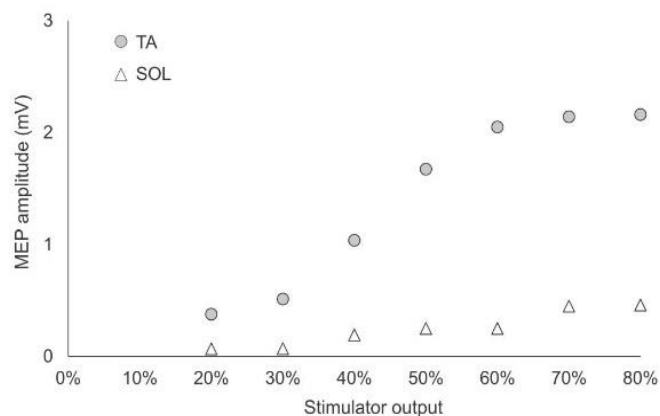


Fig. 2. Input-output curve for a representative subject. The optimal stimulation intensity was selected when MEP TA plateaued and when MEP SOL was small. For this subject, 60% of the maximal stimulator output was chosen as the optimal stimulation intensity.

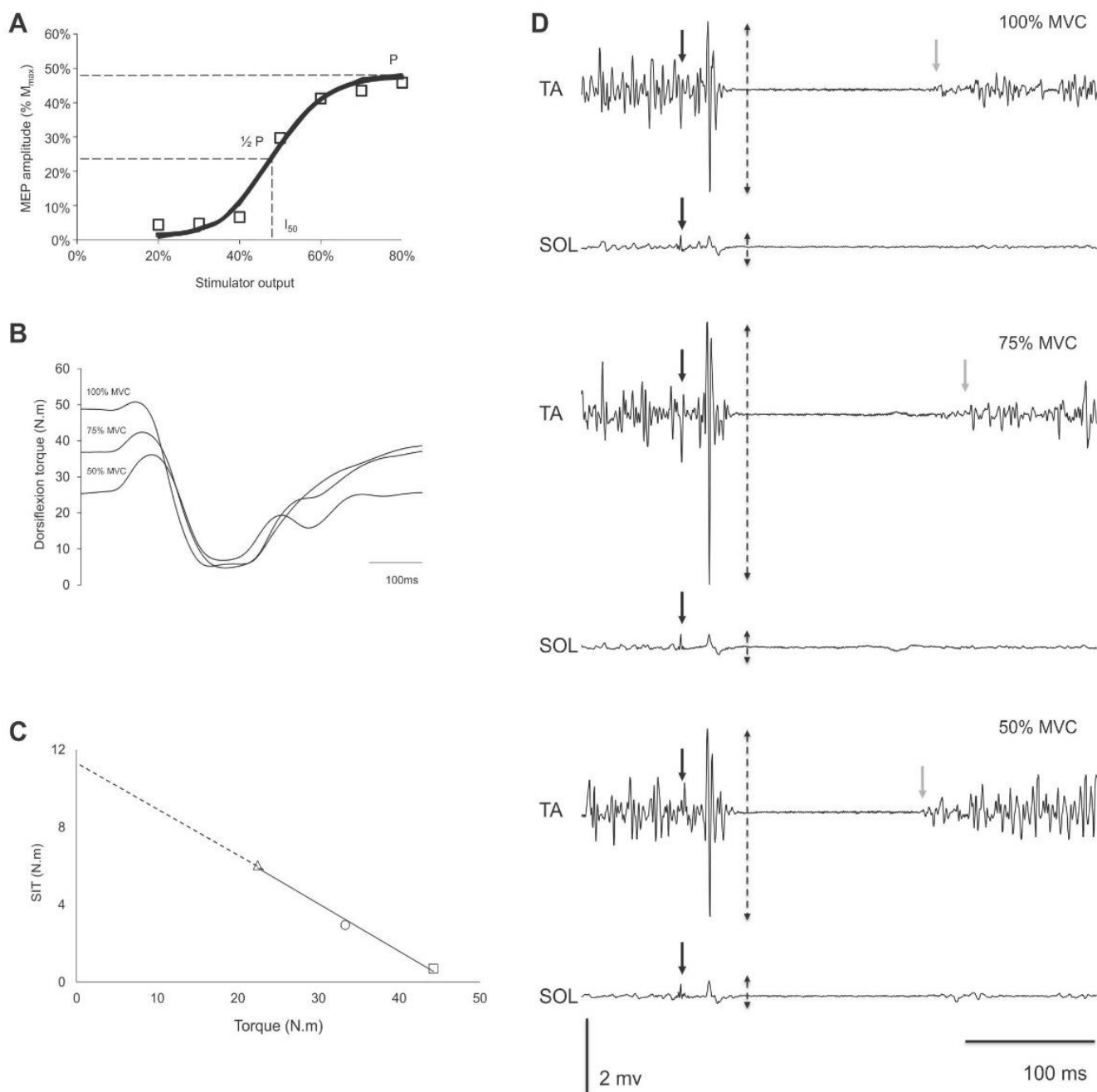


Fig. 3. *A*: typical tibialis anterior (TA) MEP input-output curve. Mean TA MEP amplitudes (\square) are presented as a function of TMS intensity from 20% to 80% of maximal stimulator output. Solid line represents the Boltzmann sigmoid function fit to that set of data. Dashed lines indicate I_{50} [i.e., stimulus intensity required to obtain a MEP amplitude of half the size of the plateau ($\frac{1}{2}P$) and P (i.e., the maximum MEP defined by the function)]. *B*: superimposed twitch force evoked with TMS during maximal (i.e., 100% MVC) and submaximal (i.e., 75% and 50% MVC) voluntary contractions. *C*: amplitude of superimposed twitches (SIT) produced by TMS during contraction at 50% (Δ), 75% (\circ), and 100% (\square) MVC. The linear regression was extrapolated, and the y-intercept (dashed line) was interpreted as the ERT amplitude. *D*: example of electromyographic recording in response to transcranial magnetic stimulation (TMS) during maximal (100% MVC) and submaximal (75% and 50% MVC) voluntary contractions for the agonist (TA) and antagonist soleus (SOL) muscles. The time interval between black and gray arrows represents a method of assessing cortical silent period (CSP) duration. Black arrows represent the time of TMS stimulation. Gray arrows represent the resumption of continuous voluntary EMG. Dashed arrows represent the MEP peak-to-peak amplitude. Data are from a representative subject.

MVC, VA_{TMS} , M_{max} , P , k , and I_{50} [group (CON or VIB) \times time (PRE, MID, POST, POST_{2w}) \times leg (right or left) \times sex (male or female)]. A five-way repeated-measures ANOVA was performed on MEP and CSP [group (CON or VIB) \times time (PRE, MID, POST, POST_{2w}) \times leg (right or left) \times force level (100%, 75%, or 50% MVC) \times sex (male or female)]. One should acknowledge here that sample size was not calculated for such multiple-way repeated-measures ANOVA (see above) and this is likely to reduce the power

of the performed analysis, i.e., this was calculated to be 0.41 for MVC. However, despite reduced power, the results of the present statistical analysis corroborated those obtained when two-way repeated-measures ANOVA was performed on each leg separately and by pooling the other factors. Post hoc analyses were performed with Student-Newman-Keuls testing when the ANOVA identified significant differences. A level of $P < 0.05$ was used to identify statistical significance.

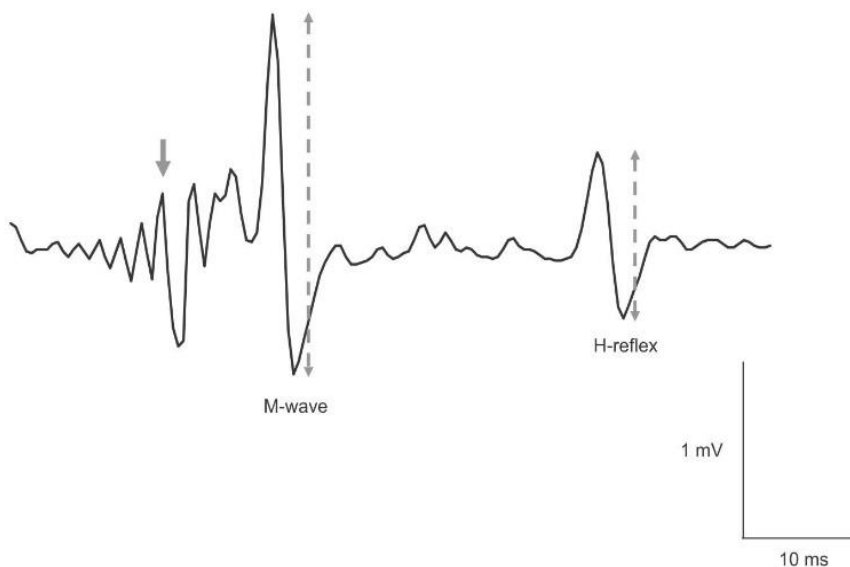


Fig. 4. Representative trace of H reflex and associated M wave for tibialis anterior muscle recorded during submaximal voluntary contractions at 20% MVC. Gray arrow represents the time of peripheral nerve stimulation. Dashed arrows represent M-wave and H-reflex peak-to-peak amplitude.

RESULTS

MVC and VA_{TMS}

No differences between groups or between legs were found at baseline for any parameters ($P > 0.05$). There was a significant group \times time interaction for MVC ($P < 0.001$) with no further interaction with the leg factor ($P = 0.96$). In VIB for the right leg, MVC was significantly increased at MID (53.5 ± 14.6 N·m, $P = 0.001$), POST (55.8 ± 15.1 N·m, $P < 0.001$), and POST_{2w} (55.2 ± 15.1 N·m, $P < 0.001$) compared with PRE (49.8 ± 13.2 N·m). Similarly, MVC of the left leg was greater at MID (50.8 ± 12.5 N·m, $P < 0.01$), POST (52.6 ± 13.5 N·m, $P < 0.001$), and POST_{2w} (51.7 ± 13.0 N·m, $P < 0.001$) compared with baseline (47.8 ± 12.2 N·m) (Fig. 5). For CON, no significant differences were observed at MID, POST, and POST_{2w} compared with baseline (Fig. 5; $P > 0.05$ for all time points and both legs). Although there was a main effect of sex ($P < 0.001$), no significant group \times time \times sex interaction was found for MVC ($P = 0.25$).

There was also a significant group \times time interaction for VA_{TMS} ($P < 0.001$) recorded with no group \times time \times leg interaction ($P = 0.73$). In VIB for the right leg, VA_{TMS} was significantly increased at MID ($97.9 \pm 3.7\%$, $P < 0.01$), POST

($98.4 \pm 2.4\%$, $P = 0.001$), and POST_{2w} ($98.1 \pm 3.4\%$, $P = 0.001$) compared with PRE ($93.8 \pm 7.1\%$). For the left leg, VA_{TMS} was significantly increased at MID (96.4 ± 6.1 , $P < 0.01$), POST (97.9 ± 4.8 , $P = 0.001$), and POST_{2w} ($98.1 \pm 4.6\%$, $P = 0.001$) compared with PRE ($92.1 \pm 10.2\%$) (Fig. 6). For CON, no significant differences were observed at MID, POST, and POST_{2w} compared with baseline (Fig. 6; $P > 0.05$ for all time points and both legs). No significant main effect for sex ($P = 0.69$) or group \times time \times sex interaction was found ($P = 0.55$).

Corticospinal Properties

MEP, CSP, and M-wave measurement are presented in Table 1. No significant group \times time interaction was found for M_{max} . Similarly, no significant group \times time interaction was reported for MEPs and CSPs ($P > 0.05$). There was, however, a main force level effect ($P < 0.001$), with greater MEP amplitude and CSP duration during submaximal voluntary contractions at 75% ($P < 0.001$ and 0.05 respectively) and 50% ($P < 0.01$ and 0.009, respectively) MVC compared with MVC. As shown in Table 1, there was no group \times time interaction for the input-output curve-related parameters ($P > 0.05$).

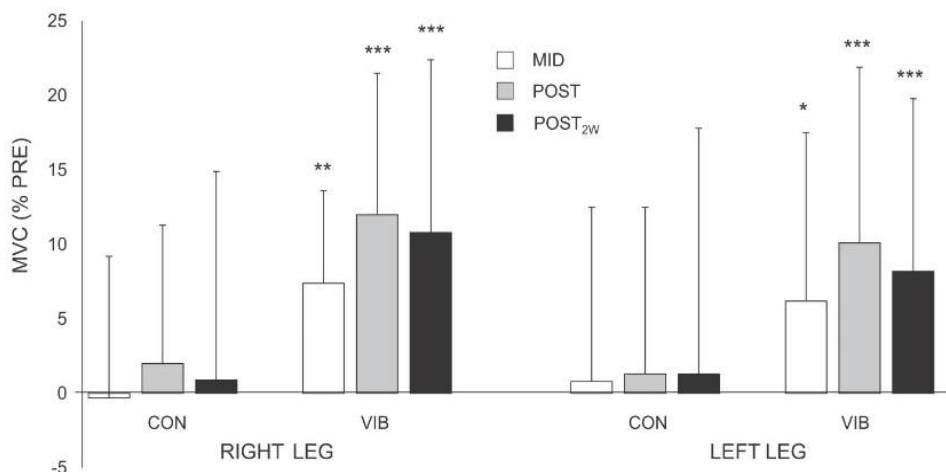
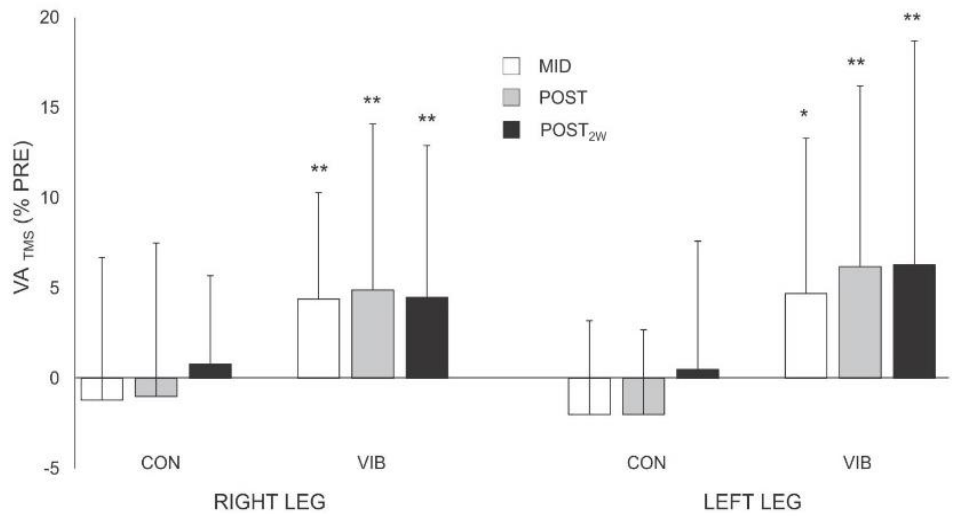


Fig. 5. Mean changes in dorsiflexion maximal voluntary contraction (MVC) isometric torque during (MID), immediately after (POST), and 2 wk after (POST_{2w}) the training period for control (CON) and vibration (VIB) groups and for right and left legs. Results are expressed as % of baseline values (PRE). Error bars indicate SD. Posttraining values significantly different from PRE: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Fig. 6. Mean changes in cortical voluntary activation (VA_{TMS}) during (MID), immediately after (POST), and 2 wk after ($POST_{2w}$) the training period for control (CON) and vibration (VIB) groups and for right and left legs. Results are expressed as % of baseline values (PRE). Error bars indicate SD. Post-training values significantly different from PRE: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.



No significant group \times time interaction was found for MEP_{SOL} ($P = 0.90$) or H_{20} on the right leg ($P = 0.45$) (Table 2). For these parameters, there were no main interaction effects or interaction effects involving the factor sex or leg ($P > 0.05$).

DISCUSSION

The main findings of the present study are that an 8-wk LVT program 1) significantly enhanced maximal cortical voluntary activation (VA_{TMS}) and MVC on the trained (i.e., right) leg and 2) induced similar gains on these two parameters on the contralateral (i.e., left) leg despite 3) inducing no identifiable changes in corticospinal properties in any leg.

Effects of Unilateral Local Muscle Vibration Training on MVC

While a large number of studies have reported strength improvement after WBV training (55), only a few studies have assessed the effect of LVT (34, 36, 53, 66), and these studies used a variety of training protocols (i.e., different training duration, vibration frequency, number of sessions, etc.). Hence, no standard training protocol exists for LVT. Our training protocol was based on 1) acute results recently reported by our team on the TA muscle (15) and 2) the practical applicability of the training and/or rehabilitation protocol currently used (40).

Increases of ~7% (36) and 10% (34) were previously found in plantar flexion MVC after 14 days of local Achilles tendon vibration training and ~14% knee extension MVC after 6 mo of LVT (66). In line with these findings, 4 wk of LVT in the present study was sufficient to induce significant strength enhancement (+7.4 and +6.2% on the right and left legs, respectively). Thereafter, MVC tended to (not significantly) increase to week 8 (+12% and +10% on the right and left legs, respectively) (Fig. 5), the gains being still present 2 wk after the end of LVT. Hence, the present study confirms that LVT is an appropriate method to improve maximal strength in previously untrained young, healthy individuals.

The present study further documents a significant cross-education effect. While the cross-education effect has been consistently reported after strength training (22), the present results concur with those of the only study that investigated cross-education with LVT (34). It is interesting to note that unilateral LVT led to similar strength gain in the right and left legs (Ref. 34) while most (e.g., Ref. 47) but not all (Ref. 33) studies reported higher strength increase on the trained rather than the untrained leg after voluntary (i.e., conventional) strength training. This may be explained by a combination of muscular and neural adaptations occurring in the trained leg while only neural adaptations are suggested to occur in the contralateral limb (7). Since only neural adaptations seem to

Table 1. Input-output curve parameters and M_{max} amplitude before, during, and after training period for control and vibration groups

	Control				Vibration			
	PRE	MID	POST	POST _{2w}	PRE	MID	POST	POST _{2w}
	<i>Right leg</i>							
k	0.067 ± 0.035	0.061 ± 0.039	0.068 ± 0.025	0.067 ± 0.031	0.064 ± 0.037	0.067 ± 0.046	0.057 ± 0.050	0.075 ± 0.076
P, % M_{max}	18.5 ± 14.6	15.9 ± 17.1	16.6 ± 12.8	17.4 ± 16.4	16.7 ± 10.8	15.7 ± 15.4	22.3 ± 22.1	20.4 ± 17.1
I_{50} , % stimulator output	35.6 ± 9.6	37.0 ± 11.9	36.7 ± 8.3	33.8 ± 5.3	34.1 ± 8.9	37.1 ± 11.4	31.8 ± 8.5	35.7 ± 17.3
	<i>Left leg</i>							
k	0.070 ± 0.054	0.072 ± 0.051	0.070 ± 0.030	0.072 ± 0.036	0.064 ± 0.044	0.072 ± 0.049	0.074 ± 0.061	0.078 ± 0.076
P, % M_{max}	26.6 ± 23.9	17.6 ± 13.9	19.4 ± 12.6	14.7 ± 9.8	26.4 ± 29.1	15.3 ± 14.7	16.4 ± 13.7	20.1 ± 17.1
I_{50} , % stimulator output	37.2 ± 10.0	36.9 ± 8.6	36.1 ± 5.7	33.1 ± 7.0	33.7 ± 11.2	34.8 ± 11.2	37.3 ± 9.7	34.2 ± 16.5

Values are mean ± SD values before (PRE), during (MID), immediately after (POST), and 2 wk after ($POST_{2w}$) the training period for control and vibration groups. k , Slope parameter; P, function plateau; I_{50} , stimulus intensity required to obtain a MEP amplitude of half the size of the plateau.

Table 2. MEP, CSP, M-wave, and H-reflex measurements before, during, and after training period for control and vibration groups

	Control				Vibration			
	PRE	MID	POST	POST _{2w}	PRE	MID	POST	POST _{2w}
<i>Right leg</i>								
MEP _{MVC} , %M _{max}	60.9 ± 21.7	53.8 ± 26.0	53.5 ± 18.2	50.2 ± 21.8	65.1 ± 20.9	50.3 ± 23.8	52.2 ± 25.3	49.2 ± 23.8
MEP ₇₅ , %M _{max}	82.1 ± 27.9	81.7 ± 42.2	79.7 ± 28.5	79.5 ± 33.6	77.8 ± 20.8	68.1 ± 25.7	81.7 ± 25.1	81.2 ± 21.4
MEP ₅₀ , %M _{max}	69.5 ± 27.4	69.8 ± 36.8	68.9 ± 24.5	73.4 ± 33.7	67.3 ± 19.5	63.9 ± 30.7	75.7 ± 27.1	69.0 ± 22.1
MEP _{SOL} , mV	0.43 ± 0.18	0.41 ± 0.17	0.45 ± 0.19	0.46 ± 0.18	0.40 ± 0.19	0.39 ± 0.22	0.43 ± 0.21	0.41 ± 0.18
CSP _{MVC} , ms	278 ± 66	283 ± 66	298 ± 78	284 ± 54	279 ± 85	269 ± 66	282 ± 64	278 ± 67
CSP ₇₅ , ms	304 ± 78	309 ± 64	315 ± 61.4	317 ± 51	304 ± 70	293 ± 60	282 ± 68	298 ± 56
CSP ₅₀ , ms	299 ± 76	300 ± 68	306 ± 62	315 ± 47	294 ± 72	280 ± 58	271 ± 65	284 ± 53
M _{max} , mV	4.5 ± 1.7	5.4 ± 2.3	4.4 ± 1.8	4.9 ± 2.0	4.5 ± 2.0	4.6 ± 2.0	4.2 ± 2.4	4.5 ± 2.0
H ₂₀ , %M _{max}	13.1 ± 5.9	13.9 ± 7.3	14.1 ± 6.9	14.9 ± 9.5	13.0 ± 5.6	13.2 ± 7.7	16.8 ± 9.4	15.1 ± 7.8
<i>Left leg</i>								
MEP _{MVC} , %M _{max}	56.5 ± 24.9	53.1 ± 18.4	51.7 ± 17.5	49.2 ± 17.1	56.7 ± 23.7	49.8 ± 25.0	53.2 ± 23.9	52.1 ± 12.8
MEP ₇₅ , %M _{max}	89.0 ± 33.3	83.5 ± 36.0	81.7 ± 21.5	70.5 ± 23.8	82.4 ± 30.5	69.7 ± 18.9	69.0 ± 19.5	77.6 ± 20.8
MEP ₅₀ , %M _{max}	73.7 ± 17.5	62.8 ± 24.0	70.1 ± 17.7	58.5 ± 16.7	76.4 ± 36.6	64.2 ± 27.3	64.8 ± 33.8	69.5 ± 18.0
MEP _{SOL} , mV	0.39 ± 0.11	0.41 ± 0.14	0.43 ± 0.16	0.44 ± 0.13	0.43 ± 0.18	0.42 ± 0.16	0.46 ± 0.22	0.43 ± 0.21
CSP _{MVC} , ms	266 ± 61	261 ± 72	273 ± 68	278 ± 64	258 ± 84	254 ± 84	258 ± 94	265 ± 86
CSP ₇₅ , ms	282 ± 62	291 ± 71	292 ± 59	296 ± 49	276 ± 64	272 ± 60	259 ± 70	289 ± 58
CSP ₅₀ , ms	280 ± 77	277 ± 70	281 ± 58	287 ± 54	292 ± 84	277 ± 60	257 ± 74	271 ± 47
M _{max} , mV	3.9 ± 2.0	4.5 ± 1.9	3.9 ± 1.1	4.9 ± 2.7	3.9 ± 1.6	4.8 ± 1.8	4.1 ± 1.4	4.4 ± 1.5

Values are mean ± SD motor evoked potential (MEP), cortical silent period (CSP), M-wave, and H-reflex values before (PRE), during (MID), immediately after (POST), and 2 wk after (POST_{2w}) the training period for control and vibration groups. MEP_{MVC}, MEP recorded during MVC; MEP₇₅, MEP recorded during submaximal voluntary contractions at 75% MVC; MEP₅₀, MEP recorded during submaximal voluntary contractions at 50% MVC; MEP_{SOL}, MEP recorded on the soleus during MVC; CSP_{MVC}, CSP recorded during MVC; CSP₇₅, CSP recorded during submaximal voluntary contractions at 75% MVC; CSP₅₀, CSP recorded during submaximal voluntary contractions at 50% MVC; M_{max}, M wave recorded at rest; H₂₀, H reflexes recorded during submaximal voluntary contractions at 20% MVC.

occur after LVT (36, 66), the similar strength gains observed in the present study may be ascribed to the bilateral activation in cortical areas during the application of vibration (23, 43). However, the reasons for these similar gains require further investigation.

Effects of Unilateral Local Muscle Vibration Training on Cortical Voluntary Activation

Since no studies have presented any evidence for muscle adaptations after LVT (36, 53), neural adaptations have been suggested to be the main reason for maximal strength increase after LVT (34, 37). Potential involved mechanisms of increased motor drive within the central nervous system may come from spinal and/or supraspinal levels (19). Increased spinal excitability after LVT has been previously reported through the assessment of H reflexes (34, 37). While supraspinal adaptations have been suggested after strength training (e.g., Refs. 10, 24), the present study was designed to investigate such potential adaptations after LVT by using TMS-related parameters. The presence of a SIT produced by TMS during a MVC has been suggested to evidence that motor cortical output from the cortex is insufficient to fully activate the motor units and produce a maximal force (20). However, while VA_{TMS} has been suggested to preferentially inform about neural adaptations at or above the motor cortex level (20), mechanisms occurring at the spinal cord level cannot be ruled out (71). Nonetheless, VA_{TMS} is a relevant parameter in the investigation of neural adaptations but has surprisingly only rarely been used to assess the effects of training on neural mechanisms (41, 42). This may be explained by some limitations when using TMS to assess voluntary activation (e.g., TMS-induced antagonist coactivation that may influence the size of the superimposed twitch) (71).

In the present study, an 8-wk LVT program led to an improvement of VA_{TMS} on both right and left legs (+4.9% and +6.2%, respectively), while 4 wk of LVT was sufficient to observe significant gains. In line with the increases in MVC, VA_{TMS} remained improved 2 wk after the end of the training intervention (Fig. 6). These results demonstrate that LVT may induce short-term and persistent (at least in the short term) neural adaptations leading to higher maximal neural drive.

The present findings could be linked to the strong activation of Ia spindle afferents during vibration (14, 56, 57). While muscle or tendon vibration may induce a “tonic vibration reflex” depending on the experimental conditions (14), vibration also elicits bilateral somatosensory and motor cortex activation during its application (32, 48–50), via afferent fiber activation from muscle and/or cutaneous receptors (18). This may induce a modulation of corticospinal excitability (31) and explain the contralateral effect observed in our study.

Increased corticospinal excitability has been demonstrated in plantar flexor (39) and extensor carpi radialis (31) muscles during local vibration application. Since long-term potentiation of corticospinal excitability was not induced by LVT in the present study (see below), it remains to be determined how repeated activation of Ia afferents during vibration sessions may have led to greater maximal cortical voluntary activation level. Any changes upstream of the motor cortical output cells (i.e., circuitry of the primary motor cortex, adaptations in the secondary motor cortical areas) may explain the VA_{TMS} augmentation observed after training (8), although changes in spinal/motoneuronal excitability cannot be totally ruled out since it is a single continuous pathway. However, unchanged H-reflex and MEP amplitudes observed in the present study may suggest that 1) an increased intrinsic motoneuronal excitability, 2) an enhanced fusimotor activity, and/or 3) a diminu-

tion of the presynaptic inhibition level exerted on Ia afferents did not contribute to an increased excitability of the motoneuron pool that would have led to higher VA_{TMS} for the same TMS-induced corticospinal volley (34).

Effects of Unilateral Local Muscle Vibration on Corticospinal Excitability

The present study investigated corticospinal excitability through assessment of MEP amplitude and input-output curve-related parameters. MEPs reflect the effect of the summation of excitatory postsynaptic potential onto the alpha motoneuron due to descending volleys from cortical output neurons following TMS (61). Larger MEP values were found during submaximal voluntary contractions (i.e., MEP_{50} and MEP_{75}) than MVCs (i.e., MEP_{MVC}), which is in agreement with previous studies, including some conducted on TA (63, 65). This may be explained by the higher probability for the TMS pulse to be evoked during the refractory period during a maximal (i.e., higher discharge rate) rather than a submaximal voluntary contraction, leading to a lower MEP amplitude (21, 63, 65, 72, 73). To date, only one study has investigated the effect of a chronic vibration intervention on MEP amplitude (76) and reported that WBV coupled with 4 wk of strength training did not further increase the corticospinal excitability over the strength training stimulus alone. In the present study, there were no LVT-induced significant changes in MEP amplitude obtained during MVC or submaximal contractions (Table 2). Since MEP amplitude depends on the synaptic relays of the corticospinal projections at both the cortical and spinal levels (12), spinal excitability was further investigated in the present study through H-reflex recordings. Despite previous work from our team demonstrating increased H-reflex amplitudes in the vibrated leg (34, 37), the present results failed to show similar findings. These discrepancies may be related to differences in 1) the investigated muscles (i.e., TA vs. SOL) or 2) the vibratory protocol parameters (i.e., three 100-Hz sessions per week for 8 wk vs. one 50-Hz session per day for 14 days). However, one must keep in mind that H reflex recorded during submaximal voluntary contractions (20% MVC) does not necessarily reflect the state of spinal circuitry during MVCs (1, 2).

Boltzmann modeling of the input-output curve was further performed to describe corticospinal excitability (6, 12). While several studies have reported significant changes of the extracted parameters after strength training (22, 77), no changes were reported after LVT in the present study. Altogether, these results suggest no effect of LVT on corticospinal excitability, although the assessment of cervico-medullary evoked potential should be considered in future studies to further investigate the effects of LVT on motoneuronal excitability (19, 45).

The discrepancy between strength training and LVT may speculatively be explained by the fact that heavy load and complex movement patterns may facilitate sensorimotor inputs onto the primary motor cortex (54), which could facilitate potential corticospinal adaptations. Although local vibration has been reported to modulate corticospinal excitability during (39) and immediately after (15) exposure, the stimulation provided by vibration in the present study may not have been sufficient to induce long-term potentiation of corticospinal excitability. Alternatively, the relevance of investigating MEP to evidence potential corticospinal excitability might be ques-

tioned (see below). The absence of CSP variations in the present study also suggests that LVT did not lead to alterations in $GABA_B$ receptors within the primary motor cortex, a mechanism suggested to contribute to the reduction of intracortical inhibition observed after short-duration strength training programs (10, 40).

Limitations of Study

Why VA_{TMS} was increased without any remarkable spinal (H reflexes) and/or supraspinal (MEPs and CSPs) changes is unclear. Interestingly, similar results are commonly reported after fatiguing exercise (i.e., decreased VA_{TMS} without any MEP changes) (21, 29, 62). Since it has been shown that MEP amplitude can be altered during (38, 39) or after (17, 35, 64) the application of acute vibration, an increase of the MEP amplitude might have been expected after repeated exposure to local vibration because of neural adaptive processes similar to those reported after strength training interventions (16, 51). The use of MEPs to inform about potential corticospinal adaptations must be questioned. Indeed, MEPs recorded during MVC may be influenced by the high probability for the TMS pulse to be evoked during the refractory period because of the high discharge rate of cortical neurons (21, 63, 65, 72, 73). Since one of the main neural adaptations to training is the increase in motor unit discharge rate (25, 75, 78), it could have masked potential MEP amplitude increases recorded during MVC. On the other hand, MEPs recorded during submaximal voluntary contractions (50% and 75% MVC in the present study) do not necessarily reflect the state of corticospinal excitability during maximal contraction. Since VA_{TMS} informs about the maximal neural drive from the motor cortex through the muscles, it seems hazardous to investigate MEPs evoked during submaximal voluntary contractions to explain VA_{TMS} changes. Furthermore, there is no consensus with regard to MEP changes after strength training when investigated at rest and during submaximal voluntary contractions or MVCs (for review see Refs. 8 and 30). To our knowledge, only one strength training study investigated MEPs recorded during MVCs and no MEP_{max} amplitude changes were observed despite increased VA_{TMS} (42), as reported in the present study.

To better examine cortical adaptations after LVT, the use of functional magnetic resonance imaging or positron emission tomography might be considered in future studies even though such techniques also present some limitations (8). Accordingly, it has been demonstrated that strength training may lead to neural adaptations, such as an enlarged region of activation in sensorimotor cortex (16). With regard to vibration, various studies (49, 50, 59) have shown that application of vibratory stimuli strongly activates the same motor cortical areas as those that are activated during a voluntary contraction (i.e., both motor and sensorimotor cortex and contralateral supplementary motor area). As a result, it has been recently demonstrated that illusory movements provided by vibration may prevent, when performing voluntary movement, the reduced cortical activation of several areas (e.g., sensorimotor cortex, supplementary motor area) induced by immobilization (58). The occurrence of such adaptations, to potentially explain the present results, remains to be determined. Moreover, given the limitations of the methods to assess training-induced corticospinal adaptations (e.g., TMS, EMG, functional magnetic resonance imag-

ing, positron emission tomography) (8), future LVT studies should now use a combination of these methods, and agreement in findings will need to be found before it can be ultimately concluded that central drive changes have occurred.

In conclusion, the present study reports for the first time an increased VA_{TMS} after LVT in both the trained and untrained legs. This was not accompanied by changes in corticospinal excitability and/or inhibition. The present results have practical relevance since the demonstrated neural adaptations, together with functional MVC gains, suggest that LVT is an interesting method of strength training in clinical or aging populations. Indeed, this technique does not require any active contribution from the subject and can easily be performed by patients with weight-bearing restrictions. The long-term effects of LVT, particularly in these populations, remain to be investigated.

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DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the authors.

AUTHOR CONTRIBUTIONS

R.S., L.F., G.Y.M., and T.L. conceived and designed research; R.S. and A.F. performed experiments; R.S. and A.F. analyzed data; R.S., G.Y.M., and T.L. interpreted results of experiments; R.S. prepared figures; R.S., G.Y.M., and T.L. drafted manuscript; R.S., A.F., L.F., A.B., G.Y.M., and T.L. approved final version of manuscript; R.S., G.Y.M., and T.L. edited and revised manuscript.

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Synthèse de l'étude #2 :

Cette étude confirme que l'entraînement par vibration locale est une technique d'entraînement efficace permettant d'augmenter les capacités de production de force maximale chez des sujets sains et jeunes, et s'accompagnant d'adaptations d'origine nerveuse. Suite aux résultats des études #1 et #2, ce travail de thèse visait à apporter de nouvelles évidences sur les effets aigus et chroniques de la vibration locale sur la fonction neuromusculaire en considérant i) de nouvelles méthodes d'évaluation, i.e. stimulation électrique thoracique (étude #3), ii) un nouveau groupe musculaire, i.e. extenseurs du genou et iii) une nouvelle population, i.e. sujets sains et âgés.

ETUDE #3

**UNE EXPOSITION AIGUE À LA VIBRATION MUSCULAIRE DIMINUE
LA CAPACITE DE PRODUCTION DE FORCE DES MUSCLES
EXTENSEURS DU GENOU ET MODULE L'EXCITABILITE DU
SYSTEME NERVEUX CENTRAL**

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EXTENSORS FORCE PRODUCTION AND MODULATES ASSOCIATED CENTRAL
NERVOUS SYSTEM EXCITABILITY*

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RESUME :

Objectif : La vibration locale a récemment été validée comme une méthode efficace pour améliorer la force musculaire. Comprendre les effets aigus de l'application de la vibration locale peut alors aider à comprendre les mécanismes qui sous-tendent cette augmentation de performance musculaire. Cette étude évaluait les effets d'une application prolongée de la vibration locale sur les capacités de production de force et d'excitabilité cortico-spinale des muscles extenseurs du genou, chez de jeunes adultes sains ainsi que chez des sujets sains âgés. **Méthodes :** Vingt-trois sujets adultes (20–75 ans) ont participé à cette étude et étaient testés i) avant et après une exposition prolongée de 30 minutes à la vibration locale vs ii) avant et après une période de repos de 30 minutes. La force maximale volontaire isométrique (MVC) des extenseurs du genou était mesurée. La stimulation magnétique transcrânienne était utilisée pour évaluer le niveau d'activation cortical (VA_{TMS}), les potentiels évoqués moteurs (MEPs) et les périodes de silence (SPs). La stimulation électrique thoracique du faisceau pyramidal, i.e. l'obtention des potentiels évoqués moteurs thoraciques (TMEPs), permettait l'analyse de l'excitabilité spinale de façon plus directe. **Résultats :** La MVC était significativement diminuée après la vibration ($-12,9 \pm 7,7\%$, $p < 0,001$). L'activité électromyographique (EMG) enregistrée lors des MVCs était également diminuée pour les muscles vaste latéral ($-25,1 \pm 10,7\%$, $p = 0,001$) et droit fémoral ($-20,9 \pm 16,5\%$, $p = 0,004$). Les TMEPs ainsi que le ratio MEP/TMEP étaient respectivement diminués et augmentés ($p = 0,01$) après la période de vibration. Aucun changement n'était observé pour les paramètres évalués par TMS (MEPs, SPs). **Conclusion :** Ces résultats confirment notre hypothèse selon laquelle des modulations centrales accompagneraient la diminution de MVC, comme mis en évidence par la diminution de l'activité EMG maximale. Une diminution de l'excitabilité motoneuronale semble être une explication probable à cette moindre commande nerveuse, comme suggéré par la diminution des TMEPs (données obtenues pour 11 sujets jeunes).



An Acute Exposure to Muscle Vibration Decreases Knee Extensors Force Production and Modulates Associated Central Nervous System Excitability

Robin Souron^{1,2}, Thibault Besson^{1,2}, Chris J. McNeil³, Thomas Lapole² and Guillaume Y. Millet^{1*}

¹Human Performance Laboratory, Faculty of Kinesiology, University of Calgary, Calgary, AB, Canada, ²Laboratoire Interuniversitaire de Biologie de la Motricité, UJM Saint-Etienne, University Lyon, Saint-Etienne, France, ³School of Health and Exercise Sciences, University of British Columbia, Kelowna, BC, Canada

Local vibration (LV) has been recently validated as an efficient training method to improve muscle strength. Understanding the acute effects may help elucidate the mechanism(s). This study aimed to investigate the effects of a single bout of prolonged LV on knee extensor force production and corticospinal responsiveness of vastus lateralis (VL) and rectus femoris (RF) muscles in healthy young and old adults. Across two visits, 23 adult subjects (20–75 years old) performed pre- and post-test measurements, separated by 30-min of either rest (control; CON) or LV. Maximal voluntary contraction (MVC) force was assessed and transcranial magnetic stimulation (TMS) was used to evaluate cortical voluntary activation (VA_{TMS}) as well as the motor evoked potential (MEP) and silent period (SP). In 11 young adults, thoracic electrical stimulation was used to assess the thoracic motor evoked potential (TMEP). Although MVC decreased after both CON ($-6.3 \pm 4.4\%$, $p = 0.01$) and LV ($-12.9 \pm 7.7\%$, $p < 0.001$), the MVC loss was greater after LV ($p = 0.001$). Normalized maximal electromyographic (EMG) activity decreased after LV for both VL ($-25.1 \pm 10.7\%$) and RF ($-20.9 \pm 16.5\%$; $p < 0.001$), while it was unchanged after CON ($p = 0.32$). For RF, the TMEP and MEP/TMEP ratio decreased ($p = 0.01$) and increased ($p = 0.01$) after LV, respectively. Both measures were unchanged for VL ($p = 0.27$ and $p = 0.15$, respectively). No changes were reported for TMS-related parameters. These results confirm our hypothesis that modulations within the central nervous system would accompany the significant reduction of maximal voluntary force. A reduced motoneuron excitability seems to explain the decreased MVC after prolonged LV, as suggested by reductions in maximal EMG (all subjects) and TMEP area (data from 11 young subjects).

Abbreviations: BF, Biceps femoris; EMG, Electromyography; ERT, Estimated resting twitch amplitude; LV, Local vibration; M_{max} , Maximal M-wave recorded on relaxed muscles; MEP, Motor evoked potential; MVC, Maximal voluntary contraction; PNS, Peripheral nerve stimulation; RF, Rectus femoris; RMS, Root mean square; SIT, Superimposed twitch amplitude; SP, Silent period; Pt, Potentiated peak twitch; TMEP, Thoracic motor evoked potential; TMS, Transcranial magnetic stimulation; VA_{TMS} , Voluntary activation assessed with TMS; VL, Vastus lateralis.

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 Australia

Vanesa Bochekezanian,
 Central Queensland University,
 Australia

*Correspondence:

Guillaume Y. Millet
 gmillet@ucalgary.ca

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A concomitant increased cortical excitability seems to compensate for lower excitability at the spinal level.

Keywords: cortical voluntary activation, corticospinal excitability and inhibition, local vibration, thoracic electrical stimulation, transcranial magnetic stimulation

INTRODUCTION

In recent years, a prolonged (20–60 min) period of local vibration (LV) has been validated as an efficient training method to increase muscle strength in healthy young subjects for plantar flexor (Lapole and Pérot, 2010) and dorsiflexor muscles (Souron et al., 2017) as well as for knee extensor muscles in old subjects (Tankisheva et al., 2015). Because this method does not require an active contribution and may be applied while the subject is relaxed (sitting, lying down), prolonged LV may be particularly beneficial for specific populations; e.g., older subjects (Tankisheva et al., 2015). In order to better consider chronic uses, it is important to understand acute effects. A single exposure to prolonged LV can induce a significant neuromuscular workload in healthy young subjects, as indicated by the decrease of maximal voluntary contraction (MVC) force reported after 20–30 min of LV for knee extensor (Kouzaki et al., 2000; Jackson and Turner, 2003), plantar flexor (Ushiyama et al., 2005) and first dorsal interosseous muscles (Shinohara et al., 2005).

As with neuromuscular fatigue induced by “traditional” exercise, the vibration-induced decreased MVC may arise from central and/or peripheral mechanisms. An acute exposure to 20–30 min of LV failed to modulate mechanisms downstream of the neuromuscular junction (Ushiyama et al., 2005; Herda et al., 2009), so it appears the decreased MVC is explained by neural alterations, likely induced by the well-reported strong activation of Ia afferents by vibratory stimuli (Burke, 1980). When vibration exposure is prolonged, a decrease in alpha motoneuron activity has been reported (Bongiovanni and Hagbarth, 1990; Bongiovanni et al., 1990). This is likely linked to an attenuation of Ia afferent discharge, supported by reductions in spinal loop excitability after prolonged LV (Heckman et al., 1984; Hayward et al., 1986; Fry and Folland, 2014; Farabet et al., 2016). Based on the lack of changes in the F-wave (Christova et al., 2011; Lapole et al., 2012b), it has been argued that intrinsic motoneuronal excitability is not impacted after prolonged LV; however, many authors have suggested the F-wave provides a flawed measure of motoneuron excitability (for review, see McNeil et al., 2013). Responses to electrical stimulation of the descending corticospinal tract at the level of the mastoids (cervicomedullary motor evoked potential, CMEP) or thoracic spine (thoracic motor evoked potential, TMEP) provide the most direct assessment of the motoneuron pool’s responsiveness to synaptic input because: (i) a large proportion of the response is monosynaptic for the upper limb (Petersen et al., 2002) and probably the lower limb (Martin et al., 2008); and (ii) evidence exists that descending tracts are not influenced by presynaptic inhibition (Nielsen and Petersen, 1994). Despite the utility of corticospinal tract stimulation, to date, no study has examined the response of CMEPs or TMEPs to prolonged LV.

Although it is intuitive that prolonged LV has the potential to modulate the spinal level, transient vibration increases Ia afferent input to both motor and sensorimotor cortices as well as the contralateral supplementary motor area (Naito and Ehrsson, 2001; Romaiguère et al., 2003) suggesting prolonged LV could also have a supraspinal impact (Pamukoff et al., 2016a, Pamukoff et al., 2016b). The motor evoked potential (MEP) in response to transcranial magnetic stimulation (TMS) of the motor cortex can provide an index of cortical excitability following an intervention, if one considers the MEP along with a valid measure of motoneuronal excitability (i.e., normalizes the MEP to the CMEP or TMEP). It is unclear how prolonged LV affects cortical excitability because no previous study has normalized the MEP in this manner. Furthermore, the data which exist are equivocal as MEPs have been reported to increase (Steyvers et al., 2003; Lapole et al., 2012b), decrease (Steyvers et al., 2003; Farabet et al., 2016), or remain unchanged (Lapole et al., 2012b; Lapole and Tindel, 2015) after prolonged LV using frequencies from 50 Hz to 100 Hz and amplitudes from 0.2 mm to 1 mm.

When applied during a voluntary contraction, TMS may also inform about GABA_B-mediated intracortical inhibition through the assessment of the silent period (SP), which is the interval of muted electromyographic (EMG) activity that follows the MEP (Terao et al., 2000). More evidence is required, but we recently showed that 30 min of LV (frequency: 100 Hz; amplitude: 1 mm) did not impact SP duration in the tibialis anterior (Farabet et al., 2016). Finally, TMS may also assess the level of corticospinal drive (voluntary activation, VA_{TMS}) by evoking superimposed twitches (SIT) during voluntary contraction (Todd et al., 2003). Our team recently showed no changes in VA_{TMS} for dorsiflexor muscles after a 30-min LV period (Farabet et al., 2016) but the effects of LV on VA_{TMS} still remain to be tested on knee extensor muscles, an important functional muscle group (Hurley et al., 1998) which is susceptible to a fatigue-related impairment of voluntary activation (Millet et al., 2011; Jubeau et al., 2014).

While chronic use of LV has been reported to be an efficient means to increase muscle strength (Lapole and Pérot, 2010; Lapole et al., 2013; Souron et al., 2017), a greater understanding of acute effects of LV is needed to inform effective long-term use (training). Thus, this study investigated the effects of a single exposure to prolonged LV on force production capacities and associated corticospinal properties (e.g., VA_{TMS}, TMEPs, MEPs, SPs) of knee extensor muscles in healthy adults. Due to the potential neuromuscular benefits LV could have in a less mobile population (e.g., elderly), we included a small sample of old subjects to probe the possibility of age-related differences in the response to prolonged LV. Without consideration of age, we hypothesized that modulations in corticospinal excitability would accompany the significant reduction of MVC force.

MATERIALS AND METHODS

Subjects

Twenty-three healthy subjects volunteered for this study after giving their informed consent. The study included 15 young (11 men and 4 women, age: 28 ± 6 year; height: 175 ± 8 cm; weight: 70 ± 9 kg) and eight old (2 men and 6 women, age: 65 ± 5 year; height: 168 ± 15 cm; weight: 72 ± 10 kg) subjects. This study was carried out in accordance with the recommendations of the local ethics committee (Conjoint Health Research Ethics Board, University of Calgary) with written informed consent from all subjects. All subjects gave written informed consent in accordance with the Declaration of Helsinki. The protocol was approved by the local ethics committee (Ethics ID: REB #15-2752). All subjects were free of lower-limb injury during the previous 3 months, had no contraindications to TMS (Rossi et al., 2011), and no acute or chronic neurological disorders and trauma. Subjects were not informed of the investigators' hypotheses, only that the effect of LV was being tested. They were instructed to abstain from caffeine for a minimum of 12 h before each session.

Experimental Design

Subjects completed a familiarization session to get used to the correct development of knee extension maximal isometric force and the electrical and magnetic stimulations. Then, subjects were tested twice in random conditions (crossover design) on two separate days with a 4-week interval. No specific recommendations were given to the subjects during the 4-week period. They were only asked not to change their usual physical activities. The subjects were randomly divided into two groups with the first one starting with the control condition (CON) and the second one starting with the vibration condition (LV). This was inverted for the second session. Both sessions took place at the same time of the day, to avoid circadian variations.

Subject Set-Up

Knee extensor force of the right lower limb was measured during voluntary contraction by a calibrated force transducer (Omega Engineering Inc., Stamford, CT, 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 three belts across the thorax and waist. During all measurements, subjects were provided real-time feedback of the force trace on a screen, and guidelines were added when subjects had to maintain a targeted submaximal level of MVC.

EMG activity of the vastus lateralis (VL), rectus femoris (RF) and biceps femoris (BF) was recorded with pairs of self-adhesive surface electrodes (Meditrace 100, Covidien, Mansfield, MA, USA) placed at the distal end of each muscle of interest in a bipolar configuration with a 30-mm interelectrode distance (Figure 1B). 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. EMG signals were amplified with an octal

bio-amplifier (ML138, ADInstruments, Bella Vista, Australia), bandpass filtered (5–500 Hz) and analog-to-digally converted at a sampling rate of 2000 Hz by PowerLab System (16/35, ADInstruments). All data were analyzed offline using Labchart 8 software (ADInstruments).

Local Vibration

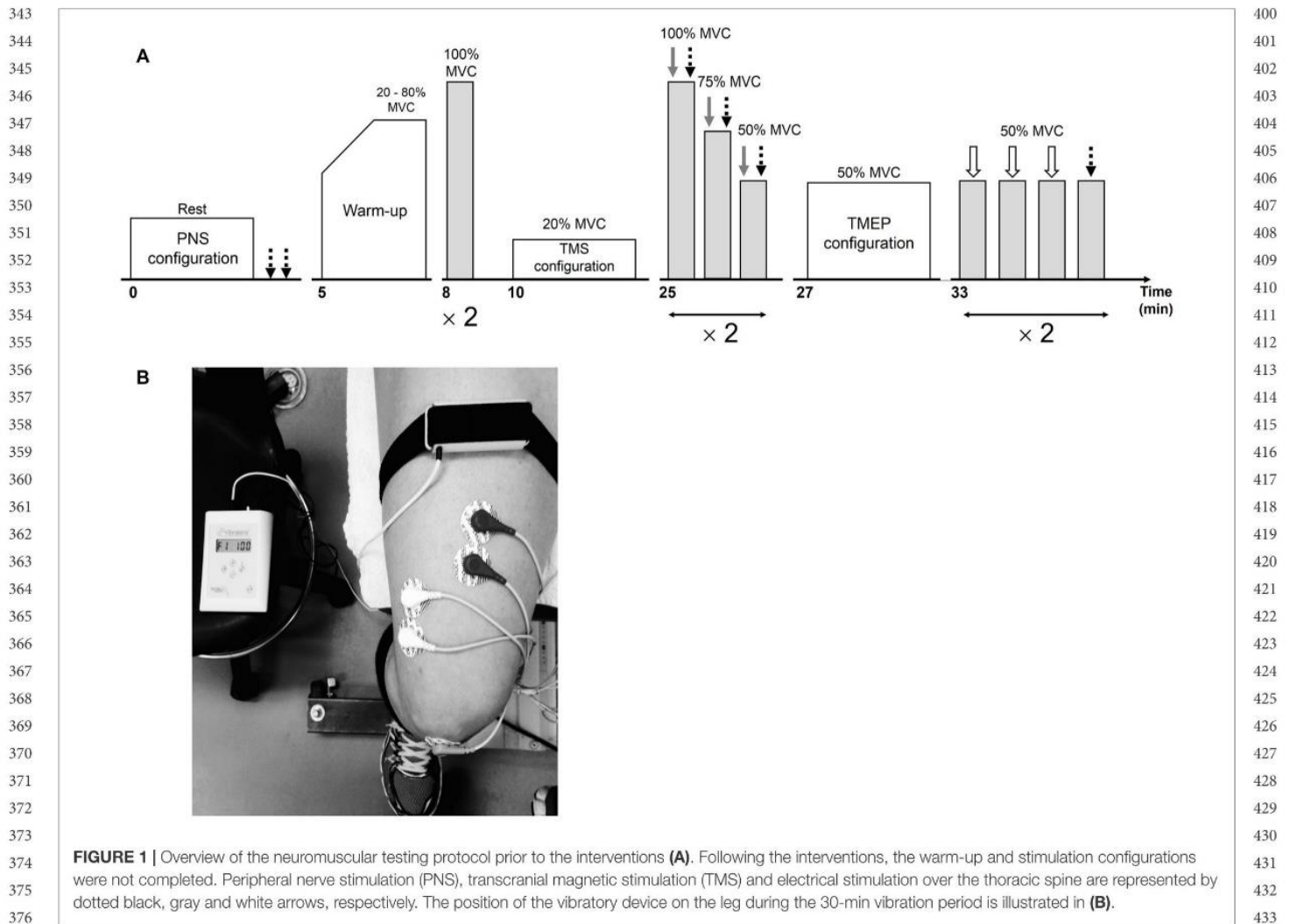
The vibrating device (VB 115, Techno Concept, Mane, France) was applied locally and strapped directly on the right RF muscle (40% of the muscle length from the upper edge of the patella to the anterior superior iliac spine) using elastic Velcro fasteners (Figure 1B) for the LV condition. During CON, the vibrating device was also placed on the leg but was turned off. The right leg was the dominant one for 21 out of 23 subjects (the two subjects with the left leg as the dominant one belonged to the young group). As Ia afferents are sensitive to a small vibration amplitude (Roll et al., 1989) and fire synchronously with vibration frequencies up to 80–120 Hz (Roll and Vedel, 1982; 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 team (Farabet et al., 2016).

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) taped to the skin into the femoral triangle and a 50×90 mm anode (Durastick Plus; DJO Global, Vista, CA, USA) in the gluteal fold. To determine the optimal intensity of stimulation for M-wave measurement, single stimuli were delivered incrementally by steps of 10 mA until resting M-wave (M_{max}) and twitch amplitudes plateaued. The optimal intensity was then increased by 30% to confirm supramaximality.

Transcranial Magnetic Stimulation

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, six marks were drawn on the cap: the vertex, 1 and 2 cm posterior to the vertex and 1 cm to the left of these three 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 a small MEP amplitude in the antagonist BF, in response to stimulation at a known suprathreshold stimulator output (50% maximum) during a 10% MVC knee extension. When optimal agonist 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, four contractions were performed at 10 s intervals. A rest period of 10 s separate each intensity. In one 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 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 to those recorded in VL and RF and did not increase substantially with an increase in stimulator output (Figure 2). Mean TMS intensities were $67 \pm 12\%$ and $65 \pm 11\%$ stimulator output for CON and LV, respectively.

Thoracic Electrical Stimulation

To find the optimal intensity used to elicit TMEPs, the descending corticospinal tract was stimulated over the thoracic level during brief voluntary knee extensors contractions at 50% MVC. Responses were collected during contraction because large TMEPs are difficult to acquire at rest, when motoneuron excitability is low (Martin et al., 2008). A constant-current stimulator (DS7A, Digitimer) was used to evoke TMEPs by passing a single rectangular electrical pulse with 1-ms duration and 400 V maximal output voltage between surface electrodes positioned between the spinous processes of T3 and T4 (cathode) and 5–10 cm above (anode; Ugawa et al., 1991; Aboudarda et al., 2015). The intensity of stimulation was incrementally increased by steps of 5 mA until the TMEP peak-to-peak amplitude was approximately 20%–30% of the M-wave obtained at 50% MVC ($M_{\max,50}$, see below). Because of: (i) the discomfort produced by the electrical stimulus of the thoracic spine; and (ii) the difficulty to obtain responses of sufficient size (McNeil et al., 2013), the old subjects were not asked to perform TMEP measurements. Thus, only 11 young subjects (9 men and 2 women) underwent electrical stimuli of the thoracic spine

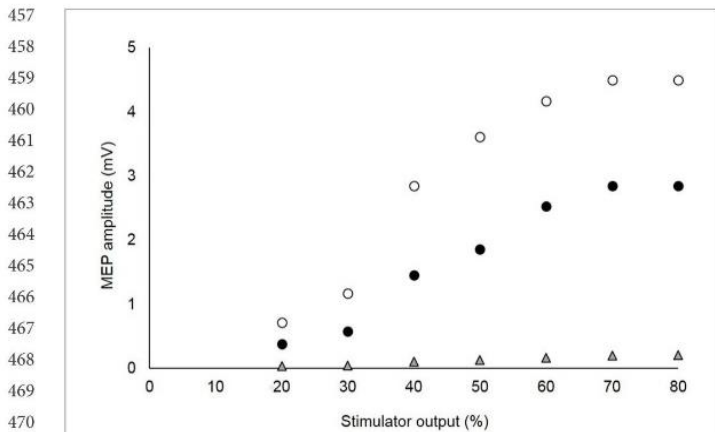


FIGURE 2 | Stimulus-response curves of motor evoked potentials (MEPs) recorded from agonist and antagonist muscles in a single, representative subject. The optimal stimulation intensity was that which showed a plateau of the vastus lateralis (VL; white circles) and rectus femoris (RF; black circles) MEPs, without a marked increase of the MEP for the antagonist biceps femoris (BF; gray triangles). For this subject, 70% of the maximal stimulator output was chosen as the optimal intensity.

(4 out of the 15 young subjects did not performed TMEP measurements due to the discomfort produced by thoracic electrical stimulation). The mean thoracic electrical stimulation intensity was 53.0 ± 14.8 mA and 52.5 ± 16.4 mA for CON and LV, respectively.

Experimental Procedures

The experimental procedures are illustrated in **Figure 1**. A testing session consisted of neuromuscular measurements performed before (PRE; **Figure 1A**) and after (POST) a 30-min resting (CON) or LV period (LV). First, the optimal position and intensity of stimulation for peripheral nerve stimulation (PNS) were determined in order to assess resting M-waves (M_{\max}) for RF and VL. Then, after a standardized warm-up consisting of three brief (~ 3 s) submaximal knee extensor isometric voluntary contractions at 20, 40, 60 and 80% MVC, the subjects performed two brief (~ 3 s) MVCs interspaced by 1 min. Optimal coil position and intensity for TMS were then established. Cortical voluntary activation, i.e., VA_{TMS} , was calculated using two series of three 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, optimal position and intensity for electrical stimulation over the thoracic spine was determined and two series of four brief (~ 3 s) contractions at 50% MVC were performed. Rest periods of 15 s and 1 min were provided between contractions within a series and between the series, respectively. Thoracic stimulation (first three contractions) or PNS (last contraction) was applied to elicit TMEPs and M-waves, respectively. The subjects who opted out of thoracic stimulation still performed these four submaximal

voluntary contractions at 50% MVC without receiving any form of stimulation. Stimulation sites and intensities were not re-established after the CON or LV period so subjects started with the first series of VA_{TMS} measurements 10 s after the intervention (the second series began at $\sim 1:55$). The two series of contractions at 50% MVC (to collect TMEP and M_{\max}) started at $\sim 3:40$ and $\sim 5:35$. Considering the time-course of the post-LV assessments, it is certainly possible there was an attenuation of some effects during our measurement period, representing a limitation in the interpretation of our normalized evoked EMG data.

Data Analysis

As results for M-wave, MEP and TMEP peak-to-peak amplitudes and areas behaved similarly, only areas are reported. M-wave, MEP and TMEP areas were measured between cursors placed at the beginning, i.e., initial deflection from baseline, and the end, i.e., second horizontal crossing, of the evoked potentials (see **Figure 1D** in Martin et al., 2006). Evoked EMG data (M-wave, MEP, TMEP and SP) are presented as the average values of all responses collected pre- and post-intervention. A representative trace of the three types of evoked potentials obtained during a submaximal voluntary contraction at 50% MVC for PRE and POST sessions in LV is displayed in **Figure 3**.

PNS

M-wave areas were measured from electrical nerve stimulations in both relaxed (M_{\max}) and contracted VL and RF ($M_{\max_{50}}$ and $M_{\max_{MVC}}$ elicited during 50% and 100% MVC, respectively). In parallel to M_{\max} measurement, the amplitude of the peak twitch (Pt) evoked during a relaxed state (**Figure 1A**) was also determined as a mean of the recorded twitches.

Force and Voluntary EMG

Maximal force was considered as the peak value recorded before the TMS stimulus from the four MVCs pre- and the two MVCs post-intervention. Root mean square (RMS) EMG was calculated for VL (RMS_{VL}) and RF (RMS_{RF}) muscles over a 500-ms period after maximal force. RMS_{VL} and RMS_{RF} were then normalized to $M_{\max_{MVC}}$.

TMS

VA_{TMS} was measured by the modified twitch interpolation technique (Todd et al., 2003). In brief, the estimated resting twitch (ERT) was determined as the y-intercept of a linear regression of SIT amplitude and absolute voluntary force during the two series of contractions at 100, 75 and 50% MVC (**Figure 3B**), i.e., one ERT derived from six data points. The regression of voluntary torque and the SIT torque was linear (i.e., $r > 0.9$; Hunter et al., 2006) for all series ($0.91 < r < 0.99$) so no data were excluded from VA_{TMS} statistical analysis. VA_{TMS} was then assessed with the equation:

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

where SIT_{MVC} is the mean SIT evoked during the two contractions at 100% MVC.

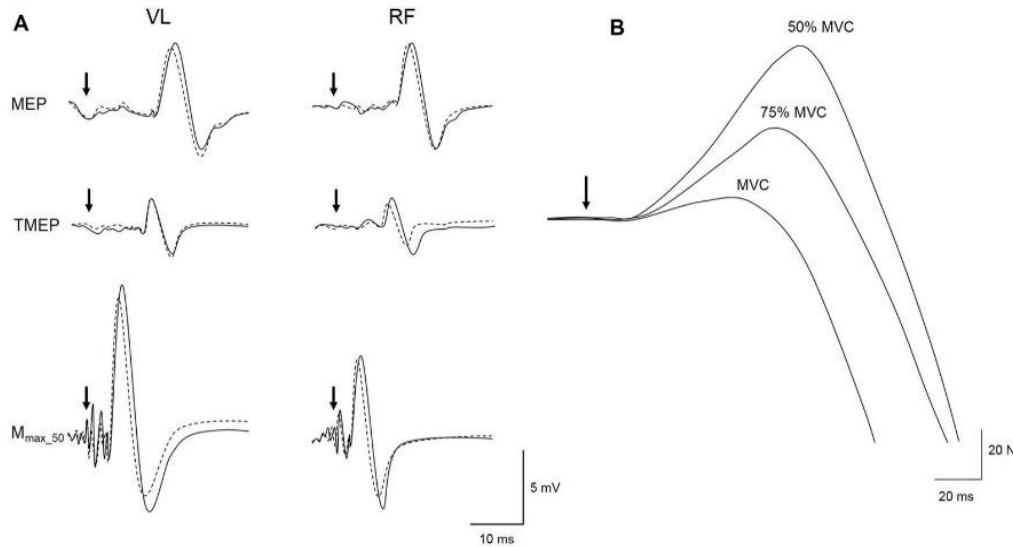


FIGURE 3 | Representative trace of a MEP, thoracic motor evoked potential (TMEP) and M-wave (M_{\max_50}) recorded for local vibration (LV) session at PRE (solid line) and POST (dotted line) during a 50% maximal voluntary contraction (MVC) submaximal voluntary contraction on VL and RF muscles (A). Raw traces from a single subject of the TMS superimposed twitches (SIT) evoked during maximal (MVC) and submaximal voluntary contractions at 75 and 50% MVC are displayed in (B). Black arrows represent the time of magnetic or electrical stimulations.

The area of VL and RF MEPs elicited by TMS during 100, 75 and 50% MVC contractions were normalized to the M-wave measured at the same contraction intensity. As a maximal M-wave was not recorded from BF in the experimental protocol, MEP_{BF} are presented as absolute areas rather than a percentage of the maximal output of the motoneuron pool. The inability to standardize the relative activation of antagonist motoneurons may compromise the validity of the VA_{TMS} measured for the knee extensors (Todd et al., 2016). 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).

TMEP

VL and RF TMEP areas were normalized to M_{\max_50} to account for possible post-intervention changes in peripheral excitability.

Statistical Analysis

The sample size was calculated at the outset for an expected “medium” effect size ($f^2 = 0.25$) for MVC change between conditions, with α level of 0.05, power ($1-\beta$) of 0.80 and correlation among repeated measures of 0.85. Thus, including at least 20 subjects was necessary to reach the desired power of 0.80 on a two-way repeated-measures ANOVA, i.e., condition (CON or LV) \times time (PRE or POST). However, the sample size calculation was performed without taking the factor “age” into consideration. Therefore, 20 subjects would theoretically be enough for detecting time and condition effects, but not group effects. Thus, it is possible that age effects were not detected due to insufficient statistical power, representing one of the main limitation of the current study. Statistical analyses

were performed with Statistica software (StatSoft Inc., Tulsa, OK, USA). All variables were normally distributed (Shapiro-Wilk normality test). For ANOVA analyses, homogeneity of variance was verified by Levene’s test. Three-way repeated measures ANOVA were performed for MVC and VA_{TMS} [group (young or old) \times condition (CON or LV) \times time (PRE, POST)], as well as for TMEP analysis [condition (CON or LV) \times time (PRE, POST) \times muscle (VL, RF)]. Four-way repeated measures ANOVA were performed for the other neuromuscular parameters, i.e., MEPs, SPs, EMG RMS and M-waves [group (young or old) \times condition (CON or LV) \times time (PRE, POST) \times muscle (VL, RF)]. *Post hoc* analyses were performed using Newman-Keuls testing when the ANOVA identified significant differences. Partial eta square (η^2) was reported as an estimate of effect size, with $\eta^2 \geq 0.07$ and $\eta^2 \geq 0.14$ used as moderate and large effects, respectively (Cohen, 1988). We also calculated difference scores for each session and report their mean and 95% confidence interval. Statistical significance was set at $p < 0.05$. All data are presented in the text and figures as mean \pm standard deviation (SD).

RESULTS

P values from all ANOVA analyses are presented in **Table 1**. No differences between the two conditions (i.e., CON or LV) were found at baseline (i.e., PRE) for any parameters ($p > 0.05$). Although insufficient statistical power could have prevented detection of age-related differences (i.e., caused a type II error), because there was no effect of the group (young vs. old) on the magnitude of changes reported in this study, as demonstrated by the lack of significant group \times condition \times time

interaction, data from young and old participants were pooled.

MVC Force, RMS and Voluntary Activation

There was a significant condition × time interaction for MVC ($F_{(1,21)} = 4.95$; $p = 0.03$; $p\eta^2 = 0.19$). Although MVC was significantly decreased at POST for both CON ($-6.3 \pm 4.4\%$, $p = 0.01$) and LV groups ($-12.9 \pm 7.7\%$, $p < 0.001$), the MVC loss was significantly greater after LV ($p = 0.001$; **Figure 4A**). Similarly, a significant condition × time interaction ($F_{(1,21)} = 17.42$; $p < 0.001$; $p\eta^2 = 0.45$) was found for EMG RMS measured during MVC, with a significant decrease reported POST LV for both VL ($-25.1 \pm 10.7\%$) and RF ($-20.9 \pm 16.5\%$) but no significant changes POST CON ($p = 0.32$; **Figure 4B**). Unlike force and RMS, there was no significant condition × time interaction for VA_{TMS} ($F_{(1,21)} = 1.08$; $p = 0.30$; $p\eta^2 = 0.04$); however, there was a significant main effect of time ($F_{(1,21)} = 12.15$; $p = 0.02$; $p\eta^2 = 0.36$), with decreased VA_{TMS} for POST measurements (**Table 2**).

MEP, SP, M-wave and Pt

Condition × time × muscle interactions were not significant for MEP, SP or M-wave at any contraction strength ($F_{(1,21)} = 0.11-1.74$; $p > 0.05$; $p\eta^2 = 0.04-0.21$; **Table 2**). However, in some instances, there was a main effect of time (**Table 1**) such that SP duration increased and M-wave area decreased from pre- to post-intervention for pooled CON and LV data ($p < 0.05$, **Table 2**). The condition × time interaction was not significant for Pt ($F_{(1,21)} = 0.02$; $p = 0.88$; $p\eta^2 = 0.01$); however, there was a significant main effect of time ($F_{(1,21)} = 46.64$; $p < 0.001$; $p\eta^2 = 0.71$), with decreased Pt for POST measurements (**Table 2**).

TMEP and MEP/TMEP Ratio

Based on data from 11 young subjects, a significant condition × time × muscle interaction was found for TMEP ($F_{(1,10)} = 16.95$; $p = 0.01$; $p\eta^2 = 0.32$). It was significantly decreased POST LV for the RF ($p = 0.001$) but not the VL ($p = 0.27$), while it remained unchanged after CON for both muscles ($p = 0.21$ and $p = 0.67$ for VL and RF, respectively; **Figure 5A**).

In these subjects, a significant condition × time × muscle interaction was found for MEP/TMEP ratio ($F_{(1,10)} = 9.83$; $p = 0.01$; $p\eta^2 = 0.39$). It was significantly increased POST LV on the RF ($p = 0.002$) while it was unchanged for VL ($p = 0.15$). No significant changes were detected after CON for either RF ($p = 0.96$) or VL ($p = 0.85$) muscles (**Figure 5B**).

DISCUSSION

The principal aim of this study was to investigate the effects of a single bout of prolonged LV on knee extensor force

TABLE 1 | p values from all ANOVA analyses.

	Condition	Time	Group	Condition × time	Time × group	Condition × muscle	Muscle × group	Condition × muscle × group	Muscle × time × group	Condition × muscle × time	Condition × muscle × time group
MVC	0.11	<0.001	0.002	0.03	0.04	<0.001	0.002	0.85	0.80	0.98	0.25
RMS	0.08	<0.001	0.003	<0.001	0.16	<0.001	0.002	0.85	0.80	0.98	0.25
VA_{TMS}	0.67	0.02	0.06	0.30	0.26	<0.001	0.01	0.19	0.31	0.90	0.87
MEP_{MVC}	0.80	0.75	0.30	0.93	0.27	<0.001	0.01	0.98	0.21	0.31	0.75
MEP_{75}	0.68	0.75	0.10	0.24	0.23	<0.001	0.03	0.81	0.16	0.12	0.49
MEP_{50}	0.22	0.45	0.08	0.20	0.89	<0.001	0.82	0.78	0.06	0.12	0.22
SP_{MVC}	0.65	0.05	0.54	0.45	0.46	0.73	0.99	0.31	0.15	0.02	0.64
SP_{75}	0.74	0.01	0.64	0.73	0.55	0.42	0.44	0.50	0.75	0.69	0.71
SP_{50}	0.53	0.05	0.65	0.22	0.85	0.15	0.99	0.50	0.75	0.002	0.71
TMEP	0.52	0.15	0.12	0.12	0.12	0.003	0.05	0.79	0.53	0.01	0.31
$MEP/TMEP$	0.93	0.14	<0.001	0.08	0.13	0.27	0.05	0.82	0.72	0.43	0.41
M_{max}	0.76	0.52	<0.001	0.94	0.001	<0.001	0.12	0.82	0.72	0.70	0.41
$M_{max,50}$	0.61	0.01	0.001	0.84	0.001	<0.001	0.12	0.82	0.72	0.70	0.41
Pt	0.27	<0.001	0.03	0.88	0.03	<0.001	0.12	0.82	0.72	0.70	0.41

MVC, maximal voluntary contraction; RMS, maximal EMG activity expressed as a percentage of maximal M-wave; VA_{TMS} , maximal voluntary activation assessed by TMS; MEP, motor evoked potential; SP, silent period; MEP_{MVC} , measurement performed during maximal voluntary contraction; MEP_{75} , measurement performed during submaximal voluntary contractions at 75% MVC; MEP_{50} , measurement performed during submaximal voluntary contractions at 50% MVC; M_{max} , M-wave recorded at rest.

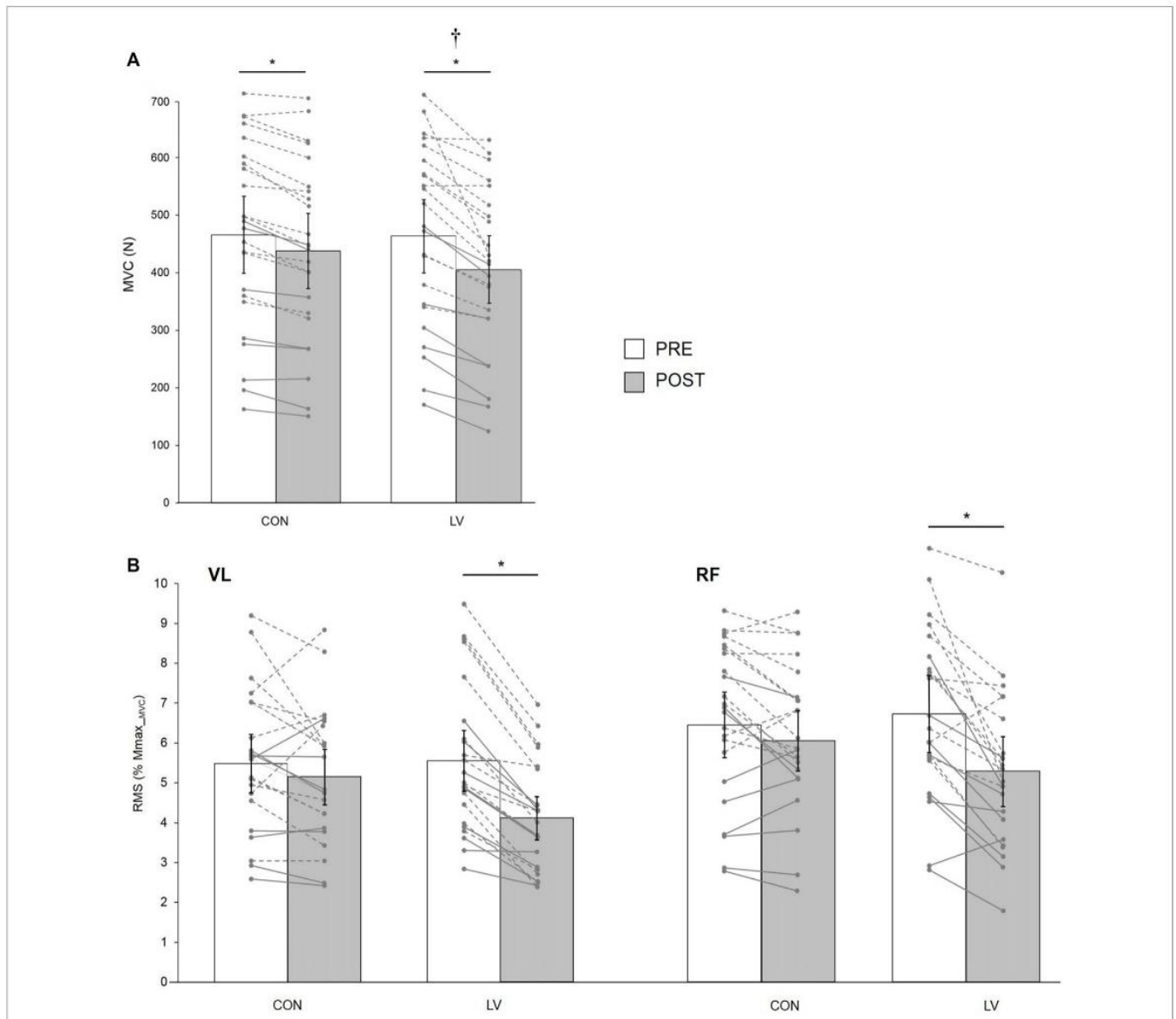


FIGURE 4 | Knee extensor MVC force (MVC, **A**) and associated maximal electromyography (EMG) root-mean-square (RMS) normalized to M_{max_MVC} for VL and RF muscles (**B**) recorded before (PRE) and after (POST) a 30-min resting (CON) or LV period. The displayed data are mean values. Error bars denote the 95% confidence interval. Data from individual young (dashed lines) and old (solid lines) subjects are displayed for both testing sessions at PRE and POST measurements. *Significantly different from PRE; † significantly different from POST CON ($p < 0.05$).

production capacities and associated corticospinal properties in healthy adults. In the current study, LV was applied for a prolonged (30-min) period. While it has been reported that the efficiency of the spinal loop is increased during the first seconds of exposure to the LV stimulus and may thus in turn evoke an extra voluntary force (Magalhães and Kohn, 2010; Magalhães et al., 2013), prolonged exposure has been reported to reduce spinal excitability (Fry and Folland, 2014) and maximal muscle output (Jackson and Turner, 2003; Saito et al., 2016a), with associated potential supraspinal adaptations (Smith and Brouwer, 2005; Lapole et al., 2012b). However, we recently showed that repeated sessions of prolonged LV can enhance both neural drive and maximal strength (Souron et al., 2017).

Here, we report a reduction in knee extensor MVC torque after a single bout of prolonged LV, which is accompanied by: (i) a reduction of maximal EMG activity for both VL and RF muscles, as well as, in young adults; (ii) a significant decrease in TMEP areas; and (iii) increase in MEP/TMEP ratio for RF only.

This study reported a significant MVC decrease after a 30-min prolonged LV period, which is consistent with previous results obtained for knee extensor (Kouzaki et al., 2000; Konishi et al., 2002, 2009; Jackson and Turner, 2003; Richardson et al., 2006; Saito et al., 2016a), plantar flexor (Yoshitake et al., 2004; Ushiyama et al., 2005; Herda et al., 2009) and first dorsal interosseous muscles (Shinohara et al., 2005) following

TABLE 2 | V_{TMS}, MEP, SP, M-wave and Pt measurements before (PRE) and after (POST) a 30-min resting (CON) or local vibration (LV) period.

	Control		Vibration	
	Pre	Post	Pre	Post
V _{TMS} (%)	92.9 ± 6.0	91.7 ± 6.9	93.0 ± 6.6	90.8 ± 7.0
MEP _{MVC_VL} (% M _{sup_100})	46.4 ± 14.9	45.6 ± 13.8	47.4 ± 15.2	45.7 ± 12.6
MEP _{75_VL} (% M _{sup_75})	61.2 ± 12.5	59.5 ± 14.2	57.0 ± 12.2	57.8 ± 13.8
MEP _{50_VL} (% M _{sup_50})	63.6 ± 17.3	62.1 ± 14.7	57.7 ± 16.7	56.0 ± 16.4
MEP _{MVC_RF} (% M _{sup_100})	63.0 ± 21.2	62.7 ± 18.0	63.2 ± 18.9	64.1 ± 21.2
MEP _{75_RF} (% M _{sup_75})	80.9 ± 19.1	77.5 ± 27.0	77.2 ± 15.2	81.3 ± 22.5
MEP _{50_RF} (% M _{sup_50})	83.6 ± 20.0	81.0 ± 19.9	80.5 ± 13.7	83.3 ± 18.8
MEP _{BF} (mV/s)	1.5E-05 ± 9.95E-06	1.4E-05 ± 8.2E-06	1.4E-05 ± 1.2E-05	1.2E-05 ± 9.2E-06
SP _{MVC_VL} (ms)	258 ± 75	267 ± 76	250 ± 76	262 ± 80
SP _{75_VL} (ms)	258 ± 80	273 ± 83	259 ± 79	266 ± 84
SP _{50_VL} (ms)	262 ± 78	264 ± 76	257 ± 73	264 ± 81
SP _{MVC_RF} (ms)	258 ± 76	262 ± 84	249 ± 78	263 ± 80
SP _{75_RF} (ms)	258 ± 79	265 ± 87	247 ± 81	269 ± 84
SP _{50_RF} (ms)	255 ± 78	263 ± 85	242 ± 79	252 ± 77
M _{max_VL} (mV/s)	0.087 ± 0.034	0.086 ± 0.031	0.088 ± 0.029	0.087 ± 0.029
M _{max_RF} (mV/s)	0.063 ± 0.019	0.063 ± 0.018	0.060 ± 0.015	0.059 ± 0.015
M _{sup50_VL} (mV/s)	0.069 ± 0.028	0.066 ± 0.025	0.070 ± 0.026	0.068 ± 0.024
M _{sup50_RF} (mV/s)	0.055 ± 0.018	0.046 ± 0.014	0.051 ± 0.013	0.042 ± 0.011
Pt (N)	132 ± 43	117 ± 37	137 ± 50	121 ± 47

V_{TMS}: maximal voluntary activation assessed by TMS; MEP: motor evoked potential; SP: silent period; MVC: measurement performed during maximal voluntary contraction; 75: measurement performed during submaximal voluntary contractions at 75% MVC; 50: measurement performed during submaximal voluntary contractions at 50% MVC; VL, vastus lateralis; RF, rectus femoris; BF, biceps femoris; M_{max}, M-wave recorded at rest; 95% CI, 95% confidence interval.

a 20–30 min LV period. For the present study, there was an unexpected decrease of MVC force for CON, i.e., after 30-min of rest. This may be explained by fatigue induced by the large number of contractions that subjects had to perform, as supported by the significant reduced of Pt for CON. Yet, the greater force loss observed for LV confirms the potential for LV to decrease force generation capacity.

To our knowledge, this was only the second study to compare the after-effects of prolonged LV between young and old subjects. The decrease in MVC was similar for young ($-11.9 \pm 8.4\%$) and old ($-14.3 \pm 7.2\%$) subjects, which contradicts the previous report of a greater MVC decrease in young than old subjects (Richardson et al., 2006). These authors suggested a gamma loop function impairment in the old due to an age-related decrease in number and size of type II muscle fibers (Snyder-Mackler et al., 1994). Indeed, the decrease in Ia afferent inputs onto alpha motoneurons has been suggested to predominantly affect the recruitment of high-threshold motoneurons that supply fast-twitch muscle fibers (Bongiovanni et al., 1990). Regardless of the mechanisms, the discrepancy between our results and those reported by Richardson et al. (2006) indicates a need for further investigation of LV-related effects in older adults. This is particularly important given the limited sample size in our study ($n = 8$) and the one conducted by Richardson et al. (2006, $n = 7$).

The ability to produce a maximal level of voluntary force depends on both peripheral and central mechanisms. Evidence based on electrically-evoked twitch (Ushiyama et al., 2005; Herda et al., 2009; Fry and Folland, 2014; Saito et al., 2016a,b) and M-wave amplitudes (Ushiyama et al., 2005; Ekblom and Thorstensson, 2011; Fry and Folland, 2014; Cattagni et al., 2016; Farabet et al., 2016; Saito et al., 2016a,b) seems to rule out an influence of peripheral mechanisms on the MVC decrease commonly seen following prolonged LV. Our results further confirm this interpretation, as there were no differences between CON and LV for: (i) M-wave areas evoked on either relaxed or contracted muscles; and (ii) potentiated peak twitch. Hence, an alteration to the neural command probably fully explains the decrement in force-generation capacity after prolonged LV. In the present study, although cortical voluntary activation (V_{TMS}) was decreased minutely over time, and so indicating some central fatigue in line with MVC impairment in both conditions, it was independent of the condition, i.e., no condition × time interaction effect, which is in agreement with what we recently reported for dorsiflexor muscles (Farabet et al., 2016). The LV-induced reduction in maximal EMG activity for both VL and RF muscles corroborates previous findings for knee extensor (Kouzaki et al., 2000; Konishi et al., 2002, 2009; Jackson and Turner, 2003; Richardson et al., 2006), plantar flexor (Yoshitake et al., 2004; Ushiyama et al., 2005; Herda et al., 2009) and first dorsal interosseous muscles (Shinohara et al., 2005). Based on EMG results, and because vibration-induced excitatory Ia afferents project to both the spinal cord (Eklund and Hagbarth, 1965; De Gail et al., 1966) and cortical structures (Goodwin et al., 1972; Roll and Vedel, 1982; Roll et al., 2012), the decreased MVC observed after LV exposure may be related to a neural drive alteration occurring at a spinal

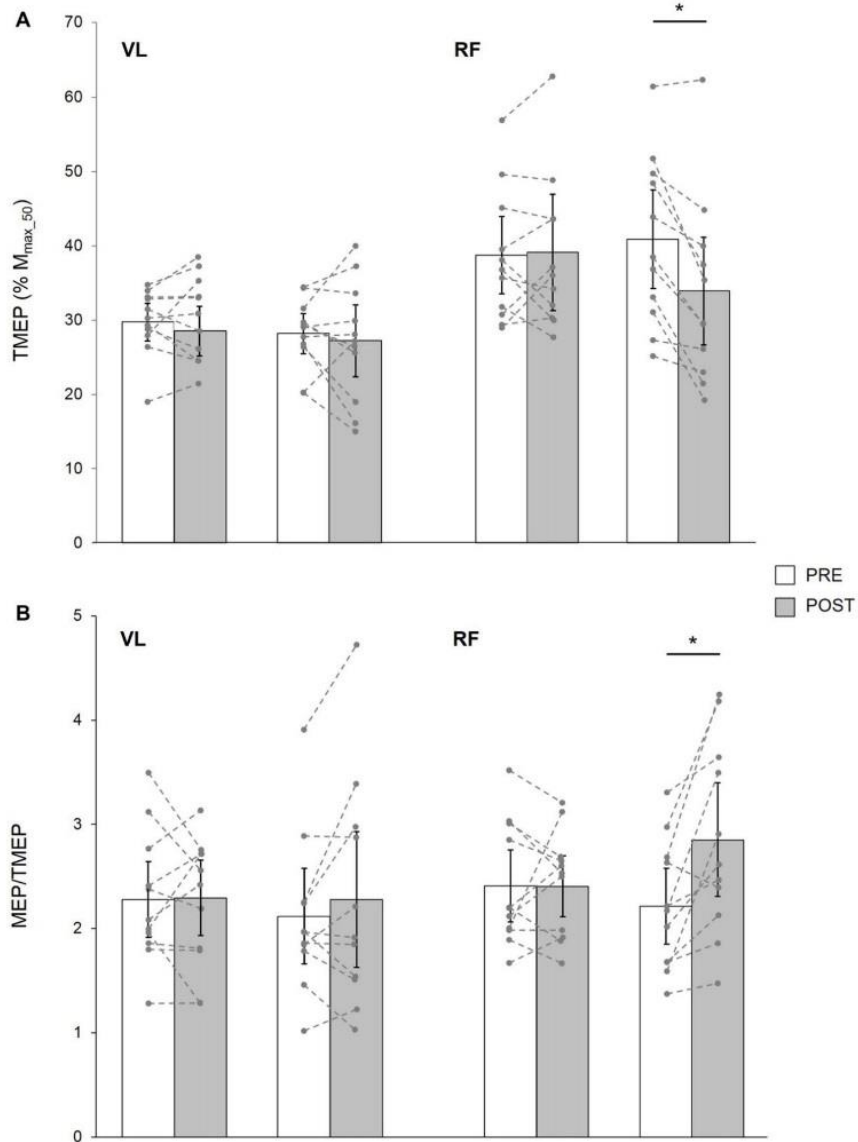


FIGURE 5 | TMEP normalized to M_{max_50} (A) and MEP/TMEP ratios (B) recorded in 11 healthy young subjects for VL and RF muscles before (PRE) and after (POST) a 30-min resting (CON) or LV period. The displayed data are mean values. Error bars denote the 95% confidence interval. Data from the individual subjects are displayed (dashed lines) for both testing sessions at PRE and POST measurements. *Significantly different from PRE ($p < 0.05$).

and/or supraspinal level. It is thus likely that VA_{TMS} was not sensitive enough to detect such neural modulations after an acute exposure to LV.

Although not investigated in the present study, previous results show H-reflex depression after prolonged LV (Heckman et al., 1984; Ushiyama et al., 2005; Ekblom and Thorstensson, 2011; Lapole et al., 2012a,b; Fry and Folland, 2014; Farabet et al., 2016), suggesting an impaired motoneuron excitability with LV. As a measure of motoneuron excitability, the H-reflex suffers the disadvantage to be potentially influenced by presynaptic inhibition at the Ia afferents level (Hultborn et al., 1996). Hence, one of the most novel aspects of this study was to assess motoneuronal excitability in healthy young adults via

stimulation of the corticospinal tract (TMEP) in order to avoid an influence of classical presynaptic inhibition (Nielsen and Petersen, 1994; Jackson et al., 2006). In the present study, TMEP_{RF} was reported to be significantly decreased following the 30-min LV period, while it remained unchanged for TMEP_{VL}. This discrepancy may be explained by the position of the vibratory device on the leg (i.e., over the RF muscle). This likely led to a stronger activation of Ia afferents supplying the RF muscle rather than the VL. The observed reduction in TMEP_{RF} after prolonged LV may imply: (i) impaired excitability of the corticospinal descending tracts; (ii) impaired efficacy in synaptic transmission between corticospinal descending tracts and alpha motoneurons; and/or (iii) impaired intrinsic motoneuronal

1141 properties (Giesebrecht et al., 2010). Although different from
 1142 a vibration intervention, studies of muscle fatigue failed to
 1143 demonstrate impaired excitability of the corticospinal tract
 1144 (Petersen et al., 2003; Giesebrecht et al., 2010) and impaired
 1145 efficacy in synaptic transmission during strong contractions
 1146 (Petersen et al., 2003). Hence, we believe that a reduction in
 1147 intrinsic motoneuronal excitability is the most likely explanation
 1148 for our observed decrease in TMEP size following prolonged
 1149 LV. Such acute modulations in motoneuronal properties may be
 1150 a plausible explanation to the functional effects reported after
 1151 longer-term use (Lapole and Pérot, 2010; Iodice et al., 2011;
 1152 Lapole et al., 2013; Tankisheva et al., 2015; Souron et al., 2017).
 1153 However, these results should be interpreted with caution since
 1154 TMEP data were collected from only 11 young subjects, reducing
 1155 the statistical power for this analysis. Also, it remains to be
 1156 investigated whether or not such adaptations could occur in old
 1157 subjects.

1158 It is worth noting that MEPs, either evoked during maximal or
 1159 submaximal voluntary contractions, were unchanged following
 1160 the 30-min prolonged LV period on RF and VL muscles. This
 1161 is consistent with some (Rosenkranz and Rothwell, 2004, 2006;
 1162 Smith and Brouwer, 2005; Lapole et al., 2012b; Lapole and
 1163 Tindel, 2015) but not all studies. Indeed, previous literature
 1164 has reported either increased (Steyvers et al., 2003; Smith and
 1165 Brouwer, 2005; Christova et al., 2011; Lapole et al., 2012b) or
 1166 decreased (Steyvers et al., 2003; Farabet et al., 2016) MEPs after
 1167 prolonged LV using vibration frequencies and amplitudes from
 1168 25 Hz to 100 Hz and 0.2–2 mm, respectively (i.e., comparable
 1169 to the 100 Hz and 1 mm of the present study). Differences
 1170 in the investigated muscles and the vibration parameters may
 1171 account for these discrepancies. Also, the method used to
 1172 determine the optimal TMS intensity (i.e., stimulus-response
 1173 curve vs. active or resting motor threshold) may contribute
 1174 to the differences reported in MEP behavior between these
 1175 studies and ours. Importantly, positioning our MEP data in
 1176 the literature is difficult because none of the aforementioned
 1177 studies included a measure of motoneuron excitability so do
 1178 not include speculation on cortical and spinal influences on the
 1179 MEP. Although MEP size did not change after LV, the reduction
 1180 in the TMEP_{RF} (observed for 11 young subjects) suggests that
 1181 cortical excitability increased with LV in order to compensate
 1182 for the reduced excitability at the spinal level; i.e., without
 1183 an increase in cortical excitability, the MEP would also be
 1184 reduced by the lower motoneuronal excitability. This presumed
 1185 increase in cortical excitability is shown by the larger MEP/TMEP
 1186 ratio after LV. However, this ratio should be interpreted with
 1187 caution because the size of the MEP and TMEP were not
 1188 matched and the potentials were separated by ~1–4 min. Indeed,
 1189 because TMS intensity was set to investigate VA, the MEP is
 1190 approximately twice the size of the TMEP, so is likely testing
 1191 a far greater proportion of the motoneuron pool than the
 1192 TMEP.

1193 Although SP duration increased in some conditions (at
 1194 MVC and 75% MVC for VL and RF, respectively), this
 1195 was independent of the condition since no interaction effect
 1196 was found. Thus, similar to our recent findings in the
 1197 dorsiflexors (Farabet et al., 2016), it appears that LV had no

1198 impact on SP duration. This suggests that acute prolonged
 1199 LV did not alter GABA_B neurotransmission (Werhahn et al.,
 1200 1999) of inhibitory neurons within the primary motor cortex
 1201 projecting onto the pyramidal cells (Inghilleri et al., 1993).
 1202 The technique of paired-pulse TMS should be considered
 1203 in parallel to SP measurement for future studies since
 1204 it has been reported as the more appropriate method to
 1205 measure changes in intracortical inhibition (Kidgell and Pearce,
 1206 2010).

1207 In a small sample of young adults ($n = 6$), it has been reported
 1208 that the effect of brief (20 s) periods of high-frequency vibration
 1209 on neuronal pathways is strongly time-dependent (Magalhães
 1210 et al., 2013). Prolonged LV is unlikely to induce effects with such
 1211 a strong dependence on time, but it is probable that the relative
 1212 importance of different mechanisms would vary immediately
 1213 after, shortly after or at longer periods after stimulation. Hence, it
 1214 would be important for future work to assess the variables of the
 1215 current study at a broader range of times following prolonged LV.

1216 In conclusion, the significant decrease of MVC reported in
 1217 this study after 30-min of LV in an adult population seems to be
 1218 explained primarily by a reduced output from the motoneuron
 1219 pool, as demonstrated by the reduction in maximal EMG activity
 1220 for VL and RF in both young and old subjects. Moreover,
 1221 at least for young subjects, a reduced motoneuron excitability
 1222 may be involved as indicated by decreased TMEP area for RF,
 1223 this finding being reported for the first time in this scientific
 1224 framework. The current results for young subjects also show a
 1225 concomitant increase in cortical excitability after prolonged LV
 1226 as indicated by the increased MEP/TMEP ratio, likely occurring
 1227 to compensate for reduced excitability at the motoneurons.
 1228 Although the absence of TMEP data from old subjects prevents
 1229 speculation on motoneuron excitability in this group, similar
 1230 findings of reduced force generation capacities and EMG activity
 1231 for both young and old subjects may suggest that LV could be as
 1232 efficient to induce neural adaptations in old subjects. In support
 1233 of this suggestion, positive long-term adaptations to prolonged
 1234 LV (e.g., increased maximal strength) have been shown in both
 1235 young (Lapole and Pérot, 2010; Lapole et al., 2013; Souron et al.,
 1236 2017) and old adults (Tankisheva et al., 2015). Notably, any
 1237 speculation on the effects of LV in the elderly is limited by our
 1238 small number of older adults, so future research to elucidate
 1239 the mechanisms of prolonged LV must employ a larger sample
 1240 size.

1241 Although the functional link between the recorded
 1242 parameters and motor performance remains to be elucidated,
 1243 our findings suggest that a single bout of prolonged LV has the
 1244 potential to induce neural modulations in healthy adults. Current
 1245 and previous findings (e.g., Tankisheva et al., 2015; Souron et al.,
 1246 2017) suggest it is conceivable that LV could trigger chronic
 1247 neural adaptations in both healthy young and old subjects that
 1248 may eventually lead to an improvement in muscle performance.
 1249 If, in the future, this proposition is supported by stronger
 1250 experimental findings (especially with a larger sample size for
 1251 the old population), LV could be considered as an efficient
 1252 and alternative training method to the ones classically used
 1253 (e.g., resistance training, neuromuscular electrical stimulation),
 1254 but which have identified limitations in rehabilitation settings.

For example, resistance training may not be applicable to everyone, especially those with significant motor impairments that limit the capacity for volitional exercise (e.g., old or clinical populations). Neuromuscular electrical stimulation avoids such an issue and has been shown to acutely modulate the central nervous system (Bochkezanian et al., 2017) and to improve muscle performance in clinical (Hauger et al., 2017) or old (de Oliveira Melo et al., 2016) populations. However, some limitations (e.g., pain, restricted spatial recruitment of muscle fibers) are commonly associated with this technique (Maffiuletti, 2010) that may make LV a more attractive method for some sensitive subjects.

AUTHOR CONTRIBUTIONS

RS was involved in the conception of the research, the acquisition, analysis and interpretation of the data. RS was also involved in the

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- revision of the manuscript. TB was involved in the conception of the research, the acquisition, analysis and interpretation of the data, as well as in the revision of the manuscript. GYM, TL and CJM were involved in the conception of the research design, the analysis and interpretation of the results and the writing of the manuscript (revising the work). As the contributing author, GYM gave his final approval for submission.

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- 1553 **Conflict of Interest Statement:** The authors declare that the research was
1554 conducted in the absence of any commercial or financial relationships that could
1555 be construed as a potential conflict of interest.
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Synthèse de l'étude #3 :

Les résultats de cette étude montrent que la diminution de force observée après l'application prolongée de vibration s'accompagne de modulations au niveau central, comme suggéré par les diminutions concomitantes du niveau d'activité EMG des muscles VL et RF et des TMEPs.

Face aux modulations aiguës de la fonction neuromusculaire induites par les stimuli vibratoires chez de jeunes adultes sains ainsi que chez des sujets sains âgés, le but de l'étude #4 de ce travail de thèse était d'évaluer l'effet d'une application chronique de la vibration locale sur la fonction neuromusculaire des muscles extenseurs du genou chez ces deux populations.

ETUDE #4

ADAPTATIONS NERVEUSES INDUITES PAR UN ENTRAÎNEMENT DE 4 SEMAINES DE VIBRATION LOCALE SUR LE MUSCLE QUADRICEPS CHEZ DES SUJETS JEUNES ET AGES

Publication associée :

Souron R., Besson T., Lapole T., Millet GY. (2017)

*NEURAL ADAPTATIONS IN QUADRICEPS MUSCLE AFTER 4 WEEKS OF LOCAL
VIBRATION TRAINING IN YOUNG AND OLD SUBJECTS*

Applied Physiology, Nutrition, and Metabolism (en révision)

RESUME :

Objectif : Cette étude évaluait les effets d'un programme d'entraînement de 4 semaines par vibration locale sur les propriétés fonctionnelles et cortico-spinales du muscle quadriceps, chez de jeunes adultes sains ainsi que chez des sujets sains âgés.

Méthodes : Dix-sept sujets (respectivement $n = 9$ et $n = 8$ pour les sujets jeunes et âgés) réalisaient 3 sessions de tests neuromusculaires : avant (PRE_1) et après (PRE_2) une période de 4 semaines de repos, ainsi qu'après ($POST$) un programme d'entraînement par vibration locale consistant en 3 séances par semaine durant 4 semaines. La force maximale volontaire isométrique (MVC) était évaluée ainsi que l'activité électromyographique (EMG) maximale des muscles vaste latéral (VL) et rectus femoris (RF). La stimulation magnétique transcrânienne était utilisée pour évaluer le niveau d'activation cortical (VA_{TMS}), les potentiels évoqués moteurs (MEPs) et les périodes de silence (SPs). La performance en saut vertical était également évaluée. **Résultats :** Les adaptations à l'entraînement étaient similaires entre les sujets jeunes et âgés ($p > 0,05$). Aucun changement significatif n'était observé entre PRE_1 et PRE_2 , qui servait de condition contrôle et permettait de s'assurer de la bonne reproductibilité des données. La MVC ($+ 11,9 \pm 8,0$, $p < 0,001$) et le VA_{TMS} ($+ 3,6 \pm 5,2\%$, $p = 0,001$) étaient significativement augmentés après 4 semaines d'entraînement par vibration locale. L'activité EMG était également augmentée pour le muscle VL ($+ 21,9 \pm 33,7\%$, $p = 0,04$), alors qu'une tendance à l'augmentation était observée pour le RF ($+ 14,1 \pm 19,7\%$, $p = 0,05$). Les SPs enregistrées lors de contractions sous-maximales étaient diminuées pour les muscles VL et RF ($p < 0,05$). Aucun changement n'était observé pour les MEPs ($p > 0,05$). La hauteur de saut était significativement augmentée ($p < 0,05$).

Conclusion : L'entraînement par vibration locale semble être une méthode efficace pour améliorer les capacités fonctionnelles de sujets jeunes et âgés et induire des adaptations nerveuses sur le long terme intervenant notamment au niveau supra-spinal.

1 **Neural adaptations in quadriceps muscle after 4 weeks of local vibration training**
2 **in young and old subjects**

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5 Robin Souron^{1,2}, Thibault Besson^{1,2}, Thomas Lapole², Guillaume Y Millet¹

6 ¹Human Performance Laboratory, Faculty of Kinesiology, University of Calgary, Canada

7 ²Univ Lyon, UJM Saint-Etienne, Laboratoire Interuniversitaire de Biologie de la Motricité,

8 EA 7424, F-42023, Saint-Etienne, France

9 robin.souron@gmail.com

10 thibault.besson@yahoo.fr

11 thomas.lapole@gmail.com

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13 Running title: Neural adaptations after vibration training

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15 Corresponding author:

16 Guillaume Millet

17 Faculty of Kinesiology

18 2500 University Dr NW

19 Calgary, AB, T2N 1N4, AB, Canada

20 +1 403 220 3649

21 Email: gmillet@ucalgary.ca

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Abstract (English)

The aim of this study was to evaluate the effects of a 4-week local vibration training (LVT) on knee extensors function and corticospinal properties in healthy young and old subjects. Seventeen subjects (9 young and 8 old) 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 force (MVC) and associated electromyographic (EMG) activity on vastus lateralis (VL) and rectus femoris (RF) muscles were assessed. Transcranial magnetic stimulation (TMS) allowed to evaluate cortical voluntary activation (VA_{TMS}), motor evoked potential (MEP) area and silent period (SP). All training adaptations were similar between young and old subjects ($p > 0.05$) so that the results below reflect the pooled sample of subjects. MVC ($+11.9 \pm 8.0\%$, $p < 0.001$) and VA_{TMS} ($+3.6 \pm 5.2\%$, $p = 0.004$) were significantly increased at POST compared to PRE₂. Maximal VL EMG was significantly increased at POST ($+21.9 \pm 33.7\%$, $p = 0.03$) together with a tendency toward an increased maximal RF EMG ($+14.1 \pm 19.7\%$, $p = 0.054$). No changes were reported for MEPs on both muscles ($p > 0.05$). SPs recorded during 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 old 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 old subjects.

Keywords: local vibration training; transcranial magnetic stimulation; cortical voluntary activation; corticospinal excitability and inhibition; old population

Résumé (French)

Cette étude évaluait les effets d'un entraînement par vibration locale (« LVT ») sur les propriétés fonctionnelles et cortico-spinales des muscles extenseurs du genou de sujets sains jeunes et âgés. Dix-sept sujets (9 jeunes et 8 âgés) réalisaient 3 sessions de tests : avant et après une période sans activité de 4 semaines pour s'assurer de la reproductibilité des données ainsi qu'après le programme de LVT. La hauteur de saut, la force maximale volontaire (« MVC ») et l'activité électromyographique (« EMG ») des muscles vaste latéral (« VM ») et droit fémoral (« RF ») étaient évaluées. Le niveau d'activation volontaire cortical (« VA_{TMS} »), les potentiels évoqués moteurs (« MEPs ») et les périodes de silence (« SP ») étaient évalués via stimulation magnétique transcrânienne. Les adaptations à l'entraînement étaient similaires entre les sujets jeunes et âgés ($p > 0,05$). La MVC ($+11,9 \pm 8,0\%$, $p < 0,001$) et le VA_{TMS} ($+3,6 \pm 5,2\%$, $p = 0,004$) étaient augmentés après l'entraînement. L'activité EMG du VL était augmentée ($+21,9 \pm 33,7\%$, $p = 0,03$) et une tendance à l'augmentation de l'activité EMG du RF était observée ($+14,1 \pm 19,7\%$, $p = 0,054$). La durée des SPs enregistrées lors de contractions sous-maximales était diminuée ($p < 0,05$). La hauteur de saut vertical était augmentée ($p < 0,05$). Aucun changement n'était reporté pour les MEPs sur les deux muscles ($p > 0,05$). L'entraînement par vibration locale est efficace chez les sujets jeunes et âgés pour améliorer les capacités fonctionnelles via des modulations nerveuses intervenant en partie au niveau supra-spinal, et peut être utilisé comme une méthode alternative pour améliorer la performance musculaire chez des sujets sains jeunes et âgés.

Mots-clés: entraînement par vibration locale; stimulation magnétique transcrânienne; niveau d'activation cortical; excitabilité et inhibition cortico-spinale; population âgée

69 Introduction

70 The idea of using local vibration (LV) as an efficient training method to enhance muscle
71 performance is relatively recent. Indeed, while the chronic effects of whole-body vibration
72 (WBV) have been well described (Cochrane 2011), the concept of local vibration training
73 (LVT), i.e. the repetition of LV sessions across multiple days with the aim to improve
74 neuromuscular function, is relatively under-investigated so far. It has been reported that
75 LVT performed on relaxed lower limb muscles was efficient to improve muscle strength
76 in healthy young subjects (Lapole and Pérot 2010; Iodice et al. 2011; Lapole et al. 2013;
77 Souron et al. 2017a). Neural adaptations were proposed to mainly account for the
78 strength gains after LVT (Lapole and Pérot 2010; Lapole et al. 2013; Souron et al. 2017a),
79 as first evidenced in healthy young subjects by an increased electromyographic (EMG)
80 amplitude and increased voluntary activation during MVC after 14 consecutive days of
81 LVT on the Achilles tendon (Lapole and Pérot 2010).

82 Among the receptors that are sensitive to vibration, e.g. cutaneous receptors (Ribot-
83 Ciscar et al. 1996), Ib afferents of Golgi tendon organs (Burke et al. 1976), Ia afferents of
84 muscle spindles are the most responsive (Burke 1980; Roll et al. 1989). It has been
85 reported that Ia afferent discharge elicits an excitatory input on alpha motoneurons and
86 may evoke a reflex contraction of the vibrated muscle called the tonic vibration reflex
87 (Eklund et al. 1965; Hagbarth et al. 1966), that may in turn induce modulations in spinal
88 loop excitability (Desmedt et al. 1978). Accordingly, spinal adaptations have previously
89 been reported after LVT through an increase of soleus Hoffmann reflex (H reflex)
90 amplitude (Lapole et al. 2012b; Lapole et al. 2013). It has also been reported supra-spinal
91 modulations during LV application since vibration-induced Ia afferent discharge activates
92 the same motor cortical areas as those activated during a voluntary contraction, i.e. both

93 motor and sensorimotor cortex and contralateral supplementary motor area (Naito et al.
94 1999; Naito et al. 2001). Supra-spinal adaptations with training may be investigated using
95 transcranial magnetic stimulation (TMS). For instance, motor evoked potentials (MEPs),
96 i.e. compound muscle action potentials due to TMS, and silent period (SP), i.e. the period
97 of EMG silence that follows the MEP when elicited during a contraction, may be recorded
98 to provide information about the excitability and inhibition of cortical neurons and/or
99 motoneuron pools of the stimulated muscles (Goodall et al. 2014). Moreover, cortical
100 voluntary activation (VA_{TMS}) can be calculated by evoking superimposed twitches (SIT)
101 during voluntary contractions (Todd et al. 2003). A SIT elicited by TMS during MVC
102 highlights a suboptimal drive from the motor cortex (Goodall et al. 2014). Our team
103 recently reported that VA_{TMS} was significantly increased in healthy young subjects after 4
104 weeks of LVT applied on the dorsiflexor muscles (Souron et al. 2017a).

105 Adaptations within the central nervous system seem to enhance muscle performance
106 after LVT in healthy young subjects. It has recently been reported that this form of training
107 may also benefit for older populations (Tankisheva et al. 2015) known for neuromuscular
108 deconditioning. Indeed, aging results in decreased output from the neuromuscular
109 system, which causes reductions in force-generation capacities (Dalton et al. 2010; Kirk
110 et al. 2016). Alterations in muscle properties, such as loss in muscle mass or changes in
111 fiber type distribution (see Evans et al. (1995) for a review) have been documented with
112 aging. Alterations in neural properties may also arise at both spinal, e.g. loss of spinal
113 motoneurons, decrease in the efficiency of Ia afferents pathway to activate spinal
114 motoneurons (Aagaard et al. 2010; Baudry et al. 2012), and supra-spinal levels, e.g.
115 reductions in the availability of several cortical neurotransmitters, reduction in brain
116 volume (Volkow et al. 1998; Mattay et al. 2002), that may reduce *in fine* the number of

117 functioning motor units (Power et al. 2010). The alterations in force-generation capacities
118 may lead to an impaired mobility, a loss of autonomy and an increased risk of falling
119 representing one of the major causes of dependency in old subjects (Hepple and Rice
120 2016). Training can reduce neuromuscular deconditioning and thus improve quality of life
121 in this population. Strength (Hurley et al. 2000) and WBV training programs (Bogaerts et
122 al. 2007) have been reported to induce positive results on muscle strength and functional
123 capacities in aging populations. However, some limits may restrain the use of such
124 training programs for older subjects. Especially, WBV presents a prohibitive cost. In
125 addition, this non-portable system is unable to directly target a specific muscle group and
126 unable to be used by some subjects who have not the capacity to maintain an active
127 position during the vibration application on the platform. In contrast to strength or WBV
128 training, LV does not require any active contribution from the subject and may overcome
129 these limits by using a small and portable device that applies vibration directly over the
130 muscle or the tendon (Souron et al. 2017a), making easier its use in older populations
131 (e.g. retirement homes).

132 In the present study, we aimed to investigate the effects of a 4-week unilateral LVT
133 program on the functional capacities and associated corticospinal properties of the knee
134 extensor muscles, known for their important functional role in daily life activities and their
135 progressive weakness with aging (Hurley et al. 1998). One of the main originality of this
136 work was to assess for the first time neural adaptations due to LVT in healthy old subjects.
137 Based on recent results that reported neural modulations after an acute exposure to LV
138 in both healthy young and old subjects (Souron et al. 2007b), we hypothesised that a
139 repeated exposure to LV would trigger neural adaptations in the long term that would
140 accompany the significant augmentation of MVC force. This work will help to eventually

141 observe if the magnitude of training adaptations could be different between these two
142 populations, considering differences in i) muscle fiber composition, i.e. reduced number
143 and size of type II muscle fibers in old subjects (Grimby et al. 1982; Aniansson et al.
144 1986), and ii) muscle spindles sensitivity to LV-induced muscle stretch, i.e. lower
145 sensitivity in old subjects (Corden et al. 1996), two parameters known to influence the
146 sensitivity to LV stimuli. An understanding of the sites of neural adaptation for this muscle
147 group in response to LVT, and potential age-related differences, may help to improve
148 training and/or rehabilitation technique, with age-based specificity.

149

150 **Materials and Methods**

151 *Subjects*

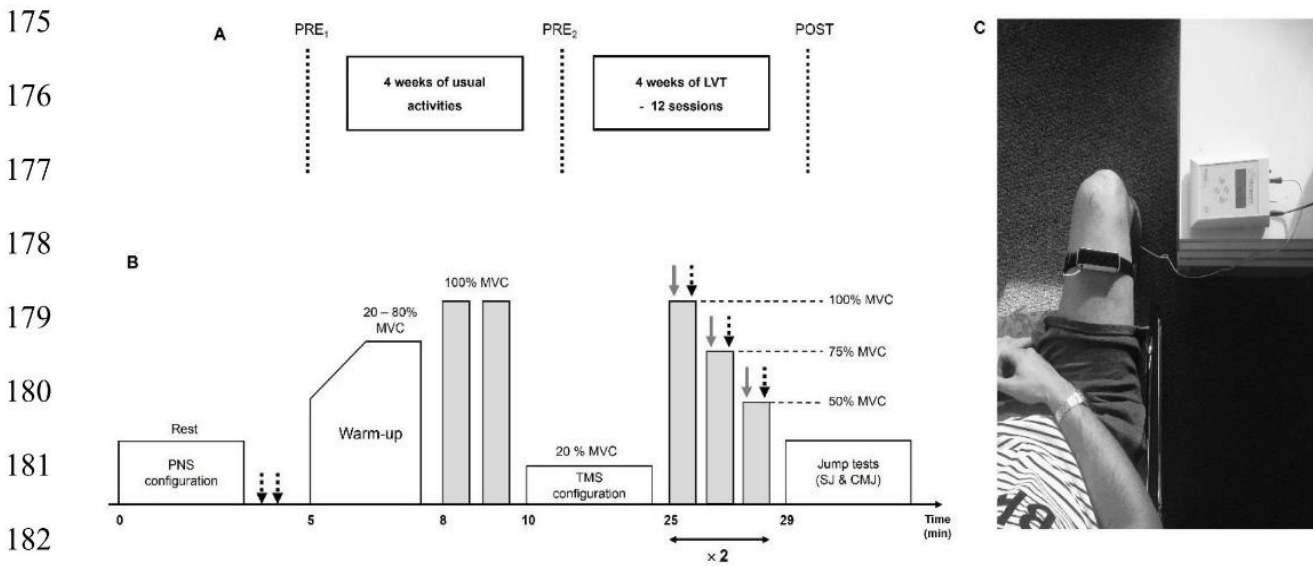
152 Seventeen healthy subjects volunteered for this study after giving their written informed
153 consent. The current study included 9 young (5 men and 4 women, age: 25 ± 1 yr; height:
154 173 ± 7 cm; weight: 66 ± 5 kg) and 8 old (2 men and 6 women, age: 65 ± 5 yr; height: 168
155 ± 15 cm; weight: 72 ± 10 kg) subjects. The level of weekly physical activity was reported
156 to be between 0 and 4 hours per week for each subject. This study conformed to the
157 standards from the latest revision of the *Declaration of Helsinki* and was approved by the
158 local ethics committee (REB #15-2752). All subjects were free of lower-limb injury during
159 the previous three months, had no contraindications to TMS, and no acute or chronic
160 neurological disorders and/or trauma. Subjects were not informed of the investigators'
161 hypotheses, only that the effect of a local vibration training was being tested. They were
162 instructed to abstain from caffeine for a minimum of 12 h before each session.

163

164

165 *Experimental design*

166 The experimental design is illustrated in Fig. 1A. All the subjects performed the
 167 experimental procedures three times, at the same time of the day, after they were first
 168 familiarized with the correct development of the knee extension maximal isometric
 169 contraction and the electrical and magnetic stimulations. The first testing session (PRE₁)
 170 was performed 4 weeks before the second one (PRE₂) in which subjects were retested
 171 to control the repeatability of data. No specific recommendations were given and the
 172 subjects were only asked not to change their usual activities during the 4-week period
 173 between PRE₁ and PRE₂. After PRE₂, the subjects started to follow the 4-week LVT and
 174 then returned for follow-up testing (POST).



183 **Fig. 1.** Panel A illustrates the experimental design of the study. Panel B gives an overview of the
 184 neuromuscular testing protocol. Dotted black and grey arrows represent peripheral nerve
 185 stimulation and transcranial magnetic stimulation, respectively. Panel C illustrates the local
 186 vibratory device and the application site for the training session.

187

188 *Local vibration training*

189 The subjects underwent a 4-week unilateral LVT. After a muscle palpation, the vibrating
 190 device (VB 115, Techno Concept, Mane, France) was applied locally and strapped

191 directly on the right rectus femoris muscle (i.e. 40% of the muscle length from the upper
192 edge of the patella to the anterior superior iliac spine) using elastic Velcro fasteners (Fig.
193 1C). The subject was seated on a chair during the entire vibration session, with a knee
194 angle of 90°. The vibrating device was always placed on the muscle by the same
195 investigator to insure that almost the same pressure was exerted on the leg. However,
196 the exact pressure was not measured in this work. The 4-week LVT program consisted
197 of three 1-h vibration sessions per week with at least one day of rest in between, for a
198 total of 12 vibration sessions. As Ia afferents are sensitive to small vibration amplitude
199 (Roll et al. 1989) and fire synchronously with vibration frequencies up to 80-120 Hz (Roll
200 et al. 1989), vibration characteristics were 100-Hz frequency and 1-mm amplitude in the
201 present study, as already set in previous works led by our team (Souron et al. 2017a).
202 Because no EMG measurement was performed during LVT sessions, it is impossible to
203 rule out an eventual occurrence of tonic vibratory reflexes during training sessions.
204 However, the vibration device and parameters used in the present study were the same
205 as in a previous one from our team (Lapole et al. 2015) that reported no occurrence of
206 tonic vibratory reflexes during LV application (frequency: 110 Hz; amplitude: 1 mm). The
207 compliance for LVT was excellent since none of the subjects missed a session. The
208 training was also reported to be well tolerated by each subject.

209

210 *Force and EMG recordings*

211 Knee extensor force of the right limb was measured during voluntary contraction by a
212 calibrated force transducer (Omega Engineering Inc., Stamford, CT). Subjects were
213 seated upright in a chair with both right knee and hips at 90° of flexion. Movement of the
214 upper body was minimized using three belts across the thorax and waist. During all

215 measurements, subjects were provided with real-time feedback of the force trace
216 displayed on a screen, and visual guidelines were added when subjects had to maintain
217 a targeted submaximal level of MVC.

218 EMG activity of the vastus lateralis (VL), rectus femoris (RF) and biceps femoris (BF) was
219 recorded with pairs of self-adhesive surface electrodes (Meditrace 100, Covidien,
220 Mansfield, MA) placed at the distal end of each muscle of interest in a bipolar
221 configuration with a 30-mm interelectrode distance. The reference was placed on the
222 patella. Low impedance (<5 k Ω) was obtained by shaving, gently abrading the skin and
223 then cleaning it with isopropyl alcohol. Signals were amplified with an octal bio-amplifier
224 (ML138, ADInstruments, Bella Vista, Australia), bandpass filtered (5-500 Hz) and
225 analogue-to-digital converted at a sampling rate of 2000 Hz by PowerLab System
226 (16/35, ADInstruments). All data were analysed offline using Labchart 8 software
227 (ADInstruments).

228

229 *Peripheral nerve stimulation*

230 Single rectangular pulses with 1-ms duration and 400 V maximal output voltage were
231 delivered via constant-current stimulator (DS7A, Digitimer, Hertfordshire, UK) to the right
232 femoral nerve via a 30-mm-diameter surface cathode (Meditrace 100) manually pressed
233 into the femoral triangle and 50 × 90 mm anode (Durastick Plus; DJO Global, Vista, CA)
234 in the gluteal fold. To determine the optimal intensity of stimulation for M-wave
235 measurement, single stimuli were delivered incrementally by steps of 5 mA until resting
236 M-wave (M_{max}) and twitch amplitudes plateaued. The optimal intensity was then increased
237 by 30% to confirm supramaximality. The determination of optimal peripheral nerve

238 stimulation (PNS) position and intensity was performed at the beginning of the
239 neuromuscular testing session to avoid any potentiation or fatigue effect.

240

241 *Transcranial magnetic stimulation*

242 The left motor cortex was stimulated by a magnetic stimulator (Magstim 200², The
243 Magstim Compagny Ltd, Whitland, UK) with a 110-mm double-cone-coil (maximum
244 output of 1.4 T). The coil was positioned to induce a postero-anterior current and manually
245 controlled by the same investigator throughout all the testing sessions. A cervical collar
246 was worn during all TMS measures to stabilize the head and neck and a swim cap was
247 worn to ensure consistent coil placement relative to the optimal position. To determine
248 this site, 6 marks were drawn on the cap: the vertex, 1 and 2 cm posterior to the vertex
249 and 1 cm to the left of these three marks along the midline. Optimal coil position was
250 determined as the site eliciting the largest SIT as well as VL and RF MEP amplitudes,
251 with minimal MEP amplitude in the antagonist BF, in response to stimulation at a known
252 suprathreshold stimulator output (50% maximum) during a 10% MVC knee extension.
253 When optimal MEPs and peak force were not recorded at the same coil position, the
254 optimal coil position was chosen according to MEP amplitude, because the evoked peak
255 force may be influenced by activation of other muscles (Todd et al. 2016). This position
256 was marked on the swim cap and was the same for both RF and VL muscles.

257 As per our recent recommendation (Temesi et al. 2014), the optimal stimulus intensity
258 was determined from SIT and MEP stimulus-response curves obtained during brief (2-3
259 s) voluntary contractions at 20% MVC. In brief, intensities of 20, 30, 40, 50, 60, 70 and
260 80% stimulator output were tested in random order. At each intensity, four contractions
261 were performed at 10 s intervals. A rest period of 10 s separate each intensity. In one

262 subject, the SIT and MEP amplitudes did not plateau using these intensities so stimulator
263 outputs of 90 and 100% were added to reach a plateau. The optimal stimulation intensity
264 was considered as the lowest which showed a plateau for VL and RF MEPs as well as
265 the SIT. The MEP evoked in the antagonist BF was also measured to make sure that its
266 size was low compared to those recorded in VL and RF.

267

268 *Experimental procedures*

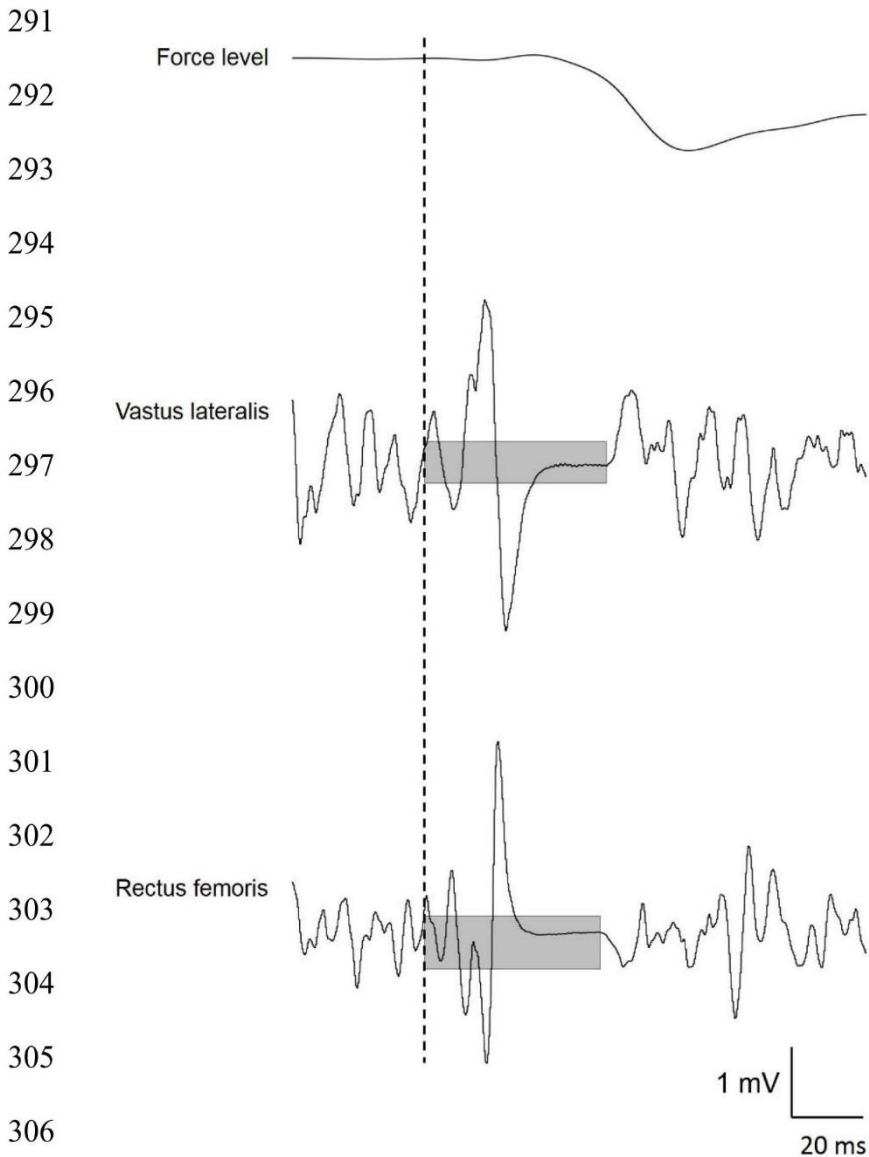
269 The experimental procedures are illustrated in Fig. 1B. All the neuromuscular
270 measurements were performed on the right (i.e. trained) leg only, which was the dominant
271 one for all the subjects. First, the optimal position and intensity for peripheral nerve
272 stimulation (PNS) were determined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

284

285

286 *Data analysis*

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



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

312 **PNS.** M-wave areas were measured from electrical nerve stimulations in both relaxed
313 (M_{\max_VL} and M_{\max_RF}) and maximally contracted ($M_{\text{sup_VL}}$ and $M_{\text{sup_RF}}$) VL and RF,
314 respectively.

315 **Force and EMG.** Maximal force was calculated as the highest peak force recorded from
316 the four MVCs. Root mean square (RMS) EMG was calculated for VL (RMS_{VL}) and RF
317 (RMS_{RF}) muscles over a 500-ms period after the force had reached a plateau. RMS_{VL}
318 and RMS_{RF} were then normalized to M_{sup} .

319 **TMS.** VA_{TMS} was measured by the modified twitch interpolation technique (Todd et al.
320 2003). Corticospinal excitability increases substantially during the transition from relaxed
321 to contracted muscle states (Ugawa et al. 1995), thus underestimating TMS evoked twitch
322 in the relaxed muscle. Hence, the estimated resting twitch (ERT) was determined as the
323 y-intercept of a linear regression of SIT amplitude and absolute voluntary force during the
324 two series of contractions at 100, 75 and 50% MVC. VA_{TMS} was then assessed with the
325 equation:

$$326 \quad VA_{\text{TMS}} = (1 - \text{SIT}_{\text{MVC}} / \text{ERT}) \times 100$$

327 where SIT_{MVC} is the superimposed twitch evoked during MVC. Two series were
328 performed with contractions and series separated by 10 s and 2 min, respectively. Thus,
329 the linear regression was performed with the 3 values from each series (R^2 range: 0.83-
330 0.99). The highest value of VA_{TMS} was kept for further analysis.

331 MEP areas were measured between set cursors placed at the beginning (i.e. initial
332 deflection from baseline) and the end (i.e. second horizontal crossing) of the evoked
333 potentials (see Fig. 1D in Martin et al. 2006) and normalized to the M-wave measured at
334 the same contraction intensity, i.e. 100; 75 and 50% MVC. To assess M-wave during
335 voluntary contractions, PNS was delivered 2-3 s after TMS once the force returned to the

336 appropriate contraction level. To ensure the lowest possible co-activation was elicited,
337 MEP areas were also recorded on the antagonist BF muscle during MVC. As no M-waves
338 were recorded on the BF, MEP are presented as absolute values for this muscle. SP
339 durations for VL and RF were determined visually and defined as the duration from the
340 TMS stimulus to the return of continuous voluntary EMG, i.e. when clear EMG bursts
341 could be identified (Taylor et al. 1996).

342 **Jump performance.** Two squat jumps (SJ) and two counter movement jumps (CMJ)
343 were performed on a jumping mat (27 × 27", Probotics Inc., Huntsville, AL) at the end of
344 the testing session. For the SJ, subjects were instructed to start from a semi-squatted
345 position, i.e. knee flexion at 90°, that was maintained for 2 s before jumping vertically
346 without making any countermovement. The CMJ started in an erect position and subjects
347 were instructed to make a downward movement to almost 90° knee flexion (visually
348 controlled by the experimenter), before starting to push-off with the lower limbs (Markovic
349 et al. 2004). For SJ and CMJ, subjects were instructed to keep their hands on the hips to
350 control for arm assistance. They were asked to jump continuously, as explosively and as
351 highly as possible. Maximal performance was identified as the highest jump obtained from
352 the two trials.

353

354 *Statistical analysis*

355 Statistical analyses were performed with Statistical software (StatSoft Inc., Tulsa, OK).
356 All variables were normally distributed (Kolmogorov-Smirnov normality test). For ANOVA
357 analyses, homogeneity of variance was verified by Levene's test. Two-way repeated
358 measures ANOVAs were performed on the neuromuscular parameters for both control
359 and training conditions. Factors included in the statistical analysis were the group (young

360 or old) and time (PRE₁ vs PRE₂ vs POST)]. Post-hoc analyses were performed using
361 Bonferroni testing when the ANOVA identified significant differences. Statistical
362 significance was set at $p < 0.05$. All data are presented as mean \pm standard deviation (SD).
363 SD is indicated by error bars on the figures.

364

365 **Results**

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

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

373

374 **Table 1.** Neuromuscular measurements for young and old before (PRE₁), after control condition (PRE₂) and after the 4-
 375 weeks local vibration training program (POST).

	YOUNG SUBJECTS			OLD SUBJECTS			Time	Group	Time x 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

376 MVC: maximal voluntary contraction; VA_{TMS}: maximal voluntary activation assessed by TMS; RMS: maximal EMG root-mean-square;
 377 MEP: motor evoked potential; SP: silent period; M_{sup}: M-wave recorded during MVC; SJ: squat jump; CMJ: counter movement jump;
 378 VL: vastus lateralis; RF: rectus femoris; 50: measurement performed during submaximal voluntary contractions at 50% MVC; 75:
 379 measurement performed during submaximal voluntary contractions at 75% MVC

380

381 **MVC and voluntary activation.** A significant group effect was found for MVC
382 ($F(1,15)=10.99$; $p=0.004$), with lower values reported at baseline (-37.9%) in old than
383 young subjects. A significant time effect was reported for MVC ($F(2,30)=24.68$; $p<0.001$),
384 with a significant increase reported after LVT ($+11.9 \pm 8.0\%$) (Fig. 3A).
385 A non-significant group effect was found for VA_{TMS} ($F(1,15)=2.24$; $p=0.15$). A significant
386 time effect was reported for this factor ($F(2,30)=8.21$; $p=0.001$) which was significantly
387 increased by $3.6 \pm 5.2\%$ after LVT (Fig. 3B). A significant group effect was reported for
388 RMS measurements, with lower values reported at baseline in old than young subjects
389 for RMS_{VL} (-34.1%; $F(1,15)=6.38$; $p=0.02$) and RMS_{RF} (-44.4%; $F(1,15)=16.17$; $p=0.001$).
390 RMS_{VL} was significantly increased after LVT ($+21.9 \pm 33.7\%$) as demonstrated by a
391 significant time effect ($F(2,30)=3.32$; $p=0.04$). Although not statistically significant, RMS_{RF}
392 tended to increase after LVT ($+14.1 \pm 19.7\%$, $F(2,30)=2.85$, $p=0.05$) (Fig. 3C).
393

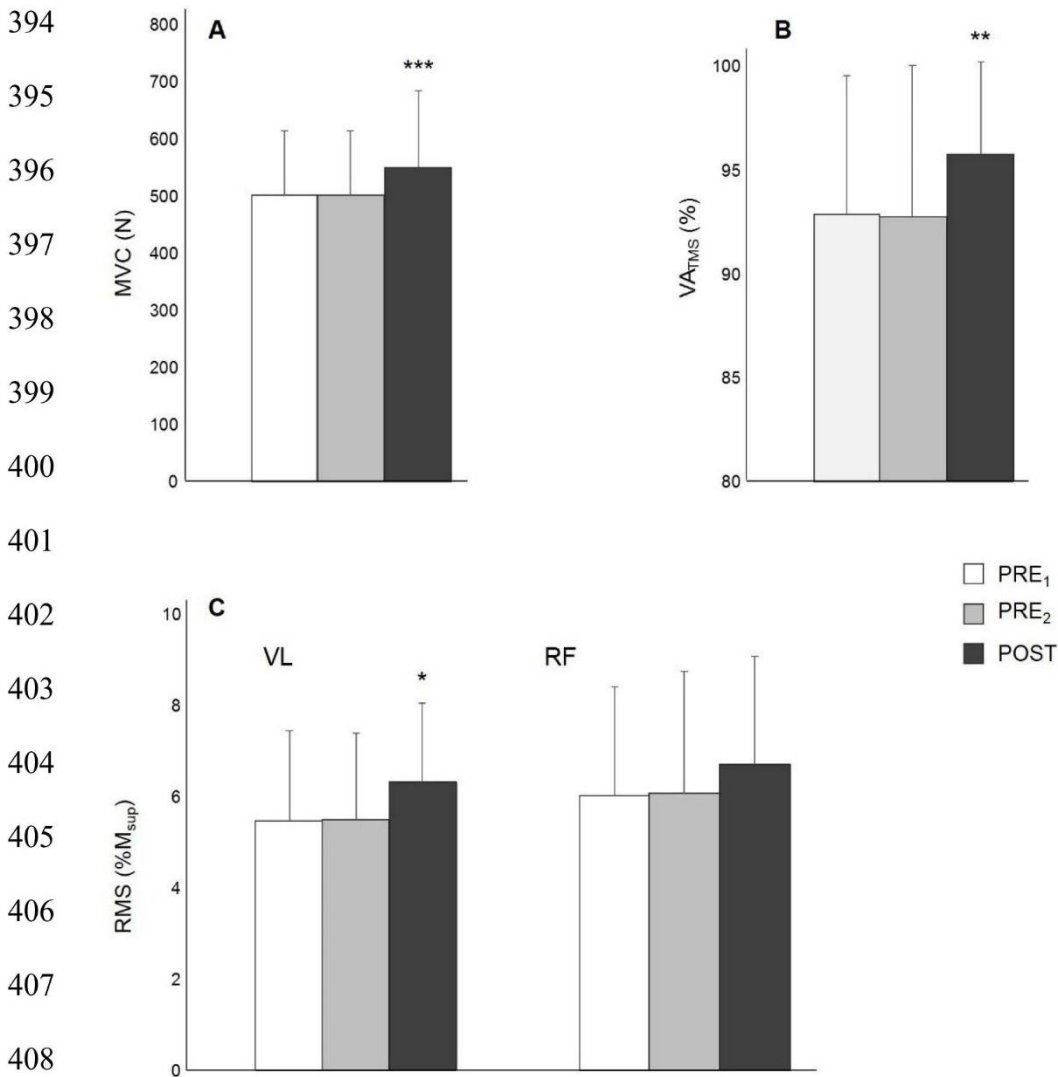


Fig. 3. Knee extensors maximal voluntary contraction (MVC) isometric force (panel A), maximal cortical voluntary activation assessed with transcranial magnetic stimulation (VA_{TMS} , panel B) and EMG root-mean-square (RMS) normalized to M_{sup} for vastus lateralis (VL) and rectus femoris (RF, panel C) muscles before (PRE₁), after control condition (PRE₂) and after the 4-week local vibration training (POST). Values are means \pm SD.

*, ** and *** Significantly different from PRE₂ (main effect of time) at $p < 0.05$, $p < 0.01$ and $p < 0.001$, respectively

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

No significant differences were found in SP durations between young and old subjects as demonstrated by the non-significant group effects ($p = 0.53 - 0.83$). While SPs recorded during MVC were not significantly changed following LVT on both VL and RF

421 (F(2,30)=2.18; p=0.12 and F(2,30)=3.18; p=0.07 for the main time effect, respectively),
422 SPs recorded during submaximal voluntary contractions were significantly reduced after
423 LVT (F(2,30)=4.25–6.38; p<0.05) on both VL (-7.0 ± 12.5% for SPs recorded at 50%
424 MVC) and RF (-6.7 ± 11.5 and -4.1 ± 12.0% for SPs recorded during 75 and 50% MVC,
425 respectively). Only a tendency for a decrease was reported for SPs recorded on VL during
426 a 75% MVC submaximal voluntary contraction (F(2,30)=2.71; p=0.051).

427 A significant group effect was found for MEPs recorded on the RF (p=0.04, p=0.04 and
428 p=0.009 for MEPs recorded during 100, 75 and 50% MVC), with lower values reported at
429 baseline in old subjects (-18.6, -21.3 and -22.3% for MEPs recorded during 100, 75 and
430 50% MVC, respectively). Non-significant time effects were found for MEPs
431 (F(2,30)=0.64–2.21; p=0.06–0.56). MEPs recorded on the antagonist BF remained
432 consistent across the three testing sessions (F(2,30)=0.01; p=0.98), suggesting that the
433 level of co-activation during the MVCs was low for all the testing sessions, which is
434 mandatory to ensure a correct evaluation of VA_{TMS} (Todd et al. 2016).

435 No differences in M_{sup} values were observed between young and old subjects as
436 demonstrated by the non-significant group effect (F(1,15)=3.36, p=0.08 and
437 F(1,15)=4.22, p=0.06 for M_{sup} recorded on VL and RF, respectively). M_{sup} was unchanged
438 following LVT for both VL (F(2,30)=0.25; p=0.77) and RF (F(2,30)=0.42; p=0.65) muscles.

439
440 **Vertical jumps.** A significant group effect was found for SJ (F(1,15)= 11.72; p=0.003) and
441 CMJ (F(1,15)=13.20; p=0.003), with lower height jumps recorded at baseline in the old
442 subjects (-39.3 and -39.5% for SJ and CMJ, respectively). Maximal jump heights recorded
443 in SJ and CMJ were significantly improved after LVT by 15.2 ± 16.2% (F(2,30)=11.97;

444 $p < 0.001$ for the main time effect) and $6.5 \pm 7.1\%$ ($F(2,30)=9.52$; $p=0.008$ for the main time
 445 effect), respectively (Fig. 4).

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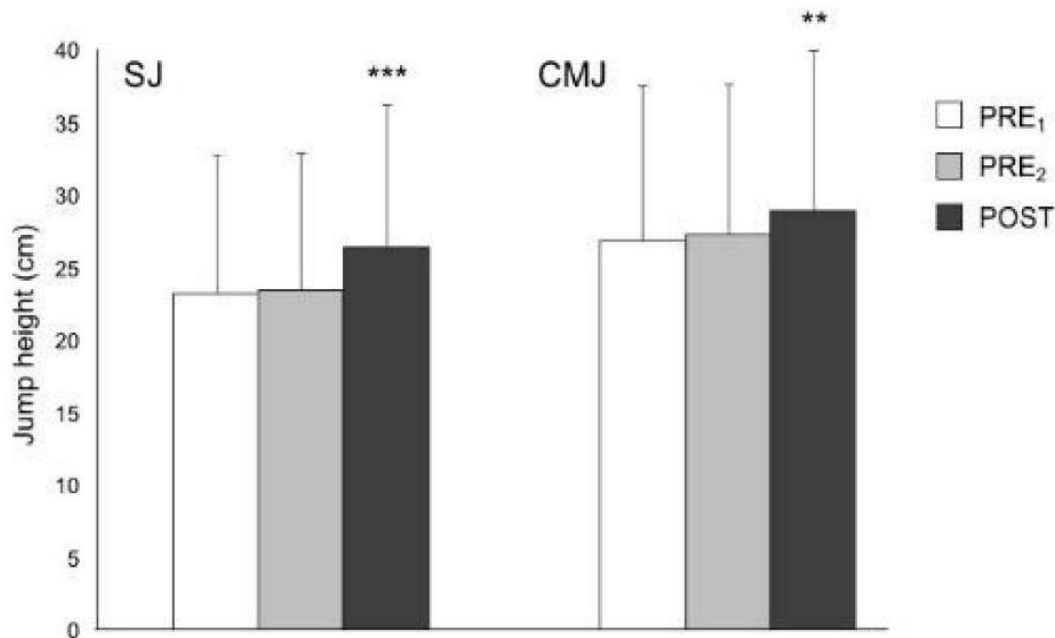
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456 **Fig. 4.** Performances in squat (SJ) and counter movement (CMJ) jumps before (PRE₁), after
 457 control condition (PRE₂) and after the 4-weeks local vibration training program (POST). Values
 458 are means \pm SD.

459 ** and *** Significantly different from PRE₂ (main effect of time) at $p < 0.01$ and $p < 0.001$,
 460 respectively

461

462 Discussion

463 The purpose of the present study was to investigate the effects of a 4-week local vibration

464 training (LVT) program on knee extensor muscles functional abilities and corticospinal

465 properties in healthy young and old subjects. We hypothesized that LVT would be

466 effective in inducing functional and neural adaptations. This hypothesis was confirmed

467 since the main findings of the present study reported that a 4-week LVT: i) significantly

468 enhances maximal voluntary contraction (MVC) and vertical jump performances and ii)

469 induces modulations within the central nervous system, i.e. maximal cortical voluntary

470 activation (VA_{TMS}), maximal electromyographic (EMG) RMS activity and silent period (SP)
471 duration. Therefore, this work was original in investigating for the first time potential age-
472 related differences in LVT-induced adaptations. Although speculative, one could have
473 expected differences in the magnitude of training adaptations between these two
474 populations. While we recently reported similar neuromuscular modulations (i.e.
475 decreased MVC, maximal EMG activity and VA_{TMS} for knee extensor muscles) after an
476 acute exposure to LV between young and old subjects (Souron et al. 2017b), Richardson
477 et al. (2006) reported age differences in the post-LV responses for MVC and quadriceps
478 EMG (i.e. decreased MVC and EMG in young but not old subjects). These authors
479 suggest that an impairment in gamma loop function due to a reduced number and size of
480 type II muscle fibres in older subjects could be a likely explanation to the absence of
481 neuromuscular modulations. Therefore, they suggested a reduced sensitivity of the
482 muscle spindle in older subjects as another explanation to these results. Although
483 insufficient statistical power due to the small sample size could have prevented detection
484 of age-related differences (i.e. have caused a type II error), we reported no differences
485 between training adaptations induced in young and old subjects (Table 1).

486

487 *Local vibration training effects on functional abilities*

488 The increased MVC reported in the present experiment (+9.8 and +14.3% for young and
489 old subjects, respectively) after LVT is consistent with previous studies. Indeed, MVC has
490 been found to increase by ~7-10% (Lapole and Pérot 2010; Lapole et al. 2013) to ~30%
491 (Iodice et al. 2011) in healthy young subjects, while similar results (~ +14%) were found
492 in healthy old subjects (Tankisheva et al. 2015). Since training parameters used in this
493 later study differed from ours, e.g. 6 vs. 1 months of training, 30-45 vs. 100 Hz of vibration

494 frequency, it is difficult to directly compare the current results with those reported by
495 Tankisheva et al. (2015) in old subjects. The present study is original in that it is the first
496 one to directly compare the effects of the same LVT program between young and old
497 subjects. One important and new result of the present study is that a 4-week LVT
498 performed on relaxed muscles was also effective for enhancing vertical jump performance
499 in both healthy young and old subjects. This result may be of clinical interest since a
500 greater leg extensor power may be important to reduce the risk of falling in old subjects
501 (Bassey et al. 1992).

502

503 *Local vibration training-induced neural modulations*

504 In the present study, significant improvements in MVC and vertical jump performances
505 are likely due to adaptations within the central nervous system, despite the lack of direct
506 correlations between changes in central adaptations and functional parameters (data not
507 shown). Neural adaptations were first evidenced by the ~4% increase in VA_{TMS} (+~3 and
508 +~5% for separate young and old subjects, respectively). This agrees with recent results
509 obtained by our team reporting an increased voluntary activation level evaluated by
510 means of the classic, i.e. nerve stimulation, twitch interpolated technique after LVT
511 (Lapole and Pérot 2010). In another study, we also recently demonstrated that an 8-week
512 LVT was efficient to significantly improve VA_{TMS} (+~5%) in healthy young subjects, with
513 the increase being significant as soon as after 4 weeks of LVT (Souron et al. 2017a).
514 Neural adaptations were also evidenced in the present work by the increase in maximal
515 EMG activity for both VL and RF muscles. These results appear consistent with a
516 previous work from our team demonstrating a 17% increased maximal EMG activity of
517 the triceps surae after 14 consecutive days of training (Lapole and Pérot 2010). The

518 strong and repeated activation of Ia spindle afferents during LV (Roll et al. 1982; Roll et
519 al. 1989) that project their excitatory input toward spinal and supra-spinal levels may likely
520 explain the greater muscle activation (i.e. increased VA_{TMS} and maximal EMG activity)
521 reported in this work.

522 As previously stated, vibratory stimuli strongly activate the motor areas which are
523 activated during a voluntary contraction, i.e. both motor and sensorimotor cortex and
524 contralateral supplementary motor area (Naito et al. 1999; Naito and Ehrsson 2001). It
525 has also been suggested that acute LV exposure can induce persistent changes in
526 corticospinal excitability (Lapole et al. 2012a). Modulations at the cortical level may also
527 be expected after LVT because it was demonstrated that a LV program designed to
528 provide illusory movements during a 5-day immobilization period can prevent the reduced
529 cortical activation of several areas (e.g. sensorimotor cortex, supplementary motor area)
530 when performing voluntary movement (Roll et al. 2012). Then, it is tempting to ascribe
531 part of the LVT-induced neural adaptations to changes at the supra-spinal level. However,
532 we demonstrated in this work unchanged MEP after LVT. It agrees with one of our recent
533 work that reported no changes in MEP after an 8-week LVT on tibialis anterior muscle
534 (Souron et al. 2017a). Previous findings also demonstrated that combined WBV with
535 strength training did not further increase corticospinal excitability compared to strength
536 training alone (Weier et al. 2012). Since long-term potentiation of corticospinal excitability
537 was not induced after LVT in one of our previous work (Souron et al. 2017a) and not
538 directly demonstrated in the present one, it remains to be determined how repeated
539 activation of Ia afferents during LV sessions may have led to a greater VA_{TMS} . Any
540 changes upstream of the motor cortical output cells (e.g. circuitry of the primary motor
541 cortex, adaptations in the secondary motor cortical areas) may explain the VA_{TMS}

542 augmentation observed after training (Carroll et al. 2011), although changes in
543 spinal/motoneuronal excitability cannot be totally ruled out since it is a single continuous
544 pathway.

545 Supra-spinal adaptations after LVT are suggested in the present study by the significant
546 decrease in SP duration during submaximal voluntary contractions in both VL and RF.
547 Although the exact mechanisms of the SP remain unclear, the initial part could be mainly
548 due to reduced spinal excitability while the final part could be cortical in origin (Inghilleri
549 et al. 1993; Chen et al. 1999). Then, the final part of SP is thought to result from the
550 activation of inhibitory cortical neurons projecting onto the pyramidal cells in the motor
551 cortex (Inghilleri et al. 1993). Decreased SP duration in the present study suggests that
552 modulations in intracortical inhibitory mechanisms mediated by GABA_B receptors, i.e. the
553 G-protein-coupled receptors (Nakamura et al. 1997), arise within the primary motor cortex
554 and may be an early adaptation to LVT in both young and old subjects. It appears in
555 contrast with the only study that investigated LVT-induced changes in SP duration so far
556 and reporting no significant results neither during maximal and submaximal voluntary
557 contractions of dorsiflexor muscles (Souron et al. 2017a). It is likely that the strong and
558 repeated sensory feedback from muscle spindle to supra-spinal areas (Naito et al. 1999;
559 Naito and Ehrsson 2001) may have induced long term modulations in the mechanisms
560 involved in corticospinal inhibition and may have *in fine* decreased the inhibitory input to
561 the motoneuron pool that can be viewed as an explanation to the increased MVC (Latella
562 et al. 2012). However, the SP-related results to inform on supra-spinal adaptations should
563 be interpreted with caution. Indeed, a recent study that assessed cervicomedullary motor
564 evoked potentials during the SP reported that the spinal portion of the TMS-evoked silent
565 period is considerably longer than previously believed (Yacyshyn et al. 2016). In that way

566 and based on the current results, it is difficult to completely rule out an eventual spinal
567 contribution to the SP decreases reported in the current study. The techniques of paired-
568 pulse TMS (i.e. assessment of intracortical inhibition and facilitation) should be
569 considered in parallel to SP measurement for future studies since they have been
570 reported as the more appropriate methods to measure changes in intracortical inhibition
571 (Kidgell et al. 2010).

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

590 in synaptic transmission between corticospinal descending tracts and alpha motoneurons
591 and/or iii) motoneuronal excitability (Giesebrecht et al. 2010).

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

598

599 **Practical applications**

600 Our results demonstrated that maximal strength and power can be enhanced by a short
601 term local vibration intervention in healthy young and aging populations, together with
602 neural adaptations as reported by the higher VA_{TMS} and maximal EMG activity as well as
603 the lower SP duration. Training adaptations were not reported to be significantly higher
604 for the older subjects despite weaker neuromuscular capacities (e.g. MVC and maximal
605 EMG activity) recorded at the beginning of the training in this population. Nonetheless,
606 the ability for a short (4-weeks) LVT period to significantly increase functional
607 performance in this study, as already reported by our team on tibialis anterior muscle
608 (Souron et al. 2017a), has important clinical relevance. It suggests that LV can be an
609 effective training method to counteract the neuromuscular deconditioning of knee
610 extensor muscles which are functionally involved in several activities of daily living such
611 as standing up, sitting down and gait (Hurley et al. 1998). Then, LVT may decrease the
612 risk of falling, one of the major causes of dependency in old subjects. The portability of
613 most LV devices is clearly an asset to directly bring the vibration to the patient (e.g.

614 hospital, retirement homes). Since different populations may benefit from LVT to enhance
615 functional abilities, i.e. healthy young (Souron et al. 2017a) and old (Tankisheva et al.
616 2015) subjects as well as clinical populations (Pietrangelo et al. 2009), future
617 investigations are now needed to precisely determine the training parameters (i.e.
618 session duration, number of sessions, number of sessions per week, vibrations
619 parameters, etc) so that the training can be optimal and tailored to these populations.

620

621 **Conflicts of Interest**

622 The authors have no conflicts of interest that are directly related to the contents of this
623 article. The authors accept the full responsibility for the conduct study, had full access to
624 all the data and controlled the decision to publish. The results of the study are presented
625 clearly, honestly, and without fabrication, falsification, or inappropriate data manipulation.

626 The present study does not constitute endorsement by ACSM.

627

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634

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Synthèse de l'étude #4 :

Les études #2 et #4 ont démontré qu'un entraînement par vibration locale de 4 (12 séances) ou 8 (24 séances) semaines (fréquence de vibration : 100 Hz, amplitude de vibration : 1 mm) est une méthode efficace pour améliorer les capacités fonctionnelles de divers groupes musculaires (fléchisseurs dorsaux de la cheville, extenseurs du genou) pour des sujets sains aussi bien jeunes qu'âgés, s'accompagnant d'adaptations intervenant au niveau central. Ces résultats nous ont permis d'envisager l'application de la vibration locale dans un cadre clinique dans une optique de réadaptation/reconditionnement neuromusculaire (étude #5).

DISCUSSION GENERALE

L'objectif général de ce travail de thèse visait à évaluer les effets aigus et chroniques de la vibration locale sur la fonction neuromusculaire de différents groupes musculaires et ce pour des populations saines et jeunes, saines et âgées, ainsi que des patients dans le cadre d'une rééducation post-ligamentoplastie du LCA. Même si les effets d'une application aiguë et prolongée de la vibration locale sur la fonction neuromusculaire sont déjà particulièrement bien documentés (voir les tableaux 1 (pages 1943-1944 de l'article publié) et 2 (pages 1946-1947 de l'article publié) de notre revue de littérature (Souron et al., 2017c) insérée en page 8 de ce manuscrit), l'originalité des études #1 et #3 résidait dans le choix des muscles évalués (fléchisseurs dorsaux de la cheville), des outils d'évaluation utilisés (TMS, stimulation électrique thoracique) et des populations recrutées (sujets sains et âgés). En plus d'évaluer les capacités fonctionnelles de divers groupes musculaires, les études #2 et #4 présentaient l'originalité d'évaluer pour la première fois les adaptations nerveuses (via l'utilisation de la TMS) induites par un entraînement par vibration locale chez de jeunes adultes sains ainsi qu'une population saine âgée. Ces quatre premières études visaient à évaluer et valider l'efficacité de la vibration locale pour améliorer les capacités fonctionnelles afin d'envisager une application clinique lors de la dernière année de thèse (étude #5 présentée en annexe 2 de ce manuscrit).

Cette partie de discussion générale s'attachera dans un premier temps à résumer et discuter brièvement des principaux résultats obtenus lors d'une application aiguë de la vibration locale. L'objectif principal de ce travail de doctorat, à savoir la détermination des effets d'un entraînement par vibration locale sur les capacités fonctionnelles de différents groupes musculaires ainsi que des adaptations nerveuses qui accompagnent ces modifications fonctionnelles, sera ensuite discuté dans une deuxième partie. Nos résultats seront en particulier comparés à d'autres méthodes d'entraînement classiquement utilisées dans une optique de développement/reconditionnement de la fonction musculaire, i.e. WBV, NMES et entraînement en force, afin de discuter l'efficacité de la vibration locale comme technique d'entraînement. Cette discussion générale sera suivie d'une dernière partie de conclusion générale qui présentera les perspectives issues de ce travail de thèse.

1. Application aigüe de la vibration locale

Les principaux résultats obtenus après une application aigüe de vibration locale lors des études #1 et #3 (durée d'application : 30 min ; fréquence de vibration : 100 Hz ; amplitude de vibration : 1 mm) sont synthétisés dans le **tableau 2** :

Tableau 2. Synthèse des résultats obtenus après une application aigüe de vibration locale sur les muscles fléchisseurs dorsaux de la cheville (étude #1) et extenseurs du genou (étude #3).

Etude	Modulations périphériques			Modulations nerveuses						
	MVC	Onde M	Secousse musculaire	EMG	Réflexe H	VA _{TMS}	MEPs	SPs	TMEPs	MEP/TMEP
#1	=	=	Non Mesuré	=	↓ 21% ¹⁰	=	↓ 14% ⁵⁰ ↓ 15% ⁷⁵ ↓ 20% ^{MVC} (p=0,11)	=	Non Mesuré	Non Mesuré
#3	↓ 13%	=	=	↓ 21% (RF) ↓ 25% (VL)	Non Mesuré	=	=	=	↓ 17% ⁵⁰ (RF) = (VL)	↑ 29% (RF) = (VL)

MVC : contraction maximale volontaire ; VA_{TMS} : niveau d'activation volontaire mesuré par stimulation magnétique transcrânienne ; MEPs : potentiels évoqués moteurs ; SPs : périodes de silence ; TMEPs : potentiels évoqués moteurs thoraciques ; ¹⁰ : mesure réalisée lors d'une contraction sous-maximale volontaire à 10% de MVC ; ⁵⁰ : mesure réalisée lors d'une contraction sous-maximale volontaire à 50% de MVC ; ⁷⁵ : mesure réalisée lors d'une contraction sous-maximale volontaire à 75% de MVC ; ^{MVC} : mesure réalisée lors d'une MVC. Les résultats en gras sont augmentés (↑) ou diminués (↓) de manière statistiquement significative.

1.1. Effets de la vibration locale aigüe et prolongée sur la force maximale

Alors que l'étude #3 a confirmé notre hypothèse de départ qui postulait une diminution aigüe des capacités de production de force à la suite d'une exposition prolongée à la vibration locale, ce n'était pas le cas de l'étude #1. Les résultats obtenus lors de ces deux études reflètent la littérature actuelle dans laquelle on retrouve un manque de consensus sur l'effet d'une application unique et prolongée de la vibration locale sur les capacités de production de force maximale (voir le tableau 1 (pages 1943-1944 dans l'article publié) de notre revue de littérature (Souron et al., 2017c) insérée en page 8 de ce manuscrit). Les paramètres vibratoires utilisés peuvent parfois offrir une explication aux différences de résultats entre les études, mais ce n'est évidemment pas le cas pour les différences entre les études #1 et #3 puisque les mêmes

paramètres vibratoires ont été utilisés. Les propriétés intrinsèques des muscles investigués apparaissent alors comme l'explication la plus probable à cette divergence de résultats. Il a été reporté que le TA possède une large proportion (~80%) de fibres de type I (Johnson et al., 1973). A l'inverse, le muscle RF possède une majorité de fibres de type II (Johnson et al., 1973). Cette différence de typologie pourrait directement impacter la réponse du muscle ciblé aux stimuli vibratoires et justifier la diminution de force seulement observée sur les muscles extenseurs du genou (étude #3). En effet, à partir de l'enregistrement de la fréquence de décharge de plusieurs unités motrices, il a été montré que la perturbation de la transmission de l'information nerveuse entre les afférences Ia et les Mn α affectait principalement le recrutement d'unités motrices à haut seuil de recrutement, i.e. à dominante rapide (Bongiovanni et al., 1990). Si certaines études confirment nos résultats (Kouzaki et al., 2000; Jackson & Turner, 2003), cette hypothèse reste cependant spéculative dans la mesure où il a récemment été montré aucune diminution de la force maximale des muscles extenseurs du genou après une exposition prolongée à la vibration locale (Fry & Folland, 2014). Finalement, les effets aigus de la vibration locale sur la force musculaire semblent être liés à une combinaison de plusieurs paramètres, i.e. muscle étudié, site de vibration, fréquence et amplitude de vibration, qui reste actuellement à être mieux déterminée.

Si la diminution de force musculaire observée post-vibration peut être liée à des perturbations intervenant en amont de la jonction neuromusculaire, i.e. versant central/nerveux, ou en aval de cette dernière, i.e. versant périphérique/musculaire, nos résultats ont permis de confirmer que la vibration locale n'est pas un stimulus suffisamment puissant pour venir directement altérer les propriétés musculaires (cf. **tableau 2**), suggérant que des modulations au sein du système nerveux central permettent d'expliquer presque exclusivement, lorsqu'elle est présente, la diminution de la capacité de production de force post-vibration.

1.2. Effets de la vibration locale aiguë et prolongée sur l'excitabilité cortico-spinale

Les études #1 et #3 confirment l'hypothèse que nous avons émise selon laquelle des modulations d'origine nerveuse seraient induites par une séance d'exposition à la vibration prolongée (cf. **tableau 2**). Nous avons montré une altération de l'efficacité de la transmission synaptique entre les afférences Ia des FNMs et les Mn α , comme

suggéré par la diminution significative de l'amplitude du réflexe H lors de l'étude #1, ce résultat apparaissant largement en accord avec la littérature actuelle (voir le tableau 2 (pages 1946-1947 dans l'article publié) de notre revue de littérature (Souron et al., 2017c) insérée en page 8 de ce manuscrit). Même si cela n'a jamais été directement évalué dans un contexte de vibration locale appliquée de manière aiguë, il est probable que cette diminution du réflexe H soit liée au moins partiellement à une augmentation du niveau d'inhibition présynaptique exercé sur les afférences Ia (Lapole et al., 2012b) et médiée par la neurotransmission GABAergique sous le contrôle de structures supra-spinales (Gillies et al., 1969; Delwaide, 1973; Hultborn et al., 1987). Cette hypothèse a en effet longtemps été considérée comme la plus probable afin d'expliquer la diminution du réflexe H post-vibration, mettant de côté d'éventuelles modifications d'excitabilité motoneuronale depuis qu'il a été montré qu'une exposition prolongée à la vibration locale ne modifiait pas l'amplitude de l'onde F (Christova et al., 2011; Lapole et al., 2012b), qui reflète la réactivation d'un certain nombre de motoneurones par les PAs propagés de façon antidromique en réponse à une stimulation électrique nerveuse d'intensité supramaximale (McNeil et al., 2013). Cependant, en plus des nombreuses limites associées à l'évaluation de l'onde F (McNeil et al., 2013), les résultats apportés par l'étude #3 remettent en cause les origines purement pré-synaptique (inhibition) de la diminution du réflexe H et permettent de considérer l'hypothèse d'une modification d'excitabilité motoneuronale après une exposition aiguë et prolongée à la vibration locale. En effet, nous avons observé une diminution des TMEPs post-vibration dans l'étude #3. Cette diminution pourrait alors être liée à i) une diminution de l'excitabilité du faisceau cortico-spinal (pyramidal), ii) une diminution de l'efficacité de la transmission synaptique entre le faisceau cortico-spinal et le Mn α et/ou iii) une perturbation des propriétés intrinsèques du motoneurone (Giesebrecht et al., 2010). Au regard des mécanismes d'action de la vibration et des résultats reportés dans des études évaluant l'effet d'un exercice fatigant (Petersen et al., 2003; Giesebrecht et al., 2010), il est possible de spéculer sur une implication probablement plus importante du troisième facteur dans la diminution des TMEPs observée.

L'utilisation de la TMS permettait d'apporter de nouvelles évidences sur les modulations d'excitabilité cortico-spinale induites par une exposition prolongée à la vibration locale. Nous avons montré une absence de modification du VA_{TMS} dans nos travaux. De manière un peu paradoxale, et comme reporté dans l'étude #1 de cette thèse, il est parfois observé des modulations d'excitabilité cortico-spinale après une

exposition aiguë à la vibration, comme suggéré par des modifications dans l'amplitude des MEPs (Steyvers et al., 2003a; Smith & Brouwer, 2005). Cependant, il existe un manque de consensus à ce sujet et le lien direct entre les résultats obtenus pour le VA_{TMS} et les MEPs est difficile à établir. En effet, il est par exemple couramment reporté après des exercices fatigants une diminution du VA_{TMS} sans aucun changement ou augmentation des MEPs (Gruet et al., 2013). Mesurées en parallèle, des méthodes plus directes évaluant l'excitabilité corticale, e.g. double stimulation magnétique, inhibition interhémisphérique (Daskalakis et al., 2002), pourraient permettre d'interpréter plus précisément ces modifications d'excitabilité cortico-spinale.

L'absence de diminution des MEPs observée lors de l'étude #3 reflète le manque de consensus actuel sur l'effet de la vibration locale sur le comportement des MEPs. En effet, alors qu'il semble qu'une augmentation des MEPs est systématiquement observée pendant l'application de la vibration (Claus et al., 1988; Kossev et al., 1999; Siggelkow et al., 1999; Kossev et al., 2001; Rosenkranz & Rothwell, 2003; Steyvers et al., 2003b; Rosenkranz & Rothwell, 2006; Lapole et al., 2015), les résultats sont plus équivoques au regard des changements reportés après une application aiguë de la vibration locale. Même si la quasi-totalité de ces études ont évalué les MEPs sur le muscle relâché, limitant alors la comparaison avec les résultats de nos études, il a été reporté une augmentation (Steyvers et al., 2003a; Smith & Brouwer, 2005; Christova et al., 2011; Lapole et al., 2012b), une diminution (Steyvers et al., 2003a; Farabet et al., 2016) ou une absence de changement (Rosenkranz & Rothwell, 2004; Smith & Brouwer, 2005; Rosenkranz & Rothwell, 2006; Lapole et al., 2012b; Lapole & Tindel, 2015) après une session unique de vibration locale (voir le tableau 2 (pages 1946-1947 dans l'article publié) de notre revue de littérature (Souron et al., 2017c) insérée en page 8 de ce manuscrit pour des résultats détaillés). Il est probable que des différences dans les muscles évalués, dans les paramètres de vibration ou dans les designs expérimentaux expliquent cette divergence de résultats. Tandis que les paramètres vibratoires utilisés lors des études #2 et #4 de ce travail de thèse étaient similaires, les différences observées dans le comportement des MEPs peuvent être majoritairement expliquées par la typologie des muscles investigués, i.e. prédominance de fibres lentes pour les muscles dorsiflexeurs de la cheville vs. composition mixte pour les muscles extenseurs du genou. La densité en FNMs, décrit comme le récepteur le plus sensible aux stimuli vibratoires (Burke et

al., 1976a; Burke et al., 1976b; Burke, 1980; Roll et al., 1989), au sein d'un muscle est en relation directe avec la fonction et la composition en unités motrices de ce dernier, i.e. la densité en FNMs est plus importante dans les muscles riches en unités motrices lentes (McCloskey, 1978; Proske et al., 2000). Ainsi, l'activation des afférences la par le stimulus vibratoire prolongé a pu être plus importante sur le muscle TA, qui contient une majorité de fibres lentes, modulant ainsi de manière plus importante les différents niveaux du système nerveux central, expliquant la tendance à la diminution des MEPs observée sur ce muscle lors de l'étude #1. Cela paraît toutefois contradictoire avec l'absence de diminution de force observée lors de l'étude #1. Cependant, cette décharge importante des afférences la pour le muscle TA expliquant probablement la diminution des MEPs pourrait avoir un moindre impact sur le recrutement des unités motrices et donc sur la capacité de production de force dans la mesure où le stimulus vibratoire prolongé impacte principalement le recrutement d'unités motrices rapides (Bongiovanni et al., 1990).

Lors de l'étude #3, la diminution d'excitabilité spinale (TMEPs) discutée plus haut semble être compensée par une augmentation de l'excitabilité corticale, comme suggéré par l'augmentation du ratio MEP/TMEP. Cependant, l'absence de modification des SPs remarquée lors des études #1 et #3, reflétant l'incapacité pour le stimulus vibratoire prolongé de venir altérer la neurotransmission GABAergique des neurones inhibiteurs situés au sein du cortex moteur primaire et se projetant sur les cellules pyramidales (Inghilleri et al., 1993), ne permet pas de conclure de manière certaine sur les effets de la vibration locale au niveau cortical. Des techniques de stimulations magnétiques doubles pourraient être utilisées dans de futures études en parallèle des mesures de SPs car elles ont été reportées comme les techniques les plus appropriées et les plus sensibles aux changements de neurotransmission GABAergique au niveau intra-cortical (Kidgell & Pearce, 2010).

Les résultats obtenus lors de ces deux études sont intéressants en montrant que la technique de vibration locale peut être utilisée de manière aigüe (i.e. une séance unique d'application prolongée) comme une méthode alternative aux méthodes classiquement utilisées, i.e. WBV (Armstrong et al., 2008), NMES (Gueugneau et al., 2016), entraînement en force (Latella et al., 2017), permettant de moduler la fonction neuromusculaire sur le très court terme. Ces modulations aigües du système neuromusculaire sont importantes dans la mesure où elles peuvent initier des

adaptations sur le plus long terme (Gathercole et al., 2015) permettant d'améliorer les performances musculaires.

2. Entraînement par vibration locale

Les principaux résultats obtenus après une application chronique de la vibration locale (fréquence de vibration : 100 Hz ; amplitude de vibration : 1 mm) lors des études #2 (24 séances d'une heure réparties sur 8 semaines) et #4 (12 séances d'une heure réparties sur 4 semaines) sont synthétisés dans le **tableau 3** :

Tableau 3. Synthèse des résultats obtenus après une application chronique de la vibration locale sur les muscles fléchisseurs dorsaux de la cheville (étude #2) et extenseurs du genou (étude #4).

Etude	Capacités fonctionnelles		Adaptations périphériques		Adaptations nerveuses				
	MVC	Hauteur de saut	Onde M	Secousse musculaire	EMG	Réflexe H	VA _{TMS}	MEPs	SPs
#2	POST ₄								
	↑ 7,5% MV	<i>Non Mesuré</i>	=	<i>Non Mesuré</i>	=	=	↑ 4,5% MV	=	=
	↑ 6% MC						↑ 4,5% MC		
	POST ₈								
	↑ 12% MV	<i>Non Mesuré</i>	=	<i>Non Mesuré</i>	=	=	↑ 5% MV	=	=
	↑ 10% MC						↑ 6% MC		
	POST ₊₂								
	↑ 11% MV	<i>Non Mesuré</i>	=	<i>Non Mesuré</i>	=	=	↑ 4,5% MV	=	=
	↑ 8% MC						↑ 6,5% MC		
#4	Echantillon général								
	↑ 12%	↑ 12% (SJ)	=	=	↑ 22% (VL)	<i>Non Mesuré</i>	↑ 3,5%	=	↓ 7%^{50,75} (VL)
		↑ 6,5% (CMJ)			↑ 14% (RF; p=0,05)				↓ 8%⁵⁰, ↓ 4%⁷⁵ (RF)
	Sujets jeunes (n=9)								
	↑ 10%	↑ 14% (SJ)	=	=	↑ 6,5% (VL)	<i>Non Mesuré</i>	↑ 2,5%	=	↓ 8-9%^{50, 75} (VL)
		↑ 8% (CMJ)			↑ 12% (RF)				↓ 7%⁵⁰ & ↓ 4%⁷⁵ (RF)
	Sujets âgés (n=8)								
	↑ 14,3%	↑ 9% (SJ)	=	=	↑ 39% (VL)	<i>Non Mesuré</i>	↑ 5%	=	↓ 5-6%^{50,75} (VL)
		↑ 2,5% (CMJ)			↑ 16,5% (RF)				↓ 4-5%^{50,75} (RF)

MVC : contraction maximale volontaire ; SJ : squat jump ; CMJ ; contre mouvement jump ; VA_{TMS} : niveau d'activation volontaire mesuré par TMS ; MEPs : potentiels évoqués moteurs ; SPs : périodes de silence ; ^{50, 75} : mesures réalisées lors d'une contraction sous-maximale volontaire respectivement à 50 et 75% de MVC ; MV : muscle vibré ; MC : muscle controlatéral. Les résultats en gras sont augmentés (↑) ou diminués (↓) de manière statistiquement significative. Lors de l'étude #2, les mesures étaient réalisées 4 (POST₄) et 8 (POST₈) semaines après le début de l'entraînement, ainsi que 2 semaines après son arrêt (POST₊₂).

2.1. Adaptations nerveuses à l'entraînement par vibration locale

Peu de données sont disponibles à l'heure actuelle pour informer sur les effets d'un entraînement par vibration locale sur le système nerveux central. Les premières évidences ont été apportées par Lapole & Pérot, (2010) qui ont observé une augmentation significative de l'activité EMG maximale du muscle soléaire après 2 semaines d'entraînement. Ce résultat est en accord avec l'étude #4 qui montre une augmentation significative de l'activité EMG maximale du muscle VL ainsi qu'une tendance à l'augmentation pour le RF. A l'inverse, aucune modification de l'activité EMG n'était observée après 8 semaines d'entraînement lors de l'étude #2 (données non reportées dans l'article publié ; Souron et al., (2017a)). La comparaison de ces différents résultats doit être réalisée avec précaution face aux limites d'interprétation du signal EMG pour détecter des changements de faibles amplitudes de l'activité des unités motrices (Farina et al., 2010). De plus, divers facteurs physiologiques et non-physiologiques peuvent contaminer le signal RMS et ainsi donner une estimation erronée sur l'intensité de la commande nerveuse volontaire. Un phénomène d'annulation de phase (*amplitude cancellation*), qui désigne l'annulation des phases positives et négatives des PAs, a été reporté (Farina et al., 2004; Farina et al., 2010; Hug, 2011), et peut conduire à la sous-estimation de l'intensité de la commande nerveuse. Le phénomène de diaphonie (*cross talk*), qui désigne la contamination du signal EMG par l'activité électrique d'un muscle proche (Farina et al., 2004; Farina et al., 2010; Hug, 2011), contribue également à une mauvaise interprétation (surestimation) du signal RMS. La normalisation du signal RMS par l'amplitude de l'onde M, comme effectué dans l'ensemble des études de ce travail de thèse, permettait de s'affranchir en partie de ces limites méthodologiques. Cependant, si cette augmentation de l'activité EMG observée par Lapole & Pérot, (2010) et lors de l'étude #4 semble confirmer le potentiel pour un entraînement par vibration locale d'induire des adaptations d'origine centrale, elle ne permet pas de distinguer précisément à quel(s) niveau(x) elles interviennent. En effet, cette augmentation de l'activité EMG pourrait être liée à des modulations d'origines spinales et/ou supra-spinales.

La diminution du réflexe H (étude #1 ; Farabet et al., 2016) et des TMEPs (étude #3 ; Souron et al., 2017b) reportée après une application aigüe de vibration locale permet d'envisager des adaptations spinales/motoneuronales sur le long terme

lorsque la vibration locale est utilisée comme technique d'entraînement. Ainsi, il a récemment été montré une augmentation du réflexe H sur le muscle soléaire relâché (Lapole & Pérot, 2012) ou maximale contracté (Lapole et al., 2013) après un entraînement par vibration locale de 14 jours. Ce résultat suggère une augmentation d'excitabilité motoneuronale et/ou diminution du niveau d'inhibition pré-synaptique exercé sur les afférences Ia, ce dernier phénomène pouvant être médié par des mécanismes supra-spinaux (Hultborn et al., 1987). Nos travaux ne confirment néanmoins pas ces résultats puisqu'aucun changement dans l'amplitude du réflexe H du TA n'a été observé dans l'étude #2 (NB : cette mesure n'était pas effectuée dans l'étude #4). Si cela reste une analyse spéculative, ces résultats contradictoires peuvent être expliqués par i) des différences dans les muscles étudiés (TA vs. soléaire) ou ii) les protocoles d'entraînement mis en place (3 sessions d'une heure par semaine pendant 8 semaines (100 Hz, 1mm) vs. 1 session d'une heure par jour pendant 14 jours (50 Hz, 1 mm)). Il est également important de souligner que l'analyse du réflexe H lors de contractions sous-maximales, comme réalisée lors de l'étude #2 (20% de MVC), ne reflète pas nécessairement l'état des mécanismes spinaux pendant une contraction maximale volontaire (Aagaard et al., 2002b; Aagaard, 2003), ce qui rend l'interprétation fonctionnelle de ce résultat difficile. Au regard de nos résultats, de futurs travaux peuvent être envisagés afin de mieux comprendre les éventuelles modifications d'excitabilité motoneuronale (via stimulation électrique thoracique ou cervicomédullaire) ou d'inhibition pré-synaptique (par conditionnement du réflexe H) après une période d'entraînement par vibration locale (voir la partie « conclusions et perspectives » pour plus de détails).

Une des originalités de ce travail de thèse était d'évaluer directement les adaptations supra-spinales intervenant à la suite d'un entraînement par vibration locale. De telles adaptations ont déjà été indirectement évaluées via l'analyse de l'onde V (Lapole et al., 2013), qui reflète l'intensité de la volée afférente atteignant le muscle due à la collision entre les PAs antidromiques évoqués par une stimulation électrique percutanée d'intensité supra-maximale et la commande nerveuse descendante (Upton et al., 1971). Cependant, de nombreuses limites liées à la signification de ce paramètre pour renseigner sur des adaptations supra-spinales (changement dans l'excitabilité axonale des afférences et/ou motoneurones, influence poly-synaptique sur l'amplitude du réflexe, e.g. inhibition pré-synaptique) limitent son interprétation (Carroll et al., 2011; McNeil et al., 2013). Une augmentation du VA_{TMS} a

ainsi été remarquée lors des études #2 et #4, avec une augmentation similaire au côté entraîné pour le membre controlatéral dans l'étude #2 (cf. **tableau 3**). Si les gains de VA_{TMS} observés permettent de renseigner sur des adaptations intervenant au niveau supra-spinal, et plus spécialement sur l'intensité de la commande nerveuse issue du cortex moteur (Todd et al., 2004), l'influence de mécanismes prenant place au niveau spinal et/ou motoneuronal est à prendre en compte dans l'interprétation de ce paramètre (Todd et al., 2016). Ainsi, l'évaluation du VA_{TMS} isolé ne permet pas de distinguer de manière précise à quel(s) niveau(x) les adaptations ont pris place. De manière similaire, parce que le MEP est affecté aussi bien par des phénomènes d'excitation et/ou d'inhibition synaptique aux niveaux corticaux et spinaux (Devanne et al., 1997), il ne permet pas de distinguer de manière précise quel niveau du système nerveux central a été modulé par l'entraînement. Dans ce travail de thèse, aucune modification dans l'amplitude des MEPs n'a été remarquée après l'entraînement par vibration locale pour les différents muscles étudiés et pour les différents niveaux de force testés, i.e. contractions maximales et sous-maximales, ce qui apparaît en accord avec la seule étude ayant évalué les MEPs après un entraînement par vibration locale (Marconi et al., 2008). La pertinence de l'évaluation des MEPs durant une contraction maximale pour informer sur d'éventuelles modulations cortico-spinales peut cependant être discutée. En effet, il existe une haute probabilité pour le stimulus magnétique d'être évoqué durant la période réfractaire lors d'une contraction maximale volontaire à cause de la haute fréquence de décharge des neurones corticaux (Todd et al., 2003; 2004; Goodall et al., 2009; Tallent et al., 2012; Souron et al., 2016). Alors qu'une des adaptations nerveuses couramment observées après une période d'entraînement est l'augmentation de la fréquence de décharge des unités motrices (Häkkinen & Komi, 1982; Zehr & Sale, 1994; Van Cutsem et al., 1998), cela aurait pu masquer une éventuelle augmentation des MEPs enregistrés pendant une MVC après l'entraînement par vibration locale. Aucune évidence directe sur l'apparition d'un tel phénomène n'a à ce jour été reportée après ce type d'entraînement, même si cette hypothèse peut être potentiellement indirectement suggérée par l'augmentation de l'activité EMG maximale reportée dans l'étude #4. D'un autre côté, les MEPs enregistrés lors de contractions sous-maximales ne reflètent pas idéalement le niveau d'excitabilité cortico-spinale lors d'une MVC. Enfin, la méthodologie employée pour déterminer l'intensité optimale de stimulation magnétique a également pu influencer les résultats obtenus pour les MEPs après

l'entraînement par vibration locale. L'intensité était déterminée comme celle permettant d'obtenir une valeur maximale de MEPs lors d'une courbe de recrutement (cf. **figure 9** à la page 50 de ce manuscrit). Même si cette méthode a permis de détecter des modifications d'excitabilité cortico-spinale (i.e. augmentation des MEPs) après un exercice fatigant (Temesi et al., 2015; Vernillo et al., 2017), elle a potentiellement pu rendre certaines mesures effectuées par TMS insensibles à des changements d'excitabilité cortico-spinale après l'entraînement par vibration, notamment en cas de légère facilitation. Une autre façon de déterminer l'intensité optimale de stimulation magnétique pourrait être de choisir une intensité de stimulation qui marque la transition entre la phase ascendante de la courbe de recrutement et le début du plateau (Groppa et al., 2012). Il serait intéressant d'envisager de futures études en considérant cette méthode afin d'évaluer d'éventuelles modifications dans le comportement des MEPs post-entraînement. Il reste donc difficile à l'heure actuelle de faire le lien entre la mesure d'excitabilité cortico-spinale via les MEPs et la performance musculaire. Des travaux récents montrent même des résultats contre-intuitifs à ce sujet, avec des amplitudes de MEPs plus élevées sur une population inactive comparativement à une population active (Hassanlouei et al., 2017).

L'analyse de la durée des SPs renseigne sur d'autres modulations d'origine supra-spinale : le niveau d'inhibition intra-corticale. La durée des SPs enregistrées lors de contractions sous-maximales à 75 et 50% de MVC était diminuée après les 4 semaines d'entraînement sur les muscles VL et RF lors de l'étude #4. Il est probable que l'augmentation du niveau d'activation musculaire puisse être médiée par des processus intervenant dès l'initiation de l'ordre moteur au niveau des structures supra-spinales, et notamment par une réduction des processus inhibiteurs corticaux mettant en jeu la neurotransmission GABAergique. Cependant, cette hypothèse mérite davantage d'investigations dans la mesure où aucune modification de la durée des SPs n'était observée après 4 et 8 semaines d'entraînement dans l'étude #2.

2.2. La vibration locale comme une méthode d'entraînement alternative et efficace

L'efficacité ou non d'un programme d'entraînement peut être évaluée au regard des adaptations qu'il induit. En effet, l'augmentation de la performance musculaire après une période d'entraînement est intimement liée aux adaptations nerveuses et/ou musculaires résultantes (Sale, 1988), ce qui sous-tend que des adaptations

intervenant au moins à un de ces deux niveaux sont nécessaires pour rendre le programme d'entraînement efficace. En ce sens, diverses méthodes d'entraînement ont montré leurs capacités à moduler le versant central de la chaîne de commande neuromusculaire, parfois de manière légèrement différente que suite à un entraînement par vibration locale. En effet, il a été montré qu'un entraînement par NMES ne semblait pas induire de changement au niveau du réflexe H (Maffiuletti et al., 2003; Gondin et al., 2006), laissant penser que des adaptations supra-spinales sont majoritaires après ce type d'entraînement, même si les marqueurs neurophysiologiques utilisés pour suggérer une telle hypothèse présentent certaines limites, e.g. onde V (Gondin et al., 2006). A l'heure actuelle, il est difficile de venir comparer nos résultats avec ceux obtenus après un entraînement par NMES car aucune étude ne semble avoir étudié l'effet de ce type d'entraînement sur l'excitabilité des structures supra-spinales en utilisant la technique de TMS, ce qui peut être envisagé comme un futur axe de recherche intéressant. S'il est largement admis qu'un entraînement en force induit des adaptations centrales, la large inconsistance des résultats actuellement reportés limite leur interprétation ainsi que la comparaison avec les résultats obtenus lors de ce travail de thèse. En effet, les nombreuses variations dans les paramètres d'entraînement altèrent la nature des adaptations induites (Carroll et al., 2011; Kidgell & Pearce, 2011), et il serait aujourd'hui intéressant d'identifier des principes généraux sur les adaptations nerveuses induites par ce type d'entraînement. Il a été montré que des séances répétées de WBV modulaient le système nerveux central et permettaient de lutter contre les effets délétères d'une période d'immobilisation prolongée (Mulder et al., 2009). Cependant, peu de travaux font état d'adaptations nerveuses induites par ce type d'entraînement, comme suggéré par l'absence de modification du niveau d'activation volontaire (de Ruyter et al., 2003) ou du niveau d'activité EMG maximal (Machado et al., 2010; Rubio-Arias et al., 2017) reportée après plusieurs semaines d'entraînement par WBV. Devant le faible nombre de données disponibles, de futures recherches sont à considérer pour développer les connaissances à ce sujet. Les tableaux ci-dessous ont pour but de faciliter la comparaison des résultats relatifs aux adaptations nerveuses induites par un entraînement par vibration locale (**tableau 4.1**), WBV (**tableau 4.2**), NMES (**tableau 4.3**), et en force (**tableau 4.4**). Cette présentation des résultats est non exhaustive et ne couvre pas l'ensemble de la bibliographie actuelle. Les études sont triées dans un ordre croissant en fonction de la durée de l'entraînement.

Tableau 4.1. Adaptations nerveuses induites à la suite d'un entraînement par vibration locale.

Références	Sujets (nombre / âge (moyenne ± ET))	Groupe musculaire	Nombre de séances / Nombre de semaines	Durée de la séance	Adaptations nerveuses
Lapole & Pérot, (2010)	29 / 21 ± 2	FP	14 / 2	1h	EMG: TS ↑ 9% VA: ↑
Lapole & Pérot, (2012)	16 / 21 ± 2	FP	14 / 2	1h	Réflexe H: SOL ↑ 34%
Lapole et al., (2013)	11 / 22 ± 3	FP	14 / 2	1h	Réflexe H: SOL ↑ 30% Onde V: SOL ↑ 43%
Souron et al., (2017a)	22 / 20 ± 1	FD	12 / 4	1h	VA _{TMS} : ↑ 4% MEP _{MVC} : TA → SP _{MVC} : TA → Réflexe H: TA →
Souron et al., (en révision)	9 / 28 ± 6 & 8 / 65 ± 5	EG	12 / 4	1h	VA _{TMS} : ↑ 4% MEP _{MVC} : VL & RF→ SP _{MVC} : VL & RF→ SP _{50&75} : VL & RF ↓ EMG: VL ↑ Adaptations similaires entre sujets jeunes & âgés
Souron et al., (2017a)	22 / 20 ± 1	FD	24 / 8	1h	VA _{TMS} : ↑ 5% MEP _{MVC} : TA → SP _{MVC} : TA → Réflexe H: TA →

EG : muscles extenseurs du genou ; EMG : électromyographie ; FD : muscles fléchisseurs dorsaux de la cheville ; FP : muscles fléchisseurs plantaires de la cheville ; MEP : potentiel évoqué moteur ; RF : muscle droit fémoral ; SOL : muscle soléaire ; SP : période de silence ; TA : muscle tibial antérieur ; VA_{TMS} : niveau d'activation volontaire mesuré par TMS ; VL : muscle vaste latéral ; ↑ : indique une augmentation statistiquement significative ; ↓ : indique une diminution statistiquement significative ; → indique un résultat statistiquement non significatif.

Tableau 4.2. Adaptations nerveuses induites à la suite d'un entraînement par vibration corps entier.

Références	Sujets (nombre / âge (moyenne ± ET))	Groupe musculaire	Nombre de séances / Nombre de semaines	Durée de la séance	Adaptations nerveuses
Rubio-Arias et al., (2017)	17 / 22 ± 5	FP & EG	18 / 6	30 min	EMG: GM, GL & VL →
Wang et al., (2014b)	12 / 21 ± 2	FP	24 / 8	NR	Augmentation plus prononcée de l'onde V dans le groupe entraînement WBV + CMJ que CMJ seul
Machado et al., (2010)	15 / 75–90	EG	38 / 10	7–22 min	EMG: VL & VM →
de Ruitter et al., (2003)	10 / 21 ± 1	EG	33 / 11	5–8 min	VA _{PNS} : →

EG : muscles extenseurs du genou ; EMG : électromyographie ; FP : muscles fléchisseurs plantaires de la cheville ; GL : muscle gastrocnémien latéral ; GM : muscle gastrocnémien médial ; NR : non reporté ; VA_{PNS} : niveau d'activation volontaire mesuré par stimulation nerveuse électrique surimposée ; VL : muscle vaste latéral ; VM : muscle vaste médial ; ↑ : indique une augmentation statistiquement significative ; → indique un résultat statistiquement non significatif.

Tableau 4.3. Adaptations nerveuses induites à la suite d'un entraînement par stimulation électrique neuromusculaire.

Références	Sujets (nombre / âge (moyenne ± ET))	Groupe musculaire	Nombre de séances / Nombre de semaines	Durée de la séance	Adaptations nerveuses
Maffiuletti et al., (2002)	8 / 20 ± 2	FP	16 / 4	18 min	VA _{PNS} : ↑ 12% EMG: SOL ↑, GL & GM →
Maffiuletti et al., (2003)	8 / 20 ± 2	FP	16 / 4	18 min	Réflexe H: SOL & GM →
Gondin et al., (2006)	12 / 22 ± 3	FP	15 / 5	18 min	VA _{PNS} : ↑ 11% EMG: SOL, GL & GM ↑ (+51, 54 & 60%) Onde V: SOL, GL & GM ↑ (+75, 80 & 84%) Réflexe H: SOL, GL & GM →
Doix et al., (2017)	10 / 56 ± 5	FD	24 / 8	20 min	EMG: TA →
Gondin et al., (2005)	12 / 23 ± 5	EG	32 / 8	18 min	VA _{PNS} : ↑ 6% EMG: VL & VM ↑ (+69 & 39%), RF →

EG : muscles extenseurs du genou ; EMG : électromyographie ; FD : muscles fléchisseurs dorsaux de la cheville ; FP : muscles fléchisseurs plantaires de la cheville ; GL : muscle gastrocnémien latéral ; GM : muscle gastrocnémien médial ; RF : muscle droit fémoral ; SOL : muscle soléaire ; TA : muscle tibial antérieur ; VA_{PNS} : niveau d'activation volontaire mesuré par stimulation nerveuse électrique surimposée ; VL : muscle vaste latéral ; VM : muscle vaste médial ; ↑ : indique une augmentation statistiquement significative ; → indique un résultat statistiquement non significatif.

Tableau 4.4. Adaptations nerveuses induites à la suite d'un entraînement en force.

Références	Sujets (nombre / âge (moyenne ± ET))	Groupe musculaire	Nombre de séances / Nombre de semaines	Durée de la séance	Adaptations nerveuses
Christie & Kamen, (2014)	15 / 22 ± 3	FD	6 / 2	~10 min	MEP: TA → SP: TA ↓ ~13% Réflexe H: TA →
Goodwill et al., (2012)	7 / 21 ± 1	EG	9 / 3	NR	MEP: RF ↑ 56% SICI: RF ↓ 26%
Del Balso & Cafarelli, (2007)	20 / 24 ± 5	FP	12 / 4	~15 min	VA _{PNS} : ↑ 3% EMG: SOL ↑ 61% Onde V: ↑ 57% Réflexe H: SOL →
Griffin & Cafarelli, (2007)	10 / 18–32	FD	12 / 4	~15 min	MEP: TA ↑ 32% (10% MVC) & → (muscle relâché)
Weier et al., (2012)	6 / 20 ± 1 15 / 73 ± 5	EG	12 / 4	NR	MEP: RF ↑ 116% SICI: RF ↓ ~30% MEP: TA → SP: TA ↓ ~8% Réflexe H: TA →
Fimland et al., (2009b)	15 / 24 ± 2	FP	16 / 4	~15 min	EMG: SOL & GM ↑ (+42 & 62%) Onde V: SOL & GM ↑ (+109 & 69%) Réflexe H: SOL & GM →
Beck et al., (2007)	8 / 20–38	FD & FP	16 / 4	60 min	MEP: TA ↑ SICI: SOL →
Lagerquist et al., (2006)	10 / 21–42	FP	15 / 5	~10 min	Réflexe H: SOL ↑
Aagaard et al., (2002b)	14 / 25 ± 5	FP	38 / 14	NR	Réflexe H: SOL ↑ 19% Onde V: SOL ↑ 55%

EG : muscles extenseurs du genou ; EMG : électromyographie ; FD : muscles fléchisseurs dorsaux de la cheville ; FP : muscles fléchisseurs plantaires de la cheville ; GM : muscle gastrocnémien médial ; MEP : potentiel évoqué moteur ; NR : non reporté ; RF : muscle droit fémoral ; SICI : inhibition intra-corticale de courte latence (short interval intracortical inhibition) ; SOL : muscle soléaire ; SP : période de silence ; TA : muscle tibial antérieur ; VA_{PNS} : niveau d'activation volontaire mesuré par stimulation nerveuse électrique surimposée ; VL : muscle vaste latéral ; VM : muscle vaste médial ; ↑ : indique une augmentation statistiquement significative ; ↓ : indique une diminution statistiquement significative ; → indique un résultat statistiquement non significatif

Les adaptations nerveuses induites par un entraînement sont généralement associées à une amélioration de la performance musculaire. Sur la base des résultats apportés par les études #2 et #4 de ce travail de thèse (cf. **tableau 3** à la page 146 de ce manuscrit) ainsi que d'autres études récentes (Lapole & Pérot, 2010; Iodice et al., 2011; Lapole et al., 2013; Tankisheva et al., 2015), il est intéressant d'observer que l'entraînement par vibration locale permet d'augmenter les capacités de production de force, comme d'autres méthodes d'entraînement plus classiquement utilisées (**tableau 5**). En effet, il a été montré qu'un entraînement en force permettait d'augmenter de manière systématique la production de force isométrique et/ou dynamique (voir le tableau 1 et le tableau 2 respectivement dans les articles de Kidgell & Pearce, (2011) et Carroll et al., (2011)). Si l'on compare, pour des durées d'entraînement similaires à celles utilisées dans nos études (i.e. 4 et 8 semaines ; **tableau 5**), l'entraînement par vibration locale avec l'entraînement en force, ce dernier induit généralement des gains de force plus importants (+ 14–44%). S'il semble hasardeux de conclure à des adaptations périphériques après seulement 4 semaines d'entraînement en force, les gains de force plus importants reportés après 8 semaines d'entraînement en force sont probablement liés à des adaptations à la fois nerveuses et musculaires (Narici et al., 1989). Inversement, nos résultats ont montré qu'un entraînement par vibration locale ne développait que le versant nerveux. Bien que moins consensuel, il est parfois observé des gains de force plus importants lors d'un entraînement de 4 et 8 semaines par NMES (**tableau 5**), ce type d'entraînement pouvant également déclencher des adaptations aussi bien nerveuses que musculaires (Gondin et al., 2005). Enfin, l'entraînement par WBV est aussi largement utilisé pour augmenter les capacités de production de force (voir le tableau 1 dans l'article de Rittweger, (2010)).

Il est également intéressant d'observer que l'entraînement par vibration locale permet d'induire des gains de force du côté controlatéral comme mis en évidence par l'augmentation de MVC (+ 10%) sur le membre non entraîné lors de l'étude #2 de cette thèse (Souron et al., 2017a). Nos résultats confirment ceux précédemment reportés par Lapole et al., (2013) sur les muscles fléchisseurs plantaires et suggèrent que des adaptations nerveuses, i.e. augmentation du VA_{TMS} (Souron et al., 2017a) et de l'onde V (Lapole et al., 2013), soient la principale cause de cette amélioration de performance musculaire du côté non-entraîné, tout comme pour le côté entraîné. Ce phénomène, dit de « *cross-education* », a largement été démontré après un entraînement en force (Manca et al., 2017) mais peut également être observé après un entraînement par

NMES (Maffiuletti et al., 2006). Notons qu'à ce jour, une seule étude s'est intéressée aux effets d'un entraînement par WBV sur les adaptations controlatérales nerveuses et fonctionnelles, sans reporter de résultats significatifs (Goodwill & Kidgell, 2012).

Cette comparaison ne remet pas en cause l'efficacité des différentes techniques d'entraînement plus classiquement utilisées pour améliorer la force musculaire aussi bien du côté entraîné que non-entraîné, mais montre qu'un entraînement par vibration locale peut être une méthode alternative et efficace permettant de s'affranchir de certaines limites associées à ces différentes techniques. En effet, la NMES présente le désavantage d'être douloureuse pour certains patients via l'activation de récepteurs nociceptifs cutanés (Sheffler & Chae, 2007). De plus, les modalités de recrutement des fibres musculaires via la NMES (i.e. superficiel, fixe et incomplet) ont amené à penser que cette méthode n'était pas optimale dans un contexte d'entraînement musculaire (Maffiuletti, 2010). Par ailleurs, l'entraînement en force, même sous l'utilisation de charges légères, présente la limite de ne pas pouvoir être mobilisé immédiatement après une période d'immobilisation prolongée ou une opération chez certains patients présentant une importante fragilité musculaire. Le même problème se pose face à l'utilisation de la WBV, qui présente en plus le désavantage d'être coûteuse, non-portable, et de ne pas pouvoir cibler un muscle de manière précise, les vibrations étant transmises à l'ensemble du corps à partir des pieds.

Tableau 5. Effets d'un entraînement par vibration locale, vibration corps entier (WBV), stimulation électrique neuromusculaire (NMES) et en force sur la capacité de production de force maximale isométrique. Les différentes études sont regroupées en fonction de la durée de la période d'entraînement.

4–5 semaines							
Mode d'entraînement	Références	Sujets (nombre / âge (moyenne ± ET))	Groupe musculaire	Nombre de séances / durée (semaines)	Durée de la séance	Gains en force	Gains moyen
Vibration locale	Iodice et al., (2011)	18 / 21 ± 1	EG	12 / 4	30 min	↑ 32%	17%
	Souron et al., (2017a)	22 / 20 ± 1	FD	12 / 4	1h	↑ 7%	
	Souron et al., (en révision)	9 / 28 ± 6 & 8 / 65 ± 5	EG	12 / 4	1h	↑ 12%	
WBV	Delecluse et al., (2005)	10 / 17–30	EG	15 / 5	~15 min	→ (+3%)	~7%
	Wang et al., (2014a)	7 / 19–23	EG	12 / 4	3 min	→ (+10%)	
NMES	Currier & Mann, (1983)	8 / 21 ± 2	EG	15 / 5	~10 min	↑ 16%	~17%
	Selkowitz, (1985)	12 / 18–32	EG	12 / 4	~20 min	↑ 40%	
	Parker et al., (2003)	9 / 18–28	EG	8 / 4	10 min	→ (+7%)	
		9 / 18–28		12 / 4		↑ 13%	
	Herrero et al., (2006)	10 / 19 ± 1	EG	16 / 4	~35 min	↑ 9%	
	Gondin et al., (2005)	12 / 23 ± 5	EG	16 / 4	18 min	↑ 15%	
	Gondin et al., (2006)	12 / 22 ± 3	FP	15 / 5	18 min	↑ 22%	
Force	Griffin & Cafarelli, (2007)	10 / 18–32	FD	12 / 4	~15 min	↑ 18%	~27%
	Geertsen et al., (2008)	14 / 26 ± 7	FD	12 / 4	~20 min	↑ 20%	
	Fimland et al., (2009b)	15 / 24 ± 2	FP	16 / 4	~15 min	↑ 44%	

Discussion générale

8–9 semaines							
Vibration locale	Souron et al., (2017a)	22 / 20 ± 1	FD	24 / 8	1h	↑ 12%	12%
WBV	Kvorning et al., (2006)	9 / 23 ± 1	EG	21 / 9	~15 min	↑ 9%	8%
	Rees et al., (2009)	15 / 74 ± 5		24 / 8	5–8 min	↑ 7%	
NMES	Portmann & Montpetit, (1991)	11 / NR	EG	24 / 8	10 min	↑ 21%	24%
	Gondin et al., (2005)	12 / 23 ± 5	EG	32 / 8	18 min	↑ 27%	
Force	Hakkinen et al., (2000)	12 / 37–44	EG	16 / 8	NR	↑ ~14%	~20%
		10 / 62–77	EG	16 / 8	NR	↑ ~27%	
	Fimland et al., (2009a)	10 / 23 ± 3	FP	24 / 8	~15 min	↑ 20%	
> 9 semaines							
Vibration locale	Tankisheva et al., (2015)	17 / 66–84	EG	130 / 26	2–8 min	↑ 14%	14%
WBV	Torvinen et al., (2002a)	26 / 23 ± 4	EG	~64 / 16	2–4 min	→ (+3%)	~15%
	Delecluse et al., (2003)	20 / 21 ± 2	EG	36 / 12	3–20 min	↑ 17%	
	Roelants et al., (2004)	18 / 21 ± 1	EG	72 / 24	3–20 min	↑ 24%	
Force	Aagaard et al., (2002a)	15 / 23 ± 4	EG	38 / 14	NR	↑ 16%	~18%
	Aagaard et al., (2002b)	14 / 25 ± 5	FP	38 / 14	NR	↑ 20%	
	Scaglioni et al., (2002)	14 / 60–80	FP	48 / 16	2–3 min	↑ 18%	
	Cannon et al., (2007)	9 / 20–30 8 / 64–78	EG	30 / 10	~20 min	↑ 16% ↑ 18%	

EG : muscles extenseurs du genou ; FD : muscles fléchisseurs dorsaux de la cheville ; FP : muscles fléchisseurs plantaires de la cheville ; NR : non reporté ; ↑ : indique une augmentation statistiquement significative ; → indique un résultat statistiquement non significatif. Les études sont triées dans un ordre croissant en fonction de leur date de publication.

Il apparaît donc que les adaptations neuromusculaires engendrées par l'entraînement par vibration locale peuvent bénéficier aux capacités fonctionnelles des sujets, comme remarqué avec l'augmentation de la hauteur de saut lors de tâches de squat jump et de contre-mouvement jump dans l'étude #4 (cf. **tableau 3** à la page 147 de ce manuscrit). Il est intéressant d'observer que nos résultats s'appliquaient également à une population âgée, avec comme originalité principale l'évaluation des adaptations nerveuses induites chez ce type de population réalisée pour la première fois dans ce cadre scientifique. Le recrutement d'une population âgée était motivé par le fait qu'un phénomène de dégénérescence neuromusculaire est couramment associé à ce type de population. Ainsi, une altération des propriétés nerveuses aussi bien au niveau spinal (Aagaard et al., 2010; Baudry & Duchateau, 2012) que supra-spinal (Volkow et al., 1998; Mattay et al., 2002) peut conduire à une diminution des capacités de production de force, une perturbation de la mobilité ou encore une augmentation du risque de chute chez ces personnes. Dans cette optique, nous avons trouvé pertinent d'évaluer les effets d'un entraînement par vibration locale sur les capacités fonctionnelles de personnes âgées et d'identifier les adaptations nerveuses qui sous-tendent ces possibles améliorations fonctionnelles, ceci dans le but de pouvoir proposer ce genre de protocole dans un cadre clinique à des populations parfois inadaptées aux protocoles de rééducation classiques, e.g. entraînement en force, par WBV ou par NMES.

CONCLUSIONS ET PERSPECTIVES

Les études #1 et #3 ont permis d'apporter de nouvelles évidences sur les adaptations nerveuses induites par une application aigüe de la vibration locale. Cependant, certains mécanismes restent encore à explorer de manière plus précise. Il serait ainsi intéressant d'évaluer de manière directe le niveau d'inhibition pré-synaptique, e.g. technique d'inhibition D1 (*inhibition D1*) (Mizuno et al., 1971; Johannsson et al., 2015), méthode de facilitation des projections hétéronymes monosynaptiques la (Johannsson et al., 2015), après une exposition prolongée à la vibration locale depuis que ce mécanisme a été suggéré comme influençant majoritairement le comportement du réflexe H post-vibration. Parallèlement à l'analyse des TMEPs, cela pourrait permettre de mieux isoler les phénomènes liés à l'inhibition pré-synaptique et ceux liés aux perturbations d'excitabilité motoneuronale intrinsèque. Devant la divergence des résultats reportés sur différents paramètres (e.g. force, MEPs) après une application aigüe de la vibration locale, il serait intéressant d'évaluer si certains paramètres vibratoires pourraient mieux convenir à certains muscles afin d'optimiser l'efficacité des séances de vibration en fonction du groupe musculaire considéré. En fixant des paramètres vibratoires précis, il pourrait être intéressant d'évaluer si les effets aigus de la vibration sont similaires entre plusieurs groupes musculaires pour un même sujet

Les études #2 et #4 ont confirmé l'efficacité d'un entraînement par vibration locale pour améliorer la performance musculaire et ont apporté des résultats nouveaux sur les adaptations nerveuses induites sur le long terme par ce type d'entraînement. Cependant, il existe actuellement un manque de clarté quant à la relation entre l'amélioration de la performance musculaire et les adaptations nerveuses observées dans la mesure où aucune corrélation significative n'a été montrée entre ces différents paramètres. Il serait intéressant d'approfondir ces résultats à l'avenir, en mobilisant notamment de nouvelles techniques pour investiguer de manière plus précise les adaptations nerveuses induites par ce type d'entraînement. La stimulation électrique du faisceau pyramidal permettrait d'évaluer d'éventuelles adaptations motoneuronales à la suite d'un entraînement par vibration locale. Des techniques de conditionnement du réflexe H (e.g. inhibition D) permettraient d'évaluer plus directement d'éventuelles modifications dans le niveau d'inhibition pré-synaptique après ce genre d'entraînement. Enfin, l'imagerie par résonance magnétique ou la tomographie permettrait d'évaluer si des modifications d'activation de certaines régions corticales surviennent à la suite de ce type d'entraînement.

Une des originalités de ce travail de thèse était de comparer les adaptations induites après un entraînement par vibration locale sur des sujets sains jeunes et âgés. Les adaptations étaient similaires pour les sujets jeunes et les sujets âgés. Cependant, le faible nombre de sujet dans chaque groupe ($n = 9$ et $n = 8$ respectivement pour les sujets jeunes et âgés) limite la puissance de l'analyse statistique, et il serait intéressant dans le futur de conduire des recherches similaires avec un échantillon plus important pour évaluer si les adaptations dues à l'entraînement diffèrent entre ces deux populations distinctes.

L'évaluation des effets de la vibration locale dans une optique de performance sportive peut également constituer un axe de recherche intéressant dans le futur. Dans cette perspective, une étude réalisée en collaboration avec Darryl J Cochrane de l'Université de Massey en Nouvelle-Zélande (non présentée dans ce manuscrit) a été menée en marge de ma troisième année de thèse pour évaluer les effets d'un échauffement par vibration locale sur la performance musculaire. Les premiers résultats semblent montrer qu'un échauffement par vibration locale n'améliore pas significativement la performance (e.g. MVC, RFD, hauteur de saut) comparativement à un échauffement actif. Cependant, il serait intéressant d'évaluer les effets d'une application chronique de la vibration locale associée à un programme d'entraînement sportif classique sur la performance sportive en condition de terrain.

La finalité de ce travail de thèse était de pouvoir offrir une perspective clinique à l'application chronique de la vibration locale. Le déroulement de ce doctorat est ainsi allé dans ce sens, en investiguant dans un premier temps les effets d'un entraînement par vibration locale sur une population saine et jeune, et dans un second temps sur une population saine et âgée. L'objectif de la troisième et dernière année de thèse était donc de s'intéresser à une population clinique, i.e. des patients victimes d'une rupture du LCA et opérés selon une technique de ligamentoplastie (étude #5 présentée en annexe 2 de ce manuscrit). Cette population spécifique a été choisie au regard du phénomène de sidération observé post-ligamentoplastie. Ce phénomène reflète une augmentation de l'inhibition nerveuse post-opération caractérisée comme un des principaux déterminants du déficit de force des muscles extenseurs du genou (Ingersoll et al., 2008; Hart et al., 2010). Les techniques de rééducation post-opératoire s'axent aujourd'hui essentiellement sur la réadaptation musculaire (e.g. électrothérapie, contraction active, etc.) notamment pour lutter contre l'atrophie. Nos résultats ont montré l'efficacité de la vibration locale à venir moduler le système

nerveux central sur le long terme (Lapole & Pérot, 2012; Lapole et al., 2013; Souron et al., 2017a). Il serait donc intéressant d'envisager l'utilisation de ces techniques afin d'optimiser les séances de rééducation en travaillant plus spécifiquement sur la composante nerveuse. Dans cette optique, un projet de recherche a été proposé et accepté par le Comité de protection des personnes Sud Est I, et a été lancé en janvier 2017. La stratégie de recrutement reposant exclusivement sur les chirurgiens, et compte tenu de leurs contraintes, ils n'ont pu à l'heure actuelle que difficilement nous envoyer des patients. Cependant, une collaboration avec l'Université de Chambéry a été mise en place pour que le projet puisse continuer au sein de leur structure, avec comme échéancier la date de juillet 2018. La stratégie de recrutement sera légèrement modifiée, avec comme point de départ le kinésithérapeute qui recevra le patient blessé et demandera l'aval des chirurgiens collaborateurs pour le recrutement ou non des patients à cette étude. Malgré des perspectives professionnelles qui me poussent à m'éloigner de la région stéphanoise et chambérienne, je resterai intégré aux travaux effectués à Chambéry. Une partie de justification scientifique détaillée ainsi que la méthodologie générale de ce projet de recherche sont présentées en annexe 2.

Dans l'attente des résultats de cette dernière étude, les données obtenues lors des différentes études présentées dans ce mémoire de thèse nous laissent entrevoir des résultats prometteurs, avec pour perspective une utilisation plus généralisée de la vibration locale dans un cadre clinique/de rééducation.

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ANNEXE 1

REPRODUCTIBILITE DES MESURES FONCTIONNELLES ET CORTICO-SPINALES DES MUSCLES FLECHISSEURS DORSAUX DE LA CHEVILLE LORS DE CONTRACTIONS MAXIMALES VOLONTAIRE

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*RELIABILITY OF THE FUNCTIONAL MEASURES OF THE CORTICOSPINAL
PATHWAYS TO DORSIFLEXOR MUSCLES DURING MAXIMAL VOLUNTARY
CONTRACTIONS*

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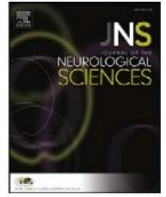
RESUME :

Objectif : Cette étude visait à déterminer la reproductibilité de l'évaluation de la fonction neuromusculaire des muscles fléchisseurs dorsaux de la cheville via l'utilisation de la stimulation magnétique transcrânienne. **Méthodes :** Treize jeunes hommes et femmes réalisaient 3 sessions de tests dans le but d'évaluer la reproductibilité intra-, i.e. deux sessions réalisées le même jour, et inter-jour, i.e. deux sessions réalisées à une semaine d'intervalle, de différents paramètres d'évaluation de la fonction cortico-spinale, i.e. i) le niveau d'activation volontaire cortical, ii) l'excitabilité cortico-spinale via l'amplitude des potentiels évoqués moteurs et iii) l'inhibition intra-corticale à partir de la durée des périodes de silence. La reproductibilité absolue, i.e. le coefficient de variation (CV) et l'erreur standard de mesure (SEM), et relative, i.e. le coefficient de corrélation intra-classe (ICC) étaient calculées. **Résultats :** Une excellente reproductibilité intra- (ICC : 0,80 ; CV : 1,7%) et inter-jour (ICC : 0,99 ; CV : 0,8%) a été reportée pour le niveau d'activation volontaire cortical. Les potentiels évoqués moteurs et les périodes de silences mesurés lors de contractions maximales volontaires ont présenté une reproductibilité intra- et inter-jour modérée à excellente (ICC : 0,47-0,98 ; CV : 8,6-14,9%). **Conclusion :** Les résultats de cette étude suggèrent que la majorité des mesures réalisées par stimulation magnétique transcrânienne sur le muscle tibial antérieur peuvent être utilisées afin de quantifier les adaptations cortico-spinales suite à des interventions aiguës, i.e. protocole de fatigue, et/ou chroniques, i.e. protocole d'entraînement.



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Reliability of the functional measures of the corticospinal pathways to dorsiflexor muscles during maximal voluntary contractions

Robin Souron^a, Adrien Farabet^a, Guillaume Y. Millet^b, Thomas Lapole^{a,*}^a Univ Lyon, UJM-Saint-Etienne, LIBM, F-42023 Saint-Etienne, France^b Human Performance Laboratory, Faculty of Kinesiology, University of Calgary, Canada

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ABSTRACT

This study aimed to evaluate the intra- and inter-day reliability of transcranial magnetic stimulation (TMS)-related measurements recorded from the tibialis anterior (TA) muscle. Thirteen healthy young men and women (23 ± 4 years) performed 3 testing sessions to assess intra- (i.e., two sessions performed the same day) and inter-day (i.e. two sessions performed one week apart) reliability of (i) dorsiflexion cortical maximal voluntary activation level (VA_{TMS}), (ii) TA corticospinal excitability assessed through the amplitude of the motor evoked potentials (MEP) recorded during 100, 75 and 50% maximal voluntary contractions (MVC), and (iii) intracortical inhibition investigated via the cortical silent period (CSP) recorded at the same % MVC. Absolute (i.e., coefficient of variation (CV) and standard error of the mean (SEM)), and relative (i.e., intraclass correlation coefficients (ICC)) reliability parameters were calculated. VA_{TMS} demonstrated excellent intra- and inter-day reliabilities (ICC: 0.80 and 0.99; CV: 1.7 and 0.8%, respectively). MEPs and CSPs presented moderate to excellent intra- and inter-day reliabilities, while input-output curves extracted parameters presented highly variable outcomes. These results suggest that most TA corticospinal measurements during voluntary contractions can be used to quantify corticospinal adaptations after acute (e.g. fatigue) or long term (e.g. training) interventions.

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1. Introduction

It is well established that training, and especially strength training, induces several adaptations to the central nervous system leading, *in fine*, to an augmentation of maximal voluntary contraction (MVC) force. The investigation of maximal voluntary activation is critical to assess neural adaptations. Voluntary activation refers to the neural drive delivered to a muscle during a voluntary contraction. The most common way to estimate maximal voluntary activation is to use the interpolated

twitch technique [1], where a supramaximal stimulus is delivered over a motor nerve during an MVC to measure the extra force evoked by the stimulation. Using this method, changes in neural drive can be identified as at or above the site of stimulation of the motor axons, without distinction between spinal and supraspinal mechanisms [2]. Since training may induce both spinal [3] and supraspinal adaptations [4], transcranial magnetic stimulation (TMS) has been proposed as an alternative technique to ascertain whether adaptations occur throughout the corticospinal pathway [5]. Indeed, the evocation of a superimposed twitch elicited by TMS during MVC has been suggested to highlight a suboptimal drive from the motor cortex [5–7], although the cause of VA_{TMS} reduction can be due to modulation at any level of the corticospinal network (i.e. through reduced spinal and/or motoneuronal excitability).

The assessment of cortical voluntary activation using TMS (i.e., VA_{TMS}) cannot be performed for all muscles since some criteria must be met, especially having strong corticomotoneuronal projections [8]. VA_{TMS} has been shown to be reliable for the elbow flexors [9] or the knee extensors [8], but not in dorsiflexor muscles thus far, despite the functional role of these muscles in particular during locomotion [10, 11]. The tibialis anterior (TA), contributing to almost half of the voluntary torque produced in ankle dorsiflexion (the remainder presumably being provided by the long extensors of the toes) [12], is known to have the strongest corticospinal projections among lower limb muscles [13]. Even though dorsiflexor muscles VA_{TMS} has already been assessed

Abbreviations: CSP, cortical silent period; CSP_{50} , cortical silent period during a 50% MVC submaximal contraction; CSP_{75} , cortical silent period during a 75% MVC submaximal contraction; CSP_{MVC} , cortical silent period during a MVC; CV, coefficient of variation; EMG, electromyographic; ERT, estimated resting twitch amplitude; I_{50} , stimulus intensity required to obtain a MEP of half the size of the plateau; ICC, intraclass correlation coefficient; k, the slope parameter of the Boltzmann modelling; M_{MVC} , M-wave amplitude during a MVC; MEP, motor evoked potential; MEP_{50} , motor evoked potential amplitude during a 50% MVC submaximal contraction; MEP_{75} , motor evoked potential amplitude during a 75% MVC submaximal contraction; MEP_{MVC} , motor evoked potential amplitude during a MVC; MVC, maximal voluntary contraction; P, the function plateau of Boltzmann modelling; RMS, root mean square; SEM, standard error of the mean; SIT, superimposed twitch amplitude; SIT_{MVC} , superimposed twitch amplitude during a maximal voluntary contraction; TA, tibialis anterior; TMS, transcranial magnetic stimulation; VA_{TMS} , voluntary activation assessed with TMS.

* Corresponding author at: Laboratoire Interuniversitaire de Biologie de la Motricité, Bâtiment IRMIS, 10 rue de la Marandière, 42270 Saint Priest en Jarez, France.

E-mail address: thomas.lapole@univ-st-etienne.fr (T. Lapole).

in fatigue studies [14,15], no study has yet investigated VA_{TMS} reliability for this muscle group. Such an approach is necessary since the constant oscillation in the elements of the central nervous system and methodological factors (e.g. subject population, muscle considered, position for magnetic stimulation) are two main sources that may affect the stability of TMS measurements [16]. Indeed, motor-evoked potential (MEP) elicited by TMS, which is known to represent the excitability of cortical neurons and/or motoneuron pools of the stimulated muscles [17], are inherently variable. For instance, MEP amplitude may be influenced by circadian variation [18]. To reduce variability, MEP amplitude is commonly expressed as ratio to M-wave to rise above the membrane excitability and conductivity influence. MEPs should also be measured during a stable voluntary contraction to further reduce variability [16,19]. Among the studies that investigated TA MEP reliability [14,16,20], only one met these last two criteria and reported high inter-day reliability for MEPs measured during submaximal lengthening and shortening contractions [16]. During maximal isometric contraction, absolute MEP was also reported to be reliable [14], as it was at rest [14,20]. Hence, intra-day and inter-day reliability of normalized TA MEPs during submaximal and maximal isometric contractions has yet to be determined. Moreover, although input-output curves (i.e. the relation between TMS intensity and MEP amplitude) [19,21] are recognized as a more sensitive measure of corticospinal excitability [22,23], its reliability for the TA muscle has only been proven during a relaxed condition [20].

Although several studies have investigated the reliability of TA TMS-related parameters [14,16,20], this topic needs further investigation. Specifically, dorsiflexor VA_{TMS} must be examined to better understand short- and long-term adaptations within the central nervous system during acute and long term interventions. This would provide complementary knowledge with regard to previous TMS studies demonstrating changes in TA corticospinal excitability after strength training [24,25].

Therefore, the present study is intended to evaluate the intra- and inter-day reliability of VA_{TMS} and associated corticospinal functional properties (e.g., MEP amplitude) for dorsiflexor muscles.

2. Material and methods

2.1. Participants

Thirteen young, healthy young subjects (9 men and 4 women, 23 ± 4 years; height: 177 ± 8 cm; body mass: 69 ± 10 kg) participated in this study. The subjects' level of weekly physical activity was reported to be between 0 and 5 h per week. Written, informed consent was obtained from all subjects prior to their participation and this study conformed to the standards from latest revision of the Helsinki Declaration and was approved by the local ethics committee. All subjects were free of lower-limb injury during the previous three months, contraindications to TMS, acute and chronic neurological disorders, and trauma. Before testing, each subject was informed about the nature and the aim of this study, as well as risks and discomfort associated with electrical and magnetic stimulation. They were instructed to abstain from caffeine for a minimum of 12 h before each session.

2.2. Design of the study

Subjects came for three visits to the laboratory at the same time of the day with a 1-week interval between visits. The first visit was a familiarization session of the entire experimental protocol. In order to assess the inter-day reliability, the same protocol was performed during the second and third visits, i.e., session 1 (S1) and session 3 (S3), respectively. Except for the TMS recruitment curve and the peripheral nerve stimulation setup (see below), the whole experimental protocol was performed twice with a 30-min resting period between measurement sessions during one of these visits (randomly designed), allowing the assessment of intra-day reliability (S1 and session 2 (S2)) (Fig. 1). The 30 minute resting period began at the end of S1 and finished at the

beginning of S2. Hence, subjects were invited to stay in a sitting position on the custom-built chair during the 30-min period.

2.3. Torque and electromyographic recordings

Dorsiflexion torque was measured during voluntary contractions by a calibrated, instrumented pedal (CS1060 300 Nm, FGP Sensors, Les Clayes Sous Bois, France). Subjects were seated upright in a custom-built chair with a hip, knee, and ankle angle of 90, 120, and 90°, respectively. The foot was securely attached to the pedal with a custom designed hook and loop fastener. Electromyographic (EMG) activity of the right TA and soleus (SOL) was recorded with pairs of self-adhesive surface electrodes (Meditrace 100, Covidien, Mansfield, USA) in bipolar configuration with a 30-mm interelectrode distance and the reference on the medial malleolus. SOL electrodes were placed 2 cm inferior to the insertion of the gastrocnemii on the Achilles tendon. TA electrodes were placed on the muscle belly parallel to the longitudinal axis of the muscle at one-third of the distance between the head of the fibula and the tip of the medial malleolus, according to SENIAM recommendations [26]. Skin impedance was measured using a classic impedance analyser (Fluke 87 V Ex, Fluke, Wallisellen, Switzerland) and low impedance (<5 k Ω) between electrodes 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; common mode rejection ratio = 85 dB, gain = 500), bandpass filtered (5–500 Hz), and analogue-to-digital converted at a sampling rate of 2000 Hz by PowerLab system (16/30-ML880/P, ADInstruments, Bella Vista, Australia). All data was analysed offline using Labchart 7 software (ADInstruments).

2.4. Stimulation

Two types of stimulation were used. Specifically, electrical stimulation of the tibialis anterior motor nerve (i.e., peroneal nerve) and transcranial magnetic stimulation (TMS) over the motor hotspot for the TA muscle. For stimulation of the tibialis anterior motor nerve, a bipolar bar stimulating electrode with 30-mm anode-cathode spacing (Bipolar Felt Pad Stimulating Electrode Part number E.SB020/4mm, Digitimer) was positioned next to the fibular head. Single rectangular pulses with 0.5 ms duration and 400 V maximal output voltage were delivered to the right peroneal nerve via a constant-current stimulator (DS7A, Digitimer, Welwyn Garden City, Hertfordshire, UK). The optimal site of stimulation was determined as the location eliciting the greatest TA

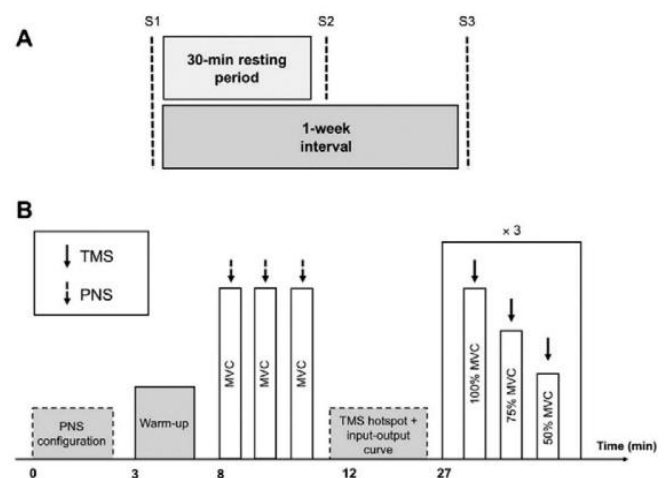


Fig. 1. Overview of the experimental design of the study (A) and the neuromuscular testing protocol (B). The measurements were performed during session 1 (S1), session 2 (S2) and session 3 (S3) except for peripheral nerve stimulation (PNS) and transcranial magnetic stimulation (TMS) setup which were performed only for S1 and S3.

M-wave for a given stimulus intensity. This site was marked with semi-permanent ink. To determine the optimal intensity of electrical stimulation, the intensity was increased by 5 mA until the magnitude of resting TA M-wave plateaued. The number of stimulations to find the optimal stimulating intensity varied among subjects (i.e., between 3 and 10). This optimal stimulating intensity was then increased by 50% to ensure supramaximal intensity of stimulation during contraction. Electrical stimulation configuration was determined at the beginning of the S1 and S3 to avoid any potentiation effects. The stimulation intensity used to evoke M-wave during MVC ranged between 30 and 97.5 mA. The mean stimulation intensities were 47.6 ± 20.2 mA in S1 (the same intensity was used for S2) and 48.2 ± 17.0 mA in S3. The whole procedure of determining stimulation site and intensity was performed in approximately 3 min.

For the TMS technique, motor evoked potentials (MEPs) and superimposed twitches (SITs) were evoked during voluntary isometric dorsiflexion via a Magstim 200² magnetic stimulator (Magstim 200², The Magstim Company Ltd., Whitland, UK) with a 110-mm double cone coil. The coil was positioned over the leg area of the left motor cortex along the nasal-inion axis to induce a postero-anterior current. The coil position to obtain an optimal activation of the TA is known to be 0.5–1 cm posterior and along the anteroposterior plane of the vertex [21]. This location was drawn on the swim cap every centimeter from 1 cm anterior to 3 cm posterior to the vertex along the nasal-inion line and also to 2 cm over the left motor cortex area (i.e., 8 marks on the swim cap). Thus, a single stimulation was delivered at each of the specified anatomical positions (i.e. 8 stimulations in total) and the optimal coil position was chosen as the site eliciting the largest SIT and TA MEP amplitude with minimal SOL MEP amplitude in response to stimulation at 50% maximal stimulator output during brief voluntary dorsiflexion at 10% MVC. The whole procedure was performed in approximately 2 min.

Subjects were provided with real-time feedback of their target force, which was displayed on a screen. This position was marked on a swim cap that was secured to the scalp. During voluntary contractions, TMS was delivered once the subject had stabilized the force on the target level. Subjects were instructed to re-contract as strongly and as fast as possible immediately after TMS delivery to permit accurate measurement of the cortical silent period (CSP). Electrodes for peripheral nerve stimulation as well as the TMS coil were placed and hand-held by the same investigator for all subjects and all visits.

2.5. Neuromuscular measurements

2.5.1. MVC

After a standardized warm-up consisting of 10 submaximal voluntary contractions performed between 30 and 80% of the MVC obtained during the familiarization session, subjects performed three maximal dorsiflexion contractions lasting approximately 3 s, with a 1-min resting period between trials to avoid fatigue. Electrical stimulation was delivered during MVCs to obtain the maximal M-wave peak-to-peak amplitude recorded during MVC (M_{MVC}) (Fig. 1.B). MVC was determined as the highest torque value achieved before the electrical stimulation. TA EMG root mean square (RMS) was calculated as the mean over a 500-ms period after maximal force had reached a plateau and was then normalized to M_{MVC} .

2.5.2. Input-output curves

TA TMS input-output curves were only assessed once during each visit to the laboratory to determine the optimal stimulation intensity. Hence, only inter-day reliability was investigated for this curve. TMS was delivered over the hotspot. Since corticospinal excitability is increased with muscle activity [27], input-output curves were determined during brief voluntary dorsiflexion at 20% MVC. Four consecutive 2–3 s contractions, with a 10 second rest between contractions, were performed at 20, 30, 40, 50, 60, 70 and 80% maximal stimulator output

(randomly ordered), and a TMS pulse was delivered during each of these contractions (i.e., 28 stimulations were initially delivered). If a TA MEP plateau was not confirmed from these intensities, higher TMS intensities were investigated. The optimal stimulation intensity obtained from the input-output curves was chosen when TA MEP and SIT plateaued. The MEP evoked in the antagonist SOL was also measured to ensure it stayed at a low value (Fig. 3). The whole procedure was performed in approximately 10 min.

The aforementioned method has been recently reported to be appropriate for determining TMS intensity in the quadriceps [28]. The size of the TA MEPs was measured as the peak-to-peak amplitude of the non-rectified EMG response and expressed relative to M_{MVC} , and then averaged and plotted against the stimulus intensity. Then Boltzmann modelling was performed on input-output curves in order to apply a nonlinear regression analysis (Fig. 2.A) [21,24,29]:

$$\text{MEPampI} = \frac{P}{1 + \exp\left[\frac{I_{50} - I}{k}\right]}$$

This function allows the determination of the relation between MEP amplitude (MEPampI) and the TMS intensity (I, in percentage of the stimulator output). Three parameters can be extracted from this relationship: the maximum MEP defined by the function (P, in % M_{MVC}), the stimulus intensity at which the MEP size is 50% of the maximal MEP (I_{50} , in percentage of the stimulator output), and the slope parameter (k) that is inversely proportional to the maximal function steepness [21]. The peak slope of the function was also calculated to provide an indication of the maximal rate of increase in MEP amplitude with stimulus intensity. The peak slope of the function is its tangent at I_{50} [19] and was further calculated by the following equation, taking into account the slope parameter (i.e., k) and the maximum MEP defined by the previous equation (i.e., P) [19,24]:

$$\text{Peak slope} = \frac{k \times P}{4}$$

2.5.3. Cortical voluntary activation

Cortical voluntary activation (VA_{TMS}) during maximal effort was calculated with the modified twitch interpolation technique as initially developed by Todd et al. [7]. Stimulus intensity used for the investigation of cortical voluntary activation was defined as the lowest stimulus intensity tested eliciting maximal SIT and TA MEP amplitude from the input-output curve test performed for corticospinal excitability measurement. The same intensity was used for intra-session reliability, but was not necessarily the same between S1 and S3 (i.e., inter-day). The stimulus intensities used to assess VA_{TMS} were $65.3 \pm 7.7\%$ and $65.3 \pm 8.7\%$ of the maximal stimulator output in S1 and S3, respectively. Corticospinal excitability increases substantially during the transition from relaxed to contracted muscle states [30], thus underestimating TMS evoked twitch in the relaxed muscle. Hence, estimated resting twitch (ERT) was determined by linear regression of the relation between SIT amplitude evoked when TMS was delivered at 100, 75 and 50% MVC and voluntary force (Fig. 2.B) [7]. This relation was extrapolated and the y-intercept was interpreted as the ERT amplitude (Fig. 4). VA_{TMS} was assessed with the equation:

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

where SIT_{MVC} is the superimposed twitch evoked during MVC. Three series were performed and averaged with contractions separated by 30 s and series by 2 min. Thus, the linear regression was run out with the 3 values from each series, and VA_{TMS} was then averaged. ERT was excluded and VA_{TMS} was not calculated when the linear regression was not linear within a series ($r^2 < 0.9$) [31]. One series was excluded from the data analysis for 5 subjects (out of 39 series in total) and the average was

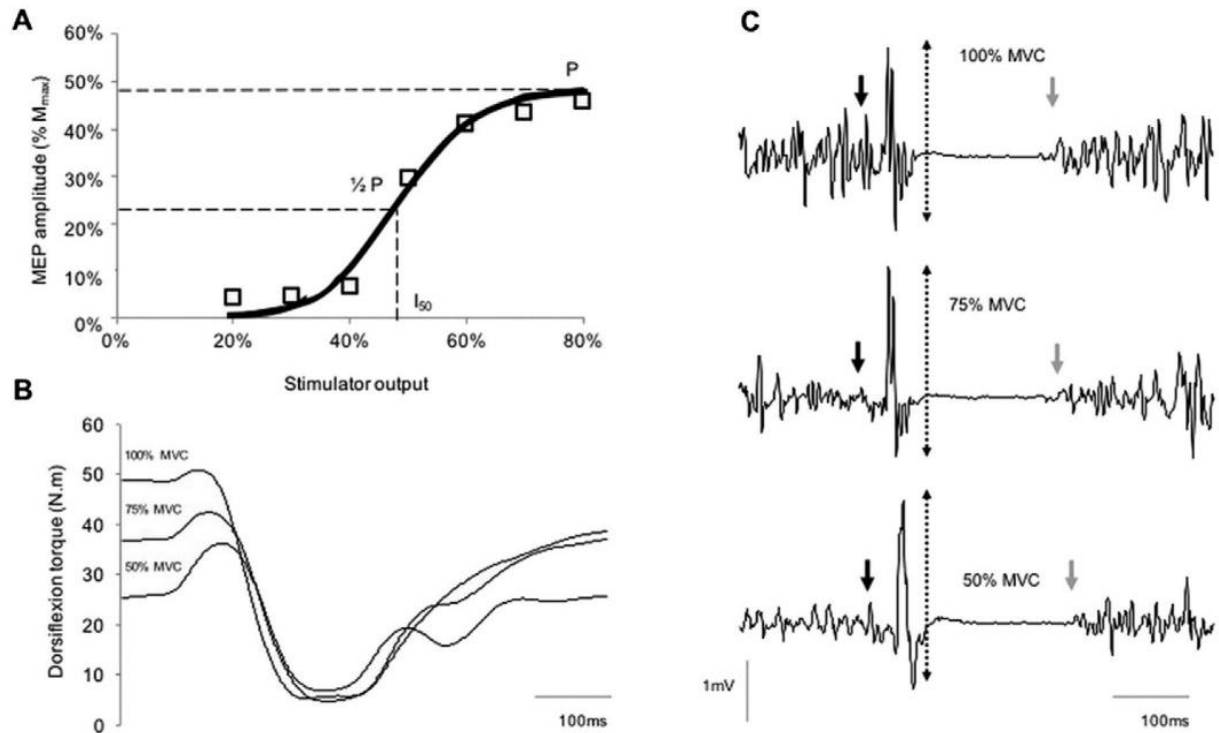


Fig. 2. (A) Typical TA MEP input-output curve. Mean TA MEP amplitudes (white squares) are presented as a function of TMS intensity from 20 to 80% of maximal stimulator output. The solid line represents the Boltzmann sigmoid function fit to that set of data. Dashed lines indicate I_{50} (i.e. stimulus intensity required to obtain a MEP amplitude of half the size of the plateau, $1/2$ P) and P (i.e. the maximum MEP defined by the function). (B) Superimposed twitch force evoked with TMS during maximal (i.e. 100% MVC) and submaximal (i.e. 75% and 50% MVC) voluntary contractions. (C) Example of electromyographic recording in response to transcranial magnetic stimulation (TMS) during maximal (100% MVC) and submaximal voluntary contractions (75% and 50% MVC). The time interval between black and grey arrows represents the way to assess cortical silent period (CSP) duration. Black arrows represent the time of TMS stimulation. Grey arrows represent the resumption of continuous voluntary EMG. Dotted arrows represent the MEP peak-to-peak amplitude. Data are from a representative subject.

done with 2 series rather than 3 in this case. ERT and SIT_{MVC} were determined on each series separately before being averaged. Mean R^2 of the linear regression was 0.97 ± 0.04 , 0.97 ± 0.05 and 0.95 ± 0.03 for S1, S2 and S3, respectively. MEPs and CSPs elicited by TMS during 100, 75 and 50% MVC contractions were also calculated and averaged over the 3 sets. Peak-to-peak amplitude of MEPs were measured and normalized to M_{MVC} (MEP_{MVC} , MEP_{75} and MEP_{50} , respectively). Since it was difficult to precisely determine the beginning and the end of the MEP, due to its polyphasic form, MEP area was not calculated. The duration of the CSPs were determined visually and defined as the duration from the TMS stimulus to the return of continuous voluntary EMG (CSP_{MVC} , CSP_{75} and CSP_{50} , respectively) (Fig. 2.C) Two investigators performed the CSP analysis, and the two values were averaged. The treatment was redone by a 3rd investigator when the difference between the two was higher than 5%. This large error occurred only for one subject (in that

case, the average was performed on the values that were these closest to each other), showing that analysing CSP duration visually was not investigator-dependant and was thus an appropriate method.

2.6. Statistical analysis

As recommended by Hopkins [32], intra-session and inter-day reliabilities were assessed using the intra-class correlation coefficient (ICC), standard error of the mean (SEM) and coefficient of variation (CV). The ICC represents a measure of relative reliability showing the degree to which individuals maintain their position in a sample with repeated measurements [33]. According to Fleiss [34], $ICC > 0.75$ represents an excellent reliability; an ICC ranging between 0.74 and 0.40 represents a moderate to good reliability and an ICC smaller than 0.40

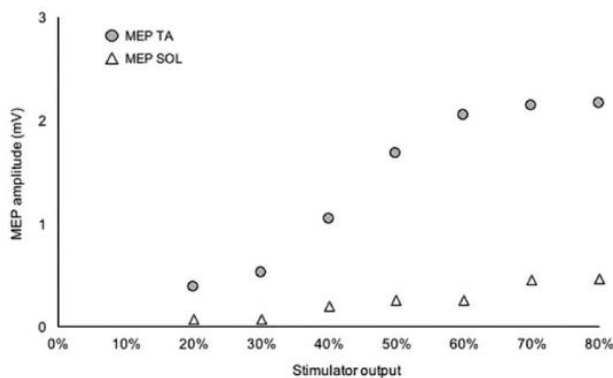


Fig. 3. Input-output curve for a representative subject. The optimal stimulation intensity was selected when MEP TA plateaued and when MEP SOL was small. For this subject, 60% of the maximal stimulator output was chosen.

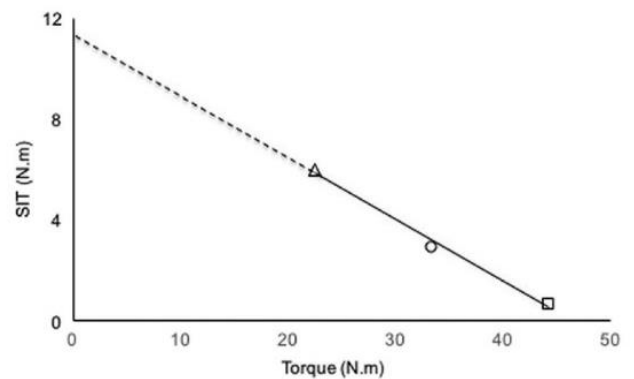


Fig. 4. Amplitude of superimposed twitches (SIT) produced by TMS during contraction at 50% (triangles), 75% (circles) and 100% MVC (squares). The linear regression was extrapolated and the y-intercept (dashed line) was interpreted as the ERT amplitude. Data from a representative subject.

represents poor reliability. The SEM scores were also calculated to quantify absolute reliability and give an indication of the precision of a recorded parameter. Thus, a low SEM value means a strong reliability and vice versa [35]. The CV ((standard deviation (SD) / mean) was calculated to represent the degree to which repeated measurements vary for individuals [33]. Data are presented as means \pm SD.

3. Results

3.1. MVC and cortical voluntary activation (VA_{TMS})

The results of intra- and inter-day reliabilities of MVC, M_{MVC} , RMS/ M_{MVC} and VA_{TMS} are presented in Table 1. Intra-day ICCs were 0.96 and 0.80 while inter-day ICCs were 0.95 and 0.99, for MVC and VA_{TMS} , respectively. For these two parameters, all CVs for intra- and inter-day conditions were lower than 4.1%, and were associated to low SEM values. VA_{TMS} across the three testing sessions was $96.0 \pm 4.9\%$. Mean SIT_{MVC} and ERT values as well as their associated ICC, CV and SEM values are reported in Table 1.

3.2. Corticospinal excitability and intracortical inhibition

Fig. 2.C represents typical torque and EMG recordings (i.e., MEP amplitude and silent period duration) in response to TMS during 100, 75 and 50% MVC contractions.

Mean results for CSP and MEP recorded at 100, 75 and 50% MVC are presented in Table 1 as well as their reliability outcomes. For these two parameters, ICCs ranged from 0.51 to 0.99 and CVs from 3.5% to 14.9%. The parameters of the input-output curves are presented in Table 2. R^2 of the Boltzmann sigmoid function were 0.83 ± 0.12 and 0.88 ± 0.10 for S1 and S3, respectively. For the four parameters extracted, ICC values ranged from 0.71 to 0.87 and CVs from 8.0% to 43.9%.

4. Discussion

This study aimed to assess the intra- and inter-day reliability of several TMS-related measures (VA_{TMS} , MEP amplitude, CSP, input-output curve parameters) related to corticospinal output to a voluntarily activated muscle responsible for dorsiflexion in healthy subjects. The main findings of the present study are that i) dorsiflexor muscles VA_{TMS} was reported for the first time to be highly reliable, ii) MEPs and CSPs showed reliable intra- and inter-day outcomes and iii) highly

Table 2

Intra- and inter-day reliabilities for input-output curves parameters.

	Mean \pm SD		Inter-day		
	S1	S3	ICC	CV (%)	SEM
k	0.06 \pm 0.03	0.07 \pm 0.03	0.73	43.9 \pm 37.7	0.02
P (% M_{MVC})	55.8 \pm 12.3	49.0 \pm 12.6	0.71	14.8 \pm 11.3	6.7
I_{50} (% stimulator output)	37.1 \pm 7.4	37.2 \pm 9.1	0.87	8.0 \pm 6.3	3.0
Peak slope	0.81 \pm 0.55	0.88 \pm 0.43	0.71	40.4 \pm 37.9	0.27

Absolute data and CV are expressed as mean \pm standard deviation.

S1: session 1; S3: session 3.

k: slope parameter; P: function plateau; I_{50} : stimulus intensity required to obtain a MEP amplitude of half the size of the plateau; ICC: intraclass correlation coefficients; CV: coefficient of variation; SEM: standard error of the mean.

variable results are reported for Boltzman modelling extracted parameters.

4.1. MVC and cortical voluntary activation

As expected, MVC presented good intra- and inter-day reliability. To the best of our knowledge, cortical voluntary activation level assessment using TMS during MVCs has only been demonstrated to be reliable for elbow flexors [9] or knee extensors muscles [6,8]. Although previous fatigue studies investigated dorsiflexor VA_{TMS} [14,15], the present study is the first one to investigate its intra- and inter-day reliability. VA_{TMS} , as well as ERT, demonstrated good to excellent intra- and inter-day reliabilities. An important result of the present study is that VA_{TMS} recorded between days (i.e., inter-day reliability) showed excellent reliability (i.e., 0.99 ICC, 0.8% CV and 0.4 SEM). Since neural adaptations have been reported after strength training through CSP [24] and MEP [25] increases, our results suggest that VA_{TMS} may be a relevant parameter to inform on possible changes in the maximal neural drive from the motor cortex in longitudinal studies although this may also reflect on a modification of spinal excitability.

VA_{TMS} was found to be $96.0 \pm 4.9\%$ across the three testing sessions, highlighting the inability of the nervous drive originating from the motor cortex to fully activate motoneurons [5]. Voluntary activation measured in our study appears to be higher compared to cortical voluntary activation recorded for elbow flexors (91–95%) [9,31,36–38] or knee extensors muscles (89–93%) [6,8,39,40], and seem to be in agreement with others showing that TA activation, quantified by the classical superimposed stimulation method, was reported to be maximal or near

Table 1

Intra- and inter-day reliabilities of neuromuscular parameters recorded during maximal (MVC) and submaximal (75% and 50% MVC) voluntary contractions.

	Mean \pm SD			Intra-day			Inter-day		
	S1	S2	S3	ICC	CV (%)	SEM	ICC	CV (%)	SEM
MVC (N·m)	52.4 \pm 12.6	52.6 \pm 12.9	51.4 \pm 12.1	0.96	3.2 \pm 2.4	2.7	0.95	4.1 \pm 3.0	2.7
RMS / M_{MVC} (%)	9.9 \pm 2.3	10.8 \pm 2.2	10.5 \pm 2.6	0.87	7.7 \pm 5.2	0.82	0.68	7.9 \pm 6.1	1.4
VA_{TMS} (%)	95.7 \pm 5.1	95.9 \pm 4.7	96.4 \pm 4.9	0.80	1.7 \pm 1.5	2.3	0.99	0.8 \pm 0.9	0.4
SIT_{MVC} (N·m)	0.76 \pm 0.97	0.67 \pm 0.88	0.60 \pm 0.40	0.73	46.4 \pm 40.5	0.5	0.95	38.3 \pm 41.7	0.2
ERT (N·m)	16.4 \pm 8.1	16.2 \pm 4.9	17.4 \pm 7.3	0.47	13.2 \pm 13.2	4.9	0.94	13.9 \pm 14.5	1.8
M_{MVC} (mV)	5.5 \pm 1.1	5.7 \pm 1.1	6.2 \pm 1.7	0.94	6.5 \pm 3.7	0.3	0.36	14.1 \pm 8.7	1.1
MEP ₅₀ (mV)	3.1 \pm 0.6	3.1 \pm 0.8	3.3 \pm 1.2	0.83	8.6 \pm 6.3	0.28	0.55	13.1 \pm 9.3	0.42
MEP ₇₅ (mV)	3.5 \pm 0.8	3.5 \pm 0.8	3.6 \pm 0.9	0.92	5.6 \pm 4.6	0.23	0.92	6.7 \pm 6.5	0.26
MEP _{MVC} (mV)	3.1 \pm 0.6	3.1 \pm 0.8	3.3 \pm 1.2	0.80	8.9 \pm 6.9	0.31	0.47	11.2 \pm 10.7	0.67
MEP ₅₀ (% M_{MVC})	65.2 \pm 14.7	65.3 \pm 11.4	61.9 \pm 14.9	0.75	10.3 \pm 7.5	6.6	0.70	13.4 \pm 8.1	8.1
MEP ₇₅ (% M_{MVC})	75.8 \pm 19.1	74.7 \pm 13.7	74.4 \pm 18.9	0.86	7.1 \pm 5.0	6.1	0.88	7.5 \pm 7.4	6.4
MEP _{MVC} (% M_{MVC})	57.0 \pm 14.0	50.1 \pm 12.3	57.0 \pm 14.4	0.51	14.9 \pm 8.1	8.7	0.52	9.9 \pm 10.4	9.2
CSP ₅₀ (ms)	246 \pm 58	266 \pm 67	230 \pm 58	0.84	6.4 \pm 7.4	25.2	0.79	7.8 \pm 9.2	26.2
CSP ₇₅ (ms)	261 \pm 64	271 \pm 63	246 \pm 59	0.99	3.5 \pm 3.9	6.4	0.86	7.6 \pm 8.3	23.3
CSP _{MVC} (ms)	250 \pm 51	267 \pm 54	229 \pm 62	0.98	7.3 \pm 10.9	7.4	0.95	8.6 \pm 11.6	13.2

Absolute data and CV are expressed as mean \pm standard deviation.

S1: session 1; S2: session 2; S3: session 3.

MVC: maximal voluntary contraction; RMS: root mean square; VA_{TMS} : cortical voluntary activation; SIT_{MVC} : superimposed twitch amplitude evoked during MVC; ERT: estimated resting twitch amplitude; M_{MVC-PP} : M wave amplitude recorded during MVC; MEP: motor evoked potential recorded at 50% MVC (MEP₅₀), 75% MVC (MEP₇₅) and 100% MVC (MEP_{MVC}). CSP: cortical silent period recorded at 50% MVC (CSP₅₀), 75% MVC (CSP₇₅) and 100% MVC (CSP_{MVC}).

ICC: intraclass correlation coefficients; CV: coefficient of variation; SEM: standard error of the mean.

maximal in a healthy young population [41]. This may be explained by the fact that the TA has the strongest corticospinal projections among all lower limb muscles [13].

Our values also appear to be greater than those reported by Ross et al. and Mileva et al. who found VA_{TMS} to be $75.5 \pm 16.0\%$ and $89.5 \pm 2.9\%$, respectively [14,15]. These discrepancies may be due to differences in the TMS intensity and/or the type of TMS coil used to evaluate VA_{TMS} . Ross et al. evaluated the VA_{TMS} at 100% of maximal stimulator output using a 70 mm figure-of-eight coil [15], while a 110-mm double-cone coil was used in the present study. This difference in coil size in the present study may have caused an increased activation of the antagonist muscles leading to misinterpretation of the evoked superimposed twitches. In the study of Mileva et al., TMS intensity was set at 120% of the resting motor threshold [14]. According to a recent study, this may not have been optimal to fully activate the motor cortical neurons since such intensity selection does not precisely identify the minimum stimulus intensity needed to elicit SIT and MEPs of maximal amplitude [28]. The authors of the present study suggest that determining TMS intensity from an input-output curve (i.e., using optimal intensity identified as the minimum stimulus intensity needed to elicit MEPs of maximal amplitude with minimal co-activation) is more appropriate to assess corticospinal excitability and VA_{TMS} .

4.2. Corticospinal excitability

Input-output curves performed in the present study to determine TMS intensity for VA_{TMS} assessment were further used to characterize the excitability of the corticospinal pathway, through the Boltzmann modelling [21,42]. According to the ICC and SEM, the extracted parameters (i.e., the function plateau, the stimulus intensity required to obtain a MEP amplitude of half the size of the plateau, the slope parameter, and the peak slope) demonstrated good reliability and these values are in agreement with previous studies performed on first dorsal interosseous [19] or TA [20]. However, the present study demonstrated high CVs for the slope parameter and the peak slope (43.9 and 40.5%, respectively). The high reported CVs may question the reliability of these two parameters in the current study. Although Carroll et al. suggested that the slope parameter (i.e., the k parameter in our study) might be a more reliable index of corticospinal excitability than the peak slope for the first dorsal interosseous, similar reliability was reported for these two parameters in the present study [19]. Nevertheless, regarding the high CV described above, it seems difficult to use these two parameters to investigate the chronic and/or acute adaptations of TA corticospinal excitability.

While input-output curves were used in the present study to investigate TA corticospinal excitability during a low level of contraction, corticospinal excitability was also assessed at higher levels of contraction (100, 75 and 50% MVC) through MEP recordings. The current results present higher MEP values during submaximal (i.e., MEP_{50} and MEP_{75}) than during maximal voluntary contractions (i.e., MEP_{MVC}), which is in agreement with other results obtained on the TA [16]. It has been suggested that the probability for the TMS pulse to be evoked during the refractory period is higher during a maximal (higher discharger rate) rather than a submaximal voluntary contraction, leading to a lower MEP amplitude [8]. MEP_{MVC} presented good intra- and inter-day reliabilities. These results are consistent with a recent study that found that the TA has a good inter-day reliability (ICC: 0.80) for MEPs recorded during MVC [14]. Even if ICC values are lower in our experiment (ICC: 0.51 and 0.52, for intra- and inter-day condition respectively), we can conclude that there was a moderate to good reliability regarding the low associate CV and SEM values, informing about small intra-subject variation. One aim of the present study was to investigate the intra-day reliability of MEP amplitude, which is known to represent corticospinal pathway excitability. Our results have shown that MEPs recorded at maximal or submaximal levels of voluntary contraction may be used as reliable parameters to investigate acute phenomenon

such as fatigue. The good reliability observed in the present study is also in agreement with several studies performed on knee extensors [8] or elbow flexors [9]. Yet, unlike the studies where the reliability was independent on force level, in the present study, MEP reliability was higher at low level of voluntary contraction (i.e., MEP_{50} and MEP_{75}) than during MVC (i.e., MEP_{MVC}). The good reliability observed for MEPs recorded during submaximal contraction is consistent with previous studies investigating the knee extensors [8], first dorsal interosseous [43], elbow flexor [9] or TA [16] muscles. The lower reliability observed for MEPs during MVC is consistent with previous studies, suggesting that high contraction intensities may cause a larger desynchronization of the action potential at the membrane level [16, 19]. Hence, the excitability of corticospinal pathway of the TA muscle can be reliably tested through the recording of MEP amplitude in response to TMS during maximal and submaximal contractions for acute interventions (e.g., fatigue) or longitudinal studies (e.g. training).

4.3. Intracortical inhibition

Cortical silent periods (CSP) associated with MEPs were also measured at 100, 75 and 50% MVC (i.e., CSP_{MVC} , CSP_{75} and CSP_{50} , respectively). When applied during a voluntary contraction, TMS may provide information about GABA mediated intracortical inhibition through the assessment of the CSP [44]. Although the exact mechanisms of the CSP remain unclear, it is accepted that the initial part is mainly due to reduced spinal excitability while the final part of the CSP is cortical in origin [45]. CSP results from the activation of inhibitory cortical neurons projecting onto the pyramidal cells in the motor cortex [46], and is thought to be mainly influenced by GABA (gamma aminobutyric acid) neurotransmission [47]. In the present study, CSP_{MVC} was highly reliable, as shown by high ICC and low CV-SEM values for both intra- and inter-day comparisons. To date, only one study recorded CSP in TA during MVC [14] and similar ICC (0.93) were observed. In the present study, CSP_{75} and CSP_{50} were also found to be highly reliable, both between S1 and S2 (intra-day) and between S1 and S3 (inter-day), in agreement with previous studies that assessed CSP during submaximal voluntary contractions in TA [16,20], first dorsal interosseous [43] and the extensor digitorum communis [48] muscles. Hence, CSP can be reliably used during maximal and submaximal dorsiflexion to investigate TA intracortical inhibition.

As most reliability studies, the principal limitation of the present work is that TMS-related parameters were investigated for a healthy young population, and that current outcomes may not be applicable to other populations (i.e., clinical, elderly).

In conclusion, the present study reports for the first time the excellent intra- and inter-day reliability for VA_{TMS} of dorsiflexor muscles. The outcomes were found to be highly reliable within and between days. A good reliability in the assessment of corticospinal excitability and intra-cortical inhibition directed towards the TA was also observed. TMS can thus be used to better understand the effects of training interventions on TA neural adaptations (e.g., neural drive from the cortex, corticospinal pathway excitability) in a healthy young population. This has important practical consequences because, besides the fact that TA has the most corticospinal projections among all lower limb muscles, it also plays an important functional role in daily life abilities such as lifting the foot in the swing phase during locomotion.

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ANNEXE 2 (étude #5)

EFFETS CHRONIQUES DES VIBRATIONS LOCALES SUR LE RECONDITIONNEMENT NEUROMUSCULAIRE APRES RUPTURE DU LIGAMENT CROISE ANTERIEUR

Souron R. (Expérimentateur principal) ; Coulondre C. (Kinésithérapeute et expérimentatrice) ; Lapole T. (Responsable scientifique) ; Millet GY. (Responsable scientifique) ; Rupp T. (Responsable scientifique) ; Carnesecchi O. (Chirurgien orthopédiste) ; Verdot FX. (Chirurgien orthopédiste) ; Edouard P. (Médecin du sport et investigateur coordinateur) ; Féasson L. (Médecin du sport et investigateur associé) ; Dalmais E. (Médecin du sport et investigateur associé) ; Rambaud A. (Kinésithérapeute)

1. Justification scientifique et description générale de la recherche

L'entorse de genou constitue une blessure fréquemment recensée. Les données épidémiologiques indiquent que la majorité des entorses avec rupture du LCA sont provoquées par un accident de sport, dans des disciplines de type « pivot-contact » (e.g. basket-ball, rugby, football) ou « pivot-sans contact » (e.g. ski alpin) (Anderson et al., 2002; Quelard et al., 2010).

Anatomiquement, le LCA est placé au sein même de l'articulation du genou. Il forme avec le ligament croisé postérieur le « pivot central » de l'articulation du genou. D'un point de vue fonctionnel, il permet de stabiliser l'articulation du genou. Son rôle est double : i) il s'oppose à la translation antérieure du tibia par rapport au fémur et empêche un mouvement dit de « tiroir antérieur » ; ii) il s'oppose à la rotation interne du tibia par rapport au fémur.

Le traitement d'une entorse avec rupture du LCA peut être médical ou chirurgical. Une intervention chirurgicale de ligamentoplastie est motivée par plusieurs indications : sportif souhaitant reprendre une activité de type « pivot-contact », patient présentant une grande instabilité de genou... Lorsque l'intervention est recommandée, deux techniques de ligamentoplasties sont préférentiellement employées : la ligamentoplastie de type « Kennet-Jones » consiste à prélever une partie du tendon rotulien pour venir remplacer le LCA ; la ligamentoplastie de type « DIDT » consiste à prélever une portion des tendons de deux muscles (i.e. le gracile et le semi-tendineux) afin d'obtenir une nouvelle plastie. Il est couramment rapporté un déficit de force des extenseurs du genou (en moyenne entre 7 et 15%) en période pré-opératoire (Keays et al., 2000). Ces faiblesses musculaires s'accroissent en période post-opératoire. Une étude récente fait écho d'une diminution de 42, 21 et 18% de la force isométrique en extension de genou respectivement à 4, 8 et 12 semaines post-opératoires, par rapport au niveau de force produit en période pré-opératoire (Harput et al., 2015). Il a également été rapporté que la récupération de force des muscles extenseurs du genou en condition dynamique n'était pas complète (i.e. déficit de 25%) à 6 mois post-opératoires, comparativement à la force mesurée en pré-opératoire (Anderson et al., 2002).

Même si l'atrophie musculaire liée à la sous-utilisation temporaire et/ou les douleurs peut en partie expliquer la réduction de force musculaire (Dauty et al., 2006), il semble qu'une augmentation de l'inhibition nerveuse (liée en partie à la douleur) soit un des principaux déterminants du déficit des muscles extenseurs du genou (Ingersoll

et al., 2008; Hart et al., 2010). Ce phénomène appelé « sidération » induit un important déficit d'activation volontaire, comme suggéré par des valeurs de VA reportées entre 55–93% pour ce genre de population, alors qu'un déficit d'activation volontaire a été défini comme un $VA < 95\%$ (Hart et al., 2010). Ce déficit d'activation peut perdurer plusieurs mois et conduire à l'incapacité pour le patient d'activer son muscle de façon maximale (Drechsler et al., 2006).

Des stratégies de rééducation post-opératoire précoces sont ainsi mises en place pour limiter l'installation prolongée de la faiblesse musculaire. Le premier objectif est de contrôler la douleur post-chirurgicale pour permettre une rééducation la plus précoce possible. Il est nécessaire de lever la sidération du quadriceps, grâce à des techniques d'électrothérapie (objectif de favoriser la vascularisation du muscle) ou de contraction statique du quadriceps. Cette première étape est réalisée de J1 à J7 post-opératoire. Il est également nécessaire de diminuer l'œdème (technique de drainage, de glaçage) afin d'optimiser la récupération des amplitudes articulaires par des techniques de mobilisation passive manuelle et active-aidée, puis de J8 à J25 de tonifier le quadriceps par des techniques d'électrothérapie, de lever de jambe avec genou en extension, etc.... Ainsi actuellement, la rééducation post-opératoire s'axe essentiellement sur la réadaptation musculaire. C'est pourquoi il serait intéressant d'utiliser des techniques complémentaires permettant d'optimiser les séances de rééducation en travaillant également sur la composante nerveuse.

Nos précédents travaux ont montré que des séances de vibrations du tendon d'Achille (Lapole & Pérot, 2010; Lapole et al., 2013), du muscle TA (Souron et al., 2017a) ou du muscle quadriceps (étude #4) conduisent à des gains de force, concomitants d'adaptations d'origine centrale chez le sujet sain jeune et âgé. L'enjeu majeur de ce projet est donc de vérifier si des séances répétées de vibrations locales sur le muscle quadriceps permettent, en complément de la rééducation classique par kinésithérapie, d'améliorer la réadaptation post-opératoire d'une ligamentoplastie du LCA. Le choix de ce groupe musculaire a été réalisé au regard du lourd déficit de force des muscles extenseurs du genou généralement observé après une ligamentoplastie du LCA, ce qui est un problème majeur susceptible de limiter les capacités de marche et de course (Robineau et al., 2000).

Afin de valider la relation à l'effet des vibrations chroniques, un groupe de patients contrôles ne bénéficiant que des séances classiques de kinésithérapie (sans le programme de vibration locale associé) est constitué de façon aléatoire. Ce projet

permet d'évaluer pour la première fois les éventuels bénéfices d'un programme d'entraînement par vibrations musculaires locales dans un contexte de déficit moteur secondaire mais réversible. Le premier bénéfice pourrait être la réduction du temps de récupération de la fonction motrice et un retour *ad integrum* qui peut parfois prendre plusieurs mois. Le second intérêt de cette étude est d'envisager une approche thérapeutique de la rééducation après ligamentoplastie du LCA, selon une méthode susceptible d'agir sur deux processus physiopathologiques potentiels d'amyotrophie de sous-utilisation et de sidération nerveuse. Enfin, l'application de cette technique à très faible risque et simple d'accès, présente toutes les caractéristiques pour une utilisation encadrée en ambulatoire ou à domicile, en complément des méthodes rééducatives classiques actuelles.

2. Design expérimental

L'étude se déroule en cinq étapes : inclusion (V1), évaluations initiales (V2), période de rééducation (et entraînement par vibration pour le groupe test), évaluations post-entraînement (V3) et évaluations terminales (V4) (**figure 13**).

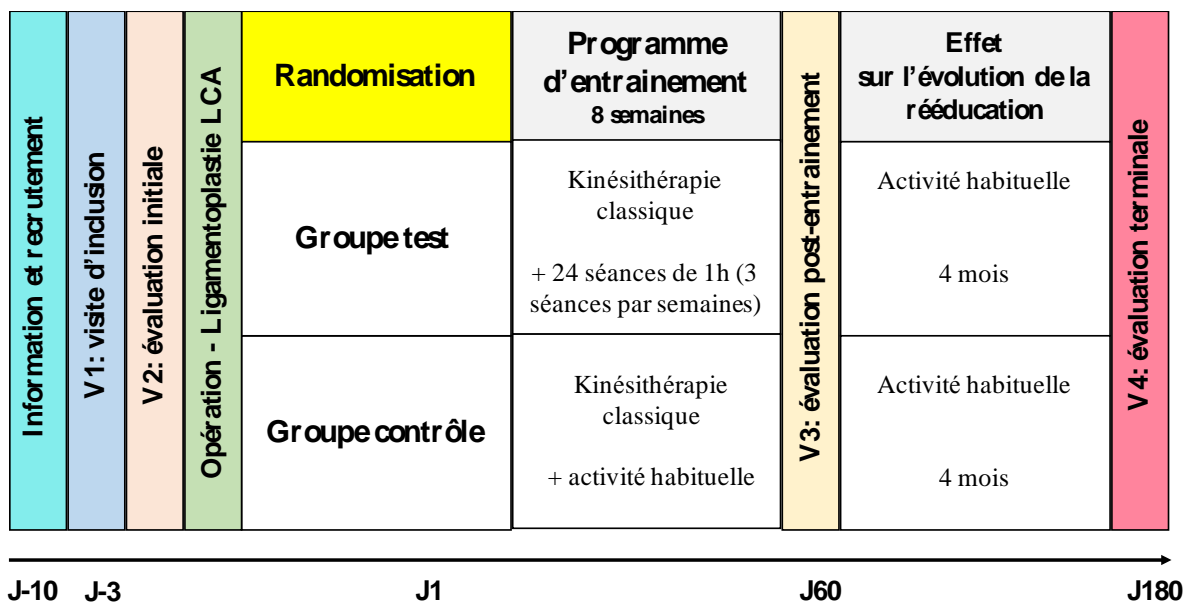


Figure 13. Déroulement global de l'étude #5.

Les patients (âgés de 18 à 50 ans, de sexe masculin ou féminin) sont recrutés via les chirurgiens et médecins du bassin de l'agglomération stéphanoise et chambérienne et suivant les patients victimes d'une rupture du LCA. Leur rôle est

d'expliquer en détails les conditions de l'étude et les éventuels bénéfices pour leur rééducation post-opératoire.

La visite d'inclusion (V1) se fait dans les dix jours précédant l'opération, permettant au médecin de vérifier les critères d'inclusion et de non inclusion et de recueillir le consentement écrit du patient. Cette visite d'inclusion se poursuit par une séance de familiarisation aux tests neuromusculaires, i.e. MVC en extension de genou, stimulation nerveuse électrique surimposée à la contraction volontaire. Après le respect d'un délai minimum de 2 jours après la V1, les patients réalisent l'évaluation initiale V2 en pré-opératoire (**figure 14**).

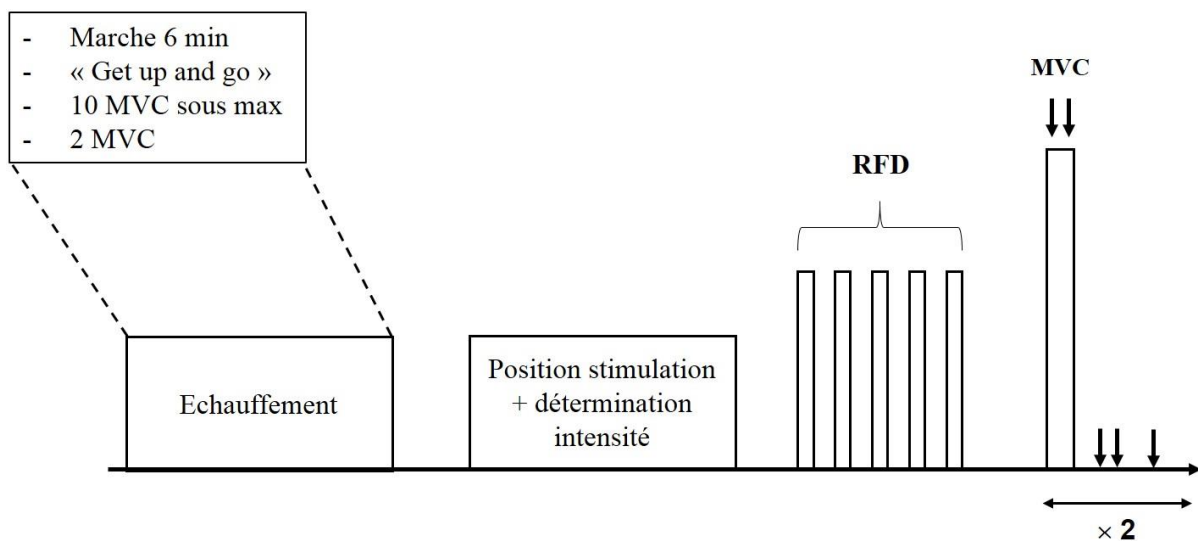


Figure 14. Evaluation neuromusculaire réalisée en pré- et post-opératoire. Le sujet réalise dans un premier temps un test de marche de 6 minutes et un test de « get up and go ». Après avoir déterminé la position et l'intensité optimales de la stimulation électrique périphérique, il est demandé au sujet de réaliser 3 contractions (Aagaard et al., 2002a; Blazeovich et al., 2009) avec pour consigne de contracter le plus explosivement possible, afin d'évaluer le taux de montée en force (RFD). Par la suite, le sujet réalise deux contractions maximales volontaires (MVC) en extension de genou. Pour évaluer le niveau d'activation volontaire, une stimulation électrique périphérique (doublet à haute fréquence ; double flèche noire) est délivrée pendant le maintien de la MVC et sur le muscle relâché. Une stimulation unique (flèche noire) est également délivrée pour évaluer l'amplitude de l'onde M. L'ensemble des tests neuromusculaires est réalisé toujours dans le même ordre, i) sur la jambe saine et ii) sur la jambe opérée.

Le processus de randomisation intervient après l'intervention chirurgicale afin de connaître le groupe alloué au patient, i.e. i) entraîné, où le patient suit les séances de vibration locale (fréquence de vibration : 100 Hz ; amplitude de vibration : 1 mm) sur une durée de 8 semaines (3 séances d'une heure par semaine pour un total de 24

séances d'entraînement) en plus des séances de kinésithérapie ou ii) contrôle, où le patient ne réalise que les séances de kinésithérapie. Lors des séances d'entraînement, le vibreur était appliqué localement et directement attaché sur le muscle droit fémoral de la jambe opérée à environ 40% de la longueur musculaire entre le bord supérieur de la rotule et l'épine iliaque antéro supérieure (cf. panel B de la **figure 2** à la page 40 de ce manuscrit). Un protocole de rééducation précis a été rédigé avec un des kinésithérapeutes collaborateurs (Alexandre Rambaud) afin de proposer le même protocole à chaque patient et d'ainsi permettre une homogénéisation des protocoles de rééducation (cf. annexe 3). L'évaluation post-entraînement (V3) est réalisée à 2 mois post-opératoire, et une évaluation terminale (V4) est réalisée à 6 mois post-opératoire.

Deux sujets sont actuellement inclus dans cette étude. Un sujet masculin a complété l'ensemble des tests prévus dans le protocole et un sujet féminin a réalisé les tests pré-opératoires, mais a dû être exclu en raison d'une atteinte méniscale remarquée lors de l'opération, constituant un des critères d'exclusion. Aucun autre sujet n'a été inclus à l'heure actuelle.

3. Tests neuromusculaires et fonctionnels & traitement des données

De manière similaire au dispositif présenté sur la **figure 4** (page 42 de ce manuscrit), le sujet était positionné sur une chaise ergométrique spécialement conçue au laboratoire lors de la réalisation des différents tests neuromusculaires présentés ci-dessous.

3.1. Mesures de force

La force maximale isométrique produite par les extenseurs du genou était mesurée. Les sujets étaient assis sur le siège de l'ergomètre et les angles articulaires étaient fixés à 90° pour la hanche et le genou. L'utilisation de deux ceintures attachées au niveau du thorax permettait de minimiser les mouvements du haut du corps. La description détaillée du traitement des données relatives à la force maximale isométrique est présentée dans la partie 4.1 à la page 51 de ce manuscrit.

Lors de cette étude, le taux de montée en force (*rate of force development*, RFD) était calculé. Les sujets avaient alors pour consigne de contracter le plus explosivement possible lors de 5 essais successifs séparés de 20 secondes. Le RFD était alors mesuré i) à partir du début de la contraction jusqu'à 50 ms, ii) de 50 à 100

ms et iii) de 100 à 150 ms. L'activation nerveuse expliquera principalement le RFD dans les premières ms de la contraction tandis que les facteurs musculaires expliqueront principalement le RFD dans les phases suivantes (Maffiuletti et al., 2016). Le début de la contraction était défini comme le point à partir duquel la force augmentait au-dessus d'une valeur de force égale à 7,5 N (Andersen & Aagaard, 2006; Blazeovich et al., 2009) (**figure 15**).

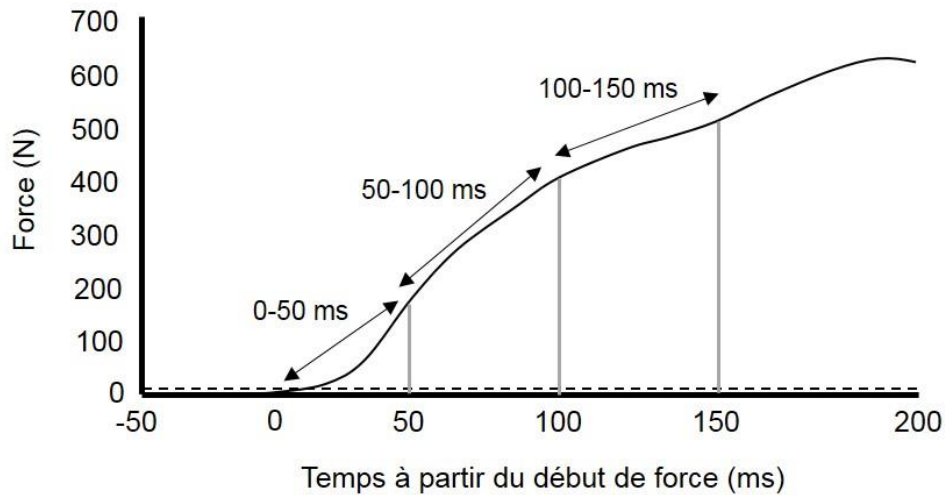


Figure 15. Schéma représentatif d'une relation force-temps obtenue lors d'une contraction explosive des muscles extenseurs du genou. Le taux de montée en force était calculé i) à partir du début de la contraction (ligne pointillée noire, représentant le point à partir duquel la force augmentait au-dessus d'une valeur égale à 7,5 N) jusqu'à 50 ms, ii) de 50 à 100 ms et iii) de 100 à 150 ms.

3.2. Electromyographie de surface

De manière similaire aux études #3 et #4, des électrodes EMG étaient disposées sur la partie distale des muscles RF, VL et biceps fémoral. En plus de ces 3 muscles, des électrodes EMG étaient disposées sur la partie distale du muscle vaste médial dans cette dernière étude. L'évaluation du vaste médial était motivée par le fait qu'il est le principal muscle touché par une opération de ligamentoplastie de genou (en comparaison des trois autres chefs impliqués dans l'extension de genou, i.e. VL, RF et vaste intermédiaire) (Rosenberg et al., 1992). De plus, son important rôle fonctionnel (e.g. verrouillage du genou en fin d'extension) en faisait un muscle d'intérêt pour cette étude. La description détaillée du traitement des données relatives aux signaux EMG est présentée dans les parties 4.1 et 4.2 à la page 51 de ce manuscrit.

3.3. Niveau d'activation volontaire

En utilisant la technique de neurostimulation électrique surimposée (voir la partie 3.3 à la page 43 de ce manuscrit pour une description détaillée des paramètres de stimulation fémorale), le niveau d'activation volontaire était évalué comme suit (**figure 16**) :

$$VA = [1 - (DB_{SUR}/DB_{REST})] \times 100$$

DB_{SUR} étant l'amplitude de la force surimposée à la MVC évoquée par stimulation électrique (doublet : 100 Hz), et DB_{REST} l'amplitude de la force évoquée sur le muscle relâché par stimulation électrique (doublet : 100 Hz).

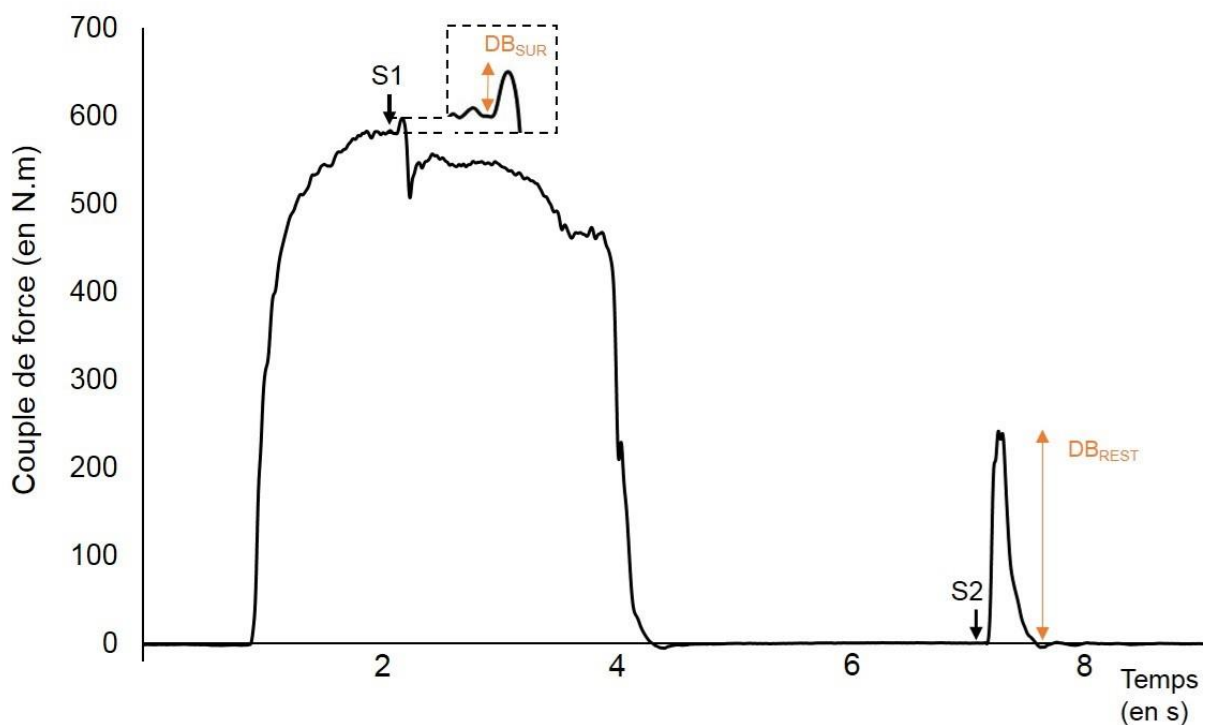


Figure 16. Calcul du niveau d'activation volontaire selon la technique de neurostimulation électrique surimposée. Une première stimulation (doublet : 100 Hz ; S1) était délivrée pendant le maintien d'une contraction maximale volontaire, et une seconde stimulation (doublet : 100 Hz ; S2) était délivrée sur le muscle relâché. DB_{SUR} est la différence entre le couple de force maximal volontaire isométrique mesuré avant S1 et le couple de force obtenu juste après S1. DB_{REST} est la différence entre le couple de force mesuré au repos juste avant S2 et le couple de force obtenu en réaction à S2.

3.4. Tests de marche

Lors de cette étude, les capacités fonctionnelles des patients victimes d'une rupture du LCA étaient évaluées via des tests de marche. Le premier était un test de marche de 6 minutes où les patients devaient réaliser le plus possible d'allers-retours en

marchant sur une distance de 30 mètres (Enright, 2003). La distance totale parcourue par le patient (en mètres) était retenue comme critère d'évaluation principal. Le second test était un test de « get up and go ». Ce test permettait d'évaluer les transferts assis, debout, la marche et les changements de direction du patient. Il était demandé au patient, qui se trouvait au départ en position assise sur une chaise, de se lever, de parcourir 3 (Podsiadlo & Richardson, 1991) ou 10 (Mathias et al., 1986) mètres, de faire demi-tour et de revenir s'asseoir sur la chaise sans l'aide des mains. Le patient devait également réaliser le même parcours sur 15 mètres, mais cette fois sans le demi-tour (Fitzgerald et al., 2004). Le temps mis pour réaliser le parcours servait de critère d'évaluation pour ce test. Chaque patient réalisait le test de marche de 6 minutes ainsi que les trois variantes du test de « get up and go ».

ANNEXE 3

Protocole de rééducation kinesithérapeutique utilisé dans l'étude #5.

Reconstruction chirurgicale du Ligament Croisé Antérieur Protocole de Rééducation post-opératoire

De semaine 1 à semaine 6 (semaine 0 = semaine de l'opération)

1 – Prévention des troubles trophiques

Massage position déclive



Cryothérapie

Mobilisation latérale et verticale de la rotule



Massage du cul de sac sous-quadricipital (éviter adhérences au niveau du système extenseur)



2 – Pour le réveil musculaire

Contractions rapides (20 contractions en 10 secondes) entraînant une mise en tension du tendon rotulien. On évite ici tout risque de flexum actif et de rotule basse.

+ Contractions longues (20-30 secondes de contraction tenue)

→ *enchaîner alternativement « contraction rapide – contraction longue » sur une durée totale de 5 min*



3 – Pour la récupération des amplitudes articulaires

En activo-passif : Mobilisation manuelle en flexion active, aidée des ischio-jambiers dans les amplitudes de 0° à 120° avec rodage articulaire doux dans les amplitudes obtenues (possibilité d'Arthromoteur...). Le gain en extension doit être réalisé passivement et peut être adapté en fonction d'une éventuelle hyperlaxité constitutionnelle (garder un très discret flexum s'il existe un important récurvatum controlatéral). Il est de toute façon important de ne pas chercher à récupérer le récurvatum.



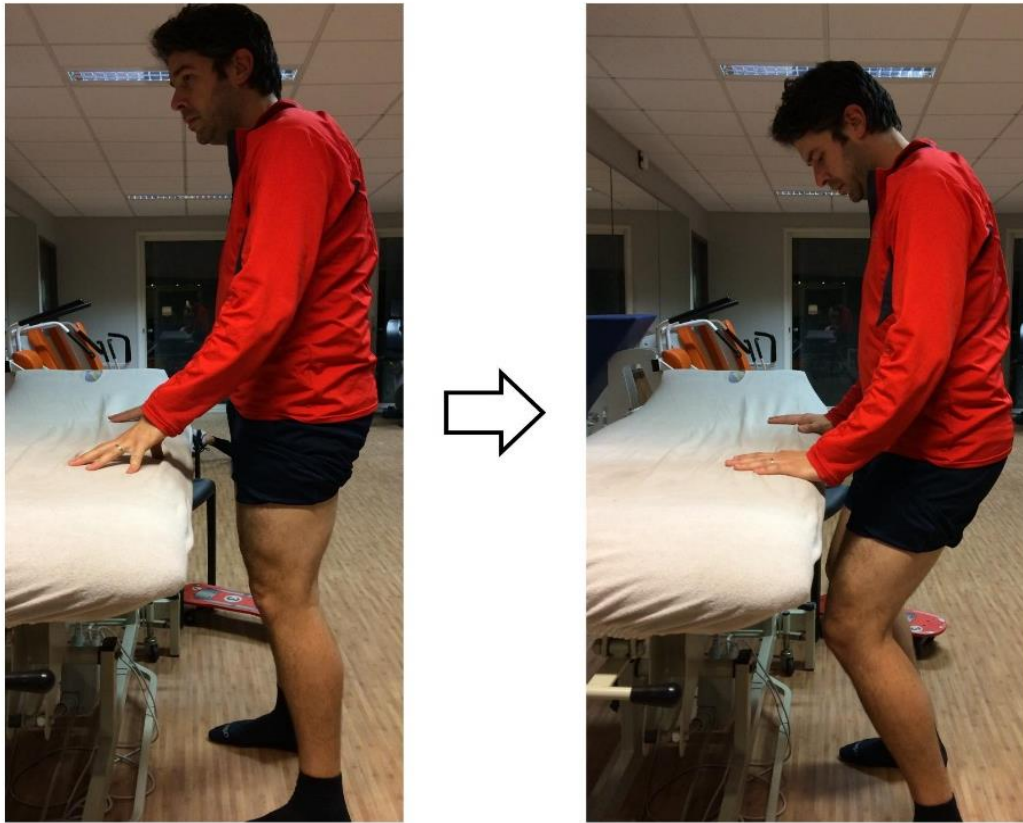
En actif : Pour les exercices présentés, respecter une amplitude de 30°-90°



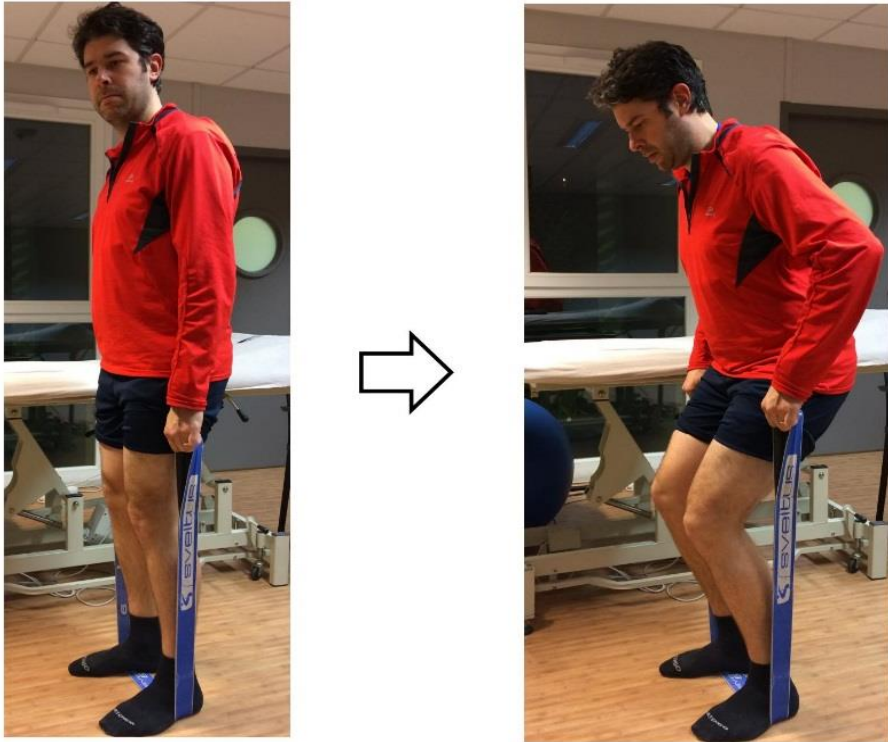
4 – Pour le renforcement musculaire

Statique ou actif avec skate board (cf ci-dessus)

Travail léger en chaîne cinétique fermée tels que des mini-squats (10-70°) : appui bipodal, la charge correspondant au poids du patient (peut éventuellement s'aider d'une table, d'un espalier etc... Si trop craintif au départ)



Ce travail peut être par la suite augmenté en passant un élastique sous les pieds du patient qui sera mis en tension par la flexion des membres supérieurs (voir ci-après) :



Travail d'étirements : chaîne postérieure doux (mettre en tension un peu les ischio-jambiers et le site de prélèvement). Décubitus dorsal, éviter le risque de flexum.

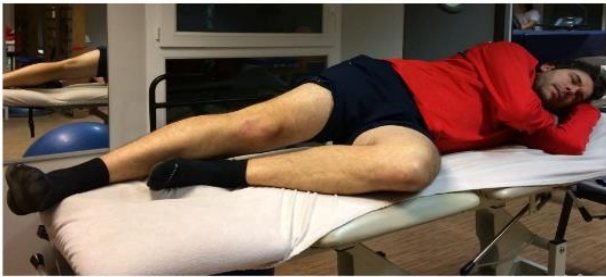


5 – Pour l'appui - Déambulation

Reprise d'appuis : sous couvert de deux cannes canadiennes. Les cannes doivent être gardées par précaution entre 20-30 jours. Lors de l'appui, vérifier le verrouillage du genou activement par le quadriceps en extension maximum mais sans recurvatum ni flexum. **L'abandon des cannes n'est permis que si la marche est correcte (pas de boiterie, pas de flexum).**

6 – Pour l'entretien général :

Travail des muscles de la hanche



A partir du 21^{ème} jour (début semaine 4), il est possible d'ajouter aux exercices de la première phase (S1-S2-S3) les exercices suivants :

Travail proprioceptif en chaîne fermée (bipodal) par déséquilibre manuel provoqué par le thérapeute



Travail des ischio-jambiers en manuel (statique)



Exercice de vélo : rodage doux sans résistance si le passage en flexion se réalise sans douleur

Des étirements du droit antérieur : hanche en extension, en ventral ou en bord de table. La tension doit être ressentie au tiers supérieur de la cuisse et **non dans le genou**.



Exercices à la presse couchée : avec des charges progressives, toujours inférieures au poids de corps (amplitudes de 20° à 80°)



ATTENTION :

Si

- **Augmentation de l'hydarthrose**
- **Diminution des amplitudes (surtout en extension)**
- **Augmentation des phénomènes inflammatoires**
- **Douleurs nocturnes**

Ne pas hésiter à diminuer la quantité de travail ou à supprimer momentanément certains exercices que vous jugeriez responsables de ces problèmes.

A partir du 45^{ème} jour post-opératoire (semaine 7 & 8 ; dans notre protocole cela consistera aux deux dernières semaines d'entraînement par vibrations).

1 – Sur le plan articulaire

Augmenter la flexion (environ 120-150° en mobilisation passive)

L'extension doit être totale, passivement et activement, en analytique et au cours de la marche, sans recurvatum.

2 – Sur le plan musculaire

Renforcement des ischio-jambiers en statique, excentrique et en concentrique



Travail résistant aux déséquilibres rotatoires du bassin provoqués par le thérapeute, en monopodal, en chaîne fermée, entre 20° et 50° de flexion du genou (contrôle rotatoire stabilisateur).

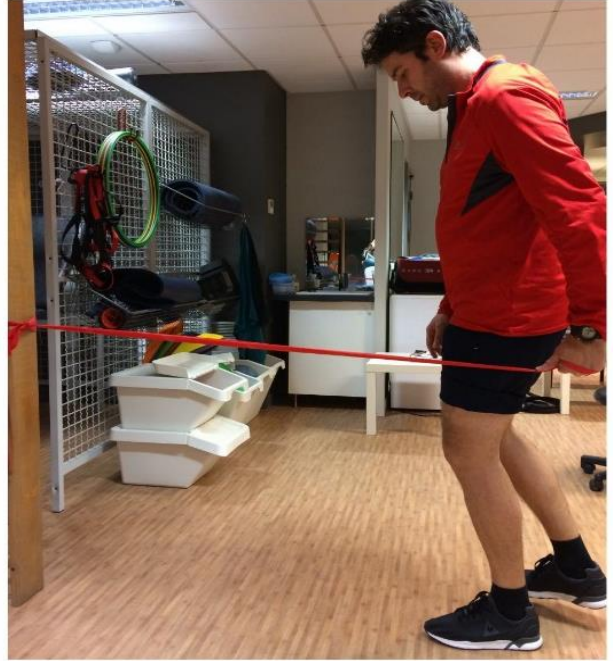


En statique : par une mise en charge totale à des degrés de flexion du genou progressivement croissants ($20^{\circ} \Rightarrow 90^{\circ}$) avec des temps de maintien de la position de l'ordre de 15 secondes, l'appui préférentielle talonnier et la rectitude du tronc permettant un recrutement plus important du quadriceps.



ANNEXE 3

En proprioception, pratiquée maintenant en monopodal à base d'auto-déséquilibre (sol stable puis instable) mais aussi à base de déséquilibres provoqués par le thérapeute (nécessitant une anticipation sur les contrôles réflexes automatiques ; cf ci-dessus pour déséquilibres provoqués par le thérapeute).

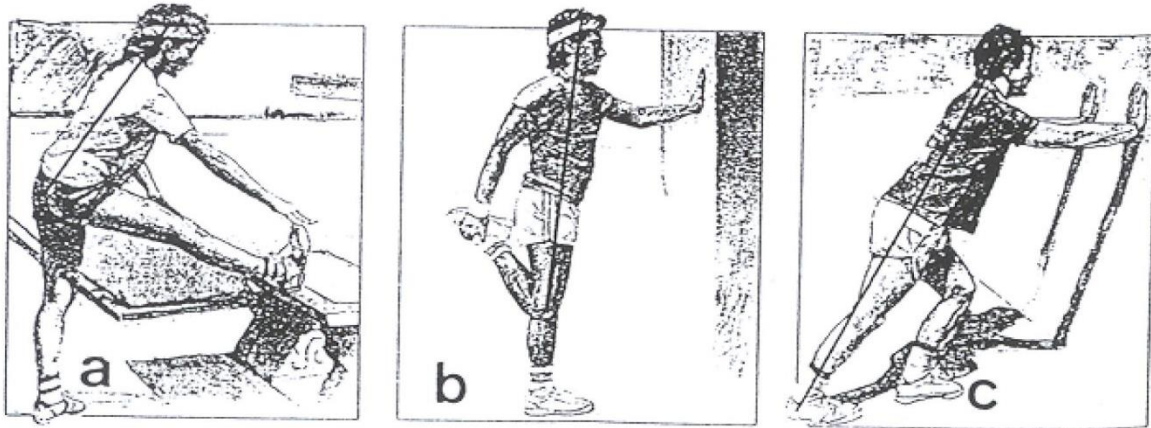


Exercices à la presse : rester en bipodal en augmentant progressivement la charge. Ne pas chercher les 20 derniers degrés d'extension

Exercices de vélo : avec légère résistance sans cale pied

Rameur : avec l'utilisation des bras

Après tout le travail musculaire, pensez à pratiquer un d'étirements des ischio-jambiers (a) du quadriceps (b) et du triceps sural (c).





Robin SOURON – Laboratoire Interuniversitaire de Biologie de la Motricité – Université de Lyon –
Université Jean Monnet

ADAPTATIONS FONCTIONNELLES ET NERVEUSES A L'ENTRAÎNEMENT PAR VIBRATION LOCALE : DU SUJET SAIN A LA REEDUCATION

RESUME :

La recherche de méthodes permettant de lutter contre le déconditionnement neuromusculaire à la suite par exemple d'une opération chirurgicale ou d'une immobilisation prolongée intéresse la communauté scientifique depuis de nombreuses années. Ce projet visait à proposer la technique de vibration locale (LV) comme une méthode alternative aux méthodes classiquement utilisées (e.g. vibration corps entier, stimulation électrique neuromusculaire) pour lutter contre ce déconditionnement neuromusculaire. Le premier objectif de ce travail de thèse était de déterminer les effets d'une application aiguë de LV sur la fonction neuromusculaire des muscles fléchisseurs dorsaux et extenseurs du genou de sujets sains. Nos résultats montrent une modulation de l'excitabilité du système nerveux central en réponse à l'application aiguë de LV, ce qui nous a permis d'envisager de potentielles adaptations si cette technique était utilisée de façon répétée sur plusieurs semaines. Ainsi, la seconde orientation de ce travail était d'évaluer les effets d'une application chronique (entraînement) de LV sur les propriétés fonctionnelles (force, hauteur de saut) et nerveuses (mesurées par stimulation magnétique transcrânienne) de sujets sains, jeunes et âgés. Nos résultats ont montré qu'un entraînement par LV était efficace pour améliorer les capacités fonctionnelles de ces deux populations, ces gains s'accompagnant d'adaptations nerveuses. Ces travaux nous ont alors conduits à la mise en place d'une dernière étude (en cours) à visée clinique, qui évaluait l'efficacité de LV en rééducation post-ligamentoplastie du ligament croisé antérieur du genou.

FUNCTIONAL AND NEURAL ADAPTATIONS TO LOCAL VIBRATION TRAINING: FROM HEALTHY SUBJECTS TO REHABILITATION

ABSTRACT:

There is a need to find new methods to limit neuromuscular deconditioning that occurs after a surgery or prolonged immobilization. This thesis aimed to assess local vibration (LV) training as an alternative to methods classically used (e.g. whole body vibration, neuromuscular electrical stimulation) to fight against neuromuscular deconditioning. The first aim of this project was to determine the effects of a 30-min acute exposure to LV on the neuromuscular function of dorsiflexor and knee extensor muscles in a healthy population. Our results showed that acute LV intervention changed central nervous system excitability, allowing us to consider long-term adaptations to prolonged LV. Thus, the second aim of this thesis was to assess the effects of a chronic application (training) of LV on functional (maximal strength, squat jump performance) and neural (assessed with transcranial magnetic stimulation) properties of healthy young and old subjects. Our results showed that 4 to 8 weeks of LV increase functional capacities that were due to neural adaptations. Based on these results, an on-going study assessing the effectiveness of LV during a rehabilitation program for subjects who suffered from anterior cruciate ligament lesion has been proposed.