

# The effects of local vibration inducing a tonic vibration reflex or movement illusion on acute modulations of corticospinal excitability

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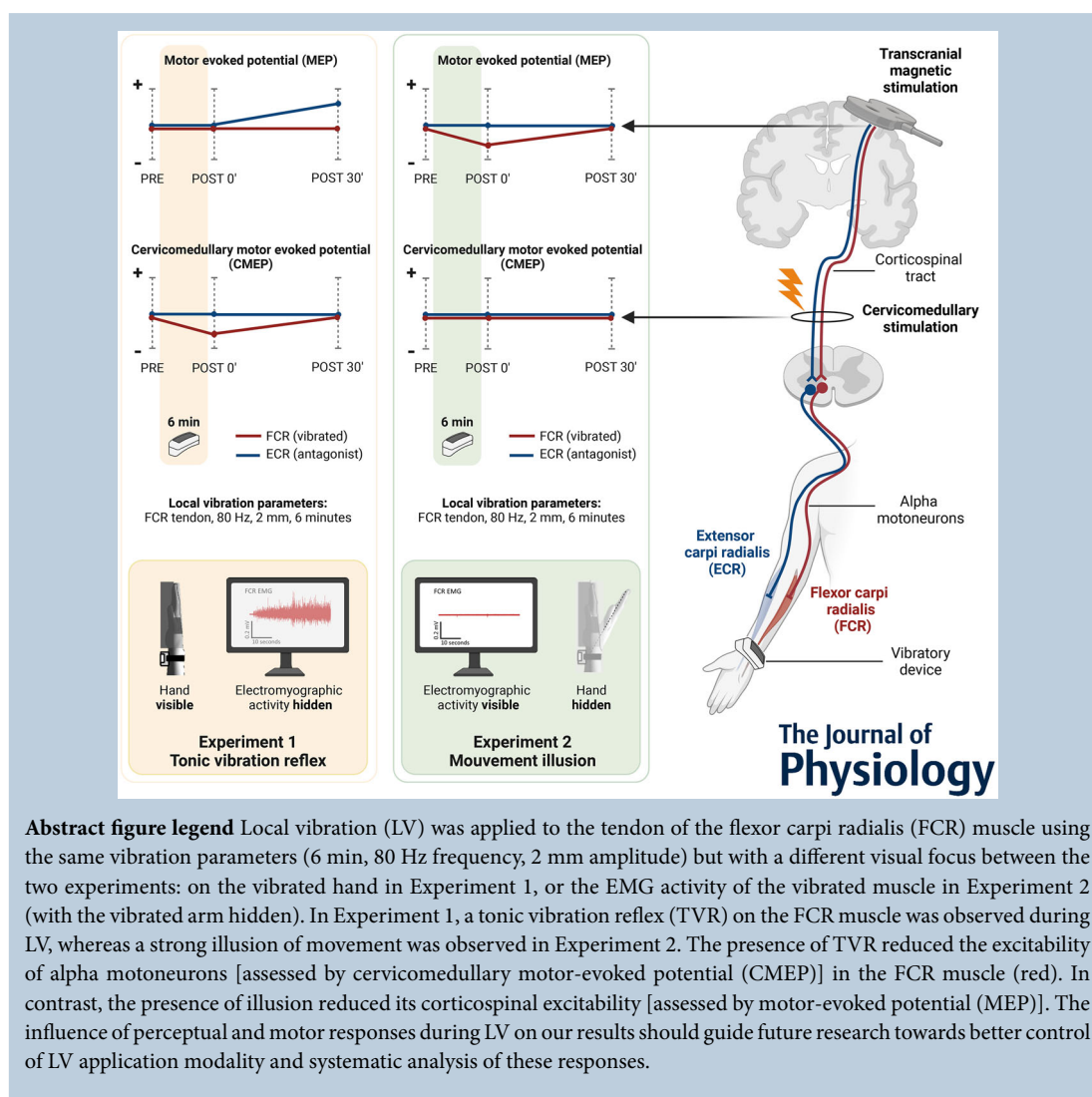
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**Abstract** Stimulation of muscle afferents by local vibration (LV) can lead to two distinct perceptual and motor responses: the tonic vibration reflex (TVR) or the movement illusion. This study aimed to evaluate the effect of TVR and movement illusion on corticospinal excitability. In two experiments, EMG activity of the vibrated flexor carpi radialis (FCR) muscle (80 Hz, 6 min) and the extensor carpi radialis (ECR) muscle were recorded. Illusion was assessed using questionnaires. LV conditions were adjusted to favour either TVR (visual attention focused on the vibrating wrist) or ILLUSION (hidden hand, visual attention focused on the EMG of the FCR muscle). Motor-evoked potential (MEP) and cervicomedullary motor-evoked potential (CMEP) were recorded at rest for both muscles before (10 and 0 min) and after (0 and 30 min) each LV condition. Only the TVR condition increased EMG of the FCR muscle (+490% compared to resting,  $P = 0.005$ ), while movement illusion was greater in the ILLUSION condition ( $P < 0.001$ ). Concerning the vibrated muscle at P0, TVR reduced the amplitude of CMEP ( $-13.8 \pm 15.8\%$ ,  $P = 0.011$ ) without altering MEP ( $0.3 \pm 27.9\%$ ,  $P = 1$ ), whereas the opposite occurred with movement illusion (i.e. CMEP:  $-4.5 \pm 13.7\%$ ,  $P = 0.891$ ; MEP:  $-25.1 \pm 17.2\%$ ,  $P = 0.002$ ). Cortical excitability (MEP/CMEP ratio) of the vibrated muscle was reduced by  $24 \pm 13.3\%$  on average compared to values obtained before LV, only in the ILLUSION condition. In conclusion, this study highlights the relevance of measuring and reporting the perceptual and motor responses induced during LV, demonstrating that TVR and movement illusion partly determine the acute effects on the neural network.

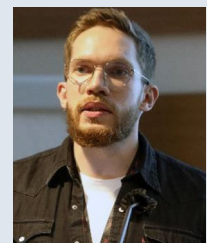
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### Key points

- Tonic vibration reflex and movement illusion are rarely controlled and measured in studies investigating the effect of LV on corticospinal excitability.
- The application of LV with visual attention focused on the vibrated muscle promotes the presence of a tonic vibration reflex (TVR). The absence of visual feedback on the latter promotes the presence of an illusion of movement.
- The cortical excitability of the vibrated muscle is influenced differently according to the perceptual and motor responses induced during LV, with an opposite effect on the cortical excitability of the antagonist muscle.
- Improved control of LV application conditions, quantification of perceptual and motor responses, and reporting of results (e.g. EMG activity of the vibrated muscle or illusion of movement during the protocol) are required to enhance our understanding of the physiological mechanisms associated with LV use and, consequently, the effectiveness of LV as a therapeutic modality.

Nicolas Amiez graduated in 2019 with a master's degree and began a PhD in 2020 in the Inserm UMR1093-CAPS laboratory (University of Burgundy, Dijon, France). His work is supported by a grant from the French Ministry of Higher Education and Research. His research focuses on the responses of the neuromuscular system in response to local vibration, particularly using different methods to investigate the excitability of the spinal and corticospinal system. His recent research focuses on the impact of perceptual and motor responses induced by local vibration on the neuromuscular system, underlining the importance of controlling the conditions under which vibration is applied.



## Introduction

The excitatory cortico-cortical connections between somatosensory and motor cortices are now well established, explaining why increasing muscular afferent input can induce lasting plastic changes in these two cortical areas (Huerta & Pons, 1990; Ridding & Taylor, 2001; Stefan et al., 2000). In this regard, local vibration (LV) is an effective tool for generating abundant afferent activation for individuals at rest (Roll et al., 1989). Indeed, micro-stretching of the muscle spindles caused by high-frequency vibration (70–100 Hz) activates primary and secondary afferent endings (Burke et al., 1976a; Hagbarth, 1973; Roll & Vedel, 1982; Roll et al., 1989) that project via mono- or polysynaptic connections to the pool of alpha motoneurons (Banks et al., 2021; Pierrot-Deseilligny & Mazevet, 2000), and via a polysynaptic pathway to the cortical level (Proske & Gandevia, 2012). Therefore, several studies have focused on changes in corticospinal excitability during short periods of LV (<1 min) using single-pulse transcranial magnetic stimulation (TMS) applied over the participants' motor cortex. In most studies, the motor evoked potential (MEP), the EMG response recorded over the target muscles, was increased during vibration for the vibrated muscle and reduced for the antagonist muscle (Claus et al., 1988; Kossev et al., 1999; Lapole et al., 2015; Rosenkranz & Rothwell, 2003; Siggelkow et al., 1999; Steyvers, Levin, Verschueren et al., 2003). More recently, several studies have investigated changes in this excitability following prolonged use of LV (>15 min) to promote its use in rehabilitation (Avvantaggiato et al., 2021). Contrary to the consistent increase in MEP for the antagonist muscle after the LV (Amiez et al., 2024; Forner-Cordero et al., 2008; Lapole et al., 2012; Steyvers, Levin, van Baelen et al., 2003), the results obtained for the vibrated muscle are more heterogeneous: some studies have observed increased MEP amplitude, while others have observed decreased or no change (for a review see Souron, Besson, Millet et al., 2017).

Such variability in MEP changes for the vibrated muscle could depend on the conditions under which the LV is applied. Indeed, positioning the vibratory device to the tendon is often suggested as an optimal position for recruiting primary afferents because it is easier to obtain the tonic vibration reflex (TVR) in this condition (de Gail et al., 1966; Eklund & Hagbarth, 1966; Roll et al., 1980), even with low vibration amplitudes ( $\leq 1$  mm) (Eklund & Hagbarth, 1966; Martin & Park, 1997; Mottram et al., 2006). This reflex, which results from the involuntary recruitment of alpha motoneurons via spinal loops (Burke et al., 1976b; de Gail et al., 1966; Roll et al., 1989; Romaguère et al., 1991), is rarely controlled and/or reported in studies. The most common solution used to prevent this reflex contraction is to suppress visual control on the vibrated limb by hiding it

or closing the eyes (Forner-Cordero et al., 2008; Lapole et al., 2015; Souron et al., 2018; Steyvers, Levin, van Baelen et al., 2003). However, under this condition, participants may experience an illusion of movement, consisting of perceiving movement in the opposite direction to the action of the vibrated muscle (Goodwin et al., 1972; Roll et al., 1980). Furthermore, the illusion of movement can elicit an involuntary activation of the antagonist muscle, called the antagonist vibratory response (AVR). This contraction occurs due to a perceptual-to-motor transformation of proprioceptive input at the cortical level (Calvin-Figuère et al., 1999). Nonetheless, the occurrence of movement illusion, AVR and TVR during prolonged LV applications remains largely underappreciated in previous research.

Controlling for the presence of the illusory movement is crucial, as it can lead to unexpected effects during LV exposure: an increase in the corticospinal excitability of the antagonist muscle alongside a reduction for the vibrated muscle, which is the opposite of the effects discussed above in the absence of illusion (Kito et al., 2006; Mancheva et al., 2017). A plausible explanation for this increase could be found in the dependence between the activation of motor cortical areas and the illusion. Indeed, several imaging studies (e.g. magnetoencephalography or functional magnetic resonance imaging) have revealed that motor areas are activated during LV mainly when the movement illusion is perceived, with the extent of this activation depending on the illusion's speed (Casini et al., 2008; Naito & Ehrsson, 2001; Radovanovic et al., 2002; Romaguère et al., 2003). The fact that the involuntary contraction occurs on the antagonist muscle (i.e. AVR) during the illusion may suggest that the cortical areas of the antagonist muscle are more activated under this LV condition (Naito et al., 2002), although data from imaging studies do not confirm the precise location of activation in motor areas. The observed effects during LV could explain the systematic increase in corticospinal excitability of the antagonist muscle following prolonged application ( $\geq 30$  min) inducing movement illusion. Moreover, this enhancement occurs concurrently with either unchanged or decreased excitability in the vibrated muscle (Amiez et al., 2024; Forner-Cordero et al., 2008; Steyvers, Levin, Verschueren et al., 2003).

While modulation of MEP for the antagonist muscle could be standardized by placing the participant under a movement illusion condition, the variability in responses for the vibrated muscle may arise from the uncontrolled presence of TVR. Indeed, it is important to recall that MEP measures corticospinal excitability while integrating spinal excitability and can be influenced by changes in alpha motoneuron excitability (McNeil et al., 2013; Spampinato et al., 2023). To assess the excitability of the latter, electrical stimulation can be applied over the corticospinal tract to elicit a mainly monosynaptic response known as cervicomedullary evoked potential

(CMEP, for upper limbs) or thoracic evoked potential (TMEP, for lower limbs) (Martin et al., 2006; McNeil et al., 2011). While a reduction in the alpha motoneuron excitability (i.e. CMEP reduction) has already been observed after a 6 min LV protocol with no TVR (visual control only) (Nito et al., 2021), it is conceivable that repeated stimulation of motor units due to the presence of TVR could lead to a greater decrease in their excitability (McNeil et al., 2011), and consequently a greater reduction in MEP. Interestingly, because these two stimulation techniques (i.e. TMS and electrical stimulation of the corticospinal tract) recruit motor units according to the size principle, the ratio between the two measures (i.e. MEP/CMEP) can be an index of cortical excitability, provided that response amplitudes are similar (McNeil et al., 2013; Taylor et al., 2002). By combining these two measures, several studies have recently shown that an absence or reduction in MEP after a 30 min LV exposure was systematically associated with a greater decrease in CMEP (Amiez et al., 2024; Pfenninger et al., 2023) or TMEP amplitude (Kennouche et al., 2022; Souron, Besson, McNeil et al., 2017), suggesting that cortical excitability was increased for the vibrated and for the antagonist muscle (Amiez et al., 2024).

Consequently, the variability in MEP responses of vibrated and antagonist muscles could be due to involuntarily induced perceptual and motor responses during LV, especially when considering the difficulty of being in a condition that does not induce either (1) the TVR or (2) the movement illusion (Roll et al., 1980). Therefore, the primary aim of this study was to compare the effect of 6 min of LV on corticospinal excitability of the vibrated muscle under conditions promoting either TVR or movement illusion. In addition, changes in the corticospinal excitability of the antagonist muscle have also been reported. To achieve this, we measured the immediate and long-term effect (i.e. 30 min after LV) of these two perceptual and motor responses on the corticospinal (i.e. MEP) and alpha motoneuron excitability (i.e. CMEP) of both vibrated [i.e. flexor carpi radialis (FCR)] and antagonist muscle [i.e. extensor carpi radialis (ECR)]. For the vibrated muscle, we hypothesized that MEP would decrease in the TVR condition due to a strong reduction in CMEP, while MEP in the ILLUSION condition would not be altered in the absence of CMEP changes. For the antagonist muscle, we hypothesized that the ILLUSION condition would favour an increase in MEP without any meaningful change in CMEP.

## Methods

### Ethical approval

Fifteen adults (three women, age:  $24.3 \pm 2.4$  years, height:  $177.4 \pm 8.5$  cm; weight:  $71.7 \pm 13.6$  kg; four left-handed)

participated in this experiment. Based on the results of a previous study, which found a significant time effect of 6 min of vibration on CMEP amplitude ( $n = 11$ ) with a large effect size ( $\eta^2 = 0.53$ ) (Nito et al., 2021), an *a priori* power analysis was run using G\*Power (version 3.1.9.7, Universität, Düsseldorf, Germany). Twelve participants were considered necessary to detect differences using standard parameters of  $1 - \beta = 0.80$  and  $\alpha = 0.05$ . None of the participants suffered from any neurological, psychological or orthopaedic disorder in the 12 months preceding their participation. Each participant gave written consent following a medical evaluation and was informed of the potential risks of participating in the research. Consumption of psychoactive substances and physical activity were prohibited for 12 h prior to an experimental session. The research was conducted in accordance with the revision of the 2013 Helsinki Declaration for Experimentation on Man, except for registration in a database, and was approved by the local ethics committee (CPP Est: A00064-49).

### Experimental design

Participants took part in two experiments that lasted 1.5 h in a randomized, cross-over design with counter-balanced order. They were spaced at least 48 h apart and took place at the same time of day. For each experiment, the participant was seated on an isokinetic dynamometer chair, and all measurements were recorded specifically from the right arm (Biodex System 4, Biodex Medical Systems Inc., Shirley, NY, USA). Each experiment began with a standardized warm-up consisting of alternating contractions of the wrist extensor and flexor muscles to homogenize participants' state prior to the start of measurements. This involved 10 submaximal isokinetic contractions at  $60^\circ/\text{s}$  and  $30^\circ/\text{s}$  ( $\sim 50\%$  of maximum perceived force), two submaximal isometric contractions ( $\sim 50\%$  and  $\sim 80\%$ , respectively) and one maximal isometric contraction. Each set was interspersed with 1 min of recovery time. Isometric contractions lasted 3 s and were alternately performed in carpal flexion and extension with 15 s of recovery between efforts.

During a 5 min rest following the warm-up, pairs of surface electrodes were positioned on the FCR and ECR muscles to record activity both at rest and during the vibration protocol, as well as EMG responses induced by stimulation. Then, muscle responses from the FCR and ECR muscles were obtained using peripheral nerve stimulation to the median and radial nerves, respectively. A recruitment curve was performed for each muscle to determine the stimulation intensity required to achieve maximal muscular contraction ( $M_{\text{MAX}}$ ), which was increased by 30% to maintain supramaximal stimulation throughout the experiment. Then, TMS was used to record MEP. The optimal stimulation position common

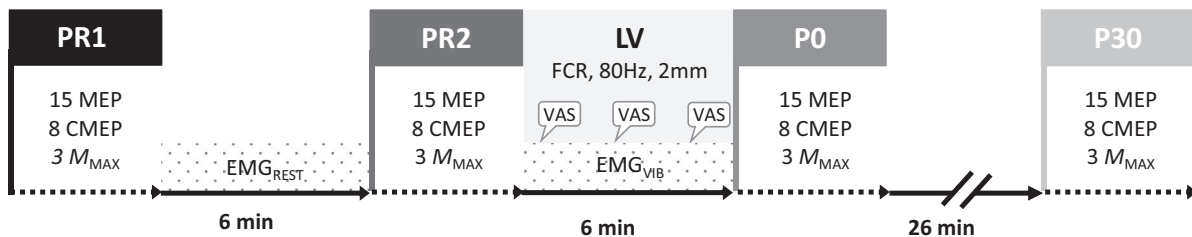


to both muscles was identified, and the resting motor threshold [rMT, in percentage maximal stimulator output (%MSO)] of the FCR muscle was measured before recording 5 MEP at 130 %rMT. Finally, electrodes were positioned at the mastoid processes to record CMEPs (Taylor, 2006). To maximize the number of motor units common to both types of stimulation, the stimulation intensity used to elicit the CMEP was adjusted to match as closely as possible the MEP amplitude previously recorded at 130% of rMT (Taylor et al., 2002). As previously used in the literature for the simultaneous evaluation of different

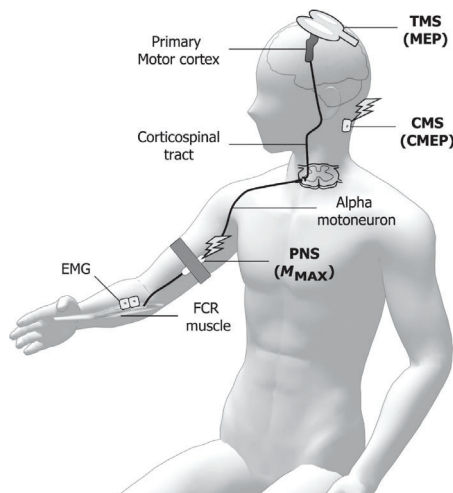
antagonistic muscle pairs, stimulations for MEP and CMEP were common between the FCR and ECR muscles using the same location and intensity (Aimonetti & Nielsen, 2001; Nuzzo et al., 2016; Steyvers, Levin, van Baelen et al., 2003).

After identifying the stimulation sites and intensities for the three stimulation techniques (MEP, CMEP and  $M_{MAX}$ ), the first measurements were taken, lasting ~4 min (PR1), in the following order: 15 MEP, 8 CMEP, 3  $M_{MAX}$  for the FCR muscle, and 3  $M_{MAX}$  for the ECR muscle (Fig. 1A). These measurements were reproduced after

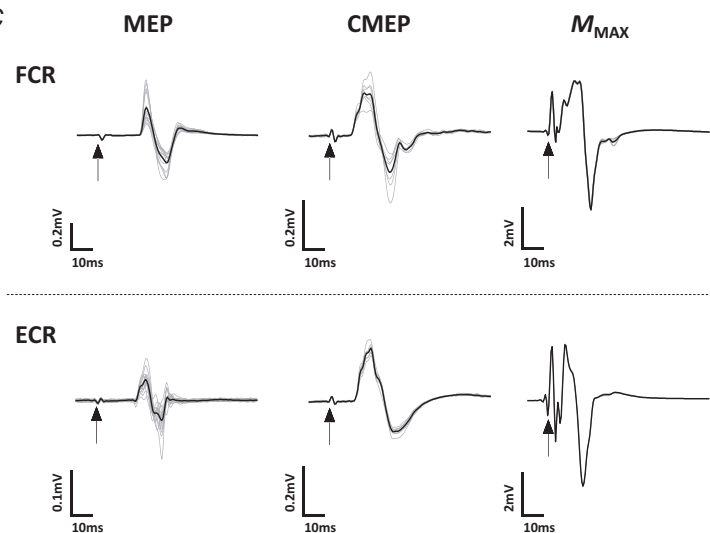
A



B



C



**Figure 1. Schematic representation of the experimental protocol used and the measurements performed**

A, experimental study design involving 15 participants. Cervicomedullary motor-evoked potential (CMEP) was not measured in two participants because of the discomfort caused by stimulation. The two experiments were spaced at least 48 h apart and differed only in the LV condition (TVR or ILLUSION). Measurements were performed at the start of the protocol (PR1), after 6 min of rest (PR2), and then 0 (P0) and 30 min (P30) after stopping the LV protocol, always using the same order of stimulation techniques: motor-evoked potential (MEP), followed by CMEP and maximal muscular responses ( $M_{MAX}$ ). EMG activity of the flexor carpi radialis (FCR) and extensor carpi radialis (ECR) muscle were recorded at rest (6 min) and during LV (6 min). The presence of illusion during LV was assessed using three visual analog scales (VAS) administered 1, 3 and 5 min after the start of the vibratory protocol. B, presentation of the stimulation sites for MEP (transcranial magnetic stimulation, TMS) and CMEP (cervicomedullary stimulation, CMS) of both muscles, and  $M_{MAX}$  (percutaneous nerve stimulation, PNS) of the flexor carpi radialis muscle (FCR). C, typical MEP, CMEP and  $M_{MAX}$  recorded on the FCR muscle (upper side) and ECR (lower side) of a participant before the LV protocol (i.e. PR2). Black line represents the average, and the grey lines represent each stimulation (i.e. MEP = 15 stimulations, CMEP = 8 stimulations,  $M_{MAX}$  = 3 stimulations). Arrows indicate the stimulation artefact. Note that the EMG amplitude scale varies depending on the muscle and the variable represented.

about 6 min of rest (PR2), immediately (P0) and 30 min (P30) after stopping the 6 min of LV (Fig. 1A). Only the LV protocol differed between the two experiments. To facilitate the occurrence of TVR, the participant was asked to focus visual attention on the vibrating wrist without feedback of EMG activity. Conversely, to enhance perception of an illusory movement, the participant was asked to focus on the sensations perceived, with the arm hidden and visual attention focused on the EMG activity of the vibrated muscle displayed on the screen in front of the participant. To assess the presence of TVR and/or AVR in both conditions, EMG activity was recorded at rest between PR1 and PR2 and during the LV protocol.

### Experimental settings

**Participant installation.** For each experiment, the participant was seated on an isokinetic dynamometer chair (Biodex System 4, Biodex Medical Systems). The position was the same across the two experiments, maintained throughout the experiment and consistent between participants (relative to the anatomical reference position, hip flexion:  $107^\circ \pm 4^\circ$ , shoulder flexion:  $31^\circ \pm 4^\circ$ , elbow flexion:  $140^\circ \pm 3^\circ$ , arm abduction:  $42^\circ \pm 5^\circ$ , dynamometer angle:  $118 \pm 3^\circ$ ). The styloid process of the ulna was aligned with the axis of the dynamometer and the hand was held in a semi-pronation position using a specific accessory. The hand was in line with the forearm, and the elbow was placed on an armrest. The feet were on support to avoid any interfering movement of the lower limbs during neurophysiological measurements (Zehr et al., 2007).

**LV conditions.** LV was applied for 6 min to the right arm at the distal portion of the tendon of the FCR muscle at a frequency of 80 Hz and an amplitude of 2 mm (manufacturer's information, Vibramoov PHYSIO, Techno Concept, Manosque, France). Before starting the warm-up for the first experiment, the vibrator's position was fine-tuned through two to three sets of 10 s of vibration to optimize illusion production and familiarize the participant (Taylor et al., 2017). The vibrator position and strap length (designed by the manufacturer for the wrist joint) were measured and reproduced in the second experiment. In the TVR condition, the participant was instructed to keep looking at his/her hand throughout the protocol to reduce the occurrence of movement illusion and promote the onset of TVR (Roll et al., 1980) (Fig. 2A). In the ILLUSION condition, the participant's arm was hidden by a home-made system (Fig. 2B). In addition, the participant was instructed to concentrate on the movement perceived during the LV and to remain fully relaxed. To facilitate muscle relaxation during ILLUSION, the EMG activity of the vibrating muscle (i.e. the FCR) was

visible to the participant on a screen in front of him/her (Roll et al., 1980; Taylor et al., 2017). Subjective perception of a movement illusion was assessed in each condition using three visual analog scales (VAS) graduated from 0 (no effect) to 10 (very strong effect) as described previously (Amiez et al., 2024; Steyvers, Levin, van Baelen et al., 2003): (1) vividness (the clarity of the illusion in relation to real extension of the wrist; score of 10: the illusory movement was perceived as if the wrist moved), (2) strength (illusory amplitude of wrist extension; score of 0: no extension, score of 10: maximal extension) and (3) continuity (subjective evaluation of the perceived duration of illusory movement in the last minute; score of 10: present without interruption).

**EMG recording.** EMG activity of the FCR and ECR muscle was recorded using electrode pairs (20 mm inter-electrode distance) with silver chloride (Ag/AgCl). After preparing the participant's skin following Seniam (<http://www.seniam.org/>) recommendations (i.e. shave the skin, clean with alcohol, and wait for dry skin). The electrodes were placed outside the innervation zones at  $\sim 30\%$  and  $20\%$  of the total length of the FCR and ECR muscle, respectively (Barbero et al., 2012). A reference electrode was positioned on the acromion of the right arm. The set-up quality was checked by observing that the root-mean-square (RMS) of the EMG signal over 5 s at rest was less than  $3.5 \mu\text{V}$  for each muscle. Resting EMG activity was recorded simultaneously for both muscles between PR1 ( $\text{EMG}_{\text{REST}}$ ) and PR2 and during the vibratory protocol ( $\text{EMG}_{\text{VIB}}$ ). The signal was recorded with a bandwidth of 10–400 Hz, amplified (gain = 1000), digitized at a frequency of 2000 Hz (Biopac Systems Inc., Goleta, CA, USA) and recorded on a computer for post-processing analysis (Fig. 2B, C).

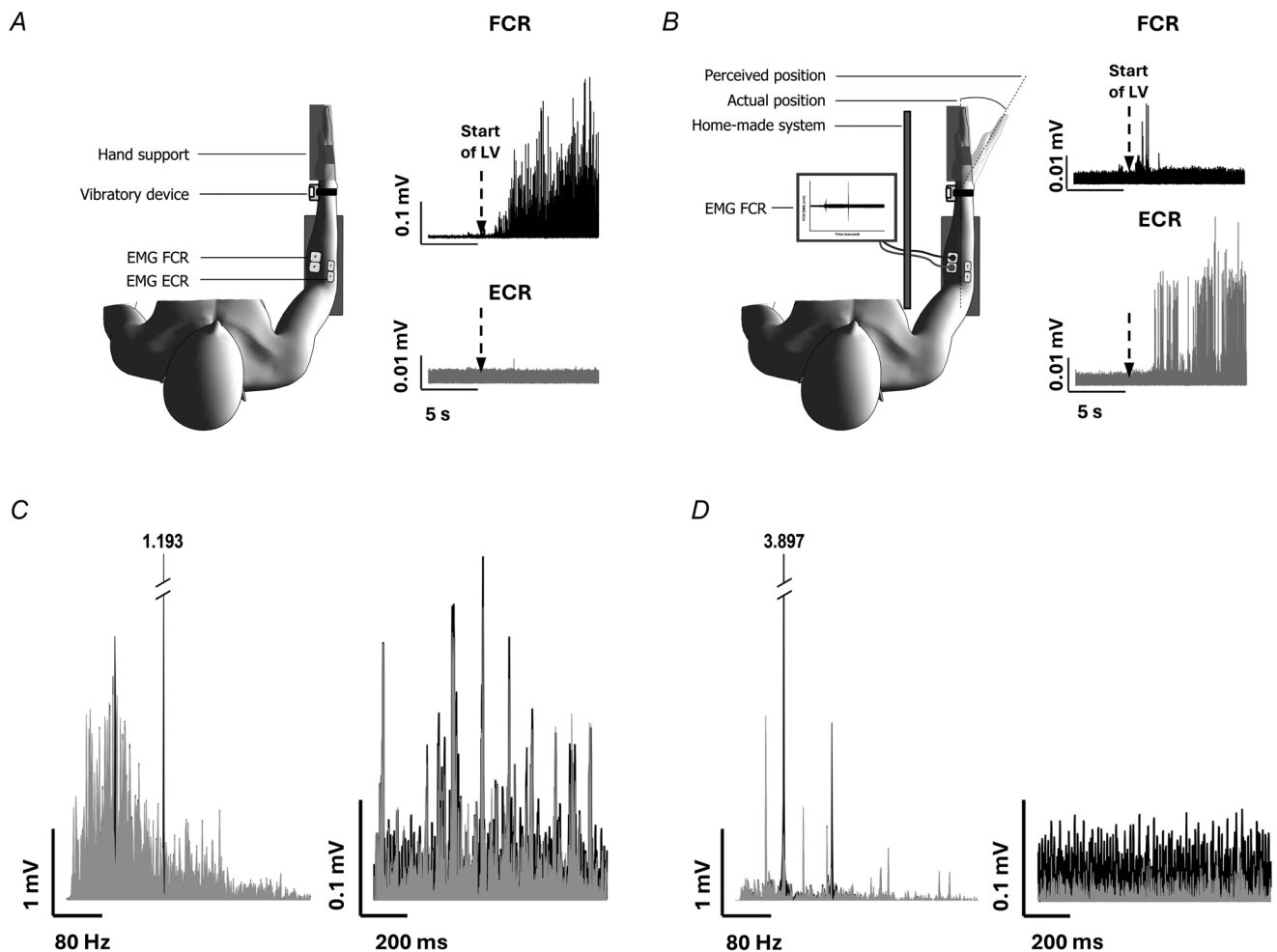
**Motor-evoked potential.** Single pulses from a figure-of-eight coil (70 mm in diameter) connected to a Magstim BiStim<sup>2</sup> monophasic stimulator (The Magstim Co., Whitland, UK) were delivered over the left motor cortex to record MEP of both muscles (Fig. 1B). The coil was oriented tangentially to the scalp, and the handle was oriented posteriorly and laterally at a  $45^\circ$  angle from the sagittal plane to induce a posteroanterior current (Balslev et al., 2007). All stimulations were performed at a fixed frequency of 0.2 Hz (inter-pulse stimulus of 5 s) to promote reproducibility and amplitude of response (Julkunen et al., 2012). The hotspot was defined as the area with the highest and most consistent response at 50 %MSO for the two muscles. Then, rMT was determined as the lowest stimulation intensity (i.e. %MSO), allowing responses with a peak-to-peak amplitude of  $50 \mu\text{V}$  to be obtained for at least four out of eight trials for the FCR muscle. For each measurement (i.e. PR1, PR2, P0 and

P30), 15 MEPs were performed at 130% of this threshold (mean stimulation intensity: 58.6 %MSO, range: 45–68 %MSO; Fig. 1C).

**Cervicomedullary motor-evoked potential.** CMEPs were obtained simultaneously on both muscles with single rectangular electrical stimulations (duration of 0.2 ms, voltage of 400 V, mean current intensity: 130 mA, range: 80–200 mA; DS7A, Digitimer, Welwyn Garden City, UK) delivered with two silver chloride (Ag/AgCl) electrodes positioned over the mastoid processes (anode on the right side) (Fig. 1B) (Taylor & Gandevia, 2004; Ugawa et al., 1991). All stimulations were performed at a fixed frequency of 0.16 Hz (6 s). An input–output curve was

constructed with a stimulation intensity increment of 10 mA to obtain a peak-to-peak response amplitude for the FCR muscle that was like the MEP amplitude obtained at 130% rMT for the same muscle, within comfortable intensities. The increment was dropped to 5 mA, approaching the target response. Once the optimal stimulation intensity had been reached, eight CMEPs were performed for each measurement period (i.e. PR1, PR2, P0 and P30) (Fig. 1C).

**Nerve stimulations.** Single rectangular electrical stimulation (duration of 1 ms, voltage of 400 V, DS7A, Digitimer) was used to assess the maximal compound muscle action potential ( $M_{MAX}$ ) of both muscles (Fig. 1B).



**Figure 2. Experimental setup and muscle activity recordings from the vibrated muscle and its antagonist during the local vibration protocol for tonic vibration reflex and movement illusion conditions**

A, experimental setup for the TVR condition (no EMG feedback of the vibrated muscle and visual attention focused on the vibrated wrist) and typical rectified EMG activity recorded on the flexor carpi radialis (FCR, black) and extensor carpi radialis (ECR, grey) muscles at the start of the LV protocol. B, experimental setup for the ILLUSION condition (visual attention focused on EMG activity of the FCR muscle and hand hidden by home-made system). C, example of data obtained for fast Fourier transform (left side) and the rectified EMG activity of the FCR muscle (right side) over 1 s of recording in the TVR condition. D, same data obtained during the ILLUSION condition. Unfiltered signals are shown in black, filtered signals in grey. Note that the amplitude scale of the rectified EMG signal is not the same for FCR and ECR muscles.

Stimulation was performed using bipolar felt electrodes on the right median nerve (cubital fossa) for the FCR muscle and on the right radial nerve (spiral groove) for the ECR muscle (30 mm anode–cathode spacing, Digitimer). For each bipolar electrode, the optimal position over the nerve was adjusted to obtain the greatest muscular response on the target muscle at a given stimulation intensity combined with the antagonist muscle's absence/low response. An input–output curve was constructed for each muscle with a stimulation intensity increment of 2 mA and a stimulation frequency 0.2 Hz. The increment was dropped to 0.5 mA as the plateau was approached. The stimulation intensity that no longer induced an increase in muscle response was increased by 30% to ensure that it remained supramaximal throughout the experiment (mean current intensity for FCR muscle: 14.4 mA, range: 3.9–32.5 mA, mean current intensity for ECR muscle: 23.3 mA, range: 4.6–41 mA). At the end of each measurement period (i.e. PRE1, PRE2, P0, P30), three stimulations (130 % $M_{\text{MAX}}$ ) were performed for the FCR and then for the ECR muscle at a frequency of 0.2 Hz (Fig. 1C).

**Control experiment.** A total of nine participants (two women, age:  $24 \pm 2.7$  years, height:  $177.1 \pm 8.2$  cm; weight:  $71.4 \pm 11.2$  kg; two left-handed) were involved in the control experiment, with seven also participating in the main experiment. The control experiment lasted 1.5 h and was conducted at the same time of day as the main experiment. The participants were positioned in the same configuration as in the main study (see 'Participant installation' section above). Following the standardized warm-up described previously, participants performed two maximal voluntary isometric contractions (MVICs) in carpal flexion. The procedures for identifying stimulation sites and intensities for MEP, CMEP and  $M_{\text{MAX}}$  were identical to those used in the main experiment. Measurements (15 MEP, 8 CMEP and 3  $M_{\text{MAX}}$  per muscle) were recorded at three time points: just before a 6 min submaximal voluntary contraction (SVC) in carpal flexion (equivalent to PR2 in the main experiment), immediately after SVC (P0), and 30 min after SVC (P30). The contraction intensity was set to produce the same relative EMG activity (i.e. % $M_{\text{MAX}}$ ) on the FCR muscle as that recorded on the vibrated FCR muscle in the TVR condition of the main experiment. The mean EMG activity from the main experiment's TVR condition was used as a target for the two participants who only performed the control experiment. Participants monitored their EMG signal throughout the 6 min SVC to maintain the required activation level. Resting EMG activity was recorded after P0 for 6 min. All other experimental settings (participant installation, EMG recording, MEP, CMEP and nerve stimulations) remained unchanged from the main experiment.

## Data analyses

All data were extracted from AcqKnowledge (Biopac Systems, Inc., Goleta, CA, USA) and analysed with a custom-made MATLAB algorithm (MATLAB; MathWorks, Natick, MA, USA). For both muscles, peak-to-peak amplitude of each stimulation within each measurement period (i.e. 15 MEP, 8 CMEP) was expressed as a percentage of the corresponding  $M_{\text{MAX}}$  (mean peak-to-peak amplitude of the three  $M_{\text{MAX}}$ ) obtained at the same time. The interquartile range method [outlier if: value  $> Q3 + 1.5 \times (Q3 - Q1)$  or value  $< Q1 - 1.5 \times (Q3 - Q1)$ ] was used to identify outlier MEP and CMEP recorded from a participant's muscle within the same measurement period (i.e. PR1, PR2, P0, P30) for a given condition (i.e. TVR or ILLUSION). Data identified as outliers were excluded prior to statistical analysis. Regarding the FCR muscle, 4.86% and 8.87% of the total number of MEPs and CMEPs recorded in this study were identified as outliers, respectively (i.e. percentages calculated across all participants, measurement periods and conditions combined). For the ECR muscle, these proportions were 6.96% and 6.27% for MEP and CMEP, respectively. MEPs were interpreted as a marker of corticospinal excitability, while CMEPs were interpreted as a marker of lower motoneuron excitability. The MEP/CMEP ratio was calculated and interpreted in terms of cortical excitability (Amiez et al., 2024; McNeil et al., 2013; Taylor, 2006).

The results of fast Fourier transformation analysis indicated that the EMG signal recorded during LV was contaminated by the vibratory device with a maximal signal amplitude at a frequency ranging from 79.3 to 79.9 Hz (vibration frequency) and a second amplitude peak from 158.6 to 159.8 Hz (first harmonic frequency). Consequently, two band-stop filters (78.5–81.5 Hz and 157–161 Hz) were applied to EMG<sub>REST</sub> and EMG<sub>LV</sub> of both muscles (Fig. 2C, D). Then, EMG activity at rest and during LV was quantified using the RMS of the filter signal. To eliminate the impact of potential peripheral alterations on the recorded EMG activity, the RMS signal was normalized for each muscle. Thus, the RMS signal recorded at rest was expressed relative to  $M_{\text{MAX}}$  obtained in PR2 ( $\text{RMS}_{\text{REST}}/M_{\text{MAX}}$ ), and the RMS signal recorded during LV was normalized relative to  $M_{\text{MAX}}$  obtained in P0 ( $\text{RMS}_{\text{LV}}/M_{\text{MAX}}$ ). Subjective perception of movement illusion within a vibration condition corresponded to the mean of the responses indicated by the participant to the different VAS (i.e. the three scales administered at 1, 3 and 5 mins).

**Control experiment.** The maximal EMG activity of the FCR muscle during the MVIC in carpal flexion corresponded to the maximal RMS signal obtained on a 500 ms window length ( $\text{RMS}_{\text{MVIC.CT}}$ ). The EMG



activity recorded during SVC and at rest after P0 were quantified using the RMS of the raw signal (RMS<sub>SVC.CT</sub> and RMS<sub>REST.CT</sub>). Each RMS signal was normalized relative to  $M_{\text{MAX}}$  obtained at P0 on the FCR muscle (i.e. RMS<sub>MVIC.CT</sub>/ $M_{\text{MAX}}$ , RMS<sub>SVC.CT</sub>/ $M_{\text{MAX}}$  and RMS<sub>REST.CT</sub>/ $M_{\text{MAX}}$ , respectively).

### Statistical analysis

Except for  $M_{\text{MAX}}$  and mean perception, RMS<sub>REST</sub>/ $M_{\text{MAX}}$ , RMS<sub>LV</sub>/ $M_{\text{MAX}}$ , MEP/ $M_{\text{MAX}}$ , CMEP/ $M_{\text{MAX}}$  and the MEP/CMEP ratio of both muscles were log-transformed. The normal distribution was checked using the Shapiro–Wilk test. For each repeated measures ANOVA described below, the sphericity of the data was checked by a Mauchly test, and the Greenhouse–Geisser correction was used when the sphericity assumption was violated. Significant factors in ANOVAs were followed by a Tukey HSD *post hoc* test.

Student's paired *t* test was used to compare the amount of illusion perceived by subjects during LV between the two experimental conditions (TVR  $\times$  ILLUSION). Repeated measures ANOVA with two within-subject factors [*Condition* (TVR, ILLUSION)  $\times$  *Time* (REST, LV)] were performed for each muscle to compare RMS<sub>REST</sub>/ $M_{\text{MAX}}$  and RMS<sub>LV</sub>/ $M_{\text{MAX}}$  between the two conditions. Repeated measures ANOVAs with two-level factor [*Condition* (TVR, ILLUSION)  $\times$  *Time* (PR1, PR2, P0, P30)] were performed on the following variables:  $M_{\text{MAX}}$ , MEP/ $M_{\text{MAX}}$ , CMEP/ $M_{\text{MAX}}$ , MEP/CMEP ratio and for each muscle (i.e. FCR and ECR). In addition to the main data discussed in the results section, details of these analyses and associated data (mean  $\pm$  SD) are available as supplementary data (Table S 1).

The variables MEP/ $M_{\text{MAX}}$ , CMEP/ $M_{\text{MAX}}$  and the MEP/CMEP ratio measured at P0 and P30 were expressed relative to the values obtained at PR2 for both muscles (i.e. P0/PR2 and P30/PR2). The results were then log-transformed, and normality was checked with the Shapiro–Wilk test. Repeated measures ANOVA with two within-subject factors [*Condition* (TVR, ILLUSION)  $\times$  *Time* (P0, P30)] were used for each variable expressed relative to PR2. In addition to the main data discussed in the results section, details of these analyses and associated data (mean  $\pm$  SD) are available as supplementary data (Table S 2). Repeated measures correlations (rmcorr R package) (Bakdash & Marusich, 2017) were performed for each variable (i.e. MEP, CMEP MEP/CMEP ratio) to assess the relationship between P0 expressed relative to PR2 for the FCR and ECR muscle, both conditions combined.

**Control experiment.** The ratio RMS<sub>SVC.CT</sub>/RMS<sub>MVIC.CT</sub> was calculated to express the SVC proportional to the

maximal activity recorded during MVIC. Repeated measures ANOVAs with one within-subject factor [*Time* (LV.TVR, REST.CT, SVC.CT)] were performed for each muscle to compare RMS<sub>SVC.CT</sub>/ $M_{\text{MAX}}$ , RMS<sub>REST.CT</sub>/ $M_{\text{MAX}}$  (both recording in the control experiment) and RMS<sub>LV.TVR</sub>/ $M_{\text{MAX}}$  (recording in the TVR condition of the main experiment). Repeated measures ANOVAs with one-level factor [*Time* (PR2, P0, P30)] were performed on the following variables:  $M_{\text{MAX}}$ , MEP/ $M_{\text{MAX}}$ , CMEP/ $M_{\text{MAX}}$ , MEP/CMEP ratio, and for each muscle (i.e. FCR and ECR).

All statistical analyses were performed using Statistica software (Statsoft, version 12, Tulsa, OK, USA). Significance was set at  $P < 0.05$  for all analyses. For each significant pairwise comparison within a *post hoc* test, the effect size (ES) corresponded to Cohen's  $d_z$  and was calculated by dividing the mean difference obtained between the two measures by the standard deviation of the differences (Lakens, 2013). The confidence interval (CI) of the ES was calculated by applying the following formula: 95%  $CI_{d_z} = d_z \pm 1.96 \times SE$  (Jané et al., 2024):

$$d_z = \frac{M_{\text{diff}}}{S_{\text{diff}}} \quad SE_{d_z} = \sqrt{\frac{1}{n} + \frac{d_z^2}{2n}}$$

where  $n$  is the data pair number (i.e. MEP:  $n = 15$ ; CMEP and MEP/CMEP ratio:  $n = 13$ );  $SE_{d_z}$  is the standard error for Cohen's  $d_z$ ;  $M_{\text{diff}}$  is the mean difference between two measurements; and  $S_{\text{diff}}$  is the standard deviation of the differences between the two measurements.

Cohen's  $d_z$  was considered according to its value as small ( $d_z \geq 0.20$ ), medium ( $d_z \geq 0.50$ ), or large ( $d_z \geq 0.80$ ). The ES of each ANOVA, determined by the partial Eta squared ( $\eta^2$ ), was considered as small, medium or large for values above 0.01, 0.07 and 0.14, respectively. The  $r$  value was considered to analyse the ES of the correlations with small ( $r \geq 0.10$ ), medium ( $r \geq 0.30$ ) or large ( $r \geq 0.50$ ) effects. Given the MEP/CMEP ratios at PR1 and PR2 were not equal to one, further analyses were performed to determine whether the effects observed in the MEP/CMEP ratios at P0 and P30, expressed relative to PR2, could be influenced by the ratio value at PR2. The application of a linear mixed model incorporating the initial value of the ratio (i.e. the MEP/CMEP to PR2 ratio) as a covariate revealed a significant effect only for the ECR muscle. This result suggests that a high ratio to PR2 was associated with greater changes after LV application. However, the inclusion of this covariate did not alter the effects of *Condition*, *Time* or the *Condition*  $\times$  *Time* interaction for both muscles. Furthermore, no interaction was observed between the covariate and the other factors. Consequently, the results of the linear mixed model were no different from those obtained for the linear model initially chosen (i.e. the repeated measures ANOVA, without covariates). Under these conditions, the

simplest model was chosen to perform the analyses. The R script (R Core Team, 2021) used to evaluate the different models, and the results of the script are provided in the supplementary data (Supplementary Analysis).

## Results

### Variables recorded during LV

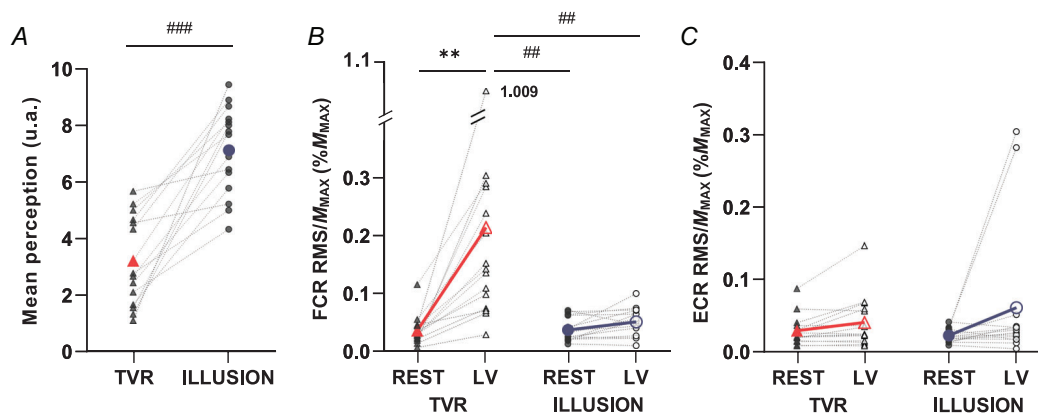
**Illusion.** The amount of illusion perceived during the LV protocol was compared between the two conditions. On average, the presence of illusory movement was higher in the ILLUSION condition ( $7.1 \pm 1.5$ ) than in the TVR condition ( $3.2 \pm 1.6$ ). This difference ( $d^+ = 3.90$ , 95% CI [2.72, 5.07]) was statistically significant ( $t(14) = 7.12$ ,  $P < 0.001$ ,  $d_z = 1.84$ , 95% CI [1.01, 2.67], Fig. 3A).

**EMG activity.** There was a significant *Condition*  $\times$  *Time* interaction effect between the EMG signal recorded at rest ( $\text{RMS}_{\text{REST}}/M_{\text{MAX}}$ ) and the signal recorded during LV ( $\text{RMS}_{\text{LV}}/M_{\text{MAX}}$ ) for the FCR vibrated muscle ( $F_{1,14} = 7.23$ ,  $P = 0.0176$ ,  $\eta^2 = 0.341$ , Fig. 3B). *Post hoc* analysis indicated that  $\text{RMS}_{\text{LV}}/M_{\text{MAX}}$  in the TVR condition ( $0.214 \pm 0.237 \% M_{\text{MAX}}$ ) was higher than the three other conditions ( $\text{RMS}_{\text{REST}}/M_{\text{MAX}}$ , TVR condition:  $0.036 \pm 0.025 \% M_{\text{MAX}}$ ,  $P = 0.00517$ ,  $d_z = 2.2$ , 95% CI [1.26, 3.13];  $\text{RMS}_{\text{REST}}/M_{\text{MAX}}$ , ILLUSION condition:  $0.037 \pm 0.019 \% M_{\text{MAX}}$ ,  $P = 0.00537$ ,  $d_z = 1.65$ , 95% CI [0.87, 2.42];  $\text{RMS}_{\text{LV}}/M_{\text{MAX}}$ , ILLUSION condition:  $0.051 \pm 0.024 \% M_{\text{MAX}}$ ,  $P = 0.00976$ ,  $d_z = 1.24$ , 95% CI [0.57, 1.91]). No change was observed in the

ILLUSION condition between  $\text{RMS}_{\text{REST}}/M_{\text{MAX}}$  and  $\text{RMS}_{\text{LV}}/M_{\text{MAX}}$  ( $P = 0.988$ ,  $d_z = 0.66$ , 95% CI [0.10, 1.22]). Regarding EMG of the ECR antagonist muscle, repeated measures ANOVA revealed no *Condition* ( $F_{1,14} = 0.238$ ,  $P = 0.634$ ,  $\eta^2 = 0.017$ ), *Time* ( $F_{1,14} = 3.836$ ,  $P = 0.0704$ ,  $\eta^2 = 0.215$ ) or interaction effects ( $F_{1,14} = 1.501$ ,  $P = 0.241$ ,  $\eta^2 = 0.097$ , Fig. 3C).

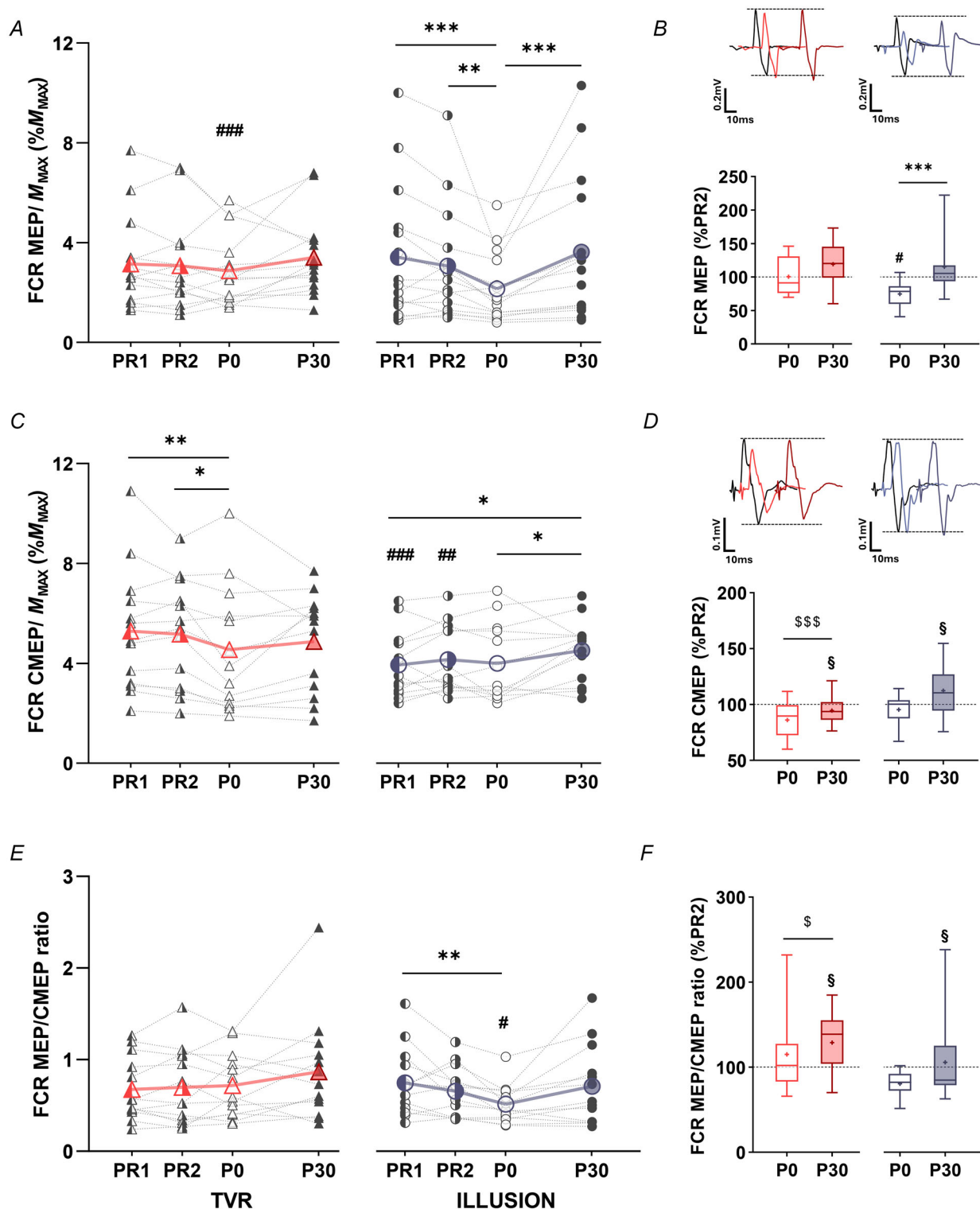
### MEP, CMEP and $M_{\text{MAX}}$

**Vibrated muscle.** As shown in Table 1, no change was observed for the  $M_{\text{MAX}}$  of the FCR muscle. Concerning MEP/ $M_{\text{MAX}}$ , the repeated measures ANOVA showed a significant *Condition*  $\times$  *Time* interaction ( $F_{3,42} = 3.598$ ,  $P = 0.0211$ ,  $\eta^2 = 0.204$ , Fig. 4A). Regarding PR1 and PR2 performed before the LV protocols, no difference was observed within each condition or between the two conditions (all  $P > 0.968$ ). No difference was observed in the TVR condition (all  $P > 0.264$ ). By contrast, a significant decrease in MEP/ $M_{\text{MAX}}$  was observed in the ILLUSION condition at P0 ( $2.15 \pm 1.39 \% M_{\text{MAX}}$ ) compared to PR1 ( $3.4 \pm 2.72 \% M_{\text{MAX}}$ ,  $P < 0.001$ ,  $d_z = 1.17$ , 95% CI [0.51, 1.83]), PR2 ( $3.07 \pm 2.24 \% M_{\text{MAX}}$ ,  $P = 0.00226$ ,  $d_z = 1.25$ , 95% CI [0.57, 1.92]) and P30 ( $3.64 \pm 2.9 \% M_{\text{MAX}}$ ,  $P < 0.001$ ,  $d_z = 1.34$ , 95% CI [0.64, 2.04]). Conversely, P30 was not different from PR1 ( $P = 0.984$ ) or PR2 ( $P = 0.853$ ). Furthermore, MEP/ $M_{\text{MAX}}$  ratio at P0 was lower in the ILLUSION condition than in the TVR condition ( $2.87 \pm 1.39 \% M_{\text{MAX}}$ ,  $P < 0.001$ ,  $d_z = 0.68$ , 95% CI [0.12, 1.24]). The repeated measures ANOVA conducted on the MEP



**Figure 3. Perceptual and motor responses assessed during the vibration protocol under tonic vibration reflex and movement illusion conditions**

A, mean of responses obtained on the three VAS at the first, third and fifth minute of the LV protocol for the TVR condition (red) and the ILLUSION condition (grey). For the Student's paired  $t$  test:  $###P < 0.001$ . B and C, EMG activity was assessed in the flexor carpi radialis (FCR) muscle (B) and extensor carpi radialis (ECR) muscle (C) both at rest ( $\text{RMS}_{\text{REST}}/M_{\text{MAX}}$ ; closed symbols) and during the 6 min application of local vibration ( $\text{RMS}_{\text{LV}}/M_{\text{MAX}}$ ; open symbols) under the TVR (red triangle) and ILLUSION (grey circle) conditions. In B, a participant has a data value outside the scale. Its individual value is indicated by a dotted line, and the precise value is displayed next to the corresponding mark. Repeated measures ANOVA revealed a significant *Condition*  $\times$  *Time* interaction. Difference between conditions:  $##P < 0.01$ ; difference within a condition:  $**P < 0.01$ . [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]



**Figure 4.** Changes in MEP, CMEP and the MEP/CMEP ratio for the vibrated FCR muscle in the tonic vibration reflex (red) and movement illusion (grey) conditions

A, representation of mean and individual motor-evoked potential (MEP) recorded on the flexor carpi radialis muscle (FCR, 15 participants) and expressed as a percentage of the maximal M-wave amplitude (% $M_{\text{max}}$ ). A 6 min LV protocol was performed in the TVR (red triangle) and ILLUSION (grey circle) conditions and measurements were taken 10 and 0 min before (PR1 and PR2, respectively) LV as well as 0 and 30 min (P0 and P30, respectively) after. B, the top panel shows typical MEP data obtained on FCR muscle at PR2 (black, also visible in Fig. 1 for the ILLUSION condition), P0 (light colour) and P30 (dark colour) for both conditions. The lower panel shows the MEP variable

at P0 and P30, expressed relative to PR2 (box: 25th to 75th percentile range, whiskers: minimum and maximum values, cross: mean, line: median). *C* and *D*, data for cervicomedullary motor-evoked potential (CMEP) recorded on the FCR muscle (13 participants). *E* and *F*, data for MEP/CMEP ratios of the FCR muscle (13 participants). Note that the amplitude scales of typical data are different depending on the condition and measurements. In the presence of a significant *Condition*  $\times$  *Time* interaction to the repeated measures ANOVA, significant difference within a same condition: \*, significant difference between the two conditions: #. \*# $P < 0.05$ ; \*\* $P < 0.01$ ; \*\*\*/### $P < 0.001$ . In the presence of a significant *Condition* effect,  $^{\S}$  indicates a significant difference between the two conditions.  $^{\S\S\S}P < 0.001$ . In the presence of a significant *Time* effect,  $^{\S}$  indicates a significant difference between P0 and P30, irrespective of the LV protocol used.  $^{\S}P < 0.05$ . [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

variable at P0 and P30, expressed relative to PR2, showed a significant *Condition*  $\times$  *Time* interaction ( $F_{1,14} = 5.163$ ,  $P = 0.0394$ ,  $\eta^2 = 0.269$ , Fig. 4B). Expressed relative to PR2, P0 in the ILLUSION condition ( $74.86 \pm 17.2$  %PR2) was significantly different from P30 in the same condition ( $115.4 \pm 37.44$  %PR2), with a mean difference of  $40.55 \pm 34.61$  %PR2 ( $P < 0.001$ ,  $d_z = 1.34$ , 95% CI [0.64, 2.04]). Additionally, P0 was different between the ILLUSION condition and the TVR condition ( $100.31 \pm 27.88$  %PR2), with a mean difference of  $-25.45 \pm 33.51$  ( $P = 0.00992$ ,  $d_z = 0.76$ , 95% CI [0.18, 1.33]).

The repeated measures ANOVA conducted on CMEP/ $M_{\text{MAX}}$  revealed a significant *Condition*  $\times$  *Time* interaction ( $F_{1,7,20.2} = 5.783$ ,  $P = 0.0135$ ,  $\eta^2 = 0.325$ , Fig. 4C). The amplitude of the responses obtained at PR1 and PR2 was unchanged within each condition (all  $P > 0.923$ ). However, CMEP/ $M_{\text{MAX}}$  ratio differed between conditions at either PR1 (TVR:  $5.29 \pm 2.49$  % $M_{\text{MAX}}$ , ILLUSION:  $3.94 \pm 1.35$  % $M_{\text{MAX}}$ ,  $P < 0.001$ ,  $d_z = 0.45$ , 95% CI [-0.12, 1.02]) and PR2 (TVR:  $5.17 \pm 2.19$  % $M_{\text{MAX}}$ , ILLUSION:  $4.14 \pm 1.36$  % $M_{\text{MAX}}$ ,  $P = 0.00597$ ,  $d_z = 0.34$ , 95% CI [-0.22, 0.90]). In the TVR condition, a significant decrease in CMEP/ $M_{\text{MAX}}$  was observed at P0 ( $4.56 \pm 2.51$  % $M_{\text{MAX}}$ ) compared to PR1 ( $P = 0.00326$ ,  $d_z = 1.12$ , 95% CI [0.43, 1.81]) and PR2 ( $P = 0.0106$ ,  $d_z = 0.86$ , 95% CI [0.23, 1.50]), but not compared to P30 ( $4.87 \pm 1.97$  % $M_{\text{MAX}}$ ,  $P = 0.265$ ,  $d_z = 0.39$ , 95% CI [-0.17, 0.96]). Concerning the CMEP/ $M_{\text{MAX}}$  ratio in the ILLUSION condition, P30 ( $4.52 \pm 1.25$  % $M_{\text{MAX}}$ ) was increased compared to P0 ( $4 \pm 1.58$  % $M_{\text{MAX}}$ ,  $P = 0.0215$ ,

$d_z = 0.58$ , 95% CI [-0.01, 1.16]) and PR1 ( $3.94 \pm 1.35$  % $M_{\text{MAX}}$ ,  $P = 0.0272$ ,  $d_z = 0.6$ , 95% CI [0.01, 1.19]). Note that, compared with PR2, the P30 value has not increased significantly ( $P = 0.346$ ,  $d_z = 0.48$ , 95% CI [-0.10, 1.05]). The repeated measures ANOVA conducted on the CMEP variable at P0 and P30, expressed relative to PR2, showed a significant effect of *Condition* ( $F_{1,12} = 24.545$ ,  $P < 0.001$ ,  $\eta^2 = 0.67$ , Fig. 4D) and *Time* ( $F_{1,12} = 4.836$ ,  $P = 0.0482$ ,  $\eta^2 = 0.29$ ). Expressed relative to PR2, the TVR condition ( $90.44 \pm 7.42$  %PR2) was significantly different across *Time* from the ILLUSION condition ( $103.93 \pm 13.13$  %PR2), with a mean difference of  $13.49 \pm 10.64$  %PR2 between conditions ( $P < 0.001$ ,  $d_z = 1.374$ , 95% CI [0.58, 2.06]). Moreover, P0 ( $90.87 \pm 13.29$  %PR2) was significantly different across conditions compared to P30 ( $103.51 \pm 13.57$  %PR2), with a mean difference of  $12.64 \pm 19.49$  %PR2 ( $P = 0.0482$ ,  $d_z = 0.63$ , 95% CI [0.03, 1.23]).

Regarding the MEP/CMEP ratio, the repeated measures ANOVA indicated a significant *Condition*  $\times$  *Time* interaction ( $F_{3,36} = 4.879$ ,  $P = 0.00601$ ,  $\eta^2 = 0.29$ , Fig. 4E). Regarding PR1 and PR2 performed before the LV protocols, no difference was observed within each condition or between the two conditions (all  $P > 0.884$ ). In the TVR condition, no comparison was significant (all  $P > 0.197$ ). Concerning the ILLUSION condition, only P0 ( $0.51 \pm 0.21$ ) was significantly lower than PR1 ( $0.75 \pm 0.37$ ,  $P = 0.00775$ ,  $d_z = 1.29$ , 95% CI [0.55, 2.03]) with no difference from PR2 despite a large ES ( $0.66 \pm 0.27$ ,  $P = 0.146$ ,  $d_z = 1.12$ , 95% CI [0.43, 1.82]). Moreover, P0 in the ILLUSION condition

**Table 1.** Mean ( $\pm$  SD) maximal muscular response amplitudes ( $M_{\text{MAX}}$ , 15 participants) for the FCR and ECR muscle

						ANOVA ( $F/P$ values/ $\eta^2$ )		
		PR1	PR2	P0	P30	C	T	C $\times$ T
FCR (mV)	TVR	$8.2 \pm 2.8$	$8.1 \pm 3$	$8.3 \pm 3$	$8.2 \pm 3$	$F_{1,14} = 2.607$	$F_{1,4,19.5} = 0.486$	$F_{2,27.6} = 2.259$
	ILL	$9.6 \pm 2.9$	$9.7 \pm 3$	$9.5 \pm 2.8$	$9.3 \pm 2.7$	0.129/0.157	0.555/0.034	0.124/0.139
ECR (mV)	TVR	$7.7 \pm 2.5$	$7.5 \pm 2.4$	$7.6 \pm 2.4$	$7.4 \pm 2.4$	$F_{1,14} = 0.511$	$F_{1,4,19.3} = 0.604$	$F_{1,3,18.2} = 0.351$
	ILL	$7.9 \pm 3.4$	$8 \pm 3.5$	$8 \pm 3.3$	$7.8 \pm 3.1$	0.487/0.035	0.497/0.041	0.618/0.024

Note: Data were recorded before (PR1 and PR2) and after the end of the 6 min local vibration (P0 and P30) in the TVR and ILLUSION conditions. Results of the two-way repeated measures ANOVA are reported for each effect.

Abbreviations: C  $\times$  T, interaction between *Condition* and *Time*; C, *Condition* effect (i.e. TVR, ILLUSION); ECR, extensor carpi radialis muscle; FCR, flexor carpi radialis muscle; ILL, illusion condition; T, *Time* effect (i.e. PR1, PR2, P0, P30); TVR, tonic vibration reflex condition.



was lower than in the TVR condition ( $0.72 \pm 0.35$ ,  $P = 0.0367$ ,  $d_z = 0.51$ , 95% CI  $[-0.07, 1.08]$ ). The repeated measures ANOVA conducted on the MEP/CMEP ratio at P0 and P30, expressed relative to PR2, showed a significant effect of *Condition* ( $F_{1,12} = 6.202$ ,  $P = 0.0284$ ,  $\eta^2 = 0.34$ , Fig. 4F) and *Time* ( $F_{1,12} = 5.115$ ,  $P = 0.0431$ ,  $\eta^2 = 0.299$ ). Expressed relative to PR2, P0 ( $97.92 \pm 26.44$  %PR2) was different across conditions compared to P30 ( $117.45 \pm 24.49$  %PR2), with a mean difference of  $19.53 \pm 38.04$  %PR2 ( $P = 0.0432$ ,  $d_z = 0.61$ , 95% CI  $[0.01, 1.20]$ ). Moreover, the TVR condition ( $122.04 \pm 29.88$  %PR2) was different from the ILLUSION condition ( $93.33 \pm 27.77$  %PR2), with a mean difference of  $28.71 \pm 46.67$  %PR2 ( $P = 0.0286$ ,  $d_z = 0.89$ , 95% CI  $[0.25, 1.54]$ ).

### Antagonist ECR muscle

As shown in Table 1, no change was observed for the  $M_{\text{MAX}}$  of the ECR muscle. Concerning MEP/ $M_{\text{MAX}}$ , the repeated measures ANOVA showed a significant *Condition*  $\times$  *Time* interaction ( $F_{1,72,24.2} = 3.655$ ,  $P = 0.0468$ ,  $\eta^2 = 0.207$ , Fig. 5A). Regarding PR1 and PR2 performed before the LV protocols, no difference was observed within each condition or between the two conditions (all  $P > 0.740$ ). In the TVR condition, a significant increase was observed at P30 ( $7.43 \pm 4.66$  % $M_{\text{MAX}}$ ) compared to PR2 ( $5.33 \pm 3.54$  % $M_{\text{MAX}}$ ,  $P = 0.0189$ ,  $d_z = 1.25$ , 95% CI  $[0.57, 1.92]$ ) and P0 ( $4.96 \pm 2.89$  % $M_{\text{MAX}}$ ,  $P = 0.00884$ ,  $d_z = 1.08$ , 95% CI  $[0.44, 1.72]$ ). Despite a medium ES, this difference was not present between PR1 and P30 ( $5.79 \pm 4.06$  % $M_{\text{MAX}}$ ,  $P = 0.0579$ ,  $d_z = 0.68$ , 95% CI  $[0.12, 1.24]$ ). P0 was not different from PR1 ( $P = 0.996$ ) or PR2 ( $P = 1$ ). Furthermore, the MEP/ $M_{\text{MAX}}$  ratio at P30 was higher in the TVR condition than in the ILLUSION condition ( $5.56 \pm 4.13$  % $M_{\text{MAX}}$ ,  $P = 0.0348$ ,  $d_z = 0.43$ , 95% CI  $[-0.10, 0.96]$ , Fig. 5A). Concerning MEP/ $M_{\text{MAX}}$  in the ILLUSION condition, no change was observed (all  $P > 0.381$ ). The repeated measures ANOVA conducted on the MEP variable at P0 and P30, expressed relative to PR2, showed a significant *Condition*  $\times$  *Time* interaction ( $F_{1,14} = 19.967$ ,  $P < 0.001$ ,  $\eta^2 = 0.588$ , 95% CI  $[0.04, 1.14]$ , Fig. 5B). Expressed relative to PR2, P0 in the TVR condition ( $101.31 \pm 29.61$  %PR2) was different compared to P30 in the TVR condition ( $141.31 \pm 34.71$  %PR2, mean difference =  $40 \pm 37.01$  %PR2,  $P < 0.001$ ,  $d_z = 1.08$ , 95% CI  $[0.44, 1.72]$ ) as well as from P0 in the ILLUSION condition ( $124.19 \pm 35.13$  %PR2, mean difference:  $22.88 \pm 42.72$ ,  $P = 0.0351$ ,  $d_z = 0.57$ , 95% CI  $[0.02, 1.12]$ ). Other comparisons were not significant ( $P > 0.183$ ).

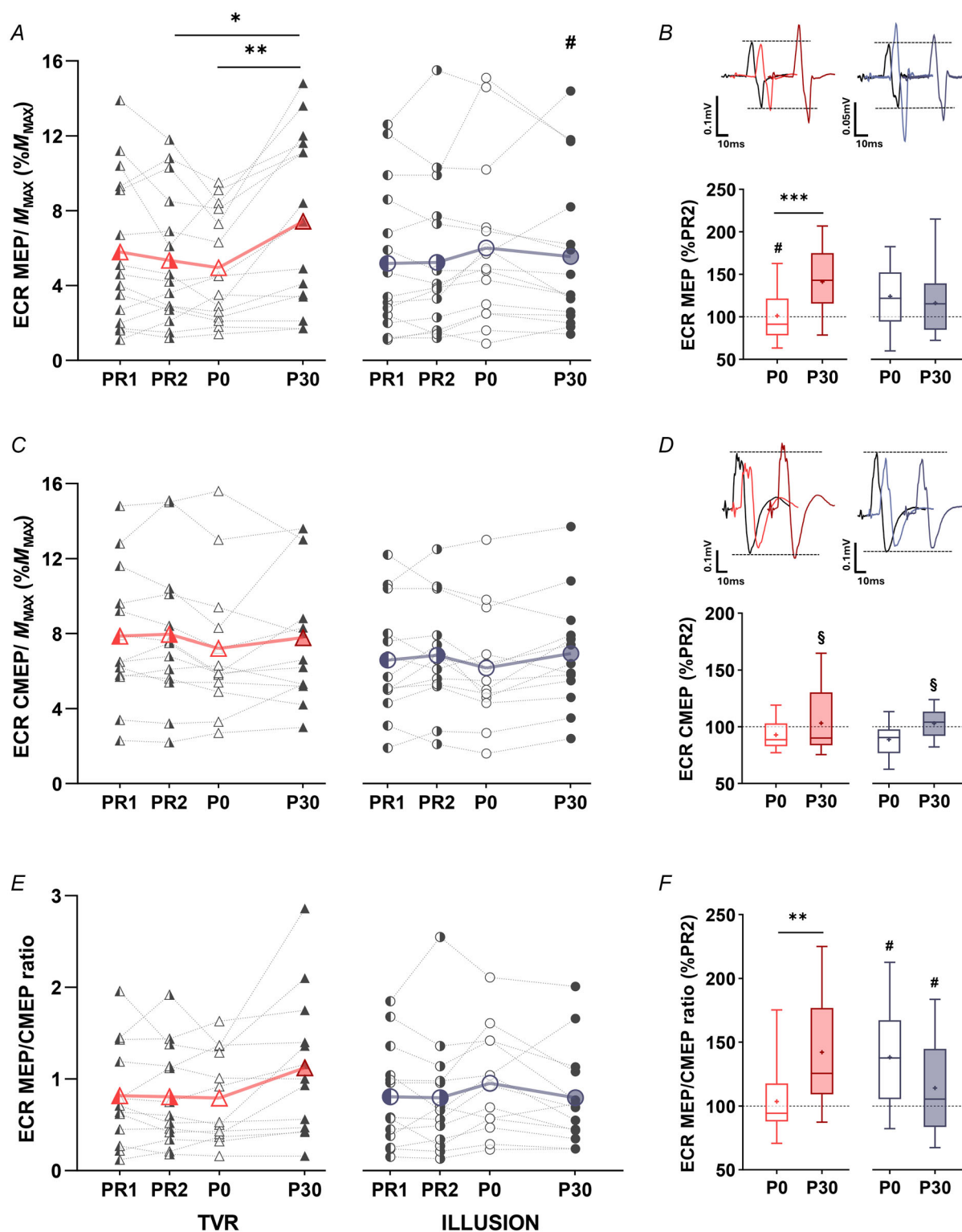
The repeated measures ANOVA conducted on CMEP/ $M_{\text{MAX}}$  revealed only a significant effect of

*Time* ( $F_{3,36} = 0.44$ ,  $P = 0.726$ ,  $\eta^2 = 0.035$ , Fig. 5C). Independent of the vibration condition used, the amplitude of the ratios obtained at PR1 was unchanged compared to PR2 ( $P = 0.936$ ). P0 ( $6.69 \pm 3.03$  % $M_{\text{MAX}}$ ) was not different from PR1 ( $7.24 \pm 2.97$  % $M_{\text{MAX}}$ ,  $P = 0.174$ ,  $d_z = 0.47$ , 95% CI  $[-0.11, 1.04]$ ) or from PR2 ( $7.4 \pm 3.01$  % $M_{\text{MAX}}$ ,  $P = 0.0513$ ,  $d_z = 0.90$ , 95% CI  $[0.26, 1.55]$ ) despite a large ES. Moreover, P0 was lower than P30 ( $7.35 \pm 2.87$  % $M_{\text{MAX}}$ ,  $P = 0.0234$ ,  $d_z = 0.89$ , 95% CI  $[0.25, 1.53]$ ). Finally, P30 was no different from PR1 ( $P = 0.796$ ) or PR2 ( $P = 0.987$ ). The repeated measures ANOVA conducted on the CMEP variable at P0 and P30, expressed relative to PR2, showed a significant effect of *Time* ( $F_{1,12} = 10.308$ ,  $P = 0.00748$ ,  $\eta^2 = 0.46$ , Fig. 5D). Expressed relative to PR2, P0 ( $90.84 \pm 10.64$  %PR2) was different across *Condition* compared to P30 ( $103.17 \pm 13.97$  %PR2), with a mean difference of  $12.32 \pm 14.52$  %PR2 ( $P = 0.00765$ ,  $d_z = 0.90$ , 95% CI  $[0.26, 1.54]$ ).

Regarding the MEP/CMEP ratio, the repeated measures ANOVA indicated a significant *Condition*  $\times$  *Time* interaction ( $F_{1,7,20.3} = 3.977$ ,  $P = 0.0407$ ,  $\eta^2 = 0.25$ , Fig. 5E). Regarding PR1 and PR2 performed before the LV protocols, no difference was observed within each condition or between the two conditions (all  $P > 0.998$ ). *Post hoc* analysis revealed no significant difference between pairs in either the TVR (all  $P > 0.0739$ ) or ILLUSION (all  $P > 0.133$ ) conditions. The repeated measures ANOVA conducted on the MEP/CMEP ratio at P0 and P30, expressed relative to PR2, showed a significant *Condition*  $\times$  *Time* interaction ( $F_{1,12} = 24.207$ ,  $P < 0.001$ ,  $\eta^2 = 0.669$ , Fig. 5F). Expressed relative to PR2, P0 in the TVR condition ( $103.48 \pm 26.35$  %PR2) was different from P30 in the same condition ( $142.17 \pm 443.79$  %PR2, mean difference =  $38.68 \pm 46.99$  %PR2,  $P = 0.00642$ ,  $d_z = 0.85$ , 95% CI  $[0.21, 1.48]$ ) as well as from P0 in the ILLUSION condition ( $138.32 \pm 0.38$  %PR2, mean difference =  $34.84 \pm 38.27$  %PR2,  $P = 0.0108$ ,  $d_z = 0.99$ , 95% CI  $[0.32, 1.65]$ ). Moreover, P30 in the TVR condition was different from P30 in the ILLUSION condition ( $114.05 \pm 0.37$  %PR2, mean difference =  $28.12 \pm 62.28$  %PR2,  $P = 0.0395$ ,  $d_z = 0.46$ , 95% CI  $[-0.11, 1.03]$ ). Finally, there was no significant difference between P0 and P30 in the ILLUSION condition despite a medium ES ( $P = 0.0669$ ,  $d_z = 0.64$ , 95% CI  $[0.04, 1.23]$ ).

### Repeated measures correlations

Repeated measures correlations were performed on each variable (i.e. MEP, CMEP and MEP/CMEP ratio) to compare P0 expressed relative to PR2 between the vibrated muscle and the antagonist muscle, independently of the condition used. Expressed relative to PR2, the modification observed for the MEP/CMEP ratios



**Figure 5. Changes in MEP, CMEP and the MEP/CMEP ratio for the antagonist ECR muscle in the tonic vibration reflex (red) and movement illusion (grey) conditions**

A, representation of mean and individual motor-evoked potential (MEP) recorded on the extensor carpi radialis muscle (ECR, 15 participants) and expressed as a percentage of the maximal M-wave amplitude (% $M_{\text{MAX}}$ ). A 6 min LV protocol was performed in the TVR (red triangle) and ILLUSION (grey circle) conditions and measurements were taken 10 and 0 min before (PR1 and PR2, respectively) LV as well as 0 and 30 min (P0 and P30, respectively) after. B, the top panel shows typical MEP data obtained on ECR muscle at PR2 (black, also visible in Fig. 1 for the ILLUSION condition), P0 (light colour) and P30 (dark colour) for both conditions. The lower panel shows the MEP variable

at P0 and P30, expressed relative to PR2 (box: 25th to 75th percentile range, whiskers: minimum and maximum values, cross: mean, line: median). C and D, data for cervicomedullary motor-evoked potential (CMEP) recorded on the ECR muscle (13 participants). E and F, data for MEP/CMEP ratios of the ECR muscle (13 participants). Note that the amplitude scales of typical data are different depending on the condition and measurements. In the presence of a significant *Condition*  $\times$  *Time* interaction to the repeated measures ANOVA, significant difference within a same condition: \*, significant difference between the two conditions: #. \* $P < 0.05$ ; \*\* $P < 0.01$ ; \*\*\* $P < 0.001$ . In the presence of a significant *Time* effect to the repeated measures ANOVA, § indicates a significant difference between P0 and P30, irrespective of the LV protocol used. § $P < 0.05$ . [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

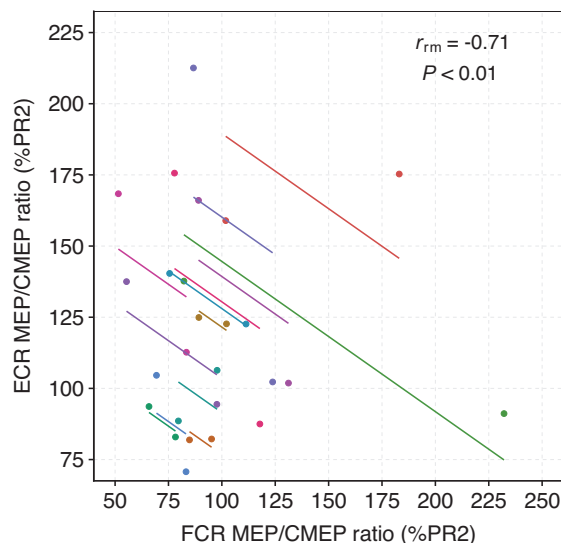
of the FCR muscle were negatively correlated with those observed for the ECR antagonist muscle ( $r_{rm} (12) = -0.71$ , 95% CI  $[-0.9, -0.284]$ ,  $P = 0.005$ , Fig. 6). In contrast, neither MEP ( $r_{rm} (14) = -0.25$ , 95% CI  $[-0.663, 0.282]$ ,  $P = 0.354$ ) nor CMEP modifications ( $r_{rm} (12) = -0.71$ , 95% CI  $[-0.408, 0.635]$ ,  $P = 0.592$ ) were correlated between the two muscles.

### Control experiment

**EMG activity.** The EMG signal recorded during the SVC ( $RMS_{SVC.CT}$ ) represented  $0.96 \pm 0.61\%$  of the maximal activity recorded during the MVIC ( $RMS_{MVIC.CT}$ ) for the FCR muscle. The repeated measures ANOVA conducted on EMG signal recorded for the FCR muscle presented a significant *Time* effect ( $F_{1,16} = 21.252$ ,  $P < 0.001$ ,  $\eta^2 = 0.727$ ; Table 2). *Post hoc* analysis indicated that  $RMS_{REST.CT}/M_{MAX}$  recorded during the control experiment was lower than both the EMG

signal recorded during sustained voluntary contraction ( $RMS_{SVC.CT}/M_{MAX}$ ) in the control experiment ( $P < 0.001$ ,  $d_z = 1.67$ , 95% CI  $[0.66, 2.68]$ ) and the EMG signal recorded during LV ( $RMS_{LV.TVR}/M_{MAX}$ ) in the TVR condition of the main experiment ( $P < 0.001$ ,  $d_z = 0.677$ , 95% CI  $[-0.05, 1.40]$ ). In contrast, there was no difference between  $RMS_{SVC.CT}/M_{MAX}$  and  $RMS_{LV}/M_{MAX}$  ( $P = 0.444$ ,  $d_z = 0.1$ , 95% CI  $[-0.55, 0.75]$ ).

There was a significant *Time* effect concerning EMG signal recorded for the ECR muscle ( $F_{0.62,9.98} = 5.259$ ,  $P = 0.039$ ,  $\eta^2 = 0.397$ ; Table 2). *Post hoc* analysis indicated that  $RMS_{LV.TVR}/M_{MAX}$  recorded during LV in the TVR condition of the main experiment was lower than  $RMS_{SVC.CT}/M_{MAX}$  recorded during the sustained voluntary contraction in the control experiment ( $P = 0.0157$ ,  $d_z = 1.01$ , 95% CI  $[0.21, 1.81]$ ). Other comparisons were not significant ( $P > 0.104$ ; Table 2). Repeated measures ANOVAs conducted on  $M_{MAX}$ ,  $MEP/M_{MAX}$ ,  $CMEP/M_{MAX}$  and  $MEP/CMEP$  ratio revealed no significant effect of *Time* for either muscle (Table 3).



**Figure 6.** Repeated-measures correlations (rmcorr) between the MEP/CMEP ratio at P0 expressed relative to PR2 for the flexor carpi radialis muscle and the extensor carpi radialis muscle, independently of the vibration condition performed. Two similar colour dots represent each participant's data from each condition (i.e. TVR and ILLUSION), and coloured lines show rmcorr fits for each participant. The result shown on the graph was obtained by conducting statistical analysis on the log-transformed data. [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

### Discussion

This study aimed to compare the conditions of LV application on the corticospinal and alpha motoneuron excitability of the vibrated and antagonist muscles. To this end, LV was applied for 6 min to the FCR muscle in a condition favouring either the appearance of the TVR or the illusion of movement. Regarding the condition of LV application, our results confirm that interference between visual and proprioceptive afferents favours the presence of TVR. In contrast, visual control over the EMG activity of the vibrated muscle and not over the vibrated limb favours the latter's relaxation and the presence of illusion. Overall, we observe a reduction in CMEP for the vibrated muscle in the TVR condition. In contrast, a reduction in MEP is observed for the same muscle in the illusion condition, with no concomitant change in CMEP. Thus, afferent feedback appears not to have the same impact at spinal and cortical levels, depending on the condition in which the LV is applied. Finally, the voluntary contraction generating EMG activity on the FCR muscle, which was similar to that observed during the application of LV in the TVR condition, had no impact on the spinal and cortical excitability of the FCR and ECR

**Table 2.** Mean FCR and ECR muscle EMG activity ( $\pm$  SD) in nine participants at rest, during voluntary contraction and during local vibration (TVR condition of main experiment)

Muscle	Variable	REST.CT	SVC.CT	LV.TVR	ANOVA ( $F/P/\eta^2$ )
FCR	RMS/ $M_{\text{MAX}}$ (% $M_{\text{MAX}}$ )	$0.06 \pm 0.03^{\text{b,c}}$	$0.28 \pm 0.12^{\text{a}}$	$0.26 \pm 0.29^{\text{a}}$	$F_{2,16} = 21.252 / <0.001 / 0.727$
ECR	RMS/ $M_{\text{MAX}}$ (% $M_{\text{MAX}}$ )	$0.04 \pm 0.02$	$0.07 \pm 0.05$	$0.03 \pm 0.02^{\text{b}}$	$F_{1,25,9,98} = 5.259 / 0.039 / 0.397$

Note: The results of the one-way repeated measures ANOVA are reported.

Abbreviations: ECR, extensor carpi radialis muscle; FCR, flexor carpi radialis muscle; LV.TVR, EMG activity recorded during local vibration in the tonic vibration reflex (TVR) condition of the main experiment; REST.CT, EMG activity recorded at rest in the control experiment; SVC.CT, EMG activity recorded during the submaximal voluntary contraction (SVC) in the control experiment.

Significant  $P$  values are presented in bold. In the presence of a significant *Time* effect, letters indicate significant differences with <sup>a</sup>REST.CT, <sup>b</sup>SVC.CT and <sup>c</sup>LV.TVR.

**Table 3.** Mean ( $\pm$  SD) maximal muscular response amplitudes ( $M_{\text{MAX}}$ ), motor-evoked potential (MEP), cervico-medullary motor-evoked potential (CMEP) and MEP/CMEP ratio for the FCR and ECR muscle (nine participants)

Muscle	Variable	PR2	P0	P30	ANOVA ( $F/P/\eta^2$ )
FCR	$M_{\text{MAX}}$ (mV)	$7.48 \pm 2.53$	$7.95 \pm 3.14$	$7.55 \pm 2.62$	$F_{1,06,8,51} = 0.862 / 0.386 / 0.097$
	MEP (% $M_{\text{MAX}}$ )	$3.12 \pm 1.29$	$3.13 \pm 1.47$	$3.63 \pm 1.72$	$F_{2,16} = 1.079 / 0.363 / 0.119$
	CMEP (% $M_{\text{MAX}}$ )	$4.44 \pm 2.95$	$4.68 \pm 3.48$	$4.87 \pm 3.36$	$F_{2,16} = 2.379 / 0.125 / 0.229$
	MEP/CMEP	$0.93 \pm 0.61$	$0.89 \pm 0.58$	$0.96 \pm 0.57$	$F_{2,16} = 0.233 / 0.794 / 0.028$
ECR	$M_{\text{MAX}}$ (mV)	$8.14 \pm 3.35$	$8.4 \pm 3.8$	$8.5 \pm 3.51$	$F_{2,16} = 1.278 / 0.306 / 0.138$
	MEP (% $M_{\text{MAX}}$ )	$4.11 \pm 2.57$	$4.16 \pm 2.29$	$4.92 \pm 3.61$	$F_{2,16} = 2.111 / 0.154 / 0.209$
	CMEP (% $M_{\text{MAX}}$ )	$4.43 \pm 2.88$	$4.12 \pm 2.48$	$4.56 \pm 2.51$	$F_{1,21,9,67} = 0.945 / 0.374 / 0.106$
	MEP/CMEP	$1.01 \pm 0.38$	$1.2 \pm 0.95$	$1.19 \pm 0.82$	$F_{2,16} = 0.266 / 0.770 / 0.032$

Note: Measurements were taken just before (PR2) the 6 min submaximal voluntary contraction (SVC), as well as 0 and 30 min after its cessation (P0 and P30, respectively). The results of the one-way repeated measures ANOVA are reported.

Abbreviations: ECR, extensor carpi radialis muscle; FCR, flexor carpi radialis muscle.

muscles. This result rules out the hypothesis that changes in excitability are induced by motoneuron output alone and therefore confirms the key role of LV in the effects observed in this study. Together, these findings suggest that the conditions under which LV is applied impact the neural network differently and that future research should control, measure and report the different perceptual and motor responses observed during LV to facilitate interpretation of results.

### LV condition

Our results confirm that TVR or movement illusion can be obtained with identical vibration parameters (i.e. vibrator positioned on the tendon, 80 Hz frequency, 2 mm amplitude) and therefore with a presumed identical stimulation of the muscle spindles. Thus, modifications to the control process of sensory information from muscle spindles result from the LV application condition and the participant's instructions. In the TVR condition, the instruction to focus visual attention on the vibrated arm results in a discrepancy between visual (i.e. no movement) and muscular afferents (i.e. wrist extension). In such

cases, the parietal cortex moderates conflicting afferents in favour of visual afferents to maintain a coherent body image (Hagura et al., 2007; van Beers et al., 1996). Consequently, the movement illusion was reduced in the TVR condition due to the decreased weight of muscle afferents in sensory information processing. It should be noted, however, that the illusion of movement was not totally suppressed despite the sensory conflict (Hagura et al., 2007; Seizova-Cajic & Azzì, 2011). Moreover, an increase in EMG activity in the vibrated muscle was observed, resulting from the activation of alpha motoneurons by the projection of primary afferents (Roll et al., 1980). Compared with the TVR condition, two reasons may explain the increase in the illusion of movement and the relaxation of the vibrated muscle in the ILLUSION condition. First, in the absence of visual afferents on the vibrated limb, only muscle afferents are used by the parietal cortex to define the exact position of the limb in space (Goodwin et al., 1972; Roll & Vedel, 1982). Second, the visual focus on the EMG activity of the vibrated muscle facilitates the voluntary suppression of the TVR, due to the control exerted by descending pathways on the involuntary alpha motoneuron activation by primary afferents (Burke et al., 1976b; Gillies et al.,



1971). The absence of AVR in our study may be due to the instructed and controlled muscle relaxation for the vibrated muscle and/or not being in an optimal condition due to open eyes during the LV protocol (Calvin-Figuère et al., 1999; Feldman & Latash, 1982; Kito et al., 2006).

### Corticospinal excitability of the vibrated muscle

Corticospinal excitability, estimated using MEP, evolved differently depending on the LV application condition, reflecting current literature variability. In the TVR condition, MEP amplitude remained unchanged immediately and 30 min after the LV protocol. This lack of change after stopping the protocol has been previously observed in studies that used prolonged LV durations (ranging from 10 to 60 min) without specifying the presence or absence of an illusion (Kennouche et al., 2022; Lapole et al., 2012; Marconi et al., 2008; Pfenninger et al., 2023; Rosenkranz & Rothwell, 2006). In contrast, the ILLUSION condition led to a significant and temporary reduction in MEP of the vibrated muscle (i.e. only at P0), in agreement with the results observed for prolonged durations of LV performed under the same conditions (Amiez et al., 2024; Steyvers, Levin, van Baelen et al., 2003). Moreover, movement illusion is also known to reduce MEP amplitude during LV (Mancheva et al., 2017; Naito et al., 2002), which contrasts with the increase usually observed in the absence of illusion (Claus et al., 1988; Kossev et al., 1999; Lapole et al., 2015; Rosenkranz & Rothwell, 2003; Siggekkow et al., 1999; Steyvers, Levin, Verschueren et al., 2003).

Since corticospinal excitability assessed by MEP also includes spinal excitability, we estimated alpha motoneuron excitability using CMEP to distinguish the cortical from the spinal origin of the changes. As expected, the TVR condition resulted in a noteworthy decrease in alpha motoneuron excitability ( $-11.8\%$  vs.  $-3.5\%$  in the ILLUSION condition). The absence of any alteration in CMEP amplitude in our control condition leads to the hypothesis that the reduction in intrinsic excitability of alpha motoneurons also depends on the way by which they are recruited (i.e. reflex vs. voluntary) and not only from their repeated activation. A similar reduction in motoneuron excitability has been previously observed for a similarly short LV duration on the FCR muscle, with a greater reduction in CMEP ( $\approx -29.1\%$ ) (Nito et al., 2021). However, the study by Nito and colleagues does not provide a detailed analysis of EMG activity during LV to confirm the absence of TVR. Moreover, their methodological choices, such as applying the vibration directly to the muscle and adjusting the LV 'intensity' by manual pressure applied on the vibrator maintained by the experimenter throughout the protocol, complicate direct comparison with our results.

Regardless, this lack of quantification and analysis of TVR appears, to our knowledge, to be broadly applicable to all recent work that has measured the excitability of alpha motoneurons using CMEP or TMEP (Amiez et al., 2024; Kennouche et al., 2022; Nito et al., 2021; Pfenninger et al., 2023; Souron, Besson, McNeil et al., 2017, 2019). In our study, preventing involuntary motor unit recruitment in the ILLUSION condition preserved CMEP amplitude, suggesting that TVR is implicated in this reduction in alpha motoneuron excitability. Nonetheless, a decrease in CMEP or TMEP has already been observed for prolonged durations of LV (i.e. 30 min), regardless of whether the illusion was controlled or not (Amiez et al., 2024; Kennouche et al., 2022; Pfenninger et al., 2023). Methodological issues may explain this difference, including (1) a lack of TVR quantification for prolonged LV durations or (2) difficulty in maintaining an identical participant state throughout the protocol. Hence, a comparison of these two LV conditions for extended durations is necessary to better understand the independent effects of LV on corticospinal excitability (e.g. duration of application), from those arising from TVR or movement illusion.

Given the observed differences in MEP and CMEP direction and amplitude between conditions, it seems plausible that each condition induces a specific change in cortical excitability. In the TVR condition, we can assume that cortical excitability is increased since corticospinal excitability (i.e. MEP) remains unchanged despite the reduction in alpha motoneuron excitability (i.e. CMEP). However, although a rise in the MEP/CMEP ratio was observed for most participants at P0 and P30, our analysis revealed no substantial differences from the baseline for the vibrated muscle. The LV duration used in this study was potentially insufficient to increase cortical excitability, compared with the results obtained for 30 min (Amiez et al., 2024; Pfenninger et al., 2023). Interestingly, a decrease in cortical excitability is observed in the ILLUSION condition (i.e. MEP reduction despite no CMEP changes), as confirmed by the post-LV reduction in the MEP/CMEP ratio, and by the differential evolution of the ratio between the two conditions. However, the measurements conducted in this study were not intended to explore changes in the excitation/inhibition balance within cortical circuits. The hypothesis of strengthening intracortical inhibitory circuits after LV has been suggested several times, but the results are inconsistent (Christova et al., 2011; Marconi et al., 2008; Rosenkranz & Rothwell, 2006). Furthermore, these studies did not control the conditions of LV application, making interpretation of the results difficult. Another hypothesis could be a reduction in cortical excitability due to increased involvement of supraspinal circuits required for TVR inhibition (Burke et al., 1976b; Gillies et al., 1971).

### Antagonist muscle

Although measured in this study, it should be noted that the stimulation sites and intensities for MEP and CMEP were calibrated to the vibrated muscle. Consequently, the results for the antagonist muscle will be discussed briefly, which aligns with the limited research focused on the antagonist muscle. The TVR condition induced a delayed increase in MEP for the ECR muscle. This is consistent with the delayed increase in MEP of the tibialis anterior muscle observed after 60 min of LV on the soleus (Lapole et al., 2012). The positive effect of LV on this antagonist muscle could be masked when LV is stopped by reciprocal inhibition from the primary afferents of the vibrated muscle (Bertolasi et al., 1998). In contrast, the increased activation of motor areas in the presence of a movement illusion could explain the significant increase in antagonist muscle MEP at longer LV durations (i.e. 30 min), although the same effect was not observed in our study after only 6 min of vibration exposure (Amiez et al., 2024; Steyvers, Levin, van Baelen et al., 2003). This suggests that a certain amount of LV exposure duration is required to increase the corticospinal excitability of the antagonist muscle at the end of the protocol.

Furthermore, the difference in MEP change between the two conditions is not explained by an alpha motoneuron excitability change (i.e. CMEP) since only a time effect independent of the LV condition was observed in our study. Despite a large ES, the absence of a significant reduction in CMEP amplitude of the antagonist muscle between PR2 and P0 ( $P = 0.0513$ ,  $d_z = 0.90$ , 95% CI [0.26, 1.55]) does not confirm the reduction observed after 30 min of exposure under the LV condition inducing an illusion of movement (Amiez et al., 2024). Similarly to the results discussed above for the MEP, a dose–response effect could exist between the duration of LV application and changes in corticospinal and motoneuronal excitability, as has already been demonstrated for the H reflex (Abbruzzese et al., 2001; Nito et al., 2021). One hypothesis concerning the alpha motoneuron excitability reduction of the antagonist muscle could be a transient increase in the reciprocal inhibition exerted by the primary afferents of the vibrated muscle on the antagonist muscle via the inhibitory interneurons (Burke et al., 1976b; Baldissera et al., 1987; Orsatto et al., 2022). Although we cannot confirm a positive effect of LV on the cortical excitability of the antagonist muscle (MEP/CMEP ratio), the changes observed from baseline (%PR2) show that immediately after the LV protocol is stopped, cortical excitability is higher in the ILLUSION condition than in the TVR condition. Conversely, 30 min after the LV protocol was stopped, this effect is reversed, with higher cortical excitability in the TVR condition than in the ILLUSION condition.

As with the other measurements, a dose–response effect seems to be present for the antagonist muscle, since the increase in cortical excitability is observed for a 30 min duration of illusory LV (Amiez et al., 2024). Finally, the multiple correlation conducted on the MEP/CMEP ratio revealed a notable inverse relationship between agonist and antagonist muscle excitability across conditions. However, these findings should be interpreted cautiously in our study due to several limitations, including the initial MEP/CMEP ratio value (i.e. different from one) or the choice of stimulation intensities in favour of the vibrated muscle and not the antagonist muscle. Beyond these limitations, the results suggest that a significant modification in the excitability of one muscle after a brief LV protocol would not be accompanied by an equivalent modification in the antagonist muscle. Moreover, it is interesting to note that similar antagonistic behaviour has been observed in previous studies involving short-duration vibrations (Rosenkranz & Rothwell, 2003), paired associative stimulation (Stefan et al., 2000) and action observation (Borroni et al., 2005). This result highlights the need for further research into the intracortical mechanisms involved after prolonged exposure to LV. For future studies on this research topic, we recommend: (1) explicitly selecting LV application conditions to standardize the perceptual and motor responses to vibration between participants, and (2) measuring and evaluating these responses. The absence of either of these recommendations in future research could increase the lack of consensus observed in previous studies regarding intracortical inhibition after LV, as well as the distinction between responder and non-responder subjects (Mancheva et al., 2014; Pfenninger et al., 2024).

In conclusion, focusing the participant's visual attention on the vibrated limb or on the EMG activity of the vibrated muscle produces two different perceptual and motor responses for a supposedly identical stimulation of muscle afferents: a TVR in one case and an illusion of movement in the other. The corticospinal excitability of the vibrated muscle is more influenced by the spinal stage in the TVR condition. In contrast, in the case of movement illusion, the site of change appears to be cortical. Moreover, shifts in cortical excitability after LV are directly opposed for the vibrated and antagonist muscles. The effect of these two perceptual and motor responses on corticospinal excitability should be compared for prolonged durations of LV and chronic training. Although our measurements cannot explain all the physiological mechanisms involved in the two conditions, we demonstrate the importance of quantifying and reporting the perceptual and motor responses occurring during LV. This approach aims to reduce the variability of results and deepen our understanding of the LV effect on the neuromuscular system.

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## Additional information

### Data availability statement

The data supporting this study's findings are available from the corresponding author, N. Amiez, upon reasonable request.

### Competing interests

The authors have no competing interests or conflicts of interest related to this work.

### Author contributions

All authors contributed to the conception and design of the work. N.A. acquired and analysed the results. N.A. drafted the manuscript and plotted the figures. N.A., A.M. and C.P. contributed to the interpretation of the results and the drafting of the manuscript. All authors revised the manuscript critically for important intellectual content. All authors have approved the submitted manuscript's definitive version and agreed to be accountable for all aspects of the work in ensuring that questions related to the accuracy or integrity of any part of the work are appropriately investigated and resolved. All persons designated as authors qualify for authorship, and all those who qualify for authorship are listed.

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### Keywords

alpha motoneuron excitability, corticospinal excitability, local vibration, movement illusion, tonic vibration reflex

### Supporting information

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