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TOPICAL REVIEW

Muscle tendon vibration revisited: Why tonic vibration reflex and kinaesthetic illusions matter

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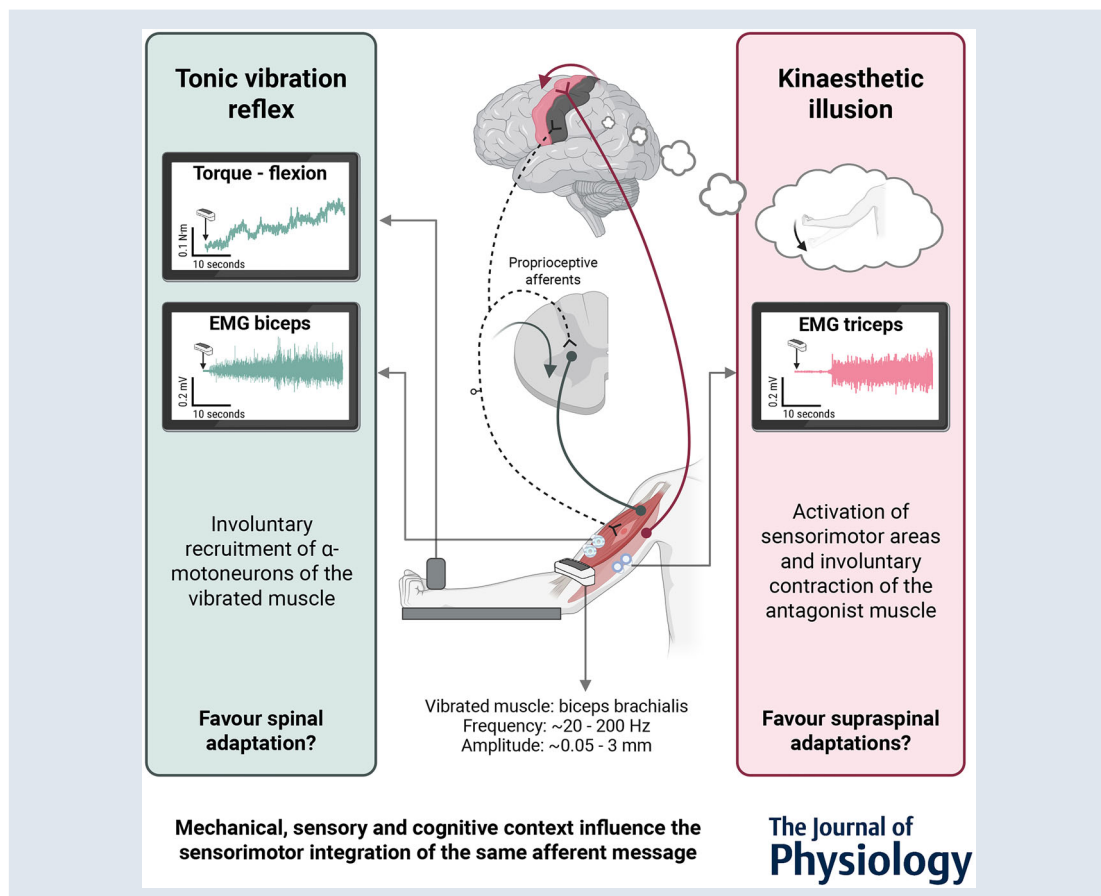
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Abstract figure legend Muscle-tendon vibration generates a strong proprioceptive inflow that can be expressed through different vibratory responses depending on the mechanical, sensory and cognitive context in which it is integrated. Under conditions favouring spinal integration, this afferent input produces a tonic vibration reflex (TVR) in the vibrated muscle (left panel). When integrated within higher-order sensorimotor networks, the same input can elicit a kinaesthetic illusion (KI), sometimes accompanied by an antagonist vibratory response (AVR), reflecting perceptually driven motor output (right panel). These responses arise from differences in sensorimotor integration rather than from differences in afferent recruitment, and they impose distinct constraints on spinal and corticospinal structures. Systematically identifying whether vibration elicits a TVR, a KI (with or without AVR), or remains non-expressive is therefore essential for interpreting how a common proprioceptive input is processed and how it shapes subsequent neuromuscular adaptations.

Abstract Muscle-tendon vibration (MTV) has long been employed in both experimental and clinical settings, and its interest as a neurorehabilitation tool continues to grow. Yet, two primary physiological responses elicited by MTV, the tonic vibration reflex (TVR) and the kinaesthetic illusion (KI), remain inconsistently described across studies. This raises a fundamental limitation: how can vibration-induced adaptations be interpreted when the underlying reflexive or perceptual contributions are unclear? In this topical review, we examine the key mechanisms driving these responses and clarify the conditions that shape their expression. We outline how sensory, attentional and motor contexts can transform the same vibratory-induced afferent into strikingly different physiological and behavioural effects. We also address how the variability in these responses – including the antagonist vibratory responses – may contribute to heterogeneous findings and blur the distinction between responders and non-responders to MTV. We conclude that reflexive or perceptual expression should ideally be systematically monitored, or at minimum that experimental conditions be explicitly reported, as their emergence reflects a configuration in which proprioceptive drive and sensorimotor integration are strongly engaged. By reframing TVR, KI and antagonist vibratory responses as informative physiological markers rather than confounds, this review provides a conceptual and methodological framework to improve the design, interpretation and reproducibility of future studies. This perspective may also support the refinement of MTV as a cost-effective and non-invasive neuromodulatory approach for health and performance applications.

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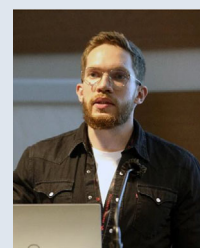
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Introduction

Muscle-tendon vibration (MTV) was first introduced as an experimental tool to probe proprioception and neuromuscular physiology, by mechanically stimulating muscle proprioceptors through a cyclic stretching of the muscle-tendon complex. The seminal work of Eklund & Hagbarth (1966) established that high-frequency tendon

vibration reliably elicits the tonic vibration reflex (TVR), demonstrating that cyclic activation of spindle afferents can drive sustained motor output in humans (Eklund & Hagbarth, 1966). A few years later, Goodwin et al. (1972) showed that selective activation of the same spindle pathway was sufficient to generate vivid kinaesthetic illusions (KI) in the absence of joint displacement, thereby revealing that primary spindle discharge contributes

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directly to conscious kinaesthesia (Goodwin et al., 1972a).

When applied continuously over several minutes, MTV often induces a reduction in maximal voluntary force, along with decreased spinal excitability and increased cortical activity (for review: Souron, Besson, Millet, et al., 2017; Souron et al., 2019). Repeated exposure over days or weeks has also been shown to improve strength, postural control and functional capacity in both healthy individuals and clinical populations (e.g. stroke or neurological disorders), highlighting the potential of MTV in rehabilitation and performance contexts (Aman et al., 2015; Celletti et al., 2020; Lauzier et al., 2024; Souron, Farabet, et al., 2017, Souron, Besson, Millet, et al., 2017). However, most of these studies do not explicitly report whether TVR, KI or the KI-associated antagonist vibratory response (AVR) are expressed during MTV (Fig. 1, Table 1). This lack of reporting has important mechanistic implications, as uncontrolled α -motoneuron recruitment (i.e. TVR or AVR) or heightened perceptual engagement (KI) may influence the targeted neural or functional effects of MTV (Amiez, Géhin, et al., 2024, 2025).

As scientific and clinical interest in MTV continues to grow, clarifying the role of these vibratory-induced responses has become essential. Previous reviews focused on TVR (Monjo & Shemmell, 2020), KI (Grünbaum & Christensen, 2024; Taylor et al., 2017) or on the broader effects of prolonged MTV on neuromuscular function (Souron, Besson, Millet, et al., 2017), without

addressing how the induced response shapes neural adaptations. Rather than treating TVR, KI and AVR as confounds to be avoided, this review reframes them as physiological markers of proprioceptive integration and examines them within a unified framework to clarify how different vibratory-induced sensorimotor states influence MTV outcomes. Drawing on historical and contemporary evidence, we argue that their systematic identification enables MTV to serve not only as a tool to characterize neuromuscular function, but also to induce targeted and interpretable neuromuscular modulations across fundamental and applied contexts.

Physiological bases of MTV responses

MTV is generally assumed to act primarily through activation of primary muscle spindle endings, whose dynamic sensitivity makes them particularly responsive to periodic stretch. Early tendon-mounted preparations in animals demonstrated strong phase-locked activations of spindle primary endings under mechanically simplified conditions involving micrometric longitudinal deformations (Brown et al., 1967; Echlin & Fessard, 1938; Matthews, 1966). However, these invasive preparations differ markedly from contemporary human protocols, in which vibration is applied non-invasively at the skin surface and produces local tissue deformation rather than controlled musculotendinous stretch. Consistent with this mechanical difference, microneurographic recordings in humans show that surface-applied vibration elicits

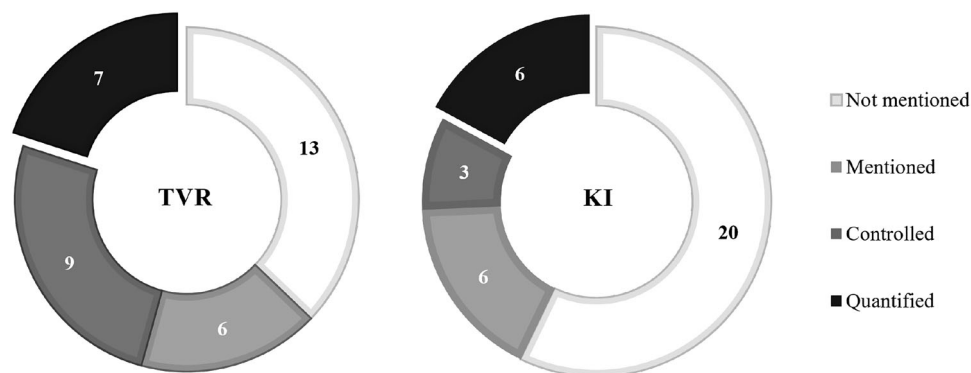


Figure 1. Overview of how 35 studies addressed the presence of vibration-induced responses (tonic vibration reflex (TVR), antagonist vibratory response and/or kinaesthetic illusion (KI)) during muscle-tendon vibration at rest or under slight contraction

'Not mentioned' indicates that none of these responses were referenced in the article; 'Mentioned' indicates that at least one response was cited but neither checked nor measured; 'Controlled' indicates that the presence or absence of at least one response was verified; and 'Quantified' indicates that at least one response was measured. Counts for each category are displayed on the charts. Studies were first identified through a Web of Science search using the following title/abstract keywords: (local vibration OR tendon vibration OR muscle vibration OR musculotendinous vibration) AND (spinal excitability OR corticospinal excitability OR motor evoked potential OR motoneuron excitability OR maximal voluntary contraction OR maximal voluntary isometric contraction OR maximal contraction), for publications between 2000 and 2025. They were then filtered to include only those primarily assessing the acute effects of prolonged MTV on maximal force production or on corticospinal and motoneuronal excitability in healthy participants.

Table 1. Presentation of protocols used in studies published between 2000 and 2025 evaluating the acute effects of prolonged vibration on spinal excitability, corticospinal excitability and maximum force production in healthy participants, with a particular focus on the monitoring of TVR, KI and AVR.

| Study | N (M/F) and age (Mean \pm SD) | MTV: vibration site; duration; frequency (Hz); amplitude (mm) | Visual context and instructions | Mention of TVR, KI and/or AVR in the article | Control and analysis of TVR/AVR and KI |
|---|---------------------------------|---|-----------------------------------|--|--|
| No motor or perceptual response was mentioned in the entire article | | | | | |
| Barrera-Curiel et al., 2019 | N = 10/14 25 \pm 6 | Suprapatellar tendon; 20 min; 66–70 Hz; 1.5 mm | Vision: NR; Instructions: NR | No | No |
| Cattagni et al., 2016 | N = 10/0 22 \pm 4 | Achilles tendon; 30 min; 40 or 100 Hz; 0.2 mm | Vision: NR; Instructions: NR | No | No |
| Eklblom et al., 2011 | N = 0/8 23 \pm 2 | Achilles tendon; 30 min; 100 Hz | Vision: NR; Instructions: NR | No | No |
| Farabet et al., 2016 | N = 9/4 23 \pm 4 | Tibialis anterior muscle; 30 min; 100 Hz; 1 mm | Vision: NR; Instructions: NR | No | No |
| Fry & Folland, 2014 | N = 18/0 20 \pm 2 | Infraspatellar tendon; 30 min; 80 Hz; 1.5 mm | Vision: NR; Instructions: NR | No | No |
| Herda et al., 2009 | N = 15/0 24 \pm 3 | Achilles tendon; 20 min; 70 Hz; amplitude NR | Vision: NR; Instructions: NR | No | No |
| Pfenninger et al., 2023 | N = 11/8 28 \pm 7 | Flexor carpi radialis muscle; 3 \times 10 min; 100 Hz | Vision: NR; Instructions: relaxed | No | No |
| Pfenninger et al., 2024 | N = 10/10 25 \pm 4 | Flexor carpi radialis muscle; 3 \times 10 min; 100 Hz, 1 mm | Vision: NR; Instructions: relaxed | No | No |
| Richardson et al., 2006 | N = 14 23 \pm 1 | Infraspatellar tendon; 20 min; 50 Hz; 1.5 mm | Vision: NR; Instructions: NR | No | No |
| Souron et al., 2017 | N = 11/4 28 \pm 6 | Rectus femoris muscle; 30 min; 100 Hz; 1 mm | Vision: NR; Instructions: NR | No | No |
| Souron et al., 2019 | N = 10/1 26 \pm 6 | Achilles tendon; 30 min; 100 Hz; 1 mm | Vision: NR; Instructions: NR | No | No |
| Yoshitake et al., 2004 | N = 8/0 27 \pm 4 | Achilles tendon; 30 min; 100 Hz; 0.75 mm | Vision: NR; Instructions: NR | No | No |

(Continued)

Table 1. (Continued)

| At least one motor or perceptual response was mentioned, but not controlled | | | | | | |
|--|-----------------|---|-----------------------------------|---|------------------|--|
| Jackson et al., 2003 | N = 10/0 26 ± 2 | Rectus femoris muscle; 30 min; 30 or 120 Hz; 1.5–2 mm | Vision: NR; Instructions: relaxed | TVR: discussion | No | |
| Kennouche et al., 2022 | N = 16/4 27 ± 6 | Rectus femoris muscle or tendon; 30 min; 100 Hz; 1 mm | Vision: NR; Instructions: relaxed | TVR: introduction/discussion | No | |
| Konishi et al., 2002 | N = 8/4 25 ± 4 | Infraspatellar tendon; 20 min; 50 Hz; 1.5 mm | Vision: NR; Instructions: relaxed | TVR: method | No | |
| Konishi et al., 2009 | N = 8/0 18 ± 0 | Infraspatellar tendon; 20 min; 50 Hz; 1.5 mm | Vision: NR; Instructions: relaxed | TVR: method | No | |
| Lapole et al., 2012 | N = 12 21 ± 3 | Achilles tendon; 60 min; 50 Hz; 0.2 mm | Vision: NR; Instructions: NR | TVR: discussion | No | |
| Saito et al., 2016a | N = 9/0 25 ± 4 | Vastus lateralis muscle; 30 min; 80 Hz; 1 mm | Vision: NR; Instructions: relaxed | TVR: method | No | |
| Zinke et al., 2019 | N = 0/11 16 ± 1 | Achilles tendon; 5 min; 80 Hz; 1 mm | Vision: NR; Instructions: NR | TVR: discussion | No | |
| At least one motor or perceptual response was mentioned and controlled, but not analysed | | | | | | |
| Kouzaki et al., 2000 | N = 7/1 25 ± 2 | Rectus femoris muscle; 30 min; 30 Hz; 2–3 mm | Vision: NR; Instructions: relaxed | TVR: 'tonic muscle vibration' (used in the entire article) | TVR: EMG | |
| Lapole et al., 2015 | N = 8/2 27 ± 9 | Abductor pollicis brevis muscle; 15 min; 80 Hz; 0.8–1 mm | Vision: NR; Instructions: relaxed | KI: 'Subthreshold for perceiving an illusory movement' | KI: verbal check | |
| Marconi et al., 2008 | N = 6 NR | Flexor carpi radialis muscle, contracted (20% maximal voluntary contraction); 10 min; 100 Hz; 0.05–0.1 mm | Vision: NR; Instructions: NR | TVR: 'Subthreshold for the tonic vibration reflex' and 'continuous EMG monitoring' | TVR: EMG | |
| Nishikawa et al., 2024 | M/F 14 24 ± 4 | Biceps femoris tendon; 30 s, 80 Hz, 0.1 mm | Vision: NR; Instructions: relaxed | TVR/AVR: 'instructed to keep their muscles relaxed' and 'The tester monitored muscle activity by visual observation.' | TVR/AVR: EMG | |
| Nito et al., 2021 | N = 14/4 21–36 | Flexor carpi radialis muscle; 6 min; 100 Hz; 3 mm | Vision: NR; Instructions: NR | TVR: 'The intensity of [MTV] was adjusted (...) to be just subthreshold to elicit [TVR]' | TVR: EMG | |

(Continued)

Table 1. (Continued)

| At least one motor or perceptual response was mentioned and controlled, but not analysed | | | | | | |
|--|------------------|---|--|--|---------------------------------|--|
| Rosenkranz & Rothwell, 2006 | N = 4/2 30–48 | First dorsal interosseous and abductor pollicis brevis muscle; 15 min (2'' on/2'' off); 80 Hz; 0.2–0.5 mm | Vision: NR; Instructions: NR | TVR: 'monitored EMG in the vibrated' (i.e. no TVR) / KI: 'below the threshold for perceiving an illusory movement' | TVR: EMG; KI: verbal check | |
| Saito et al., 2016b | N = 9/0 25 ± 4 | Infraspatellar tendon; 30 min; 80 Hz; 1 mm | Vision: NR; Instructions: relaxed | TVR: 'Tonic tendon vibration was applied (...)' (method) | TVR: EMG, torque | |
| Shinohara et al., 2005 | N = 15/17 22 ± 3 | First dorsal interosseous muscle; 30 min; 75 Hz; amplitude NR | Vision: NR; Instructions: relaxed | TVR: 'at an intensity that produced a tonic vibration reflex' (method) | TVR: EMG | |
| Smith et al., 2005 | N = 6/4 26 ± 3 | Extensor carpi radialis muscle; 15 or 30 min (30'' on/15'' off); 100 Hz; 0.5 mm | Vision: NR; Instructions: NR | TVR: 'monitored EMG activity (...) to ensure that muscles remained relaxed.' | TVR: EMG | |
| Ushiyama et al., 2005 | N = 13/0 22–49 | Achilles tendon; 30 min; 100 Hz; 1.5 mm | Vision: NR; Instructions: relaxed | TVR: 'checked their EMGs to ascertain that no tonic vibration reflex was evoked in the plantar flexors' | TVR: EMG | |
| At least one motor or perceptual response was controlled and quantified | | | | | | |
| Amiez et al., 2023 | N = 14 23 ± 1 | Suprapatellar tendon; 1–6 min, 100 Hz; 0.5 mm | Vision: NR; Instructions: NR | TVR | TVR: EMG | |
| Amiez, Géhin, et al., 2024 | N = 14/2 24 ± 3 | Flexor carpi radialis tendon; 6 min, 80 Hz, 2 mm | Vision: hidden/visible; Instructions: relaxed/no instruction | TVR/AVR, KI | TVR/AVR: EMG; KI: Likert scales | |
| Amiez, Martin, et al., 2024 | N = 15/6 23 ± 2 | Flexor carpi radialis tendon; 30 min, 80 Hz, 2 mm | Vision: hidden; Instructions: relaxed | TVR/AVR, KI | TVR/AVR: EMG; KI: Likert scales | |

(Continued)

Table 1. (Continued)

At least one motor or perceptual response was controlled and quantified

| | | | | | |
|-----------------------------|-----------------|---|--|-------------|---------------------------------|
| Amiez et al., 2025 | N = 12/3 24 ± 2 | Flexor carpi radialis tendon; 6 min, 80 Hz, 2 mm | Vision: hidden/visible; Instructions: relaxed/no instruction | TVR/AVR, KI | TVR/AVR: EMG; KI: Likert scales |
| Forner-Cordero et al., 2008 | N = 6/5 23 ± 6 | Flexor carpi radialis tendon; 60 min (25" on / 5" off); 80 Hz | Vision: eyes closed; Instructions: relaxed, focused on KI | TVR/AVR, KI | TVR/AVR: EMG; KI: reproduction |
| Lauzier et al., 2023 | N = 7/13 24 ± 3 | Flexor carpi radialis tendon; 10"; 80 Hz; 1 mm | Vision: hidden; Instructions: focused on KI | TVR/AVR, KI | TVR/AVR: EMG; KI: Likert scales |
| Steyvers et al., 2003a | N = 10/6 20–27 | Flexor carpi radialis tendon; 30 min (25" on/5" off); 80 Hz; 0.5 mm | Vision: hidden; Instructions: relaxed | TVR/AVR, KI | TVR/AVR: EMG; KI: Likert scales |

Search strategy: Articles were identified through a Web of Science search using the following title/abstract keywords: (local vibration OR tendon vibration OR muscle vibration OR musculotendinous vibration) AND (spinal excitability OR corticospinal excitability OR motor evoked potential OR motoneuron excitability OR maximal voluntary contraction OR maximal voluntary isometric contraction OR maximal contraction), for publications between 2000 and 2025. Only studies primarily aiming to quantify the acute effects of prolonged MTV applied at rest (or <20% of maximal voluntary contraction) on maximal voluntary force production or on corticospinal or motoneuronal excitability in healthy participants were included.

Abbreviations: AVR: antagonist vibratory response, EMG: electromyographic recording, on/off: intermittent protocol alternating vibration (on) and rest (off) phases, KI: kinaesthetic illusion, MTV: muscle-tendon vibration, N: number of participants (male/female), NR: not reported, SD: standard deviation, TVR: tonic vibration reflex.

a multimodal afferent response, engaging cutaneous mechanoreceptors alongside primary and secondary spindle endings and Golgi tendon organ afferents (Fallon & Macefield, 2007; Ribot-Ciscar et al., 1989). Fast-adapting cutaneous fibres can even follow each cycle in phase at frequencies up to ~200–300 Hz (Ribot-Ciscar et al., 1989), indicating that human MTV constitutes a less selective afferent stimulus than classical tendon-mounted preparations.

Determinants of afferent recruitment during muscle–tendon vibration. The relative recruitment of proprioceptive afferent groups depends on both vibration parameters and the mechanical state of the muscle–tendon unit. Lower frequencies in the 10–20 Hz range preferentially engage secondary spindle afferents and Golgi tendon organ receptors, whereas higher frequencies increasingly promote phase-locked discharge of primary spindle endings. As noted in classical analyses by McCloskey (1973), this frequency dependence reflects the differential dynamic sensitivities of primary and secondary endings (McCloskey, 1973). Frequencies between 80 and 100 Hz are most commonly used, as they effectively entrain primary endings in phase with each vibration cycle, along with a substantial proportion of secondary and Golgi tendon organ afferents (Burke et al., 1976a; Roll & Vedel, 1982; Roll et al., 1989). Amplitude – defined as the peak-to-peak displacement of the vibrator during each cycle – is another key determinant of vibratory recruitment. Very small displacements (<0.5 mm) may favour a stronger contribution of primary spindle endings at rest, but this apparent selectivity often reflects a weaker and less reliably phase-locked afferent drive (Burke et al., 1976a; Fallon & Macefield, 2007; Pierrot-Deseilligny & Burke, 2012). As amplitude increases, the afferent drive from spindle and tendon organ receptors strengthens, as evidenced by the emergence of TVR and KI at higher vibration amplitudes, suggesting that large-amplitude vibrations engage a greater number of afferents and promote more reliable phase-locked activity, albeit at the cost of receptor selectivity (Eklund & Hagbarth, 1966; Taylor et al., 2017). Regardless of vibration frequency and amplitude, afferent recruitment remains state dependent, being strongly shaped by the mechanical state and recent history of the muscle. Passive shortening dampens spindle discharge, whereas stretch or voluntary contraction enhances primary spindle firing and increases Golgi tendon organ responsiveness as tension builds (Fallon & Macefield, 2007; Proske & Gandevia, 2012; Roll et al., 1989). Taken together, these observations indicate that, despite the influence of vibration parameters and muscle mechanics, human MTV reflects the combined contribution of

multiple mechanosensitive receptors (Macefield, 2022; Pierrot-Deseilligny & Burke, 2012).

Spinal mechanisms underlying the TVR. The TVR represents the primary spinal motor expression of the synchronized afferent drive generated by MTV. Rhythmic proprioceptive discharges initially excite α -motoneurons via monosynaptic connections, but high-frequency Ia activity rapidly depresses this pathway through activity-dependent homosynaptic mechanisms, as evidenced by H-reflex suppression during vibration (De Gail et al., 1966; Gillies et al., 1969; Hultborn et al., 1996; Wood et al., 1996). Despite this monosynaptic depression, the TVR persists and can even increase – a dissociation classically termed the ‘vibratory paradox’ – indicating reliance on polysynaptic spinal circuits that remain functionally engaged during vibration (Desmedt & Godaux, 1975, 1978; Godaux & Desmedt, 1975).

Multiple observations converge to indicate that the TVR depends predominantly on polysynaptic spinal pathways under supraspinal control. Pharmacological suppression of polysynaptic transmission with barbiturates markedly reduces or abolishes the TVR while sparing monosynaptic reflexes and selectively suppresses vibration-induced asynchronous motor unit firing, consistent with a substantial polysynaptic contribution (De Gail et al., 1966; Hori et al., 1989; Kanda, 1972). Likewise, complete spinal cord lesions abolish the TVR despite preserved stretch reflexes, demonstrating that segmental Ia excitation alone is insufficient and that descending facilitation is required (Burke et al., 1972; Hagbarth & Eklund, 1968; Lance et al., 1973). Post-tetanic potentiation of heteronymous afferents further supports the involvement of shared excitatory interneuronal networks linking spindle input to α -motoneurons (Kanda, 1972), likely within laminae V–VI where Ia and Ib inputs converge (Fetz et al., 1979). The magnitude and persistence of the TVR are critically shaped by descending brainstem pathways. Reticulospinal and vestibulospinal projections provide a tonic facilitatory drive to the last-order interneurons of these polysynaptic circuits, whereas medullary reticular regions exert inhibitory control (Andrews et al., 1973; Gillies et al., 1971).

From a spinal perspective, the TVR should not only be interpreted as a sustained reflex driven by continuous primary afferent inflow, but also as the expression of self-sustained motoneuronal firing supported by intrinsic membrane properties. In fact, sustained input from primary muscle spindle afferents and convergent polysynaptic excitation depolarize α -motoneuron dendrites and facilitate the activation of persistent inward currents (Heckman et al., 2008; Lee & Heckman, 2000; Magalhães & Kohn, 2010). Once engaged, these voltage-dependent

currents amplify synaptic input and can maintain motoneuronal discharge even when synaptic drive is reduced or withdrawn (McPherson et al., 2008; Trajano et al., 2014). The expression and gain of these intrinsic currents are strongly shaped by descending monoaminergic brainstem drive, conveyed primarily through reticulospinal and vestibulospinal pathways, which increases motoneuronal excitability and thereby enhances the magnitude and persistence of the TVR (Heckman et al., 2008; Lee & Heckman, 2000). This facilitation is further modulated by the balance of excitatory and inhibitory spinal inputs, such that changes in reciprocal inhibition, muscle length or afferent context can markedly alter motoneuronal output and the emergence of self-sustained firing (Trajano et al., 2014). Together, these converging observations indicate that the contribution of persistent inward currents to vibration-induced motor responses reflects a dynamic interaction between intrinsic motoneuronal properties, sustained synaptic excitation, neuromodulatory drive, and inhibitory spinal circuitry (Fig. 2) (Monjo & Shemmell, 2020).

Consistent with this view, single-unit recordings show that once the TVR develops, spindle responses to vibration often decline due to extrafusal shortening and receptor unloading, without compensatory fusimotor activation, further indicating that reflex persistence relies on intrinsic α -motoneuronal mechanisms and polysynaptic drive rather than sustained primary afferent inflow (Burke et al., 1976b; Vallbo et al., 1979). This interplay between intrinsic motoneuronal properties and state-dependent synaptic drive accounts for the progressive force increase during sustained vibration, the orderly recruitment of motor units, and the rapid decay of the contraction upon vibration offset (Burke et al., 1972, 1976a; Desmedt & Godaux, 1978; Lance, 1966; Marsden et al., 1969; Romaiuguère et al., 1991).

Another functional distinction between phasic mono-synaptic reflexes (i.e. the stretch reflex or Hoffmann reflex) and the TVR is the influence of voluntary control. Unlike these synchronous responses, the TVR can be markedly attenuated or suppressed once the reflex contraction becomes perceptible, suggesting that voluntary gating acts preferentially on polysynaptic circuits or persistent inward currents rather than monosynaptic connections (De Gail et al., 1966; Marsden et al., 1969; Monjo & Shemmell, 2020). Conversely, voluntary muscle activation facilitates TVR expression, consistent with early observations that the reflex is more readily elicited in active than in relaxed muscles. This facilitation involves both α - γ coactivation, which maintains spindle responsiveness and Ia inflow, and descending monoaminergic drive, which enhances motoneuronal excitability and facilitates persistent inward currents that amplify vibration-induced synaptic inputs (Eklund & Hagbarth, 1966; McPherson et al., 2008; Romaiuguère et al., 1993; Vallbo et al., 1979).

Together, these findings indicate that TVR amplitude and persistence arise from spinal transformation of vibratory input mediated by polysynaptic circuits, permissively regulated by brainstem pathways, and sustained by intrinsic motoneuronal properties (Frigon et al., 2011; Gillies et al., 1971; Thompson et al., 2022).

Supraspinal mechanisms underlying the KI. The KI constitutes the perceptual expression of how the brain consciously interprets the proprioceptive volley elicited by MTV. Under appropriate conditions, such as the absence of conflicting visual or cutaneous cues, vibration of a muscle or tendon generates a conscious sensation of movement consistent with muscle lengthening, despite the absence of actual joint displacement (Goodwin et al., 1972a, 1972b; McCloskey, 1973, 1978). This percept arises predominantly from primary spindle afferents, whose dynamic sensitivity to vibration makes them the principal contributors to illusory movement at rest. It should be distinguished from position error, a static misjudgement of limb orientation occurring without perceived motion, which is more closely associated with secondary spindle signalling under conditions that suppress dynamic primary afferent activity (Eklund, 1972; McCloskey, 1973; Pierrot-Deseilligny & Burke, 2012). Thixotropic properties of muscle spindles further modulate this perceptual response, as prior length changes or conditioning contractions alter intrafusal tension and thus the efficacy of subsequent vibratory input. A brief isometric contraction tends to increase intrafusal tension and enhance spindle firing during subsequent vibration, whereas prior shortening reduces baseline tension and diminishes the resulting illusion (Gooney et al., 2000; Proske & Gandevia, 2012). When vibration stops, the abrupt drop in spindle discharge can produce a brief 'return' illusion in which the limb is perceived as moving back to its true position (Kito et al., 2006; Ribot-Ciscar et al., 1998; Seizova-Cajic et al., 2007; Tidoni et al., 2014). Neuroimaging studies indicate that KI engages a distributed cortical network including primary and secondary somatosensory cortices, premotor areas, posterior parietal regions and subcortical structures such as the cerebellum and basal ganglia (Goble et al., 2012; Kenzie et al., 2018; Naito et al., 1999; Romaiuguère et al., 2003). Some studies further report hemispheric asymmetries or stronger illusions in non-dominant limbs, but these findings are based on small samples and remain inconsistent across studies (Cignetti et al., 2014; Goble et al., 2012; Naito et al., 2005; Tidoni et al., 2014). Within this network, activity in the primary motor cortex scales with the perceived velocity of the illusory movement, but this relationship emerges only several hundred milliseconds after vibration onset, reflecting the time required for proprioceptive signals to reach and be integrated

within motor circuits (Casini et al., 2006, 2008). Posterior parietal regions, including the angular gyrus, support the interpretation and reconstruction of limb motion by integrating proprioceptive inputs with other sensory cues; this process mediates visuo-kinesthetic interactions, particularly under ambiguous or conflicting conditions (Hagura et al., 2007, 2009).

In some individuals and contexts, KI is accompanied by involuntary activation of the muscle that is antagonist to the vibrated muscle – the AVR – that is, the

muscle that would normally act to produce the perceived movement (Calvin-Figuère et al., 1999, 2000; Cordo et al., 2005; Gilhodes et al., 1986; Roll et al., 1980). Notably, this activation occurs despite the well-established spinal projection of Ia afferents from the vibrated muscle onto interneurons mediating reciprocal inhibition of the antagonist (Lance, 1966; Marsden et al., 1969; Orssatto et al., 2022). This activity typically emerges only when the illusion is present, often scales with illusion strength, and occurs at latencies incompatible with spinal circuitry

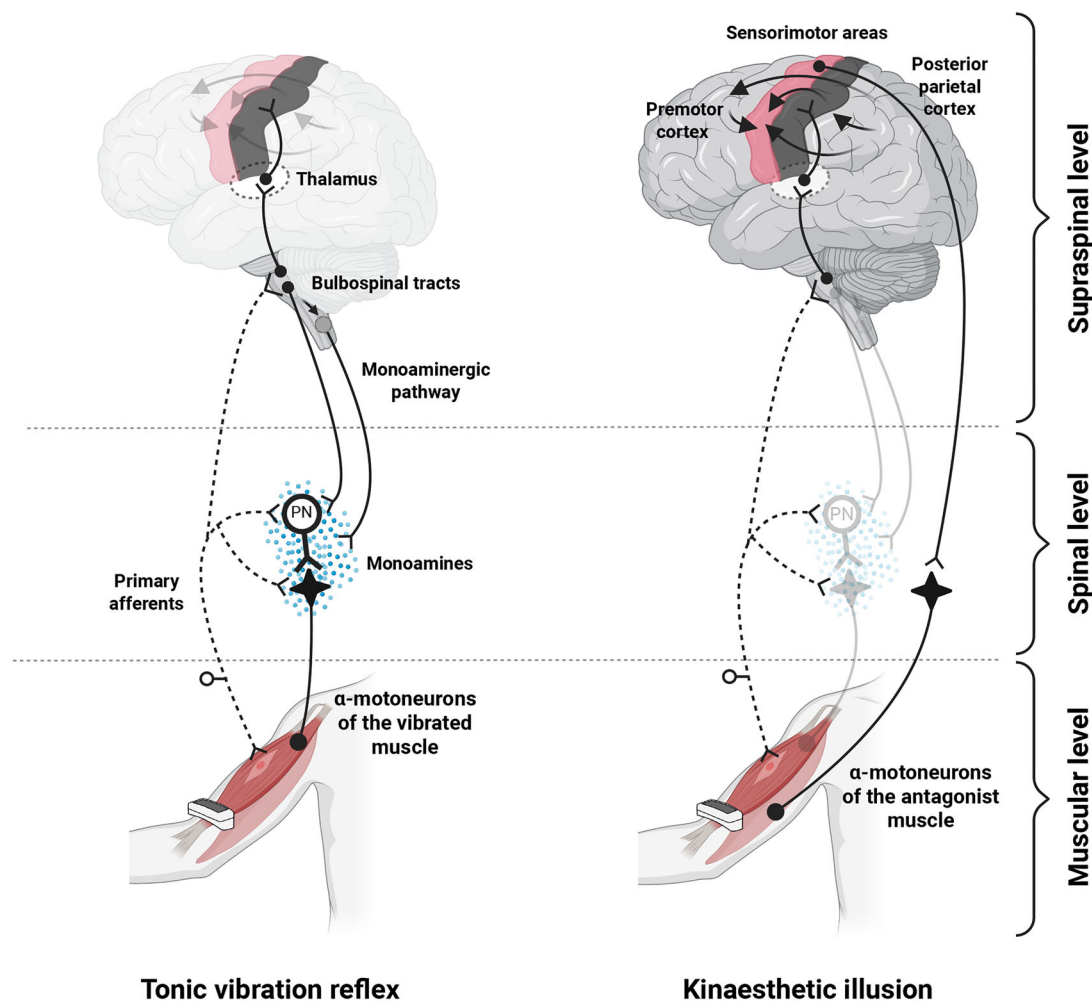


Figure 2. Overview of the presupposed human circuitry involved in the tonic vibration reflex (TVR) and kinaesthetic illusion (KI)

Muscle–tendon vibration (MTV) generates a strong proprioceptive inflow, primarily driven by Ia afferents (dotted lines) but also involving group II, Ib and cutaneous afferents. These afferents project to spinal circuits and ascend to the somatosensory cortex via brainstem and thalamic relays. Depending on task context and sensorimotor integration, this input can induce a TVR, characterized by a slowly progressive recruitment of motor units via polysynaptic spinal circuits, likely involving propriospinal interneurons (PNs). This pathway is critically facilitated by bulbospinal tracts (reticulospinal and vestibulospinal) and monoaminergic neuromodulation (e.g. serotonin, represented by blue dots), which enable the generation of persistent inward currents and plateau potentials in motoneurons. Conversely, when processed through primary motor, premotor and posterior parietal cortices, the same afferent input can evoke a KI of movement, occasionally accompanied by an antagonist vibratory response (AVR). These divergent responses reflect distinct sensorimotor integration modes rather than differences in peripheral afferent recruitment. The exact pathways described above remain partially identified and are likely more complex than those illustrated.

(Calvin-Figuère et al., 1999, 2000; Naito et al., 2016). These features support the view that AVR represents a perceptually driven motor output, reflecting a partial read-out of supraspinal state estimation into descending motor commands rather than a mechanically induced reflex. Although AVR temporal characteristics suggest it arises as a consequence of illusion processing, motor cortex activity during vibration correlates with illusion strength, raising the possibility that motor engagement – whether sub-threshold for motoneuronal recruitment or manifest as AVR – may amplify or sustain the perceptual experience through predictive feedback loops (Grünbaum & Christensen, 2024; Naito et al., 2016). Consistent with this view, combining vibration with motor imagery, that is, the mental representation of a movement without intention to physical execution, may enhance KI and elicit agonist or antagonist activity aligned with the imagined movement (Shibata et al., 2017). However, co-occurrence of KI and AVR is not obligatory. Strong illusions can occur without any detectable antagonist activity, and visual or attentional manipulations can attenuate both illusion strength and AVR expression (Kito, 2016; Seizova-Cajic & Azzi, 2010, 2011). Overall, AVR appears to be a context-dependent manifestation of supraspinal engagement whose mechanisms are only partially understood and should not be equated systematically with the presence or absence of KI.

Together, TVR, KI and AVR illustrate how the same vibratory input can give rise to distinct motor and perceptual outcomes depending on spinal gain modulation and supraspinal integration. Rather than discrete, unrelated phenomena, they represent different expressions of proprioceptive feedback integration, dynamically shaped by sensory, attentional and motor contexts. Systematically identifying these vibratory responses and the factors influencing their expression is essential for interpreting inter-individual and contextual variability. Such assessment also clarifies how these modes of integration may contribute to the heterogeneous neuromuscular outcomes reported across MTV studies.

Determinants and variability of vibratory responses during MTV

Experimental studies on vibration-induced proprioceptive responses have shown that both motor (Eklund & Hagbarth, 1966; Martin & Park, 1997) and perceptual responses (Gilhodes et al., 1986; Naito et al., 1999) can be elicited over a wide range of frequencies (~20–200 Hz) and amplitudes (~0.2–3.3 mm). Even stimulation parameters intended as ‘control’ settings, that is, assumed not to elicit a KI or remain below the TVR threshold, can nonetheless evoke vibratory responses in some individuals, revealing substantial inter-individual

variability in proprioceptive responsiveness (Mottram et al., 2006; Naito et al., 1999). Taken together, these findings indicate that while the mechanical properties of the stimulus shape the strength of the afferent input, they do not by themselves determine whether vibration gives rise to motor (TVR, AVR) or perceptual (KI) expressions. Rather, MTV-induced responses reflect how the nervous system interprets and integrates the resulting proprioceptive input within the broader sensorimotor context, shaped by sensory weighting, attentional state, motor conditions and prior experience.

Visual modulation and sensory weighting. Visual input strongly shapes the interpretation of vibratory inflow, reinforcing the broader principle that contextual factors, rather than stimulation parameters alone, determine how a synchronous proprioceptive volley is interpreted. Stable visual feedback biases the sensory estimate of limb position towards the visually defined state, thereby reducing the likelihood that the proprioceptive perturbation will be reconstructed as an illusory movement (Burgess et al., 1982; Hagura et al., 2007; Van Beers et al., 1996; van Beers et al., 1998). Conversely, occluding vision increases reliance on proprioceptive cues, thereby increasing the likelihood that the afferent volley will be expressed perceptually as a KI (Lackner, 1984; Roll et al., 1980). Importantly, even when vision contradicts proprioception, posterior parietal regions do not fully suppress proprioceptive processing. Rather, they mediate the weighting required to reconcile discrepant inputs, and their activity scales with the attenuation – but not the elimination of the illusion (Hagura et al., 2007, 2009). In other words, vision does not suppress proprioceptive processing; both sources of information remain available, and the perception that reaches consciousness reflects the most coherent combination of these cues (Hagura et al., 2007; Roll et al., 1980). This also explains why, even in experimental conditions arranged to favour or suppress a given response (e.g. KI), vibration does not consistently yield a single response mode: depending on sensory, attentional and motor context, as well as inter-individual differences in proprioceptive weighting, the same afferent volley may be expressed as a KI, a TVR, an AVR, or remain non-expressive (Cordo et al., 2005; Seizova-Cajic & Azzi, 2010). These observations indicate that visual weighting constrains but does not rigidly determine how vibratory input is ultimately experienced.

Attentional and motor context. Beyond sensory availability, attentional engagement critically determines whether vibratory input reaches conscious awareness. KI is more likely to arise when attention is directed towards limb sensations, a condition that increases the perceptual weighting of proprioceptive cues and reduces

uncertainty in their interpretation (Feldman & Latash, 1982; Roll et al., 1980; Schofield et al., 2015; Seizova-Cajic & Azzi, 2010). Neuroimaging studies show that the transition from early sensorimotor processing to explicit kinaesthetic awareness typically unfolds over several seconds and depends on the progressive recruitment of distributed fronto-parietal networks whose activity tracks the emergence of the illusion rather than its initial cortical encoding (Casini et al., 2008; Cignetti et al., 2014). This temporal dissociation underscores the idea that the illusion becomes consciously accessible only once central integration has accumulated sufficient evidence across sensory and contextual cues, a process that varies considerably between individuals and does not rely on a strictly lateralized pathway (Cordo et al., 2005; Naito et al., 2016; Schofield et al., 2015). Moreover, sustained attentional demands can gradually degrade perceptual fidelity, contributing to fluctuations in illusion vividness over repeated or prolonged stimulation (Abd-Elfattah et al., 2015; Jacquet et al., 2021). Beyond sensory and attentional factors, the motor context critically shapes KI expression, as vibration applied during voluntary contraction strongly attenuates the percept. Classic studies show that contractions of ~25–30% of maximal force markedly suppress or abolish vibration-induced movement illusions (Ansems et al., 2006; Goodwin et al., 1972a; McCloskey, 1973). This attenuation does not reflect a purely mechanical effect of loading but arises from changes in the central interpretation of spindle-derived inflow: increased background spindle discharge, altered fusimotor drive and efference-related predictive signals accompanying voluntary force production all reduce the perceptual salience of the vibration-evoked perturbation (Grünbaum & Christensen, 2024; McCloskey, 1973). Consistent with this interpretation, vibration applied to a fatigued, yet relaxed muscle, generally preserves the illusion, whereas vibration during a fatiguing or load-bearing contraction reduces its perceived velocity or abolishes it, indicating that KI attenuation results from increased voluntary drive rather than fatigue *per se* (Grünbaum & Christensen, 2024; McCloskey, 1973; Taylor et al., 2017).

Inter-individual variability. Substantial inter-individual variability persists even when frequency and amplitude are rigorously standardized, reflecting differences in both mechanical and neural factors shaping the transmission and integration of the vibratory input. Mechanical contributors include individual differences in musculo-tendinous stiffness and in the spread of vibration to adjacent tissues, which may partly account for the wide dispersion of TVR thresholds (0.05–0.70 mm) reported under constant stimulation parameters (Mottram et al., 2006). Vibrations may spread to neighbouring muscles,

mechanically stimulating their spindles and altering reflex pathways outside the targeted region, including presynaptic inhibition or involuntary activation of antagonist muscles (Dindar & Verrier, 1975; Lance et al., 1973). Beyond mechanical influences, inter-individual variability also reflects differences in how proprioceptive cues are weighted and interpreted, shaped by factors such as sensory-weighting tendencies, attentional engagement and perceptual susceptibility (Assländer & Peterka, 2016; Isableu & Vuillerme, 2006; Isableu et al., 2003). Characteristics such as age or habitual physical activity may further influence sensorimotor integration, although direct evidence linking these factors to vibration-induced expressions remains limited (Goble et al., 2012; Proske & Gandevia, 2018). This combined mechanical–neural diversity is reflected in the recurrent observation that some participants exhibit clear illusions or AVR, whereas others show minimal or no expression under identical conditions (Calvin-Figuère et al., 1999; Cordo et al., 2005; Naito et al., 1999). A similar finding holds for AVR, which emerges in only a subset of participants even when KI is robustly expressed (Calvin-Figuère et al., 1999), an effect also evident in recent datasets where AVR was present in some but not all individuals despite equally clear illusions (Amiez, Géhin, et al., 2024, 2025). Consequently, the absence of a motor (TVR, AVR) or perceptual (KI) response should not be interpreted as evidence that afferent recruitment was absent or insufficient.

Intra-individual variability and temporal dynamics.

Variability also emerges within subjects across a single session. KI often develops gradually, reaches a peak and then fades during sustained stimulation, sometimes disappearing entirely with prolonged exposure (e.g. 30 mins) (Amiez, Martin, et al., 2024; Seizova-Cajic et al., 2007; Taylor et al., 2017). This attenuation reflects both peripheral adaptation of spindle afferents whose sensitivity remains transiently reduced following vibration (Ribot-Ciscar et al., 1998) – and a sustained mismatch between the vibration-driven proprioceptive input and other concurrent sensory and motor signals. As prolonged stimulation persists in the absence of corresponding changes in actual limb position or motor output, this conflict reduces the reliability of the sensory evidence available for perceptual inference, causing unstable or fading kinaesthetic perceptions (Grünbaum & Christensen, 2024; Taylor et al., 2017). Moreover, these fluctuations suggest that even a constant proprioceptive input can alternate between competing perceptual interpretations over time, yielding variable or even opposite movement perception despite unchanged stimulation (Holcombe & Seizova-Cajic, 2008). TVR expression also shows heterogeneous temporal dynamics, ranging from stable sustained contractions to partial or complete

extinction despite continuous stimulation (De Gail et al., 1966; Eklund & Hagbarth, 1966). Collectively, these inter- and intra-individual patterns illustrate how a stable mechanical stimulus can yield markedly different outcomes depending on mechanical coupling, afferent dynamics and the evolving balance of sensory, cognitive and motor influences. These response states not only shape motor or perceptual expression during MTV; they also condition how subsequent neuromuscular adaptations emerge.

Variability of acute and chronic responses to prolonged MTV exposures

One of the most robust signatures of prolonged MTV is the post-vibration depression of the Hoffmann reflex. This reduction in the effectiveness of primary afferents to elicit motoneuronal discharge persists well beyond the stimulation period and is now understood to arise from several converging mechanisms. Sustained vibratory activation increases the electrical activation threshold of Ia afferents (Coppin et al., 1970) and may induce activity-dependent reductions in their axonal excitability (Fetz et al., 1979), thereby limiting the effective recruitment of spindle afferents by peripheral stimulation. In parallel, prolonged vibration induces a long-lasting depression of Ia-mediated transmission that cannot be explained solely by classical GABAergic presynaptic inhibition (Hultborn et al., 1996). A sustained reduction in motoneuronal excitability is now considered a major contributor to this post-vibration depression (Souron et al., 2019), consistent with evidence of decreased transmission efficacy between primary afferents and α -motoneurons in humans (Abbruzzese et al., 2001; Cavallari & Katz, 1989; Hayward et al., 1986).

Neuromuscular adaptations and inter-study variability.

Building on these classic observations, more recent work has expanded the analysis beyond spinal reflex pathways. Prolonged vibration (5–60 min) generally reduces maximal voluntary force and electromyographic activity during subsequent maximal contractions, and depresses spinal motoneuron excitability, whereas corticospinal excitability is often maintained or increased (Amiez, Géhin, et al., 2024; Barrera-Curiel et al., 2019; Herda et al., 2009; Kennouche et al., 2022; Kouzaki et al., 2000; Souron, Besson, McNeil, et al., 2017, 2019; Ushiyama et al., 2005). However, even when vibration frequency, amplitude and duration are tightly standardized, the magnitude and distribution of these adaptations vary markedly both between and within studies. Across experiments using broadly comparable mechanical parameters, reported changes in maximal force have varied markedly, from no detectable effect

to reductions approaching 20% (Amiez et al., 2023, Amiez, Géhin, et al., 2024; Amiez, Martin, et al., 2024; Barrera-Curiel et al., 2019; Kennouche et al., 2022; Souron, Besson, McNeil, et al., 2017; Souron, Besson, Millet, et al., 2017; Zinke et al., 2019). Comparable variability is often observed within a single protocol: identical vibration exposure can lead to slight improvements in force production for some participants but around a 20% decrease in others, despite a group-average decline of ~9% (Barrera-Curiel et al., 2019). Neurophysiological studies likewise reveal responders and non-responders in terms of corticospinal excitability under standardized stimulation (Lapole & Tindel, 2015; Pfenninger et al., 2024), and chronic interventions report heterogeneous strength gains following similar training programmes (Souron, Besson, Millet, et al., 2017). Differences in stimulation site, joint configuration or background muscle state likely contribute and should be considered, but they appear insufficient to explain the full breadth of outcomes. Because most protocols aim to deliver a strong proprioceptive inflow with substantial spindle recruitment, a plausible additional source of variability lies in how this afferent drive is integrated within the sensorimotor system. The same mechanical input may be accompanied by a TVR, a KI with or without AVR, or no overt response at all, thereby imposing distinct patterns of sensorimotor load on spinal and supraspinal circuits. Consequently, any neuromuscular outcome measured after MTV likely reflects not only the imposed mechanical parameters but also the *response state* expressed – or not expressed – during stimulation, a factor rarely documented explicitly.

Influence of TVR expression on neuromuscular outcomes.

When a TVR is expressed, the vibratory input drives rhythmic α -motoneuron activation in the vibrated muscle, increasing motor recruitment relative to conditions in which no TVR occurs. Studies reporting preserved force after MTV typically noted the absence of a TVR or did not document whether one was present (Amiez et al., 2023; Cattagni et al., 2016; Farabet et al., 2016; Fry & Folland, 2014; Saito et al., 2016a; Zinke et al., 2019). Across comparable protocols, declines in maximal force have been observed when a TVR was elicited, whereas similar vibratory parameters in the absence of a documented TVR have been associated with preserved force production (Saito et al., 2016a, 2016b). In paradigms where all participants expressed a TVR, larger reflex amplitudes predicted greater reductions in maximal force despite identical exposure, indicating that the magnitude of reflexive engagement influences the magnitude of the subsequent decrease (Amiez, Géhin, et al., 2024). A similar pattern is observed for motoneuronal excitability, which declines more when a TVR develops than when KI predominates, even

though identical MTV parameters were used (Amiez et al., 2025). Collectively, these findings suggest that, within the limited set of protocols in which TVR has been quantified, reflexive activation biases the neuromuscular response towards stronger activity-dependent motoneuron depression for a given vibration duration. Importantly, matching voluntary electromyographic activity to that observed during the TVR does not reproduce the same spinal and corticospinal excitability changes, indicating that activation level alone may not fully account for the effect (Amiez et al., 2025). It remains to be determined whether this reflex-specific effect persists during longer exposures or when force output, rather than electromyographic activity, is matched.

Influence of KI expression on corticospinal excitability.

When no KI is present, corticospinal excitability during MTV typically increases in the vibrated muscle and decreases in its antagonist – a pattern arising from a combination of cortical facilitation of the agonist and spinal mechanisms such as reciprocal inhibition targeting the antagonist (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). By contrast, during KI-induced vibration, corticospinal changes diverge from those observed under purely mechanical recruitment, with reduced facilitation in the vibrated muscle and context- or timing-dependent shifts towards the antagonist. This pattern ranges from clear antagonist facilitation to vision-dependent effects and transient early suppression evolving towards baseline during the build-up of the illusion (Kito et al., 2006; Lauzier et al., 2023; Mancheva et al., 2017; Naito et al., 2002). This inversion suggests that, once the perturbation is reconstructed as movement, redistribution of excitability primarily reflects supraspinal processing of the illusory state rather than spinal modulation. Findings from controlled-duration paradigms reinforce this interpretation. When assessed before and after conditioning, protocols that favour KI while preventing reflex recruitment reduce corticospinal excitability in the vibrated muscle despite preserved motoneuronal responsiveness. This dissociation indicating that the perceptual expression of the afferent input can reconfigure cortical output with minimal motoneuronal load (Amiez et al., 2025). The selective post-conditioning reduction in corticospinal excitability of the vibrated muscle observed following a KI-inducing protocol raises the possibility of increased intracortical inhibition. However, this interpretation remains unresolved because most studies assessing short- or long-interval intracortical inhibition have either not verified whether a KI occurred or have deliberately prevented its emergence, thereby limiting mechanistic conclusions (Christova et al., 2011; Marconi

et al., 2008; Pfenninger et al., 2024; Rosenkranz & Rothwell, 2006).

Cumulative dose effects independent of vibratory responses.

Finally, acute neuromuscular effects induced by MTV do not require the expression of either a TVR or a KI. Across studies applying prolonged vibration within a single session (typically ≥ 30 min), reductions in maximal voluntary force or motoneuronal excitability have been observed both when KI predominates and when vibratory responses are absent or deliberately suppressed (Amiez, Martin, et al., 2024; Kennouche et al., 2022; Lapole et al., 2012; Pfenninger et al., 2023; Rosenkranz & Rothwell, 2012; Souron, Besson, McNeil, et al., 2017; Ushiyama et al., 2005). Convergent evidence comes from very high-frequency, low-amplitude ‘acoustic’ vibrations (≈ 300 Hz, < 0.1 mm), which do not elicit TVR or KI yet produce functional or trophic adaptations after repeated exposure – likely through engagement of cutaneous or mixed somatosensory pathways (Costantino et al., 2017; Pietrangelo et al., 2009). Collectively, these observations emphasize that prolonged exposure to MTV can induce adaptations provided that the cumulative proprioceptive or somatosensory inflow is sufficient to modify neuromuscular function. By contrast, recent findings indicate that, for comparable mechanical parameters and exposure durations, the motor (TVR or AVR) and perceptual expressions that emerge during MTV shape both the distribution and magnitude of neuromuscular adaptations (Amiez, Géhin, et al., 2024, 2025).

Methodological recommendations

Establishing and explicitly reporting experimental conditions should be considered a first essential step for both fundamental and applied investigations employing MTV, as these conditions define how vibratory responses can be expressed, interpreted and meaningfully compared across studies. Frequency and amplitude shape the strength and coherence of the afferent volley, yet effective amplitude is rarely measured directly and may differ markedly from manufacturer specifications due to preload-dependent attenuation (Ferrari et al., 2019). Stimulation site and orientation (tendon vs. muscle belly), muscle state (rest, stretch, submaximal contraction) and joint configuration all influence spindle sensitivity and motoneuronal excitability, thereby modulating the balance between reflexive and perceptual integration. Given that visual and attentional conditions modulate sensory weighting and the expression of KI, they should also be explicitly reported to contextualize vibratory outcomes. Participant instructions, familiarization procedures and any voluntary suppression of the TVR represent additional factors that may bias response

expression. Taken together, these parameters do not impose a specific response but determine the conditions under which the vibratory drive is integrated at spinal and supraspinal levels.

Quantifying motor responses. A second, more specific step for studies employing MTV to probe neuromuscular adaptations is the systematic assessment of motor and perceptual responses using shared and operationally defined criteria. The approaches outlined below therefore integrate objective mechanical, electrophysiological and perceptual indices to characterize central proprioceptive processing. Quantifying the TVR can be approached through involuntary force production or electromyographic activity during vibration, each providing complementary but non-equivalent information. Force or joint-angle displacement offers a mechanical index of reflex expression (De Gail et al., 1966; Goodwin et al., 1972a), although these signals can be extremely small and therefore highly dependent on measurement precision. Electromyographic activity remains more widely used because it integrates naturally into neurophysiological protocols and allows simultaneous monitoring of agonist and antagonist muscles. A first limitation is that conventional bipolar surface electromyography samples only a limited muscle volume, so vibration-induced activation of motor units outside the recording area may remain undetected, particularly in large muscles (Farina et al., 2004; Merletti & Muceli, 2019). A second major challenge is the mechanical contamination of electromyographic signals under vibratory conditions. In humans, motor-unit discharge may show partial synchronization with the vibration frequency and its harmonics (Burke & Schiller, 1976; Desmedt & Godaux, 1975; Hagbarth et al., 1976; Romaguère et al., 1991), but strict cycle-to-cycle phase locking – characteristic of spindle afferents under specific MTV parameters – is not observed in α -motoneurons and appears far less stereotyped in humans than in reduced cat preparations (Burke et al., 1976b; Roll & Vedel, 1982; Thompson et al., 2022). As a result, spectral peaks at the vibration frequency offer limited evidence of genuine reflex activation, as they may arise from mechanical artefact rather than motoneuronal recruitment, a distinction emphasized primarily in whole-body vibration studies (Abercromby et al., 2007; Fratini et al., 2009; Xu et al., 2015). Peaks observed in antagonist muscles – where reciprocal inhibition should reduce excitability – further reinforce the likelihood of artefact contamination. Pragmatic quantification therefore relies on indices that minimize stimulus-locked components. Removing the fundamental frequency and its first harmonic can isolate asynchronous motor-unit activity, and root mean

square amplitude provides a simple estimate of overall recruitment when compared with a pre-stimulation baseline or normalized to a maximal response (e.g. maximal voluntary contraction or maximal muscular response). These approaches do not resolve the ambiguity inherent in vibration-evoked electromyographic activity, but they can improve interpretability when combined with mechanical outcomes. Transparent reporting of signal-processing steps therefore remains essential for comparing reflex expression across studies.

Assessing perceptual responses. Assessment of KI presents analogous challenges and can be evaluated using subjective procedures, complemented when appropriate by simple physiological indices compatible with standard neuromuscular recordings. The Standardized Kinaesthetic Illusion Procedure (SKIP) offers a structured approach in which participants identify the joint angle that elicits the clearest movement percept, rated on a four-level clarity scale and verified for directional accuracy (Beaulieu et al., 2020). While SKIP optimizes illusion strength by individualizing joint position, this adjustment may confound studies in which joint angle is an experimental variable (Collins et al., 2017; Dongés et al., 2019; Forman et al., 2019; Nuzzo et al., 2016). A pragmatic alternative is post-vibration angular reproduction using either the contralateral or vibrated limb. This approach avoids the perceptual attenuation induced by voluntary movement, but still depends on short-term sensorimotor memory, making it an inherently imperfect method (Hagura et al., 2007; Izumizaki et al., 2010; Kito et al., 2006; Schofield et al., 2015). Recording reproduced amplitude and velocity separately helps distinguish illusory movement from positional displacement (Taylor et al., 2017). Subjective ratings (e.g. visual analogue or Likert scales) can complement behavioural measures by capturing vividness or temporal continuity, although they generally do not differentiate movement from positional components (Naito et al., 1999; Roll et al., 2012; Schofield et al., 2015; Steyvers, Levin, Van Baelen, et al., 2003). Because perceptual outcomes rely on self-report measures, inter-individual and contextual differences may lead to under-reporting of KI despite substantial proprioceptive processing (Grünbaum & Christensen, 2024). Accordingly, an absence of reported illusion should not be equated with absence of central integration. In this context, recording the AVR when present can provide additional information indicating that the vibration paradigm has effectively activated the sensorimotor pathways at rest, thus enabling a more objective characterization of response profiles (Amiez, Géhin, et al., 2024; Calvin-Figuère et al., 1999; Feldman & Latash, 1982; Gilhodes et al., 1986).

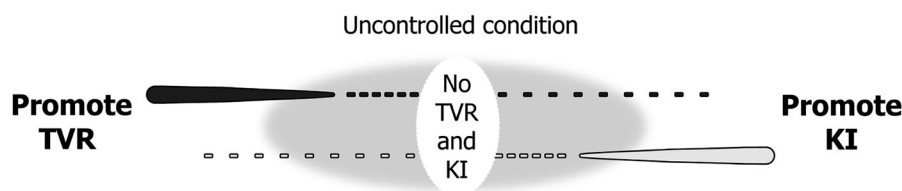


Figure 3. Conceptual continuum linking the tonic vibration reflex (TVR) and the kinaesthetic illusion (KI)
 The central light-grey region represents non-expressive states in which neither response emerges during vibration. Several factors may lead to this state, including subthreshold spindle activation, voluntary or involuntary suppression of reflex expression, or sensorimotor contexts that hinder perceptual reconstruction. The surrounding grey zone denotes uncontrolled sensory or attentional conditions – such as distraction or inconsistent visual input – that further interfere with response expression. These two opposites show contexts that promote integration towards reflexive (i.e. TVR) or perceptual expression (i.e. KI and the antagonist vibratory response), influenced by the stimulation site, muscle state, joint configuration, attentional state and the coherence of the afferent volley. Inter-individual variability and temporal adaptation may shift a given individual across the continuum, even under theoretically optimal conditions. Recognizing these different states helps to clarify that the absence or presence of TVR, KI or antagonist vibratory response reflects the conditions under which the vibratory input was integrated, underscoring the importance of reporting sensory, mechanical and attentional parameters when analysing the effects of muscle–tendon vibration.

Conclusion

This review outlines how a common spindle-driven proprioceptive input can be expressed as reflexive, perceptual or non-expressive responses, depending on the mechanical, sensory and attentional context in which MTV is applied. These responses, which arise from the integration of the afferent signal, show substantial inter-individual variability and are rarely documented explicitly, despite recent evidence that they influence vibration-induced neuromuscular adaptations (Amiez, Géhin, et al., 2024, 2025). Systematic identification of TVR, KI and AVR is therefore essential for understanding why conceptually similar vibration protocols can produce divergent effects along a continuum that reflects how a common proprioceptive input is integrated under different sensorimotor conditions (Fig. 3). This does not imply that exhaustive monitoring of all responses is required in every experimental or applied setting. Rather, it highlights that when neuromuscular mechanisms are under investigation, failure to document – or at least to control for – how the vibratory input was expressed constitutes a substantive limitation for interpretation.

Beyond characterizing vibratory responses, an important direction for future work is to determine whether systematically biasing response expression towards reflexive or perceptual configurations influences acute or chronic adaptations. Tendon-based application, slight background activation or manoeuvres known to facilitate spinal reflexes (e.g. Jendrassik (Eklund & Hagbarth, 1966; Lance et al., 1973)) may increase the likelihood of reflexive expression. Conversely, combining vibration with stretching, using intermittent stimulation, alternating stimulation between agonist and antagonist muscles, or applying optimized joint-positioning procedures such as SKIP can favour perceptual expression

(Beaulieu et al., 2020; Ribot-Ciscar et al., 1998; Roll & Vedel, 1982; Steyvers, Levin, Verschueren, et al., 2003). Integrating vibration with imagery- or observation-based paradigms may further enhance the probability of eliciting an illusory movement or, in some individuals, an antagonist response (Bisio et al., 2019; Dilena et al., 2019; Shibata et al., 2017). Whether such manipulations alter the magnitude or distribution of vibration-induced adaptations remains unresolved, but they provide a mechanistic framework for testing how specific sensorimotor contexts shape the effects of MTV. By explicitly distinguishing between the afferent drive imposed by vibration and the way this drive is centrally integrated and expressed, future studies can better account for variability in neuromuscular outcomes and more precisely define the physiological conditions under which MTV is effective.

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Additional information

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

Author contributions

All authors contributed to the conception or design of the work and drafting the work or revising it critically for important intellectual content. All authors have approved the final version of the manuscript and agree to be accountable for all aspects of the work. All persons designated as authors qualify for authorship, and all those who qualify for authorship are listed.

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Supporting information

Additional supporting information can be found online in the Supporting Information section at the end of the HTML view of the article. Supporting information files available:

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