**Chapter 8a: Supraspinal responses and spinal reflexes**

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**Abstracts:**

When vibration, induced by harmonic mechanical oscillations, is applied to the entire human body or individual segments and structures, various short- and long-term neural changes occur. This chapter presents an overview of vibration stimulus effects on the central nervous system. First, we address the modulatory impact of vibration on supraspinal level, e.g. on the excitability of the sensorimotor networks as well as on the intra- and inter-hemispheric cortical processes. Effects on neural conduction, motoneuron activation thresholds, facilitation and inhibition are highlighted. Second, we review the inhibitory and facilitatory effects of vibration on spinal level, e.g. on alpha-motoneuron pool excitability as well as on pre- and post-synaptic neural transmission. Combined, the findings from experiments in humans using focal or whole-body vibration suggest that vibration amplifies the acute and chronic neuromuscular responses achieved during low intensity exercise, such as enhanced strength and power, improved mobility and flexibility, balance and postural control. These effects can be used strategically during training and therapy and are particularly beneficial for the elderly and patients suffering from neuronal disorders.

**Keywords:** vibration exercise, spinal reflexes, cortical excitability, neuroplasticity, presynaptic inhibition

**6.1 The effects of the vibration stimulus on the neuromuscular system**

Vibration imparts mechanical oscillations into the human body and this has inspired the use of this physical modality both as a tool to study the sensorimotor connectivity and integration of the human neuromuscular system and as a stimulus with potential detrimental or beneficial effects on human health and performance (1). In contrast to occupational vibration, vibration exercise constitutes the performance of dynamic or static exercises while delivering sinusoidal oscillations to the body. Accelerations imparted into the human body at rest or during submaximal exercise elicit acute (2, 3) and chronic (4) neuromuscular adaptations and strength gains similar to traditional resistance training with high loads. Scientific evidence manifests that during vibration neuromuscular activity is increased compared to that seen during equivalent exercises performed without a vibratory stimulus (5, 6) in a dose-dependent manner.

The physiological mechanisms underlying the human body responses to the vibration stimulus are not fully understood, and the existing evidence with regard to the size and direction of evoked effects is equivocal (7).Yet, the interest in vibration exercise continues to grow. It has been promoted as a modality for augmented benefits from training for flexibility (30 Hz, (8)), power (10 Hz, (2)), dynamic and isometric strength (30–50 Hz, (9); 35 Hz, (3); 25–45 Hz, (10)); from rehabilitation and physical therapy for improved balance and mobility in elderly individuals (10 and 26 Hz, (11)) and patients with neurological conditions (1.0–4.4 Hz, (12); 20 Hz, (13)), for reduced nonspecific low back pain (14), falls and fracture rates in adults over 50 years of age (15) and improved bone turnover (16), for prevention of physical deconditioning due to prolonged immobilization (i.e. bedrest; 19–25 Hz (17); 18-26 Hz, (18)) and unloading (19). Recent evidence points to the potential of using focal muscle vibration (100 Hz) to induce long-term depression-like plasticity in specific spinal cord circuits related to the vibrated muscle (20). Thus, a complete understanding of the basic mechanisms underlying the effects of vibration and their dependence on the intervention characteristics and the exercise protocol may help to develop more effective protocols for vibration exercise.

The prevailing evidence attributes the enhanced neuromuscular activation and performance to the ability of the vibratory stimulus to influence the neural processes on both spinal and supraspinal levels of the human central nervous system (CNS, Figure 1A). The spinal circuitry is the first stage within the sensorimotor feedback loop for generating of fast and effective responses to proprioceptive input. Additionally, the direct input from muscle afferents, particularly from Ia afferents to the cerebral cortex (21), cortical motor areas (22) and the corticospinal projections (23) has been shown to contribute up to 30% of the central neural drive to the muscle(s) during activity (24) and thus, to play a significant role in motor control. In the following two subsections, the effects of vibration on the supraspinal and spinal neural pathways are discussed with reference to their functional relevance (7).

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Caption for Fig 1: Schematic diagram of the neuromuscular structures and pathways contributing to the neuromuscular responses to vibration exercise.

A – Vibration applied directly to a muscle activates the primary (Ia), the secondary (II) muscle receptors, the Golgi tendon organ (Ib) as well as the cutaneous and muscle metabo-nociceptors (III/IV). The resultant excitatory volley is transmitted along the homonymous afferent axons (blue solid lines with upward arrows) and reaches the spinal interneurons and motoneurons affiliated with the vibrated muscle via the dorsal root of the spinal cord. This volley also travels via the fasciculus gracilis nerve tract in the posterior spinal cord directly to the supraspinal structures of the CNS. The sensory input is projected via the thalamus to the contralateral somatosensory cortex where conscious sensation results. The posterior column-medial lemniscal pathway and the anterolateral spinothalamic pathway are the two main neural pathways connecting the sensory receptors and the cortex. Output from the sensory cortex is then conveyed to the motor cortex. The motor response, resulting from the changed excitability of the facilitatory and inhibitory interneurons and motor neurons in the primary motor cortex, is then transmitted via the direct pyramidal motor pathways (red dashed lines with downward arrows), which connect via nuclei in the spinal cord to the spinal motoneurons related to the vibrated muscle as well as that of its antagonist and their contralateral analogues. The nerve impulses then travel along the peripheral efferent axons (α and γ) to the muscle spindles causing muscle specific response to the vibratory stimulus. This response is presented as facilitated activation of the agonist and inhibited activation of the antagonist muscle.

B – When applied to the whole body, the vibratory stimulus activates the sensory receptors of both agonist and antagonist muscles bilaterally. Despite following the same principles for sensorimotor integration this application mode creates a much more complex sensory input to the respective spinal and supraspinal neural structures, resulting in a platform-type (e.g. vertical or side-alternating) specific differential neuromuscular response.

**6.2 Supraspinal effects**

First evidence for supraspinal effects of vibration comes from studies using application of 80-120 Hz vibration directly to muscles and/or tendons in the upper limb. It has been shown that the cortical brain areas receive direct proprioceptive information during focal vibration (blue afferent volleys; Figure 1A), in addition to the activation the primary (Ia) and, to a lesser extent, the secondary (II) and the Ib afferents from the Golgi tendon organs (25). Using electro-encephalography (EEG) to study the effects of vibration on the somatosensory evoked potentials, Munte et al. (26) have reported that vibration of different frequencies (40-80-160 Hz) delivered to forearm muscles evokes phasic cortical potentials with a highly lateralised component, i.e. originating from the primary sensory cortex, and a later focally distributed portion located in the central sulcus (Figure 1B) contralateral to the stimulated arm. The authors also observed negative evoked potentials that were symmetrically distributed over the fronto-central regions, which was interpreted as evidence for vibration-induced cortical activation beyond the primary sensory fields, most likely related to the kinesthetic phenomenon. As recently classified by Taylor et al. (27), muscle vibration induced kinesthetic illusion is of great interest as a tool for scientists in research on proprioception, for practitioners in rehabilitation of sensorimotor function and for creating of multisensory virtual environments. The taxonomy makes explicit distinctions between focal and global application mode, which induce different illusions and emphasize the impact of vibration on the sensorimotor interplay. The neuromuscular effects of focal vibration depend mostly on the stimulus frequency, amplitude and duration as well as on the properties and the state of the vibrated muscle (e.g. contraction level, fresh or fatigued), whereas during whole-body vibration contextual factors play additional role and cause sensory side effects.

Modulatory effects of single session focal muscle (28, 29), tendon and whole-body (30, 31) vibration on motor evoked potentials (MEPs) have been demonstrated using the technique of transcranial magnetic stimulation (TMS) combined with surface electromyography (EMG, Figure 2A). TMS is a non-invasive neurophysiological technique, which uses electromagnetic induction to generate an electric current across the scalp and skull to stimulate the neuronal networks in the brain. During the procedure, a magnetic coil is positioned at the head of the individual and aligned to the region of the motor cortex affiliated with the studied muscle(s) using anatomical landmarks (Figure 1B). Short-duration (typically 200μs pulse-width) single or multiple magnetic pulses of high intensity (up to 2T peak amplitude) and pre-defined inter-pulse intervals (between 1 - 200ms) are delivered to activate the neurons in the target brain area. Motoneuron activation by TMS evokes MEPs on the EMG signal recorded using surface electrodes positioned over the muscle belly. The peak-to-peak MEP amplitude and the minimal intensity of the single TMS pulse required to evoke appreciable MEP responses to 5-10 consecutive TMS pulses (called motor threshold), are the most frequently-used parameters to evaluate the excitability of the corticospinal pathways. Paired TMS pulses with short (< 7ms), medium (7-15ms) or long (50-200ms) inter-pulse intervals are used to explore inhibitory and facilitatory intracortical networks. Two TMS coils can be used simultaneously to deliver pulses at the synonymous points of the motor cortex within each hemisphere in order to explore inter-hemispheric inhibition (or transcallosal inhibition). The EMG responses together with the additional force (superimposed twitch) evoked by TMS during exercise provide invaluable information about the dynamics of the voluntary muscle activation and the excitability of the corticospinal and intracortical pathways to the vibrated muscles.

Focal muscle vibration can acutely modulate the afferent input to the CNS and induces neuroplastic changes on cortical, subcortical and spinal levels that can last up to several hours. Modulatory effects of focal vibration applied to m. abductor pollicis brevis for 15min at 80 Hz were observed on the three main intracortical mechanisms for sensorimotor integration - decreased short-latency and long-latency afferent inhibition and increased afferent facilitation, which suggest that projections from the somatosensory cortex are involved in the modulation of motor cortical excitability during muscle vibration (32). Experimentally, these modulatory effects have been evidenced by changes in the MEP peak-to-peak amplitudes as illustrated in Figure 2B. Vibration has been shown to affect the excitability of the intracortical and corticospinal neural pathways to both vibrated (excitatory effects, (28)) and non-vibrated (inhibitory effects, (33) antagonistic muscle groups. Experimentally, excitatory neural effects are confirmed by reduced motor threshold, increased MEP amplitude and total area as well as shortened MEP latency and silent period (29, 30, 34). Similar to the effects of prolonged exercise, the facilitatory effects of focal vibration (80 Hz) on extensor carpi radialis muscle activation are shown to be accompanied by inhibition of the cortical output to the antagonistic muscle (35) and to the non-vibrated contralateral antagonist muscle (29, 34). Most likely the vibration-induced interhemispheric inhibition takes place via the well-known transcallosal pathways (35). The potential of using muscle vibration for inducing lasting neuroplasticity has been long recognised as a powerful tool to assist rehabilitation of neurological disorders and injuries.

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Caption for Fig 2: Illustration of the neuro-mechanical signals recorded using surface electromyography (EMG) and dynamometry (force) in response to a single pulse transcranial magnetic stimulation (TMS) of the motor cortex area related to m. tibialis anterior (TA).

A - EMG and force signal parameters most frequently extracted when using the TMS technique to quantify the effects of an intervention on supraspinal excitability by measuring the changes in: corticospinal excitability (pre-stimulation mean voluntary muscle EMG activity, MEP peak-to-peak amplitude and latency); motor cortical inhibition (duration of the silent period following the interruption of voluntary muscle contraction by TMS); muscle activation level (pre-stimulation force output as percentage from maximal voluntary isometric contraction); force inaccessible in a voluntary effort (peak superimposed twitch). Note, that despite the maximal voluntary effort, the force output drops significantly during the silent period due to temporary unresponsiveness of the cortical motoneurons post-TMS.

B - Examples of the MEP responses recorded in m.TA while performing a static squat exercise at 30 deg knee flexion in conditions with (WBV trial) or without (control trial) before (PRE), during and after (Post) superimposed 30Hz vibration has being delivered to the human body by a platform vertical synchronous WBV (Fitvibe, Germany). Highlighted is the increased MEP size during vibration in the WBV trial, which is not seen during the same period in the control (no vibration) trial.

More recently, similar transient effects on corticospinal and intracortical processes related to lower limb muscle activation has been shown during (30) and up to 10 min after short exposure to 30 Hz whole-body vibration compared to control (31). During squatting exercise performed on a vertical synchronous WBV platform (Fitvibe, Germany), 50% augmentation in corticospinal excitability, and 20% reduction in both facilitatory and inhibitory intracortical excitability to m. tibialis anterior compared to a control condition involving squatting on a switched-off WBV platform were seen (30, Figure 2B). Interestingly, during this study only the intracortical inhibition to the antagonistic m. soleus was reduced by ~13%, which highlights the muscle-specificity of the vibration effects (30). Despite using a different approach to conduct the vibration exercise, i.e. during a relaxed up-right stance on a side-alternating WBV platform (Galileo sport, Germany), Krause et al. (31) observed up to ~30% retention of the increased MEP amplitudes for at least 10 min after the WBV accompanied by ~20% reduction in the H-reflexes recorded in m. triceps surae in response to peripheral nerve stimulation.

It is noteworthy that similar reduction of the short-interval intracortical inhibition processes related to the contracted muscle but enhanced excitability of the inhibitory pathways to the contralateral and antagonist muscles in the upper limb (36) have been shown in response to focal 80 Hz vibration. This evidence highlights the importance to consider the potential of vibration to produce differential supraspinal effects depending on the mode of application. During WBV all synonymous movement agonist and antagonist muscles bilaterally are exposed to the same level of accelerations (Figure 1B), which is not the case when focal muscle/tendon vibration is employed (Figure 1A).

In conclusion, findings from studies employing WBV exercises enforce and expand the evidence for vibration-enhanced intra- and inter-hemispheric cortical processes collected in studies using focal muscle and/or tendon vibration. Combined, they point to supraspinal effects from vibration exercise that matter for sporting, health and clinical practice. Increased reliance on cortical- and subcortical- rather than reflexive spinal- contributions to the central motor command sent to the active musculature has been observed both during and after vibration. This implies that vibration exercises can enhance sensorimotor integration and muscular performance bilaterally and hence, have beneficial implications for training and recovery of muscle activation and coordination during both uni- and bi-manual voluntary actions. Given the complexity of the supraspinal structures and their responses to vibration as well as the lack of vibration application guidelines, the translation of these effects into short- and long-term fitness and therapeutic benefits requires not only sound understanding of the brain’s physiology, but also good observational skills from practitioners.

**6.3 Spinal effects**

With an emphasis on the alpha motoneuron pool, studies are mainly concerned with the somatic reflexes affecting muscle activity related to the control of muscle length and tension, but giving less attention to withdrawal reflexes elicited on the ipsi- and contralateral sides (7). Numerous studies have investigated the vibration-induced modulation of spinal excitability by assessing the changes in the Hoffmann reflex (H-reflex) and muscle spindle stretch reflexes. The spinal stretch reflex is induced after a muscle stretch, whereas the H-reflex is the result of electric stimulation. Therefore, The H-reflex is the electrical analogue of the muscle stretch reflex and is elicited by bypassing muscle spindle and directly depolarizing the afferent nerve (37).

\*\*\* insert Figure 3 here \*\*\*

Caption for Fig 3: Acute vibration effects on the H-reflex and stretch reflex: A - Modulation of m. soleus H-reflex amplitudes (open rectangles) in response to whole body vibration (WBV): H/M recruitment curves (H-reflexes, M-waves triangles) recorded before, during, 1 and 5 min after the exposure to WBV. The maximal M-wave remained the same across all time intervals, whereas the maximal H-reflex amplitude was reduced during WBV and gradually recovered after WBV. Grand means of ten (B) H-reflexes and (C) stretch reflexes recorded before, during, 1 and 5 min after the exposure to WBV.

Figure 3 illustrates the inhibition of the H-reflexes and stretch reflexes during and immediately after vibration, as indicated by a decline in amplitude. The amplitudes progressively recover afterwards within a period of 5-30 min. The scientific consensus reached in the last decades outlines significant effects of vibration on spinal excitability, which cause a temporal inhibition of both stretch reflexes and H-reflexes after focal and WBV.

**6.3.1 Spinal motoneuron activity**

Several studies have confirmed the inhibitory effect of vibration on H-reflex amplitude and H/M-ratios: lower reflex amplitude has been recorded in muscles of the upper (39) and lower extremities (31, 40-42) both during and immediately after vibration. This inhibition has been manifested both during focal vibration applied to the muscle belly or tendon (43-45) and WBV interventions (31, 40, 41). Interestingly, unilateral WBV also suppresses soleus H-reflex in the non-vibrated contralateral limb (42). Decreased T-reflex amplitude has also been shown after WBV (40, 46).

The decline in H-reflex amplitude has been shown to reach a reduction of 50 to 100% during vibration (31, 40, 41) and to gradually recover over a period of 1 min (47), 5 min (40), 10 min (31), 30 min (48, 49) post-vibration with full return to baseline values 1-h after the end of exposure (50). While the scientific evidence broadly agrees that vibration stimulation results in a significant and sustained inhibition of the H-reflex amplitude, there is still no consensus about the size and the persistency of this inhibition exerted at alpha motoneuron pool. This is most likely due to the inhomogeneous methodological approaches, vibration parameters (e.g. amplitudes and frequencies) and affected muscle groups (7).

**6.3.1 Mechanism underlying the effect of vibration on spinal motor neuron discharges**

The most likely explanation for the suppression of H-reflex response during WBV is the increase in premotoneuronal inhibition (51) via post-activation depression, presynaptic inhibition or homosynaptic depression (40, 47, 52, Fig. 4). WBV-induced effects on the muscle spindles and/or any vibration sensitive afferents may inhibit the motor neurons either directly by affecting the efficacy of the muscle spindle primary afferent endings presynaptically, or indirectly by affecting the interneurons that inhibit the spindle primaries via a number of interneurons (53). Homosynaptic depression is rate-dependent modulation of the Ia afferent– motoneuron synapse arising from prior activation of homonymous muscle afferents (47).

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Caption for Fig 4: Schematic diagram illustrating the neural mechanisms underlying the effect of vibration on spinal motor neuron discharges to m. soleus and m. tibialis anterior.

Previous studies manifest unchanged F-wave amplitudes during and after prolonged vibration of the whole hand and sole (25 Hz, (54)) or the Achilles tendon (50 Hz,(50)). The F-waves rely on the backfiring of motoneurons after being reactivated by antidromic impulses generated during supramaximal depolarization of a peripheral nerve (55). Therefore, presynaptic inhibition of Ia afferents appears to be one of the main mechanisms underlying the inhibition of spinal reflexes in response to both locally applied and whole-body vibration. Presynaptic mechanisms are characterized by affecting the conjunction between Ia afferents and the motoneuron pool without changing the overall excitability of the alpha motoneurons or the drive descending from supraspinal structures (31, 40).

Further evidence for enhancement of presynaptic inhibition by vibration comes from work demonstrating an increased firing threshold of Ia afferents (48), a significant post-activation depression due to neurotransmitter depletion at the Ia afferent terminals (47, 56) and an increased disynaptic reciprocal inhibition from antagonists to agonist muscles (57, 58). Additional increase of the presynaptic inhibition of the discharging Ia afferents has been shown to be mediated by GABAergic interneurons under supraspinal control (59, 60). Combined, these findings point to the conclusion that the high activation of Ia afferents via the muscle spindle responses to the vibratory stimuli (25) activates multiple pathways for the H-reflex depression during and after vibration exercise (7). These origins and the associated neural pathways may be differently affected depending on the characteristics of the vibratory stimulus and this may have contributed to the heterogeneous results regarding the size of the H-reflex amplitude reduction and its persistency beyond the vibration treatment.

**6.4 Functional relevance of spinal-supraspinal interaction**

The involvement of spinal circuitries and supraspinal structures in the responses of skeletal muscles to vibration is complex and therefore, a conclusive statement on their functional relevance is not easy. As outlined in this chapter, there is compelling evidence for very specific vibration effects that encompass neural adaptations and plasticity in response to vibration exposure, which manifests the significance of this mechanical stimulus for training practice (7) and therapy (61). To maximise the training and health benefits from the additional mechanical loading of the muscle(s) during vibration it is important to understand and quantify the stimulus intensity reaching the targeted sites of the body. The accelerations induced during vibration exercise depend strongly on the vibration parameters (e.g. mode of application, amplitude and frequency) but also on the body composition, posture and muscle activation type and level (5, 62). This knowledge has direct implications for the prescription of vibration exercise with consideration of the targeted body segment and health outcome. The aforementioned adaptations on spinal and supraspinal levels show that vibration has profound effects on CNS function, often opposing along the different neural pathways. Hence, practitioners need to be competent to recognize these effects in their therapy, particularly in cases when some of these pathways may be disrupted or affected by disease.

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