The potential neural mechanisms of acute indirect vibration

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Abstract
There is strong evidence to suggest that acute indirect vibration acts on muscle to enhance force, power, flexibility, balance and proprioception suggesting neural enhancement. Nevertheless, the neural mechanism(s) of vibration and its potentiating effect have received little attention. One proposal suggests that spinal reflexes enhance muscle contraction through a reflex activity known as tonic vibration stretch reflex (TVR), which increases muscle activation. However, TVR is based on direct, brief, and high frequency vibration (>100 Hz) which differs to indirect vibration, which is applied to the whole body or body parts at lower vibration frequency (5-45 Hz). Likewise, muscle tuning and neuromuscular aspects are other candidate mechanisms used to explain the vibration phenomenon. But there is much debate in terms of identifying which neural mechanism(s) are responsible for acute vibration; due to a number of studies using various vibration testing protocols. These protocols include: different methods of application, vibration variables, training duration, exercise types and a range of population groups. Therefore, the neural mechanism of acute vibration remain equivocal, but spinal reflexes, muscle tuning and neuromuscular aspects are all viable factors that may contribute in different ways to increasing muscular performance. Additional research is encouraged to determine which neural mechanism(s) and their contributions are responsible for acute vibration. Testing variables and vibration applications need to be standardised before reaching a consensus on which neural mechanism(s) occur during and post-vibration.

Key words: Spinal reflexes, muscle tuning, motor unit firing frequency, motor unit synchronisation, inter-muscular co-ordination.

Introduction

Acute vibration training is gaining popularity as a modality for sport, exercise and physical rehabilitation as it initiates a rapidly and repeating eccentric-concentric action that evokes muscular work and elevates metabolic rate (Rittweger et al., 2003). Vibration exercise has taken on many different forms; custom built vibratory devices have recently been constructed specifically for flexibility training (Sands et al., 2006), while other vibration units have been attached to resistance training equipment (Issurin and Tenenbaum, 1999) and smaller units have been directly applied to muscle and tendon. Over the past decade, two products have featured on the commercial market, an electric powered vibrating dumbbell and the vibrating platform. There are two types of vibrating platforms; the first produces vertical sinusoidal vibrations (VV), which are transmitted to the body via the platform, the second moves in a side-alternating motion (SV).

During vibration, the transference of energy occurs from the vibration source to the whole body or body part, which causes reactive forces within the body. These forces have the potential to be harmful, but also beneficial. The human body is a spring-mass system where tendons and muscles act like springs to store and release mechanical energy, where the stiffness and mass of these body parts will determine the natural frequency (Rittweger, 2010). Therefore, the body can acquire accumulated mechanical energy when the vibration frequency of the device matches parallels with the resonance frequency of the body (Rittweger, 2010). This can be controlled by adjusting body position and changing muscle stiffness (Mester et al., 2006) where muscles have innate damping characteristics that can absorb energy and generate heat (Wakeling et al., 2002).

The vibratory load is dependent on four variables: frequency (f), amplitude (A), acceleration (a), and duration (t). The number of cycles of oscillation determines the frequency (Hz); the amplitude refers to the maximal displacement of the oscillatory motion (mm); the acceleration (m·s^{-2} or g) determines the magnitude; and duration refers to the exposure time (min or s). Low vibration frequency (5-45Hz) has been reported to increase EMG activity, muscle force, and power (Bosco et al., 1999a; 1999b, Cardinale and Lim, 2003; Cochrane and Stannard 2005; Cochrane et al., 2010b; Torvinen et al., 2002; Stewart et al., 2009) where excitatory responses of the muscle spindle are speculated to play a role in enhancing muscle activation, involving a spinal reflex mechanism. The muscle tuning response is another possible mechanism where the muscular system damps the vibration stimuli to promote muscle activity that may subsequently increase muscle function.

Additionally, the neural adaptations that occur from resistance and power training have been purported to be similar to that of acute indirect vibration (Bosco et al., 1998; 1999a; 1999b; Cardinale and Bosco, 2003; Delecluse et al., 2003). Neural aspects, such as motor unit recruitment, synchronisation, and co-contraction may be responsible for force and power increases following acute vibration. Other mechanisms of vibration, such as a warm-up effect, where friction between the vibrating tissues may raise muscle temperature (Issurin and Tenenbaum, 1999), coupled with a vibratory induced increase in blood flow (Kerschan-Schindl et al., 2001) may also contribute to enhancing muscle performance. To date, there has been no direct attempt to identify which mechanism(s) may contribute to the enhancement of neuromuscular performance. Therefore, this paper explores and assesses the possible neural mechanism(s) of acute

indirect vibration.

Methodology

A search was conducted using the following electronic databases: Medline, PubMed, ISI Web of Knowledge and Scopus. Key search words included, vibration and whole-body vibration; which were used in combination with spinal reflexes, muscle tuning, neuromuscular (motor unit firing frequency, synchronisation, intermuscular co-ordination) and central motor command. Articles were checked for relevant content and were included based on the following criteria: 1. published in English; 2. examined acute (single session) vibration; 3. the participants were healthy and trained, 4. conference abstracts and proceedings were excluded.

Types of vibration

As mentioned previously there are many different methods of producing acute vibration. Small vibratory units have been applied directly to the muscle or tendon (Warman et al., 2002; Jackson and Turner, 2003); while larger custom-built vibratory units have been constructed for flexibility training (Kinser et al., 2008; Sands et al., 2006; 2008), and resistance training to elicit vibration transmission through cables of various machines (Issurin and Tenenbaum, 1999).

Over the last decade, two commercial forms of acute indirect vibration are available for consumer use, the vibrating platform and vibrating dumbbell, which produce vertical sinusoidal vibration. As stated earlier, two types of vibrating platforms exist that involve standing and/or performing dynamic and/or static exercises. One type of platform oscillates around a central axis, where a crankshaft on each side of the platform translates to a rotationalmotion of the electro-motor into a vertical displacement, inducing a seesaw motion, of which the amplitude is either small closer to central axis or larger near the edge of the platform (0-10 mm). The second commercial machine has electro-motors that produce vertical synchronous vibration where both legs vibrate as the platform moves predominately in the vertical direction, which results in simultaneous and symmetrical movement of both sides of the body during the vibration exposure. The foot placement of this platform is independent of amplitude and has a pre-setting of two ranges; 0-2 mm or 4-6 mm. Commercially manufactured hand-held powered vibrating dumbbells have also been developed to target the upper-body where the central handle of the dumbbell rotates producing oscillatory movements to the body.

Various vibration protocols have examined the purported neural mechanism(s), through the investigation of different vibration equipment, varying vibration frequencies, amplitudes and durations, various exercises and participant types; all of the above could potentially influence the outcome measures. Additionally, a difference exists in applying the vibration by direct or indirect methods. Direct vibration is normally applied to muscle or tendon at a high vibration frequency (100-150 Hz), at a small amplitude (1-2 mm) for a short period of time (2-15 s), resulting in a transient increase in muscle activity known as the tonic vibration reflex (Eklund and Hagbarth,

1966). However, indirect vibration typically uses a lower vibration frequency (25-45 Hz), set at a high amplitude (2-10 mm) with longer duration time of either continuous (3-5 min) or intermittent exposure (30-60 s), where the vibration is applied through the feet (platform) or hands (cable or dumbbell).

Even so, there is still a lack of prescriptive guidelines for vibration, which makes it difficult to compare the various studies. The optimal vibration frequency, amplitude, duration and the type of exercises to perform remains equivocal due to inadequate validation of these variables. This aside, some experiments have failed to include appropriate control and/or sham conditions, giving uncertainty to the value of vibration. There is additional concern over the potential difference in vibration transmission between side-alternating (SV) and vertical (VV) vibration platforms. Earlier, Rittweger et al. (2001) proposed a hypothesis that in SV, the feet alternate between up and down positions, causing pelvis rotation and flexion of the spinal column, which decreases vibration transmission to the head. To test this hypothesis Abercromby et al. (2007b) compared SV and VV platforms at a set vibration frequency and amplitude (f=30 Hz, A=4 mm) while performing slow dynamic squats (4s up and 4 s down) from 10 to 35° knee flexion. They found that vibration transmitted to the upper-body and head was 71 to 189% greater during VV than SV and concluded that the pelvis damped the vibration energy more during SV than the VV. However, a complete kinematic analysis of SV and VV conducted over a larger range of knee angles across different vibration frequencies and amplitudes are required to validate this claim.

In another study, the same authors (Abercromby et al., 2007a) investigated muscle activity of SV and VV (f = 30 Hz, A = 4 mm). They reported that during dynamic (from 10° to 35°of knee flexion, at a tempo of 4 s up 4 s down) and static squatting (18.5° knee flexion) the lower limb extensors (vastus lateralis and gastrocnemius) were activated significantly more during SV than VV; and the activation of the tibialis anterior was significantly greater during VV than SV. Therefore, it would be of interest to conduct additional static squat experiments at a variety of fixed knee angles and perform dynamic squats over a larger range of knee flexion to identify if further differences in muscle activation exist between VV and SV.

Spinal reflexes

It is suggested that acute vibration may improve muscular performance via neurogenic potentiation involving the spinal reflexes and muscle activation (Cardinale and Bosco, 2003, Rittweger et al., 2003). The main evidence in supporting neurogenic potentiation is based on measurements of the tonic vibration reflex (TVR). Previous studies have reported that a vibration stimulus is capable of augmenting muscle spindle activity, which causes an excitatory response in the primary endings of non-contracting muscle (Burke et al., 1976; Ribot-Ciscar et al., 1998). As a result of direct vibration, an ensuing muscle contraction occurs with reciprocal inhibition of its antagonists, which has been termed the TVR (Eklund and Hagbarth, 1965; 1966; Matthews, 1966). This elicits an excitatory response of the muscle spindle Ia fibres

Table 1. Evidence for Spinal Reflexes.

Author	Participants	Vibration Method (type)	Exercise Type	Frequency (Hz)	Amplitude (mm)	Duration	Results
Armstrong et al., 2008	19 RA (8♂, 11 ♀)	VV platform	SS	40	2-4mm	1 min	There was a significant suppression of the H-Reflex 1 min post-vibration.
Burke et al., 1976	18 H (♂, ♀ = NR)	Direct vibration	Static	20-220	1.5	4 s	Both primary and secondary spindle endings respond with repetitive discharge when vibration was applied to the tendon of the non-contracting muscle. The responses of the primary endings were reduced during muscle vibration
Cochrane et al., 2008	12 RA Young, 12 RA Old (6♂, 6 ♀)	VV leg press	SS & Jendrassik	30	1	4 mins	VV + Jendrassik contraction increased VO_2 by 27.6% for the old and 33% for the young group but there were no significant difference between the groups
Cochrane et al., 2009	9 RA (♂)	SV platform Control	SS SS	6 0	3.1 0	15 s 15 s	6 Hz significantly increased muscle-tendon complex, contractile length, and EMG modulation compared to 0 Hz.
Hopkins et al., 2008	11 RA (6♂, 6 ♀) 11 RA (6♂, 6 ♀)	SV platform Control	SS SS	26 0	~ 4 0	5 x 1 min 0	Vibration did not show any significant changes in quadriceps stretch reflex amplitude or latency.
Melnyk et al., 2008	13 RA (♂, ♀=NR) 11 RA (♂, ♀=NR)	VV platform Normal activity	SS NA	30 NA	4 NA	2 x 1 min NA	Vibration significantly decreased tibial translation and significantly increased short latency response o lateral and medial hamstring muscles.
Nishihira et al., 2002	17 HP (♂, ♀=NR)	SV platform	SS	25	NR	3 x 3mins	The H/M ratio was significantly greater post-vibration compared to pre values.
Rittweger et al., 2003	19 RA (9♂, 10♀)	SV platform	DS to exhaustion	26 0	6 0	349 s 515 s	Immediately post-vibration tendon patellar tendon reflex amplitude was significantly greater compared to exhaustive dynamic squatting without vibration.
Ritzmann et al., 2010	10 RA ♀ (5♂, 5♀)	SV platform Ankle Ergometer	SS Standing upright	5-30 NA	4 NA	10 s	The ankle ergometer used to evoke the stretch reflex latency of tricep surae was almost identical to the latency of the same muscle group that received vibration, supporting the idea that vibration induces stretch reflexes.
Roll et al., 1989	27 H (♂, ♀ = NR)	Direct vibration	Static	10-200	0.2-0.5	20 s	Muscle spindle primary endings were the most sensitive to the vibration.

RA = Recreationally active; **H** = Healthy; **SV**= Side alternating vibration; **VV** = Vertical vibration; **DS**= Dynamic squat; **SS** = Static squat; **NA** = Not Applicable; **NR** = Not reported

(Burke et al., 1976, De Gail et al. 1966, Roll et al. 1989), which is mediated by monosynaptic and polysynaptic pathways (Matthews, 1966; Romaiguere et al., 1991). The excitability of the motoneurons innervating the antagonist muscles are depressed by reciprocal inhibition (De Gail et al., 1966; Lance et al., 1966), and the monosynaptic stretch reflexes of the vibrated muscle are suppressed during the vibration (De Gail et al., 1966; Marsden et al., 1969).

Burke et al. (1976) found that when direct vibrations of 20-220 Hz (Table 1) were applied to a tendon of non-contracting muscle, the primary endings responded more during high frequency vibration than secondary endings, which corresponded to earlier findings from cat studies conducted by Bianconi and van der Meulen (1963) and Brown et al. (1967). However, Burke et al. (1976) also found that both primary and secondary endings respond by discharging in synchrony to the vibration stimulus, which contradicts Bianconi et al. (1963) findings. The explanation for this discrepancy is that Bianconi et al. (1963) did not differentiate between endings that were unresponsive and those capable of being activated from vibration.

When the vibratory stimulus is applied to an agonist muscle it causes reciprocal inhibition of the antagonist motoneurons (Bishop, 1974); but when vibration is applied simultaneously to the agonist and antagonist muscles, the facilitatory effect of each muscle group is inhibited (Hagbarth, 1967). However, when both muscles independently vibrate they show a strong TVR (Bishop, 1974). Vibration also causes suppression of the muscle's phasic stretch reflexes (De Gail et al., 1966; Marsden et al., 1969). Arcangel et al. (1971) observed that during tendon vibration, the Achilles tendon reflex and the Hoffmann response (H response) were suppressed, but in the post-vibratory period the reflexes were potentiated, indicating that pre-synaptic inhibition of the Ia afferent terminals occurred (Gillies et al., 1969). Desmedt et al. (1978) confirmed that motor unit recruitment was suppressed by the direct application of high vibration amplitudes, which caused pre-synaptic inhibition of Ia afferents.

According to Bishop (1974), four factors affect the TVR response: 1) the location of the vibration; 2) the excitability state of the CNS; 3) the initial length of muscle i.e. pre-stretch; and 4) the vibration frequency and amplitude. Research has suggested that the initial muscle length influences the strength of the TVR where further lengthening of a muscle will induce a stronger TVR (Bishop, 1974; Eklund and Hagbarth, 1966). Vi

bration amplitude can determine the amount of stretch occurring within the muscle. Matthews (1966) and Brown et al. (1967) reported that in decerebrated cats increasing the vibration amplitude caused an increase in TVR, as this activated a larger number of muscle-spindle endings and caused more α motoneurons to be activated (Luo et al., 2005). However, the range of amplitude, which caused augmentation, occurred between 25-150 μm (Bishop 1974). Moran et al. (2007) argued that higher vibration amplitudes may only benefit sub-maximal contractions and proposed that in maximal voluntary contractions the Ia afferent discharge may reach a saturation threshold, where vibration is unable to cause further increases in Ia afferent inflow. Supporting evidence is based on observations that state, vibration can only increase maximal isometric contraction force and EMG activity when fatigue is present in the intrafusal fibres (Bongiovanni and Hagbarth, 1990) or when α-fibre are blocked (Hagbarth et al., 1986).

The Jendrassik manoeuvre is a procedure that involves contracting remote muscles, normally of the upper-body (particularly the forearm and jaw muscles) to induce a reflex response (Jendrassik, 1885). A common method for eliciting a reflex is to grasp the hands and pull them apart – this potentiates the stretch reflex and H-reflex (Delwaide and Toulouse, 1980; Dowman and Wolpaw, 1988). Using a prototype vibration machine consisting of a motorised horizontal leg press fitted with two electrically powered motors to the rear of the foot plate; young (21.5y) and old (69.2y) participants were vibrated at 30 Hz (A = 1 mm), whilst performing the Jendrassik manoeuvre for four minutes (Cochrane et al., 2008). This involved pulling with both arms a dual handle load cell at 10% maximal voluntary contraction while seated with their feet on the vibrating plate of the leg press with the knees flexed at 70°. The authors reported that superimposing the Jendrassik manoeuvre upon vibration enhanced metabolic rate in both young (27.6%) and old (33%) groups, but there were no significant differences between the groups (Table 1). Further, using a side-alternating vibration (SV) platform, acute low frequency vibration (f = 6 Hz, A = 3.1 mm) produced a temporal association between EMG activity and muscle contractile tissue displacement suggesting that muscle lengthening may be a prerequisite to eliciting probable stretch reflexes (Cochrane et al., 2009).

However, in a follow up study (Cochrane et al., 2010a) reported that after five minutes of continuous acute indirect vibration (f = 26 Hz, A = 6 mm, SV) there was minimal change in patellar tendon reflex properties, but muscle twitch characteristics were potentiated indicating that a greater myogenic response was present compared to a neural-mediated effect of a reflex potentiation. Likewise, Hopkins et al. (2008) found no effect on the patellar tendon reflex after intermittent (5 x 1 min bouts) vibration exposure (f = 26 Hz, A = 4 mm, SV). Other studies have reported enhancement of the stretch reflex, for example, Melnyk et al. (2008) initiated the stretch reflex in the hamstrings by inducing an anterior tibial translation during standing; they also compared the reflex

response between two groups that performed either intermittent (2 x 1 min) vibration (f=30 Hz, A= 4 mm, VV) or normal activity (control). The researchers found post-vibration, that anterior tibial translation displacement decreased with a corresponding increase in EMG of the hamstring short latency response. The authors concluded that the effect of increased knee stability caused reflex excitability. However, it is inconclusive whether the stretch reflex was the causal factor in decreasing anterior tibial translation because the control group did not perform the same protocol without vibration. An earlier study reported an increase in the patellar tendon reflex immediately following exhaustive squatting exercise with continuous vibration (f = 26 Hz, A = 12 mm, SV) and extra load (40% of body mass). The authors concluded that α motoneurons were augmented by the vibration, which recruited high-threshold units and muscle fibres (Rittweger et al., 2003). To date, only one study has confirmed that stretch reflexes were induced during vibration (f = 5-30 Hz, A = 4 mm, SV) (Ritzmann et al., 2010). This study measured the EMG activity of the soleus and medial gastrocnemius muscles during different vibration frequencies in comparison to an evoked stretch reflex of the same muscle groups using a custom-built ankle ergometer and found that the EMG activity was identical between the vibration and the evoked stretch reflex, indicating the existence of vibration-induced reflexes.

Currently, two studies have examined the response of the H-reflex following acute indirect vibration, both producing different results. Nishihira et al. (2002) found that the H-reflex and H max/M max ratio was enhanced, suggesting that motoneuron excitability was heightened; while Armstrong et al. (2008) found the H-reflex was suppressed (Table 1). The disagreement in these findings was most likely due to different vibration and H-reflex protocols. Nishihira et al. (2002) used three sets of three minute vibration protocol (f = 25 Hz, A = not reported, SV) where the H-reflex was activated from a seated position, which differed to Armstrong et al. (2008) one minute duration performed on a VV platform (f = 40 Hz, A = 2-4 mm) where the H-reflex was activated from a supine position. Major limitations to the above studies were that both lacked a control group and both failed to disclose the exact testing protocol of the H-reflex.

In summary, the proposed mechanism of acute indirect vibration causing a response similar to that of TVR cannot be supported (Nordlund and Thorstensson, 2007). TVR requires vibration to be directly applied to the muscle or tendon at high vibration frequencies (>100 Hz), typically other vibration methods such as, platforms and dumbbells are not directly applied to the body and are subjected to lower frequencies (20-45 Hz) and longer exposure times (>30s). Therefore, it is difficult to uphold the view that acute indirect vibration may act through a spinal mechanism, such as TVR. However, vibration may cause an indirect involvement of muscle spindles, where other sensory inputs may influence gamma (γ) motoneuron activity, causing changes to spindle input (Gandevia 2001). Additionally, the evidence is inconclusive whether acute indirect vibration potentiates stretch reflexes, this is

Table 2. Evidence for Muscle Tuning

Author	Participants	Vibration Method (type)	Exercise Type	Frequency (Hz)	Amplitude (mm)	Duration	Results
Wakeling and Nigg, 2001	14 HP (7♂, 7♀)	Voluntary contractions	Isometric & isotonic	NA	NA	NA	Soft tissue vibration frequency and damping increased with both the force production and the shortening velocity of the muscle.
Wakeling et al., 2002	10 HP (♂)	VV platform	Standing upright	10-65	5	6 s	Increased EMG activity and damping of vibration occurred when the frequency input was close to the natural frequency of the soft tissue.

HP = Healthy participants; **VV** = Vertical vibration; **NA** = Not Applicable

due to the different vibration protocols, applications and durations; therefore it remains undetermined whether spinal reflexes are the causal mechanism.

Muscle tuning

There is evidence to suggest that the body is capable of tuning its muscle activity in order to reduce the vibrations that are passing through the soft tissue that may produce a detrimental effect (Nigg, 1997). The amount of muscle activity required is dependent on the level of vibration, where maximal muscle activation can reduce or purge oscillations within the tissues. Everyday activities such as walking, running and jumping result in impact forces, from the collision of the heel with the ground, producing vibrations of 10–20 Hz to the lower limbs (Wakeling and Nigg, 2001), where an input signal from the impact force produces muscle activity or 'tuning' response to reduce soft tissue vibrations. This activation or tuning supposedly occurs shortly before the heel strikes the ground (Nigg, 1997). Consequently, muscle tuning relies on three components: i) the frequency and amplitude of the input force, ii) the vibration resonance of the soft tissue and iii) the level of muscle activity. To test the activation level of additional muscles from vibrations, a hydraulic actuator was used to mimic the force during running, by directly evoking vibrations onto the sole of a foot using a range of vibration frequencies (10-65 Hz) (Wakeling et al., 2002). The study found that damping occurred in the lower limb soft tissues and resonance reduction occurred at heel strike (Table 2). However, the natural frequency of the soft tissues did not change and paralleled the frequency of the input. The mechanism of this response remains unclear, but if damping does occur in soft-tissues, where resonance is minimised at heel strike and the changes in frequency are a consequence of altered muscle activity then energy absorbed by the muscle is likely to involve cross-bridge cycling (Ettema and Huijing, 1994, Wakeling et al., 2002). Consequently, damping vibration will depend on the individual's neuromuscular (muscle spindle) response, the sensitivity of joint and skin receptors, the proportion of muscle fibre types and viscoelastic (stiffness) elements (Bazzett-Jones et al., 2008). Due to impact forces, there is a possibility of vibrations occurring in soft tissues that have viscoelastic properties. Mechanical energy from the vibration can be stored and returned from the elastic structures of the muscle-tendon complex where the damping of vibrations may result in a net dissipation of mechanical energy that can be absorbed by activated muscle.

In summary, impact forces create vibrations in the foot where the vibrations travel through the lower limb musculature. To prevent resonance, soft tissues damp the vibrations, which cause sensory organs to send impulses to the CNS to increase muscle activity and adjust joint stiffness. The muscle tuning mechanism relies on the input force, the vibration response of the tissue and the level of muscle activity, which can make it difficult to analyse (Cardinale and Wakeling, 2005). There are similarities between single repeated impact inputs and continuous vibrations suggesting that the tissues minimise vibrations despite the input force mode. However, the validation of the muscle tuning hypothesis is dependent on developing further studies to determine the effect of vibration amplitude on tissue response.

Neuromuscular

The increase in muscle force and power following acute indirect vibrations are purported to be similar to resistance training (Bosco et al., 1998; 1999a; 1999b; Cardinale and Bosco, 2003; Delecluse et al., 2003). According to Cardinale and Bosco (2003), resistance training and vibration place load on the neuromuscular system. During resistance training, extra load is added to increase the influence of gravity, in the form of barbells, dumbbells, rubber bands or manual resistance. Resistance in terms of vibration is altered by adjusting vibration frequency and/or amplitude, which increases the acceleration and force placed on the body. Increasing the acceleration has the ability to modify the neuromuscular aspects through neurogenic and myogenic factors. The initial changes (1-3 weeks) due to resistance and power training are often attributed to neural adaptations (Aagaard et al., 2002; Gabriel et al., 2006; Sale 1988; Staron et al. 1994). However, protein synthesis, a precursor for hypertrophy can occur after one resistance training session (Chesley et al. 1992), changes in muscle size (hypertrophy) occur four to six weeks after training commences (Kraemer et al., 2002). Therefore, a closer examination of how acute indirect vibration may influence neural responses of motor unit firing, motor unit synchronisation, inter-muscular coordination is required.

Motor unit firing frequency

Motor unit firing frequency refers to the number of impulses per second that the muscle fibre of a motor unit receives from the motoneuron. The force output of every motor unit can be varied by the firing frequency from 10 to 60 impulses per second during sustained contractions

(Sale, 2003). However, in high speed movements firing rates of 60-120 impulses per second are common during force production (Desmedt and Godaux, 1977). Force production increases as a result of increased motor unit recruitment and/or firing frequency. Therefore, when motor unit recruitment patterns and firing frequency rates are optimized, a maximal contraction force may occur. However, not all muscles exhibit the same characteristics; firing frequency and recruitment may differ from muscle to muscle.

Rapid changes in motor unit firing frequency have been reported in both young and older adults, after completing six weeks of resistance training (Kamen and Knight 2004). The authors found that vastus lateralis motor unit firing frequency increased by 15% and 49% in young and older adults, respectively during maximal isometric knee extension. Likewise, Patten et al. (2001) reported that the firing frequency of the abductor digiti minimi was significantly increased 48 hours after completing maximal isometric contractions. These results indicate that early increases in force output due to resistance training are partly caused by increased firing frequency. When high frequency vibrations (150 Hz) were applied over the tendons of ankle dorsiflexor muscles, Bongiovanni and Hagbarth (1990) reported that the firing frequency in non-fatigued muscle did not change; but the vibration caused an increase in force, EMG and firing frequency during fatiguing isometric maximal voluntary contractions (Table 3). Similarly, Griffin et al. (2001) reported that the firing frequency increased when direct vibration was applied to the distal tendon of the triceps brachii following a two minute sustained 20% maximal voluntary contraction (MVC). The authors suggest that during the isometric contraction muscle spindle activity declined to support the motoneuron pool, and consequently firing frequency decreased. However, muscle spindles are responsive to vibration, especially the Ia afferents (Burke et al., 1976; De Gail et al., 1966; Roll et al. 1989), which may prevent a decline in muscle spindle activity to support the motoneuron pool (Griffin et al., 2001).

In summary, application of direct brief vibration (10-20 s) to fatigued dorsiflexor muscles increased motor unit firing rate, enhanced EMG and augmented maximal force (Bongiovanni and Hagbarth, 1990). Likewise, motor unit firing frequency and isometric force increased in fatigued arm muscles when short duration direct vibrations were applied every 2s for 10s (Griffin et al., 2001) suggesting that motor output facilitation occurs during brief vibratory periods. However, current research has focused on direct vibration in fatigued and non-fatigued muscle, the effects of acute indirect vibration on the rate of motor unit firing frequency of non-fatigued muscle during range vibration frequencies (25-45 Hz) and amplitudes (2-10 mm) are relatively untested. Therefore, carefully well-designed studies with the appropriate electrophysiological techniques are required to determine if motor unit firing frequency plays a role in enhancing neuromuscular measures.

Motor unit synchronisation
Motor unit synchronisation relies on the number of motor units firing at any one time. Synchronisation occurs from branched inputs of pre-synaptic neurons that produce a common synaptic input to increase the chance of motoneurons discharging simultaneously (Fling et al., 2009). Increased motor unit synchronisation is one explanation used to account for the increase in force and power production following resistance training (Gabriel et al., 2006, Sale, 1988, Semmler, 2002). Milner-Brown et al. (1975) investigated the discharge rates of the first dorsal interosseous muscle and found that synchronisation was greater in weightlifters than control participants. However, synchronisation was estimated using an indirect method of averaging surface EMG signal with respect to motor unit discharge, which has since been challenged (Yue et al., 1995). By using direct motor unit measurements, Semmler and Nordstrom (1998) reported that resistance trained weightlifters produced a higher level of synchronisation compared to highly skilled musicians, indicating that synchronisation may be an adaptation of resistance training to enhance force production. Yao et al. (2000) found that during motor unit synchronisation, EMG increased by 65-135% with corresponding force fluctuations. Martin and Park (1997) reported that when direct vibration was applied to finger and wrist muscles, harmonic synchronisation decreased. However, subharmonic synchronisation increased when vibration frequency increased from 40 to 200 Hz, where high vibration frequency (>150 Hz) produced less motor unit synchronisation (Table 4).

Following acute indirect vibration, an enhancement

Table 3. Evidence for Motor Unit Firing Frequency

Author	Participants	Vibration Method (type)	Exercise Type	Frequency (Hz)	Amplitude (mm)	Duration	Results
Bongiovanni and Hagbarth, 1990	5 H ♀ (♂, ♀ = NR)	Direct vibration dorsiflexor muscles	SS	150	1.5	20-25 s	Vibration had no effect on firing frequency of non-fatiguing muscle, however vibration caused an increase in EMG, force and firing frequency during fatiguing isometric maximal voluntary contractions.
Griffin et al., 2001	7 H (3♂, 4♀)	Direct Vibration triceps & biceps brachii	Isometric	110	3	2 s every 10 s	The firing frequency of the triceps significantly increased when vibration was applied during 20% MVC

H = Healthy; **SS** = Static squat; **MVC** = Maximal voluntary contraction

Table 4. Evidence for motor unit synchronisation.

Author	Participants	Vibration Method (type)	Exercise Type	Frequency (Hz)	Amplitude (mm)	Duration	Results
Bosco et al., 1999a	12 ♂ national boxers	DB	Elbow Flexion	26 0	6 0	5 x 60 s 5 x 60 s	During vibration %EMG$_{rms}$ significantly increased and elbow flexion power was significantly enhanced (14%) compared to no vibration.
Bosco et al., 1999b	6 AT♀	SV Control	SS SS	26 0	10 0	10 x 60s 10 x 60s	Leg press velocity-force and power-force relationship shifted to the right after vibration
Bosco et al., 2000	14 RA	SV	Standing, SS, lunge	26	10	5 x 90 s, 10 days	Vibration increased leg press power (160% of body mass) by 7% and EMG/Power ratio significantly decreased
Delecluse et al., 2003	18 UT ♀ 19 UT ♀ 18 UT ♀	VV Placebo Resistance	DS, SS, lunge DS, SS, lunge Cardio +knee & leg extensor strength	35-40 Low Cardio (20mins), 20RM (2wks), 15RM (3wks), 12RM (3wks), 10RM (4wks)	2.5-5 Low	⎱ 1-3 x 2-6 ⎰ x30-60 s (3x/wk, 12 wks)	There was a significant increase in isometric and dynamic knee extensor strength for vibration and resistance groups but there was no significant difference between the two groups. Vibration increased EMG activity in rectus femoris and medial gastrocnemius compared to placebo group.
	19 UT ♀	Control	No training	NA		NA	
Martin and Park, 1997	10 H	Direct vibration	Isometric hand grip	40, 80, 100, 120, 150, 200 at 0, 10 or 20% MVC	0.2-0.3	60 s	Vibration frequency of greater than 150 Hz induced less motor unit synchronisation. When vibration increases subharmonic synchronisation increases but harmonic synchronisation decreases.

RA = Recreationally active; **H** = Healthy; **AT** = Athletes; **UT** = Untrained **DB** = Dumbbell; **SV**= Side alternating vibration; **VV** = Vertical vibration; **DS**= Dynamic squat; **SS** = Static squat; **MVC** = Maximal voluntary contraction; **NA**= Not applicable; **RM** = Repetition maximum

in EMG, force, and power production provides evidence of improved motor unit recruitment (Bosco et al., 1998; 1999a; 2000; Cardinale and Bosco, 2003; Delecluse et al. 2003). However, according to Yue et al. (1995), surface EMG is a poor indicator of motor unit synchronisation and caution is required when interpreting results.

In summary, it has been well documented that direct vibration activates the primary afferent endings of the motor spindles which activate the α motoneurons to recruit previous inactive muscle fibres into contraction (Bishop 1974). Future indirect vibration studies should focus on whether a greater number of potential motor units are synchronised due to the transmission of vibration from proximal to distal muscle groups. Further, it is there is a suggestion that an optimal vibration frequency exists to increase motor unit synchronisation and any vibration frequencies above this level may cause motor unit synchronisation to decrease (Jackson and Turner, 2003; Martin and Park, 1997). It remains unclear to whether motor unit synchronisation occurs during acute indirect vibration, as no studies have specifically assessed single motor unit discharge.

Inter-muscular co-ordination
Inter-muscular co-ordination is the interaction between muscle groups during muscular activity. Contraction of the agonists may be associated with simultaneous contraction of

their antagonists (Sale, 1988). Tyler and Hutton (1986) reported antagonist co-contraction reduced agonist force production, indicated by a decrease in muscle activity (EMG). When performing new and complex tasks the co-contraction of antagonists through reciprocal inhibition may impair agonist contraction (Sale, 1988). However, through continual practice and training the level of co-contraction may be reduced, which could allow for a greater activation of the agonists. Carolan and Cafarelli (1992) reported that after eight weeks of knee extensor resistance training, force increased in the knee extensors with a reduction in antagonist (bicep femoris) co-contraction, which was shown by a decrease in bicep femoris EMG activity (Table 5).

It has been stated that acute indirect vibration causes neural changes synonymous to that of resistance and power training (Bosco et al., 2000). If true, an improvement in agonist activation and increased inhibition of antagonist muscles should also exist. Evidence from acute direct vibration studies suggest that an excitatory response of the muscle spindle occurs, which activates the Ia afferents. These afferents in turn, excite the α motoneurons of the homonymous muscle, which may uncouple the co-contraction of agonist-antagonists (Eklund and Hagbarth, 1966). Rothmuller and Cafarelli (1995) have reported that antagonist co-contraction increased during fatigue and vibration elicited a greater co-contraction than the control condition, but the co-contraction did not change

Table 5. Evidence for Inter-muscular co-ordination.

Author	Participants	Vibration Method (type)	Exercise Type	Frequency (Hz)	Amplitude (mm)	Duration	Results
Abercromby et al., 2007a	16 H (9♂, 7♀)	VV, SV VV, SV	DS SS	30 30	4 4	30 s 30 s	EMG activity of the leg extensors were significantly greater during SV than VV. Proximal leg muscles were activated more than distal muscles.
Mischi and Cardinale, 2009	12 H (5♂, 7♀)	Custom built isometric elbow device	Isometric (20%, 40%, 60%, 80%, 100% max force)	28	NR	15 s	Vibration significantly increased coactivation during elbow extension for lower loads (20% & 40% max effort) but no differences in coactivation were reported during elbow flexion.
			Isometric (20%, 40%, 60%, 80%, 100% max force)	0	NR	15s	
Rothmuller and Cafarelli, 1995	10 H ♂	Direct vibration	Isometric Knee extension	1500	1.5	15 s	Vibration of the agonist increased antagonist coactivity but it did not change the rate at which coactivation increased during fatigue. During vibration bicep femoris coactivation was greater during vibration. but it did not change during fatigue with or without vibration

H = Healthy; **SV**= Side alternating vibration; **VV** = Vertical vibration; **NR** = Not reported

during the fatigue of either condition.

Recently, Abercromby et al. (2007a) suggested that acute indirect vibration causes neuromuscular responses that could be partly modulated by the co-contraction of the musculature acting at the knee joint. A study conducted by Mischi and Cardinale (2009), investigated muscle activation and co-contraction of the biceps and triceps brachii muscles during isometric exercise with and without vibration. Using an electromagnetic actuator, mechanical sinusoidal vibrations generated a frequency of 28 Hz, which was applied to the biceps and triceps brachii for 15 s. They observed that co-contraction occurred at low levels of muscle force (20% and 40% maximum sustained force) during elbow extension, suggesting that co-contraction may serve to stabilise the joint, but it does not modulate agonist force production (Table 5). The authors concluded that vibration could be a viable option in the early stages of rehabilitation where low levels of muscle force are required due to limited joint mobility.

In summary, Mischi and Cardinale (2009) findings provide some new insights to the response of superimposing vibration on agonist, antagonist and co-contraction of muscles. However, caution is advised, as the study utilized a single vibration frequency (28 Hz) with brief exposures to vibration and the recorded absence of amplitude also limits the findings of the study. Therefore, further studies investigating lower and upper limb vibration would assist in explaining the role that intramuscular co-ordination has in vibration.

Central motor command

Direct application of high frequency vibration on muscle and tendon activates Ia afferent of the muscle spindles and to a lesser extent, the secondary afferents and Ib afferents of the golgi tendon organ (Roll et al., 1989). However, there is evidence to support the notion that cortical areas of the brain receive and process proprioceptive information when direct high frequency vibration is applied, which generates evoked cortical potentials (Munte et al., 1996). It appears that muscle afferent input to the cerebral cortex plays a role in motor control (Wiesendanger and Miles, 1982); 30% of central motor drive is attributed to muscle afferent excitability (Macefield et al., 1993). Moreover, it has been reported that Ia afferent input has the ability to excite the corticospinal pathway (Carson et al., 2004) and activate the cortical motor areas (Lewis et al., 2001). To examine the potential changes of the motor cortex, the transcranial magnetic stimulation (TMS) method has been used to study the excitability of the corticospinal system, as well as the intracortical inhibitory and facilitatory processes. In brief, TMS delivers pulses to the motor cortex through a double cone coil placed over the scalp. It has been reported that motor-evoked potentials of TMS were enhanced when direct vibration (f = 80 Hz) was applied to extensor carpi radialis muscle (Kossev et al., 2001). Researchers have also suggested anecdotally that acute indirect vibration may influence the motor cortex to increase muscular performance (Cardinale and Bosco, 2003).

Table 6. Evidence for central command.

Author	Participants	Vibration Method (type)	Exercise Type	Frequency (Hz)	Amplitude (mm)	Duration	Results
Kossev et al., 1999	5 H (3♂, 2 ♀)	Direct vibration arm	Static	80	0.5	4 s	Vibration significantly increased motor evoked potentials from transcranial magnetic stimulation suggesting that cortical mechanisms are involved in vibration.
Mileva et al., 2009	7 H ♀	VV platform	SS SS	30 0	1.6 0	330 s 330 s	During vibration the amplitude of the tibialis anterior motor evoked potentials were significantly increased compared to no vibration

H = Healthy; **VV** = Vertical vibration; **SS** = Static squat

Mileva et al. (2009) investigated the effects of acute indirect vibration (f = 30 Hz, A = 1.5mm, VV) on corticospinal excitability and intracortical processes by studying motor-evoked potentials in the tibialis anterior and soleus muscles in response to TMS of the contralateral motor cortical leg area (Table 6). They found that acute indirect vibration increased the tibialis anterior corticospinal excitability pathway, but the intracortical facilitatory processing for the tibialis anterior was reduced. However, no significant changes were evident in the corticospinal excitability or intracortical facilitatory of the soleus. These findings suggest that acute indirect vibration may stimulate the corticospinal pathway; however, no performance measures were included with TMS.

In summary, there have been promising findings on vibration training and central motor command. Studies both confirm and refute the concept that direct and indirect vibration elicits a motor cortex response. Therefore, extensive research is required in the area of indirect vibration training to confirm that vibration causes an excitatory response in the motor cortex. Future indirect vibration studies should focus on expanding vibration platform research utilizing a range of vibration frequencies, amplitudes, durations and postural positions. Further vibration work is also required on the quadriceps and hamstrings to determine if acute indirect vibration truly increases the excitability of the corticospinal pathway.

Conclusion

Acute direct vibration is normally applied to the muscle or tendon using a high vibration frequency (>100 Hz), a low amplitude (1-2mm) and brief duration (2-15 s). Contrary, acute indirect vibration is administered intermittently (5 x 1 min) or continuously (3-5 min) at a frequency of 25-45 Hz and amplitude of 2-10 mm, which increases muscle (EMG) activity, muscle force, and power, suggesting that neural mechanisms are the main contributor. Spinal reflexes, muscle tuning, neuromuscular aspects and central motor command have been purported as possible neural mechanisms. However, it is unclear from the current research which mechanism(s) are responsible for enhancing muscular performance, it could be, that multiple mechanisms are involved. Current acute indirect vibration research lack standardization of testing and training protocols. Therefore, direct comparisons between studies are impractical, making it difficult to identify the underlying mechanism(s). The current inconsistency that exists in reporting and standardising acute indirect vibration protocols can be eliminated if future acute indirect vibration research adheres to the procedural recommendations developed by an expert international vibration research panel in 2010 (Rauch et al., 2010). Future acute indirect vibration research should focus on assessing single motor unit discharge, as this would provide further information in regards to motor unit frequency and motor unit synchronisation and assessing spinal reflexes during vibration would further enhance valuable knowledge of confirming the possible neural mechanisms.

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Key points

- There is strong evidence to suggest that acute indirect vibration acts on muscle to enhance force, power, flexibility, balance and proprioception, but little attention has been given to the neural mechanism(s) of acute indirect vibration.
- Current findings suggest that acute vibration exposure may cause a neural response, but there is little consensus on identifying which neural mechanism(s) are specifically responsible. This is due to a number of studies using various vibration testing protocols (i.e.varying frequencies, amplitudes, durations, and methods of application).
- Spinal reflexes, muscle tuning and neuromuscular aspects and central motor command are all viable neuromechanical factors that may contribute at different stages to transiently increasing muscular performance.
- Additional research is encouraged to determine when (pre, during and post) the different neural mechanism(s) respond to direct and indirect vibration stimuli.

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