Using tendon vibration between trials to alter proprioceptive sensitivity and its influence on upper-limb control during voluntary reaching

by

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A thesis submitted in conformity with the requirements for the degree of Master of Science

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Abstract

The current study investigated the effects of a novel tendon vibration method on upper-limb position sense and upper-limb rapid movement control. The relative contributions of proprioception and vision during action were assessed. Vibration of elbow extension muscles was applied between trials to avoid reflexive activations that typically occur with vibration during movement. In the position-sense task, participants were asked to move the non-vibrated arm to match the position of the vibrated arm. In the action task, participants were asked to perform a discrete reaching movement. Vibration was found to decrease position sense precision and yielded increased trajectory variability towards the end of the movement. Notably, the influence of vibration on trajectory variability was also observed for reaches made in the presence of vision. Tendon vibration presented between trials likely perturbs proprioceptive feedback during trials. Also, it is concluded that proprioceptive information contributes significantly to the control of visually guided movements.
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1 Introduction

One ideal goal for every human being is to sustain life in a healthy and independent state. To achieve this goal, one must be able to perform activities of daily life, free from difficulty and constraints. As technology and modern medicine increase life expectancy, a larger proportion of the population is pushed simultaneously into a state of morbidity for extended periods of time. Thus, the struggle transforms from maintaining life, to maintaining function. From a motor control perspective, prolonging these independent states of life becomes problematic due to the lack of the mechanistic understanding of movement impairments. In fact, we do not even fully understand how people perform even the simplest of tasks, such as reaching for a glass of milk in the morning. Although various professionals are designing methods and technologies to improve motor function, we remain uncertain of what is occurring in the brain at the neural level when controlling a movement. More relevant to the present study, there is a need to better understand how visual and proprioceptive inputs are processed to control voluntary action.

Humans have a highly sophisticated nervous system that is responsible for the integration and coordination of incoming sensory and outgoing motor information. The central nervous system (CNS), which is comprised of the brain and spinal cord, recognizes various forms of sensory information and must instantly transform the information to prepare the appropriate motor commands. Specifically, when planning and coordinating goal-directed actions, the CNS integrates these commands to ensure that the individual is moving with the utmost efficiency and accuracy. Sensory systems contribute to motor actions in various ways, depending on the information that is available and the specific goals of the movement the individual is aiming to achieve. Our eyes provide the sensation of vision regarding the external world and our place in it, while proprioception gives us the sensation of posture and orientation of limbs relative to one another.

The purpose of this research was two-fold. First, studies of tendon vibration aftereffects were investigated by implementing vibration into a limb position sense task, using simultaneous biceps brachii and triceps brachii tendon vibration between movements. Secondly, predicting that between-trial vibration will increase movement variability, the method also was used to investigate the relative contribution of vision and proprioception on the control of goal-directed
action. More specifically, this thesis aimed to understand how individuals move their upper-limb when the visual and proprioceptive systems are perturbed. This aim was achieved by implementing visual and proprioceptive perturbations during goal-directed action. Kinematic characteristics were evaluated to make inferences about the changes to the control of voluntary movement. The practical application of this thesis is to generate knowledge that could be relevant to researchers working with individuals with sensory deficits, such as the post-stroke population.

The goals of the current thesis included the advancement of knowledge regarding multisensory integration during goal-directed action. The first section of this thesis will discuss the fundamental aspects of motor control. Previous literature on movement control mechanisms relative to both visual and proprioceptive systems will then be discussed, followed by the multisensory integration of these sensory modalities. Common methods will be discussed collaboratively for the two experiments performed, and then each experiment will be presented separately in manuscript format. The final section will include common discussions, conclusions and future directions relative to both experiments.

2 Review of Literature

2.1 Motor Planning and Online Control

In 1899, Woodworth discussed online control mechanisms during goal-directed aiming movements. His original monograph introduced a model that involved the fundamental control of movement through the use of impulse planning mechanisms prior to movement, and the need for sensory information during movement to correct for any initial errors. In his study, Woodworth recorded reciprocal movements on a rotating drum. Participants performed the task both with eyes open and -eyes closed. Woodworth noted an impact of vision availability late in the movement, emphasizing the presence of trajectory amendments. Additionally, he observed that the presence of these late amendments usually led to increased movement time. Since 1899, there has been a vast amount of research and technological advances in the area of motor control, however the two-component model is still being used to assess the impact of central control mechanisms during movement (for a review see Elliott, Helsen, & Chua, 2001).
When moving the limb, planning and online control mechanisms are implemented to accomplish the trajectory. Comparable displacement of the limb can emerge from these different planning and online control mechanisms, which can indicate various use of sensory information prior to and/or during the movements. Therefore, creating smooth and accurate movements may be the result of more efficient limb control, creating less fatigue in the trajectory. This idea fits in the energy expenditure speed-accuracy framework developed by Elliott, Hansen, Mendoza and Tremblay (2004), who describe how one can minimize error and energy expenditure by adapting accuracy and speed. If one can reduce error and variability in their movements, it can be speculated that they either have formed more precise preparation of the trajectory or better online control mechanisms (Elliott et al. 2004). It is especially important to understand how those with movement deficits adapt to their abilities to complete the same movement goals. If one aspect of the two-component model is compromised, how does the body compensate? And subsequently, what is the best method of rehabilitation training? Overall, many researchers followed-up on the work of Woodworth and led us to further understand that part of acquiring a motor skill includes the ability to learn how to use and integrate sensory information in an efficient way, both prior to and during a movement (Khan & Franks, 2003; Emken, Benitez, Sideris, Bobrow & Reinkensmeyer 2007; Elliott et al., 2004).

Sensory systems give humans neural representations of the world surrounding them. Each pathway connects unique receptors to the CNS, and in turn creates a holistic percept. The following section will discuss how vision is used to sense and perceive stimuli during movement, followed by a description of online proprioceptive information processing.

### 2.2 Vision

Vision is defined as the ability to see and recognize the surrounding environment. Human’s use vision constantly in waking hours to safely navigate through their environments and complete tasks of daily life. More specifically, vision is the ability for humans to process light by means of photoreceptors (see below), and ultimately yielding images into conscious cognition (Gardner & Johnson, 2013). In the absence of vision, one loses their ability to see their surroundings, and thus may rely on other sensory modalities to recognize the temporal and spatial characteristics of an object (e.g., touch and audition).
2.2.1 Organs of Vision

There are many structures of the visual system that must work together to create an accurate visual perception. The pupil of the eye controls the amount of light entering the eye, the lens converges the rays on the retina, where the light is then focused and processed. The light received by various types of photoreceptors, which transforms the light energy into electrical energy (i.e., a neural signal) for appropriate communication with the CNS. It is this retinal processing that enhances or limits what can be seen in the world.

There are two main types of photoreceptors located in the retina, the rods and the cones, which are classified by their appearance and sensitivity to light. Rods are responsible for vision in low light environments due to their heightened sensitivity, while cones are responsible for vision in well-lit environments, as well as the perception of colour (Gardner & Johnson, 2013). The photoreceptors synapse with bi-polar and horizontal cells by releasing neurotransmitters causing graded potentials. These potentials are received by ganglion cells, which have the ability to transfer image-forming information to various parts visual centers in the brain. The retina has the unique ability to discard excess stimulus, while relaying the most relevant information to central visual processing centers. During movement, humans rely on this visual control to ensure they receive accurate spatial information to safely complete the movement.

2.2.2 Vision and the control of movement

The CNS utilizes visual feedback efficiently during movement execution (for example see Hay, Pick, & Ikeda, 1965). The visual system is readily accessible for researchers to manipulate and investigate. For example, vision can be manipulated with liquid-crystal goggles (Milgram, 1987) or simply by having the participants close their eyes. Vision is known to have dominance within the sensory systems as people naturally rely on this sensory system to receive information about their limbs as well as the environment in which they are situated (Posner, Nissen, & Klein, 1976). Removing visual feedback during various portions of a goal-directed action allows for the possibility to speculate how vision can modulate movement. This method becomes important when investigating internal control processes, as vision is known to influence different portions of voluntary movement, such as planning and online control.
One way of evaluating the use of vision during movement is by employing a voluntary goal-directed task and observing accuracy at movement endpoint. Chua and Elliott (1993) used this method and discovered that when participants had both vision of the environment coupled with vision of their own hand, endpoint accuracy was increased relative to having no vision. Investigating the contribution of vision during both planning and executing a movement has also been studied using vision manipulation. The availability of vision at the end of a movement has the ability to alleviate endpoint errors (Abahnini, Proteau, & Temprado, 1997; Khan & Franks, 2003). Khan and Franks (2003) had participants perform rapid aiming movements in the absence of vision, with vision of the first 50% of movement, with vision of the first 75% of movement, or vision of the entire movement. Initially, it was found that the 50% group achieved comparable levels of endpoint accuracy as the no vision group. Accuracy was comparable for those who only saw the first half of their movement with those who did not see their movement at all. Conversely, the 75% condition and full vision condition yielded comparable endpoint accuracies, which were significantly better than the 50% and no-vision condition. Based on the spatial variability, the authors concluded that participants were not able to use online visual information before half way through the movement (no-vision and 50% condition). Alternatively, when participants had vision during the later stages of movement (full-vision and 75% condition) they were able to use the visual information to alter initial impulses and complete the movement as accurately as possible (Khan & Franks, 2003).

People can also adjust movements to optimize the amount of visual information available during movement. Elliott, Chua, Pollock and Lyons (1995) had participants aim with a cursor to a target with either 400 or 600 ms of visual feedback. After 120 trials of practice, participants performed a transfer test with either more or less time with visual feedback. Results showed that the individuals who trained with 400 ms of feedback exhibited better endpoint precision when transferred to the 600 ms condition. Additionally, these participants took more time to reach maximum limb velocity, possibly allowing more time for use of online feedback. On the other hand, the participants who trained with 600 ms of vision, exhibited higher maximum limb velocity values when transferred to a condition with less time to use visual feedback (i.e., 400 ms). The increase in peak velocity was thought to be a strategy to maintain the efficient use of vision (Elliott et al., 1995). Overall, if participant can anticipate how long visual feedback will be
available, they can alter their movement trajectory to optimize their use of that visual information.

Another way to investigate visual mechanisms during movement is by assessing velocity profiles after manipulating visual feedback. For example, time spent after reaching peak velocity during movement has been used as a marker to separate the contribution of control processes (e.g., Elliott, Hansen, Grierson, Lyons & Hayes, 2010). Elliott and his colleagues observed asymmetric limb velocity profiles, which are believed to be indicative of people slowing down their movements to use online visual feedback for correction of initial movement errors towards the end of movement. The results are consistent with previous work, also showing more time spent after peak velocity during goal-directed movements (e.g., Elliott, Carson, Goodman & Chua, 1991; Chua & Elliott, 1993; Elliott et al., 1995). Alternatively, when vision is withdrawn at movement onset, individuals exhibit more symmetrical velocity profiles, possibly indicating less of a reliance on online visual feedback and presumably more reliant on motor planning mechanisms.

There is evidence however, that minor trajectory amendments occur in the absence of vision, but are not large enough to reduce the endpoint errors (Elliott et al., 1991). In their study, Elliott and his colleagues investigated the relationship between number of movement corrections and endpoint error, as well as the relationship between time spent decelerating and endpoint error. The authors reported that the time spent decelerating, or slowing down a movement, was better able to predict endpoint error than the number of sub-movements made. This finding led the authors to conclude that maybe there is continuous control that cannot be observed through kinematic profiles. An alternate explanation, though, is that the corrections are based on proprioception, which may not be reliable enough to reduce endpoint error but still used to generate trajectory amendments (Elliott et al., 1991).

The above-mentioned methods have all incorporated visual manipulations to infer visual control on movement by either breaking down the movement into components or simply analyzing endpoint errors. From these studies, it can be concluded that vision not only has crucial role in identifying the target location and planning a subsequent movement, but also in the control during movement. It is important to note that these researchers have used visual manipulations to infer online control mechanisms and only can describe the use of vision during
movement. From these studies, it is also possible to make inferences regarding the up-regulation of proprioceptive feedback control. However, it is becoming increasingly important to directly perturb proprioception to accurately evaluate some of the above-mentioned contributions of proprioception to the online control of voluntary action.

2.3 Proprioception

Proprioception has been defined as the sensory feedback that includes information regarding the length of a muscle and its supplementary force production. The feedback is reliant on afferent signals from the embedded muscle spindles and Golgi tendon organs (see below) (Gardner & Johnson, 2013). In order to create and control accurate movements, the sense of our limbs and body in space is necessary. Proprioception is created by receptors in the muscle and joints (see below), which relay information to the CNS about both static and dynamic posture. In sum, proprioception is mechanical information regarding rate of change in muscle length and tension created in the muscle tendon. The mechanical information is transformed into changes in neuron firing frequency that is readily available for the CNS to use and process. Often in literature the somatosensory information associated with proprioception during movement is referred as ‘kinesthesia’, which is a generalization of the combination of many other sensory systems (Gardner & Costanzo, 1981) such as cutaneous receptors and joint mechanoreceptors. For the purpose of this thesis, proprioception will exclude vestibular and cutaneous sensations, and only refer to the somatosensory information brought to the CNS by receptors located between the origin and insertion of skeletal muscles (i.e., muscle spindle afferents and Golgi tendon organs).

When attempting to complete a motor task, the CNS must be able to accurately identify the location of one’s body in space as well as the relative location of the objects one is interacting with. These pieces of information are combined in order to complete a movement where an object and a moving limb must interact. The way humans have evolved to complete such tasks, is by use of vision from both the environment and the body in the environment (see above). Neurological mechanisms regarding the role of vision in goal-directed movements are well known and documented through the extensive research done in monkeys (e.g., Polit & Bizzi, 1979). What is less understood is how the signals from proprioceptive receptors are combined in the brain and utilized to complete voluntary movements. The CNS must be able to process both visual and proprioceptive information, as well handling the noise across sensory systems. For
example, when a person attempts to reach for a glass of milk in the morning, they must accurately code both the location of the glass and the arm position at every point until it reaches the glass (i.e., without spilling it). The role of proprioception in motor performance has shown to be important for the success of precise motor tasks.

2.3.1 Organs of Proprioception

Muscle spindles are sensory receptors embedded in the belly of skeletal muscle. The spindles ability to function is based on their ability to stretch and shorten simultaneously with the muscle itself. Muscle spindles or ‘intrafusal muscle fibers’, lie parallel beside the contractile or ‘extrafusal muscle fibers’ and detect the degree of stretch in the muscle itself. When a muscle spindle is stretched, the activity in the sensory neuron is heightened, increasing its firing frequency. Alternatively, when a spindle is unloaded or shortened, the firing frequency declines. Thus, spindle activity is directly proportional with the contractile activity of the muscle itself.

Muscle spindles send their afferent information through two types of fibers, the Type Ia fibers and the Type II fibers. Type Ia fibers carry information regarding the length of the muscle, as well as the dynamic changes in length. Type II afferents only carry information regarding the static length of a muscle, and they are less sensitive to small changes. Research has shown that Type Ia fibers are most sensitive to the influence of tendon vibration and are known to sometimes discharge individually, while Type II fibers are less sensitive to the effects of tendon vibration (Roll & Vedel, 1982). The sensitivity refers to the spindle’s ability to rapidly depolarize and increase the firing rate of action potential send to the central processing centers.

Golgi tendon organs (GTO) are located in the muscle tendon at the musculotendinous joint. Sensory neurons are depolarized when the GTO’s are compressed between the collagen fibers at the musculotendinous joint. GTO’s thus are responsible for detecting the amount of tension in a particular muscle tendon. Golgi tendon organs send information via the Type Ib fibers.

Force and stretch sensory information are combined and give the CNS an accurate depiction of both static and dynamic limb posture. It is both the muscles spindles and the GTO’s that allow humans to make fairly accurate movements in the absence of vision.
2.3.2 Proprionecption on the control of movement

Sherrington (1900) was one of the first to investigate the relationship between movement and sensation. In Sherrington’s work, he explained what it meant to have ‘muscular sense’, which encompasses information from the muscles, tendons, joints, corollary discharges (or efference copies) and perhaps skin. In his later work, Sherrington (1909) discovered reciprocal innervations and activations such that when flexor muscles are contracting, extensors are inhibited. Sherrington hypothesized that it was the efferent and afferent neural interconnections at the spinal cord level that allowed the inhibition to take place. Although Sherrington’s theories have been challenged many times in literature (see Matthews, 1982), the basic concepts of movement and sensation are still well considered when referring to muscle afferent information.

A common way to assess the ability to incorporate proprioception is by performing a limb-matching task. This task is used widely in physiotherapy practices and can be used to diagnose deficits in the sensorimotor system (see Goble, 2010 for a review). There are three types of limb matching tasks, all performed with eyes closed. The first involves the clinician moving the intended limb to a specific location and holding for a short period of time. After the time has elapsed, the limb is placed back to the neutral location and the participant must recreate this movement again using the same arm. The information to complete the task would be reliant on the proprioceptive location memory. This task is often termed the ‘ipsilateral matching’ task. Alternatively, a ‘contralateral matching’ task is when the clinician will bring a limb to the intended target location, however this time the limb is left in this location. The goal is for the participant to move their other limb to match the location. This task relies not on memory, but on the inter-hemispheric communication between sensory areas. Finally, a combination of the two, where the clinician will move the limb to a target location, move it back to neutral after elapsed time, and only then is the participant signaled to move their opposite limb to the mirrored location. This third task is the most challenging because it relies on both memory and neural communication, which in turn yields the greatest amount of absolute endpoint error (Goble, 2010).

Another way to assess the performance of proprioceptive feedback is to manipulate vision and observe the subsequent movement behaviour. This technique is usually applied to rapid goal-directed action. Researchers may employ an inaccurate virtual target location to create
a visual-proprioceptive mismatch. This discrepancy between where the participant feels a certain limb is and where they see it (e.g., Bagiśteiro, Sarlegna, & Sainburg, 2006) is commonly used because it would be impossible to simply remove the proprioceptive information from the environment, alike what one can do with vision. Bernier, Chua, and Franks (2005) predicted that in a visuomotor conflict, proprioception would not be regulated if vision was available during the movement. Participants performed a movement task using a virtual cursor presented on a screen. During the adaptation phase, the cursor was gradually displaced by 2.5 cm to the left of the actual limb position, such that the limb had to pass to the right of the target to be accurate. One group performed the adaptation phase with full vision of the cursor while another group performed the adaptation phase with vision of the cursor taken away at movement onset (i.e., no vision). For both groups, a path of the movement was also shown at the end of the trial (i.e., knowledge of results). The endpoint accuracy results for the adaptation phase indicated that both groups adapted to the cursor bias although the no-vision group exhibited more endpoint variability. Subsequently, all participants performed a post adaptation test, which involved an accurate cursor location prior to movement onset and reaches performed without vision of the cursor and no knowledge of results. The post-test revealed that the participants who performed the adaptation phase in the full vision condition compensated for the deviations in endpoint while the no-vision group was not able to re-adjust for the accurate cursor position (i.e., average endpoint bias greater than 2 cm). The authors speculated that when vision of the cursor was available, the CNS relied on the visual feedback, and in the absence of vision, the CNS was forced to rely on proprioception. Proprioception in this case was not calibrated to the displacement bias, thus did not adapt to the displacement of the cursor (Bernier et al., 2005).

Vision of limb position in space is arguably more important for planning movements to a visual target than a proprioceptive target (e.g., a limb matching task) (Sober & Sabes, 2003). To further investigate the contribution of proprioceptive feedback to movement, Bernier, Gauthier, and Blouin (2007) tested whether the information that is transformed from sensory information to motor information is the same when reaching to either a visual or proprioceptive target. All participants performed 90 reaching movements to three different illuminated targets while wearing displacement prisms. In the pre- and post-tests, participants were assigned to a visual or proprioceptive group, performing reaching movement to either a visual target or a proprioceptive target. The authors found that the prismatic adaptation resulted in significant aftereffects for the
visual group, while none were found for the proprioceptive group (Bernier et al., 2007). These findings point to the idea that different sensorimotor transformations regulate movements to visual and proprioceptive targets. However, these assertions relative to the use of proprioception were made without direct manipulation of the proprioceptive inputs.

2.3.3  Muscle Tendon Vibration

There is a multitude of methodologies associated with proprioceptive perturbations although tendon vibration is the most accessible and least invasive. The current research attempting to directly measure the effects of deafferentation has been limited to cats and monkeys. It is possible however, to study the behaviour of humans with sensory neuropathy (e.g., Sainburg, Poizner, & Ghez, 1993), though such research only provides indirect information about the use of proprioceptive information in a typically functioning person. The following are some of the reasons why muscle tendon vibration was selected for this study, as a non-invasive and pragmatic way to disrupting proprioceptive feedback.

The earliest use of muscle tendon vibration was performed on the legs of a cat to observe its perturbing abilities. Brown et al. (1967) reported that when Ia afferents of a cat are vibrated, they have the ability to discharge as if the muscle was lengthening during a voluntary action. Since this discovery, muscle tendon vibration has been used to perturb sensory input to the CNS to study its effects on the motor control. This finding led Goodwin, McCloskey and Matthews (1972) to further explore the effects of tendon vibration on limb position sense in humans. Vibration was applied in many experiments to either the biceps brachii tendon or the triceps brachii tendon to target these muscles involved in flexion-extension at the elbow joint. A typical trial had one arm assigned as the experimental arm (i.e., vibrated) while the other arm was the tracking arm. The participant was asked to move the tracking arm to the perceived position of the experimental arm. The results confirm that tendon vibration at 100 Hz was able to produce a consistent deception of forearm movement, even when the arm was still. Specifically, the illusion of muscle lengthening was observed as vibration of the biceps muscle elicited an illusion of extension at the elbow, which led to a flexion at the elbow. As well, the participants also exhibited flexion at the elbow of their non-vibrated arm. Although the non-vibrated arm was supposed to match the vibrated arm position, the perceptual bias assessed in the non-vibrated arm was not as important as the position bias in the vibrated arm. A possible explanation of this
phenomenon can be attributed to the increased spindle activation interpreted as a muscle stretch, which is expected based on the operational definition of a muscle spindle. Indeed, it was easier for a participant to track the online changes of their other arm than to match a static location. The perturbation of proprioception causing accuracy differences could be taken as an indication of disrupted online control processes taking place. The results from Goodwin and colleagues (1972) laid the grounds allowing the use of tendon vibration to study online proprioceptive control mechanisms.

Capaday and Cook (1981) attempted to break down the effects of tendon vibration by individually vibrating the antagonists and agonist muscles during an elbow flexion/extension movement. Vibration of the antagonist caused the participants to undershoot the target while vibration of the agonist was not affected. Not surprisingly, only the antagonist muscle vibration yielded an effect due to the fact that the agonist muscle in a movement is shortening and according to the known behaviors of muscle spindles, only stretch causes activation. The perception of muscle lengthening and its effect on limb position has also been demonstrated through passive movements of the upper-limb (Cordo, Gurfinkel, Bevan, & Kerr, 1995). These results help to affirm the idea that the CNS dominantly oversees the antagonist activity, however it was still unclear how the CNS integrated information from the muscles as is produced during natural muscle activation.

Vibration of the forearm muscle tendons also causes participants to alter their movement behaviors. In a follow up to Capaday and Cooke’s work, Rogers (1985) continued the investigation by blindfolding participants and asking them to make continuous slow extension or flexion movements to match the contralateral forearm position. The movements were made in the vertical plane only. Ten repetitions of the task were done prior to the vibration. All participants showed minor misalignments of the forearms during the control trials, and thus the authors were able to calculate the ‘true’ post vibration error for each individual participant. This was done by comparing the mean angle of misalignment of three trials immediately before vibration begun with the mean angle of misalignment of the first three trials after the vibration ended. Results revealed that the mean error was significantly different after the vibration was applied to the muscle that was lengthening. Indeed, there were significant differences during forearm extension following biceps vibration and during forearm flexion following triceps
vibration. Moreover, when vibrating the biceps tendon, the non-vibrated arm was more flexed during an extension-matching task, alluding to the illusion of forearm stretching or elbow extending (Rogers, 1985). A follow-up experiment had participants extend one forearm while the arm other performed elbow extension, creating a central alignment of the two arms. The difference in angles was significant for this task as well after vibration to the biceps muscle of the extending forearm. Rogers (1985) noted these errors occurred immediately following 60 seconds of vibration, but did not last longer than four minutes.

Dynamic position of the forearm is represented by proprioceptive input, encoding both angular displacement and absolute joint angle (Bevan, Cordo, Carlton, & Carlton, 1994). In a series of four experiments, Bevan et al. (1994) passively rotated the forearm of participants who were asked to open their hand as soon as their arm was perceived to pass through a specified target location. Participants performed the trials in the absence of vision, however after each trial, knowledge of results was displayed on a monitor, which included the relative distance between the angle obtained at hand opening angle and the target angle. The first three experiments involved a target at a constant joint angle with varying starting locations, while in the fourth experiment the movement distance of the arm was held constant with varying joint target angles (achieved by various starting positions). It was hypothesized that if proprioceptive feedback was related to an absolute joint angle, opposed to angular distance travelled, kinematics should have no affect on the discriminability of an absolute target angle. The results demonstrated that when using proprioceptive information to create a movement, participants could discriminate target distance more accurately than absolute target angle (Bevan et al., 1994). Altogether, the CNS appears to use proprioceptive information related to angular displacement more readily than absolute joint angle, because the former is considerably more precise and less dependent on initial position (Bevan et al., 1994). Such a perspective fits well with the idea that the use of proprioception changes significantly across the different portions of the movement. It is important to identify these results regarding the current study, as the use of online proprioception during a dynamic movement was evaluated.

Redon, Hay and Velay (1991) demonstrated the effects of vibration during active movements early versus late in the movement. In contrast with the above literature, Redon et al. (1991) used multi-joint movements to assess the use of online proprioceptive information. The
participants were asked to aim to one of four targets either with or without vibration applied during the movement to the biceps brachii muscle. The participants were required to perform the task without vision, in an attempt to isolate the effects of proprioception. In one experiment, Redon and colleagues compared reaches performed with a movement time target of 200 ms or 800 ms, while presenting tendon vibration for 200 ms. In the 200 ms movement time condition, vibration was thus presented for the entire movement. In the 800 ms movement time condition, vibration was either for the initial 200 ms or for the final 200 ms of movement. When vibration was on for the whole movement (200 ms condition) there were more errors (i.e., left deviation) than when only applied for the initial 200 ms of movement (800 ms condition). Additionally, when vibration was applied for only the last 200 ms in the 800 ms condition, there were significantly more errors than in both the 200 ms condition and in the initial 200 ms condition (of the total 800 ms). This finding led the authors to conclude that the use of proprioceptive information could be regulated late in a goal-directed movement. The results from Redon et al. (1991) along with Capaday and Cook (1981) indicate that tendon vibration has the ability to increase the error in endpoint accuracy, which further suggests that proprioception has an important role in the online control of movement. These results are also in line with the findings based on the visual feedback studies previously mentioned (e.g., Chua & Elliott, 1993; Elliot et al., 2005; Elliott et al., 2010), where late feedback helps to regulate movement accuracy.

In a nutshell, vibrating the lengthening muscle during voluntary reaches significantly influences endpoint accuracy (Capaday & Cooke, 1981; Rogers, 1985) with a stronger impact late compared to early in the trajectory (Redon et al., 1991). Yet, these studies were performed in the absence of visual feedback of the arm. It is thus also important to emphasize that in ecologically valid situations, proprioception and visual cues can be combined and integrated so the CNS can create the most accurate representations of the surrounding environment (e.g., Ernst & Bühlhoff, 2004). Thus, these observations allow further research to be done on the contribution of proprioceptive feedback during various movement tasks.

2.4 Multisensory Integration

Research has suggested that while vision is important to plan motor commands, proprioception can significantly contribute to the online control of goal-directed action (Rossetti, Desmurget, & Prablanc, 1995; Bagesteiro et al., 2006). Rossetti et al. (1995) used prism glasses
to assess the effect of visual displacement by creating a discrepancy between vision and proprioception prior to a movement. Participants performed voluntary movements to a visual target with both accurate vision of the finger, as well as displaced vision of the finger by 41 mm. Vision of the limb was removed at movement onset in both conditions, while the target location remained constant across all trials. In the displaced condition, analyses of constant error revealed a significant bias equal to one third of the displacement in the opposite direction. The authors thought this to be indicative of vision and proprioception creating a biased representation of the starting limb position to create a subsequent motor plan (Rossetti et al., 1995). Moreover, proprioceptive information regarding the real starting location of the finger must have contributed to the CNS’s perception of the limb during motor planning or else the displacement of the error would have been proportionate to the displacement of the seen finger. Thus, movement directions were most consistent with the actual start positions, rather than the virtual ones. Bagesteiro et al. (2006) supported the results of Rossetti et al. (1995) when they observed participants planning their movement based on where they saw a target, and not where they felt their limb to be, but utilized proprioceptive feedback later in the movement. Although these results are consistent, there still remains uncertainty as to which sensory modality our bodies use during the online control of a goal-directed movement.

To assess the variability and noise within the CNS, Ernst and Banks (2002) described a model, which helps to explain the minimization of this sensory commotion. The argument the authors make is based on maximum-likelihood estimation (MLE), using Bayesian rules to mitigate the sensory variability. The MLE also proposes the ability of the CNS to weigh the proportional reliability of the different sensory modalities (Ernst & Banks, 2002). The sensory modality with least amount of variability is given the most weight while others, with more variability, are deemed less reliable. This model can be a useful tool when inferring dominant sensory systems over others.

While most research has been concerned with the individual contributions of both proprioception and vision, Sober and Sabes (2003) describe a model with the idea that vision and proprioception are individually involved in different aspects of movement planning. The purpose of the model was to understand how initial portions of movement are guided by proprioceptive and visual feedback, which is known to be the time indicative of movement planning (Elliott et
The authors had participants perform a pointing task in a virtual reality, giving them the ability to shift the location of visual feedback from the starting limb position. They compared the initial reaching behaviour of the participants with computational models of movement planning. They discovered that visual cues about starting and final positioning were used to plan distance parameters while the proprioceptive system defines muscular forces required to move the proper distance (see Sober & Sabes, 2003). If proprioceptive feedback is necessary to convert desired movement vectors into motor commands, it seems probable that the same feedback will be used to correct for any of the initial movement errors as well.

The use of sensory systems is necessary to the control of a goal-directed movement. More specifically, there is evidence of differences between the roles of vision and proprioception in the planning and online control of movement. Having both sources of information readily available suggests equal a greater reliance on the most reliable source, relative to the goals of the task. The current study aimed to directly investigate these processes to expand the knowledge of the multisensory control literature. Specifically, the influence of proprioception to the online control of action was of interest.

### 2.5 Study Rationale

Many studies have been able to show how tendon vibration is effective in altering the perception of a moving limb in space. Visual and proprioceptive inputs both contribute to the accurate and efficient control of movement, however there is still more to learn about the relative contributions of each sensory system. We have seen many models attempting to break down the relative inputs, yet multisensory integration in the CNS is so sophisticated and complex. Typically, people study the influence of a single sensory modality during goal-directed movement (e.g., vision; Woodworth, 1899; Elliott et al., 1991, or proprioception; Goodwin et al., 1972; Redon et al., 1991). The current study includes both proprioceptive and visual perturbations to better understand the relative contributions each sensory modality has on the control of movement.

Currently, there is a vast amount of literature that comprises the use of proprioceptive and visual manipulations to study their deficits during movement although there might be challenges to the ecological validity of these investigations. For example, a significant proportion of the
cited studies had participants perform movements in a proprioceptive-visual mismatch environment, thus artificially creating a spatial discrepancy between the visual representation of a limb and the intact proprioceptive information. Another concern with such manipulation is the delay between the actual limb displacement and the displacement of its representation on the virtual display (i.e., cursor). While such delays might be shorter than those known to alter the normal sensorimotor processes (Smith & Bowen, 1980), it does not mean that it does not to impact the weighing of the different sensory modalities.

An additional concern with virtual environment is the difficulty to employ natural movement trajectories, or those made with the ability to move in all planes of motion. Gritsenko and Kalaska (2010) had participants perform reaching movements to a visual target on a screen using only the vision of a cursor. That is, the visual display of the limb was limited to a 2-dimensional plane. After baseline trials, some subjects were required perform the movement with a mirror transformation that inverted visual feedback. Mirror transformation trials with a target jump were introduced with either vision of the environment or knowledge of results (KR). Comparisons were made between the groups to assess online control mechanisms. The visual feedback group showed smaller errors during early exposures to the mirror transformation, while KR subjects took more time to adapt. Additionally, the onset time of corrections remained constant pre and post adaptation to the mirror transformation in both groups. The authors concluded that although visuomotor adaptations taking place with a limited 2-dimensional display can influence the planning of movements, they might not be sufficient enough to have an effect on online correction phases of control. As a result, the current study will target both sensory systems by directly perturbing each (tendon vibration and liquid-crystal goggles) while employing natural, 3-dimensional movements with direct vision of the limb (if any).

A secondary concern of the current literature involves the problems associated with applying tendon vibration during movements. When applying tendon vibration during an active movement, reflexive contractions of the same muscle are elicited, and this phenomenon has been termed the tonic vibration reflex (TVR: Eklund & Hagbarth, 1966). Thus, the use of direct tendon vibration during movement may interfere with typical muscle activations and manipulating vision with tendon vibration may not necessarily reveal voluntary sensorimotor processes. The ability to expose the muscle to tendon vibration prior to movement may allow us
to better understand the contribution of proprioception to the online control of voluntary upper-limb movements, without noise from the contractile tissues (Cordo et al., 1995; Rogers et al., 1985). This is why the present study first aimed to evaluate the effects of between-trial tendon vibration on the perception of movement before testing its effects on the control of goal-directed action.

A third and last concern in the current literature is that tendon vibration is most often applied to only one muscle, thereby causing a bias in joint position sense. While one study employed simultaneous tendon vibration of both biceps brachii and triceps brachii muscles, it was done at 20 Hz and 200 Hz, and the task was to maintain a stable joint angle and report any change in perception of position (Roll & Vedel, 1982). Vibrating a single muscle may induce a bias in joint position sense and there have been no instances of the use of dual-muscle tendon vibration during rapid goal-directed action.

Due to the aforementioned concerns of the previous literature, tendon vibration was presented between trials, which may reduce the sensitivity of muscle spindle afferent fibers. Additionally, this study employed simultaneous tendon vibration of both the biceps brachii and triceps brachii in all experimentations (i.e., dual-muscle).

Overall, this thesis tested two novel questions. Firstly, can the effect of dual-muscle between-trial tendon vibration be employed to perturb the use proprioceptive feedback for position sensing? And subsequently, how neurologically intact participants use proprioceptive and visual feedback at various portions of movement to control reaches when simultaneously manipulating the presence of vision and between-trial dual-muscle tendon vibration? For the purpose of this thesis, the term ‘dual-muscle’ refers to the application of vibration to both the biceps brachii muscle and the triceps brachii muscle. Additionally, the term ‘between-trial’ refers to the application of tendon vibration between each movement trial, when the limb is at rest.

The effects of dual-muscle between-trial tendon vibration were compared by means of two experiments. Firstly, in order to determine if between-trial tendon vibration has any effects on limb position sense, a position-matching task was employed. The goal was to create a clinical-like setting by employing a limb position contralateral remembering matching task during pronated elbow extension. The first experiment was performed with minimal technology
in order to make it as accessible as possible (e.g., implement in a clinical setting). As well, the low-tech methodology was implemented to ensure differences existed on the easily attainable measurements. The intention was not to be directly comparable to the results in the second experiment, but rather to create generalizations regarding the the ability for dual-muscle between-trial tendon vibration to perturb limb position sense. Following this experiment, the next goal was to use the between-trial dual-muscle tendon vibration during a voluntary goal-directed reaching movement. The reaching task was completed both in the presence and absence of vision, using liquid-crystal goggles. The combination of liquid-crystal goggles and tendon vibration allowed for the simultaneous perturbations of both visual and proprioceptive feedback, allowing for observations of the effects on movement. In contrast with the first experiment, the second experiment was designed to understand the fundamental processes of sensory feedback and utilization. Unlike the accessible measurement of the first experiment, the second experiment used precise motion tracking technology to confidently make observations regarding the use of both visual and proprioceptive feedback during goal-directed reaches. Although the two experiments presented in this thesis are related by means of the novel tendon vibration technique, they differ in their practical/theoretical implications.

It was hypothesized that between-trial dual-muscle tendon vibration would alter the perception of forearm position during the limb-matching task. Specifically, because tendon vibration induces continued firing of the proprioceptive receptors, which in turn yields altered muscle spindle fatiguing for at least few seconds after the tendon vibration stopped (e.g., Ribot-Ciscar et al., 1998), the between-trial dual-muscle vibration was expected to yield a less reliable proprioceptive signal of the joint position sense (re: Ernst & Banks, 2002). It was thus expected that the variability of left limb positioning would increase in the block of trials where tendon vibration is employed. In contrast, due to the simultaneous perturbation of the biceps and triceps, the average bias (i.e., constant error) was not expected to differ between the trials blocks with and without vibration. As previously mentioned, after tendon vibration, the frequencies of the muscle spindles are altered, causing the limb to feel either longer or shorter than it really is (i.e., depending on when the vibration was applied). Thus, when applying vibration to both agonist and antagonist muscles, it can be expected the lengthening or shortening effects will average out creating a relatively neutral bias (e.g., Roll & Vedel, 1982).
During the goal-directed movement task, it was hypothesized that with dual-muscle between-trial tendon vibration, participants would exhibit more endpoint variability than without vibration, for the same reasons of those raised above. Because of the hypothesized increase in proprioceptive noise with tendon vibration, it was also expected that reliance on vision would be greater in the presence than in the absence of vibration (re: MLE model: Ernst & Banks, 2002). Indeed, based on the MLE during the online control of movement participants may decrease the variability induced from tendon vibration on the trials that include vision of the trajectory. As well, in the absence of vision, it was expected that tendon vibration would have a greater impact on endpoint variability. It was predicted that when one or more sensory system are perturbed, the CNS would attempt to use and prioritize the most accurate sensory information (Ernst & Bülthoff, 2004: Tremblay & Proteau, 1998). That being said, with both visual and proprioceptive feedback perturbed, errors should be significantly greater than when the participant has two reliable sources of sensory information.

3 Common Methods

3.1 Study Design

The testing for this project took place in the Perceptual Motor Behaviour Laboratory located in the Warren Stevens Building at the University of Toronto. Informed consent was obtained from all participants in written form. Prior to arrival, the participants were told about the tendon vibration manipulations and given an opportunity to withdraw. Upon arrival to the laboratory, the participant was again briefed about the protocol and given another opportunity to withdraw before the experiment began. In the second experiment, all participants were also asked about hand dominance before coming into the lab and only right-handed participants were invited in to complete the protocol. The study involved a within-subjects design, having each participant act as their own control and partake in all aspects of the experimental protocol.

3.2 Participants

All participants were recruited from the University of Toronto community for both experiments. History of neurological impairment was assessed using a brief neurological questionnaire (see Appendix A). Hand dominance was assessed using a handedness questionnaire (Oldfield, 1971; Appendix B). Each participant had self-reported normal or
corrected-to-normal vision and was tested for eye dominance using the Miles (1930) simple target Eye Dominance Test. There is evidence to show that people tend to rely on the vision from one eye over the other (Miles, 1930), thus all participants in the current study were making movements with the same dominant visual field. Participants were naïve to the purpose of the experiment. Oral instructions were given upon arrival to the laboratory, followed by written informed consent prior to the experiment. Participants were financially compensated for their time. There was no overlap of participants between the two experiments.

3.3 Experimental Set-up

After the participants completed the consent process, they were seated in a chair as the tendon vibrators were applied. Two high-intensity cylindrical tendon vibrators (Dynatronic VB100, excursion 0.5mm, 100 Hz, 30 mm diameter, 75 width, 125 g) were affixed to the participants’ distal biceps brachii tendon and distal triceps brachii tendon. The tendon vibrators were affixed with athletic polyurethane foam wrap (7 cm width) to ensure proper placement with minimal shifting and vibration absorption. The vibrators were always placed on the right arm of the participant.

4 Manuscripts.
The Effects of Between-Trial Dual-Muscle Tendon Vibration on an Upper-Limb Perceptual Matching Task
VIBRATION MATCHING TASK

ABSTRACT

Tendon vibration (TVib) has been widely used to assess the use of upper-limb proprioception in humans (e.g., Goodwin et al., 1972). TVib creates a sensation that the muscle of the vibrated tendon has been stretched. TVib presented during voluntary movement interferes with natural muscle activation (e.g., Cordo et al., 1995). Additionally, previous literature has shown that after a bout of tendon vibration, the sensitivity of muscle spindles decreases, leading to an opposite lengthening effect (Ribot-Ciscar et al., 1998). The purpose of this study was to test if it is possible to employ dual-muscle TVib between trials to perturb the proprioceptive system and yield altered perception of limb configuration. Participants performed a contralateral limb-matching task (see Goble, 2010). The tendons of the biceps and triceps brachii of the right arm were simultaneously vibrated for 30 seconds between each trial. Ten trials were performed with TVib and ten without TVib. Unlike single-muscle seminal TVib studies, the average angular bias did not differ on trials with versus without TVib. On the other hand, the variability of the final angle at the elbow was significantly greater on trial with TVib than on trials without. The findings suggest that simultaneous TVib of both the biceps brachii and triceps brachii muscles between trials significantly reduced the reliability of the proprioceptive signals and could be employed to assess proprioceptive information use in humans.

Keywords: tendon vibration, between trial, proprioception, limb-matching
The Effects of Between-Trial Dual-Muscle Tendon Vibration on an Upper-Limb Perceptual Matching Task

Introduction

Tendon vibration has been used in recent literature to investigate the contribution of proprioceptive feedback to the sensation and perception of upper-limb position. Muscle tendon vibration has the ability to stimulate the muscle spindles (intrafusal fibers) and Golgi tendon organs embedded in skeletal muscle and tendons, which signal the central nervous system (CNS) about muscle tension, length and rate of change in length (Gardner & Johnson, 2013). Tendon vibration is thus effective in assessing proprioceptive function in humans.

Tendon vibration has been used in research to investigate the abilities of the proprioceptive system by introducing artificial stimulation of the muscle spindle afferents. Goodwin, McCloskey, and Matthews (1972) used tendon vibration to study the ability of humans to sense limb position in the absence of vision. These authors reported that when vibrating the biceps brachii muscle of a stationary limb, the participant felt their forearm extending at the elbow. When applying the vibration to movement, Goodwin and his colleagues (1972) found that after vibration of the biceps muscle, participants matched their non-vibrated arm to a location more extended than the vibration arm. The mechanistic explanation for this phenomenon is a product of the overstimulation of Type Ia afferent fibers innervating muscle spindles, resulting in an amplified message of stretch sent directly to the CNS, triggering the muscle sensation of being more extended than it actually is. In turn, the CNS uses this information to create any further movement.

In a follow up to Goodwin et al. (1972), Capaday and Cook (1981) investigated the impact of muscle tendon vibration on the control of endpoint position in a single-joint voluntary
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goal-directed movement. The authors presented tendon vibration either continuously during the movement or only during either active flexion or extension. The effect of biceps vibration revealed undershooting of the target during extension movements, while no significant bias was observed during the flexion movements. Alternatively, triceps vibration revealed undershooting of the target during the flexion movement, but no effects on the extension movements. From these results, the authors provided evidence that it is the proprioceptive receptors of the lengthening or antagonist muscle that is monitored by the central nervous system (Capaday & Cooke, 1981). Such effects were replicated using slower movements (Inglis & Frank, 1990). Furthermore, vibrating the shortening muscle tendon has no effects on movement accuracy or variability (Inglis, Frank, & Inglis, 1991).

Roll and Vedel (1982) investigated alternating and simultaneous vibration of the biceps brachii and triceps brachii tendons. As expected, when the vibration was alternating, perception of lengthening changed between flexion and extension. Alternatively, simultaneous dual-muscle vibration eliminated the lengthening illusion altogether. The authors employed this paradigm at rest, but it is of further interest to investigate if the application of simultaneous vibration can still be used as a proprioceptive assessment after movement, when a participant is required to use the conflicting information.

Tendon vibration of any skeletal muscle in the human body is known to elicit tonic reflex contraction, coined tonic vibration reflex (TVR: Eklund & Hagbarth, 1966). The TVR describes the over stimulation of Ia afferents leading to the relaxation of the antagonist muscles (Elkund & Hagbarth, 1966), alike our natural stretch reflexes (Sherrington, 1900). It is believed that the gamma motor system controls the TVR in skeletal muscle, based on evidence gathered in cats (Granit, 1962). Goodwin et al. (1972) described the TVR as the reason the bicep muscle became
immediately flexed during vibration. When investigating the effects of tendon vibration in muscle, it is important to consider the effects of TVR, thus the current study implemented between-trial vibration to mitigate the effects of TVR on the perceived limb position.

Post vibration aftereffects of skeletal muscle are also known to cause involuntary muscle contractions (Edin & Vallbo, 1990). The contractions may be due to the natural response of muscle spindle primary endings after cessation of a vibrating stimulus, similar to responses seen in muscle after maximum voluntary contraction (Gilhodes, Gurfin & Roll, 1992). Alternatively, aftereffects of vibration include perturbed proprioception (Rogers et al., 1985) as well as the reduced sensitivity of muscle spindles causing a perceptual illusion in the opposite direction (Roll, Gilhodes & Tardy-Gervet, 1980; Ribot-Cisar, Rossi-Durand & Roll, 1998), meaning a person may sense the shortening of the recently vibrated muscle. Thus, proprioception can be based on information not only from the muscle being lengthened but also contributions from aftereffects of the muscle shortening (Ribot-Cisar et al., 1998).

Cordo, Gurfin, Bevan and Kerr (1995) further investigated the effects of tendon vibration during passive movement and the subsequent activity of the muscle afferents. While many studies prior have investigated tendon vibration during movement (Capaday & Cooke 1981; Inglis & Frank, 1990), Cordo and his colleagues were interested specifically in the endpoint perception and precision. The authors had participants create one movement (i.e., open their hand) when they perceived their limb to be passing through a target angle. Vibration was applied to the right biceps tendon only. Vibration was turned on for five seconds before movement, during movement or both before and during movement. As expected, accuracy was directly related to the amount of vibration, where higher frequencies were associated with greater differences between perceptions of the limb. Consistent with all previous research on tendon
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vibration, Cordo and colleagues noticed that when vibration occurred during movement, the participant would consistently undershoot the target. Alternatively, when vibration was presented before movement, participants tended to overshoot the target, which was significantly different from no-vibration conditions as well.

Thus far, studies have been able to reveal the detrimental accuracy effects muscle tendon vibration has on the ability to perceive position both at rest and during movement. Although we know biases can be introduced with the vibration of one muscle (Capaday & Cooke, 1981), it has not yet been demonstrated what happens to the bias during an active task. According to the work of Roll and Vedel (1982) the directional bias should be eliminated when employing dual-muscle vibration. It is of interest to investigate whether this bias is independent or a result of instability in precision from the vibration. Thus, the current study intended to investigate the bias and variability of endpoint position of a position-matching task after brief dual-muscle tendon vibration. The current study employed a contralateral limb-matching task while simultaneous biceps and triceps dual-muscle vibration was applied between trials.

To assess one’s proprioceptive abilities, limb placement or matching tasks are often employed with eyes-closed to observe how people integrate internal sensory information. Clinicians use simple limb matching tasks to assess deficits in the sensory-motor systems (for a review see Goble, 2010). There are at least two distinct ways of employing a limb position-matching task in a clinical environment. Both require minimal apparatuses and are performed with the participant closing their eyes. The first involves the use of one limb and is known as the ‘ipsilateral matching’ task. The clinician will bring the limb to an intended target location, leave it there for a couple seconds and then return it back to a neutral position. The participant is then asked to recreate the position using the same limb. Alternatively, clinicians may opt to use a
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‘contralateral matching’ task, which incorporates both limbs. In this case, the clinician will move one limb to a target location and leave the limb at this perceptual reference point. The task for the participant is now to move their other limb to this same location. The reference limb remains in the target location and the participant must gather online proprioceptive information in order to accurately move their other limb to the same location.

Ipsilateral matching tasks are not always attractive in a clinical setting because of their reliance on the memory systems. Often, people needing sensorimotor rehabilitation have suffered cortical lesions and perhaps cannot rely on their memory systems anymore, thus results from the task may reflect memory problems rather than proprioceptive ability. Similarly contralateral matching tasks pose other limitations because of their reliance on communication between the two cerebral hemispheres, which may also have been effected by recent trauma. A third method that can be introduced incorporates the two methods discussed above. The ‘contralateral memory task’ is one where the clinician will take a limb of the participant, passively move it to a target location and then return it back to the starting position. The participant must then use their other limb to match the location of where the target location was. This task not only involves the memory component, but also relies on the communication between cerebral hemispheres. Previous results comparing the use of limb-matching tasks reveal twice as many errors in the contralateral memory task than in the ipsilateral matching task (Goble, 2010). The contralateral memory task was selected for this study, as it has been shown to produce the highest absolute errors, when compared to the other two tasks (Goble, 2010). The current study tested neurologically intact participants, thus this complex task was used to maximize task difficulty, while assuming the absence of memory deficits.
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In the current study, endpoint position was manually recorded and both constant error and variable error were calculated. Firstly, if between trial tendon vibration introduces noise into the CNS, we hypothesize that dual-muscle vibration aftereffects will increase variable error. Although there is evidence that dual-muscle tendon vibration of the biceps and triceps does not create the typical lengthening illusion at rest (Roll & Vedel, 1982), this discrepancy was expected to produce increased endpoint variability during an active matching task due to previously observed vibration aftereffects caused by TVR (Eklund & Hagbarth, 1966) or decreased sensitivity caused by vibration (Ribot-Ciscar et al., 1998). Based on the idea that vibration reduces the sensitivity of muscles spindles post vibration, the fatigued aftereffects from both muscles should also contribute to an increase in endpoint variability. Secondly, it is hypothesized that due to the use of dual-muscle tendon vibration, there would be no modifications of constant error from vibration (e.g., Roll & Vedel, 1982).

Methods

The experiment took place in a secluded room and the participant was asked to sit on a standard office chair that was lowered as much as possible (top of seat 40 cm from the ground) in front of a table (60 cm surface from the ground). The experimenter sat adjacent to the participant sat so the right arm of the participant was accessible (see Figure 1.1). The participant was asked to place both elbows on the table, while having their forearms pronated and aligned with one another. This position was used to maximize the ability to create horizontal arm extension movements about the elbow. The participants were instructed to align their middle fingers as close together without touching while seated comfortably. The middle finger was used for measuring movement endpoint. Once the position was established comfortably, a square of textured medical tape was placed beneath the tip of each middle finger. The tape was used as a
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reference point for the participants so they could feel where the home position for each forearm while their eyes were closed.

Participants (n=9) performed ten contralateral memory limb-matching tasks followed by ten contralateral memory limb-matching tasks with added dual biceps and triceps tendon vibration. Two high-intensity tendon vibrators (Dynatronic VB100, excursion 0.5 mm, 100 Hz, 30 mm in diameter, 75 mm in length, 125 g) were placed on the distal biceps brachii and distal triceps brachii muscle tendons of the participant’s right arm. The tendon vibrators were affixed with athletic polyurethane foam wrap (7 cm width) to ensure proper placement with minimal shifting and vibration absorption. A manual goniometer was used to place the right forearm in the intended target location. Alternatively, to measure the endpoint location of the left arm, a marked angle chart equipped with ticks at every 1-degree of displacement was used to measure where the middle finger landed.

Figure 1.1. Overview of Experiment 1 – Biceps and Triceps tendon vibrators indicated on the right arm of the participant. The experimenter sat to the right to have control over the right forearm of the participant. The participant moved their left arm to a location along the angle board so the experimenter could read the distance.
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The right forearm of the participant was horizontally rotated 25, 30, 35, 40, 45 or 50 degrees about the elbow by the experimenter (measured by use of manual goniometer), creating a pronated elbow extension motion. The distances were randomly generated for each participant for both experimental conditions. Due to the small number of trials, not every angle was repeated in each condition. The beginning of each trial began when the experimenter grasped the right forearm of the participant at the wrist bones and began moving it to one of six distances from the home position. The experimenter then held the right forearm in the target position for five seconds and then brought the arm passively back to the home position. The target angle was made to align to the right middle finger displaced by the intended degrees from the home position of the right forearm location. The participant was then free to begin moving their left forearm, attempting to mimic the displacement of the passively rotated right forearm. The participant was asked to pause at the perceived endpoint location for another three seconds and then move back to the left arm home starting position. During the three-second pause, the experimenter recorded the angle that was reached by the middle finger position on the angle board. Once the angle was recorded, the experimenter signaled the participant to return to home.

Two experimental blocks were completed, a no-vibration block and a vibration block. Each block contained ten trials. For the trials with vibration, 30 seconds of vibration was applied before the experimenter moved the right arm of the participant. During both the passive movement of the right arm to the target and the active movement of the left arm, the vibration always remained inactive. The experimenter controlled the vibration simply by using a switch for the vibrators and a standard computer timer (set for 30 second intervals). During the no-vibration block, a 30 second pause was taken between trials to match the duration taken to complete the
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vibration block. The no-vibration block was always presented first. If impairments are a function of practice, then variability should be lower in the second block.

The experimenter also made sure the participant kept their eyes closed for the entirety of the experiment. If requested, the participant was able to take a break between condition blocks, when vibration was off, however only one participant opted to do so.

Results

Spatial endpoint variables were collected and recorded using a manual goniometer and a hand-made angle chart. The angle chart was created using a protractor and ruler to extend the angles to an appropriate length to account for various arm sizes. The target angle was subtracted from the reached target angle. From the recordings, the average angle bias (i.e., constant error) and standard deviations (i.e., variable error) were recorded for each block within each participant. Next the constant errors and variable errors were averaged across participants. SPSS statistical software (IBM, Version 21) along with Microsoft Excel Processing (2011, Version 14.4.4), were used for all data sorting and analysis processing.

Paired t-tests were used to determine significant differences between both the constant and variable error the final angle. In the no-vibration trials, participants were very accurate when moving their limb with a constant error of less than -0.1 degrees (SD=5.2) from the target angle, which was not significantly different from the vibration trials with a constant error of 1.7 degrees (SD=4.1), \( t(8)=0.8, p=.47 \). On the other hand, the variable error for the final angle on the trials without vibration (Mean=3.8, SD=1.1) was significantly smaller than during the trials with vibration (Mean=6.2, SD=1.2), \( t(8)=5.7, p<.01 \) (see Figure 1.2).
Further analyses were performed to investigate whether there were differences in the overshooting and undershooting, based on the magnitude of the target angle. A 2 Phase (no-vibration, vibration) by 6 Angle (25, 30, 35, 40, 45, 50 degrees) repeated measures ANOVA on the constant error was used to compare differences between angles. Results revealed a main effect of angle, $F(5, 40) = 4.6$, $p < 0.01$, while simple contrast tests revealed significantly larger overshooting for the 40/45 degrees targets than the 25/30 degrees targets. The main effects for vibration condition did not meet significance, $F(1, 8) = 0.36$, $p = .56$, nor did the interaction between angle vibration condition $F(5, 40) = 1.72$, $p = .15$.
Figure 1.3. Constant error by vibration condition (0=target angle)

To test for between-subject differences, another set of analyses contrasted all endpoint measures for the vibration and no-vibration trials for each participant. Nine paired t-tests were performed and results revealed that two of the nine participants showed a significant directional bias in endpoint error. One participant displayed an undershoot bias while the other demonstrated an overshoot bias. Table 1.1 shows the average constant error in the no-vibration and vibration conditions for each individual participant (see also Figure 1.4).
<table>
<thead>
<tr>
<th>Participant</th>
<th>No Vibration</th>
<th>Vibration</th>
<th>Difference</th>
<th>t value</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>0.1(3.2)</td>
<td>-6.6(7.2)</td>
<td>6.7(9.2)</td>
<td>2.31</td>
</tr>
<tr>
<td>2</td>
<td>-13.2(3.4)</td>
<td>1.2(6.5)</td>
<td><strong>-14.4(4.2)</strong></td>
<td><strong>-10.78</strong></td>
</tr>
<tr>
<td>3</td>
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<td>-4.3(6.14)</td>
<td>3.3(9.1)</td>
<td>1.14</td>
</tr>
<tr>
<td>4</td>
<td>1.0(5.8)</td>
<td>-3.5(6.2)</td>
<td>4.5(9.6)</td>
<td>1.47</td>
</tr>
<tr>
<td>5</td>
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<td>2.3(7.4)</td>
<td>1.9(11.4)</td>
<td>0.53</td>
</tr>
<tr>
<td>6</td>
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<td>-7.1(3.5)</td>
<td><strong>10.4(3.9)</strong></td>
<td><strong>8.33</strong></td>
</tr>
<tr>
<td>7</td>
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<td>-3.7(6.9)</td>
<td>4.3(6.6)</td>
<td>2.10</td>
</tr>
<tr>
<td>8</td>
<td>2.6(2.4)</td>
<td>3(4.8)</td>
<td>-0.4(5.6)</td>
<td>-0.23</td>
</tr>
<tr>
<td>9</td>
<td>2.7(3.7)</td>
<td>3.2(6.7)</td>
<td>-0.5(8.5)</td>
<td>-0.18</td>
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</tbody>
</table>

Table 1.1. Paired t-test results within each participant on the difference in constant error (bold denotes p<.05)
Figure 1.4 Bar graphs for each participant’s constant error (CE) per angle. P2 and P6 had significantly different CE values between vibration conditions.
Discussion/Conclusions

Participants were asked to perform a limb-matching task without and with tendon vibration. Between-trial dual-muscle tendon vibration was used to perturb proprioceptive feedback during the perceptual limb-matching task. Results confirmed the ability of such tendon vibration methodology to alter proprioceptive feedback after cessation of vibration, thus further demonstrating the impact of between-trial tendon vibration on the sense of limb position.

Firstly, the results from the no-vibration condition replicated previous studies (Clark et al., 1985; Cordo et al., 1995), where in the absence of muscle vibration, participants were very accurate in achieving the target angle. More importantly, the results showed increased variability of end position in the vibration condition while no significant directional biases were observed. From these results, we can conclude that tendon vibration before a movement can yield decreased proprioceptive sensation, for as much as 10 seconds after the vibration has stopped. The results are consistent with previous work such that muscle vibration has the ability to alter the firing frequency of muscle spindle afferents during movement (Goodwin et al., 1972; Capaday & Cooke, 1981), even after the cessation of vibration. This method is of interest because knowing how to induce proprioceptive noise could be employed in studies designed to better understand how the CNS uses proprioception.

The simultaneous vibration can explain the lack of endpoint bias (i.e., constant error). Single-muscle vibration can over stimulate muscle spindles, yielding the sensation of muscles lengthening, thus creating undershooting of intended targets (Capaday & Cooke, 1981). As well, employing simultaneous vibration at rest reduced the perceptual illusion that the vibrated
VIBRATION MATCHING TASK

Muscles are lengthening. In the current study, no directional biases were observed even though the variability was increased. After vibration cessation, the firing rate of spindles was likely reduced, decreasing the sensitivity of the afferents (Ribot-Cisar et al., 1998). Such decrease in spindle sensitivity of both the biceps and triceps muscles in turn may have yielded the increase in limb position variability seen in the final angle results.

The results of the current study are also consistent with Roll and Vedel (1982), who used bicep and triceps vibrations and found no directional bias when simultaneously applying the vibration. The current analysis of constant error showed an overall lack of bias. However, individual analyses showed that two participants did in fact display a significant directional bias. Although this was true, the biases were not consistent (one undershooting, one overshooting). This may be indicative of the tendon vibrators perhaps not properly placed on the arm and pressure may have been unequally distributed on each muscle, giving a greater effect in one direction. Future usage of tendon vibration devices should include both precise positioning and perhaps also consider measuring forces applied against the tendon.

Further, the results were also in line with the work of Rogers and colleagues (1985) as they observed tendon vibration effects could last for 90 seconds after vibration cessation. The authors employed a similar limb-matching task to the current study, however they vibrated the biceps and triceps muscles separately. The errors in position sense were reported after a misalignment in forearm matching after 60 seconds of vibration at 100 Hz. Vibration for twice as long on the muscle may help explain why the observed effects lasted over a minute. The authors reported that it was not until 240 seconds after movement did the effects of tendon vibration significantly disappear. The current study adds the possibility to have tendon vibration
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aftereffects on position matching even when simultaneous vibration is applied, and that is with as little as 30 seconds of vibration.

While the influence of tendon vibration on the limb matching tasks are known, a unique contribution of the current study is the addition of offline control use during limb matching. The participants in the current study had to recall the information from their right limb, which was not in the target position during the task. However, there were differences observed despite the large variability attributed to the contralateral memory task itself (Goble, 2010). Prior literature investigating vibration effects (for example Capaday & Cooke, 1981; Rogers et al., 1985; Inglis et al., 1991) investigated online control by employing either step-tracking limb matching or static limb-matching tasks. The new information is important when attempting to use tendon vibration as a proprioceptive assessment tool. The participants were attempting to use the remembered information of perturbed proprioceptive information, which perhaps added to the variability seen in the results.

The results of Goble (2010) suggest that matching tasks may not be a sole representation of proprioceptive abilities, but a reflection of the cognitive demands of the task. It is important to consider the cognitive abilities of the participant when performing tasks such as these. In rehabilitations practice, a task similar to the current protocol may not be able to target proprioceptive deficits alone. However, to examine the fundamental abilities of neurologically intact participant, the use of contralateral matching tasks seems appropriate. Traditionally, the practice of physiotherapy has been focused around the ability of a person to produce efficient and accurate motor output following a deficit. In recent years, increased knowledge and understanding of the role of the sensory systems have led clinicians to adopt a different practice, which includes sensorimotor physical therapy. If we can learn how one behaves in the presence
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of altered sensory feedback, appropriate rehabilitation practices can be designed to increase function in this population.

In conclusion, the current study aimed to test the effects of between-trial simultaneous tendon vibration on limb position sense. Although no directional biases were present, the variability in endpoint error significantly increased when a 30 second bout of vibration was presented before movement onset. The study confirms that between-trial tendon vibration yields significant aftereffects, as well as adds the idea that simultaneous vibration can be used to increase the variability of position sense during movement, without creating directional biases. The implications from the current work will help to develop methodologies for testing the proprioceptive abilities of neurologically intact and patient populations.
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References


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The Assessment of Online Multisensory Control Processes Using Altered Proprioceptive and Vision Manipulations
ABSTRACT

Goal-directed action requires movement preparation and online monitoring during execution. While withdrawing vision during goal-directed movement has detrimental effects on endpoint accuracy (e.g., Keele & Posner, 1968; Elliott et al., 2001; Hansen et al., 2006), visuomotor transformations have revealed that proprioception is also important for the online control of movement (e.g., Bagsterio et al., 2006; Rossetti et al., 1995). Tendon vibration (TVib) has been used to perturb proprioceptive information during limb matching tasks (Goodwin et al., 1972), and goal-directed movements (Redon et al., 1991). However, because TVib presentation can yield a tonic vibration reflex (TVR), which interferes with natural muscle activation (Eklund & Hagbarth, 1966), it is difficult to use proprioceptive manipulations during voluntary to assess voluntary sensorimotor mechanisms. The current study employed novel dual-muscle between-trial TVib, coupled with vision occlusion conditions, to further assess the relative use of vision and proprioception to the online control of movement. Participants (n=17) performed an upper-limb reaching task (30 cm). Amplitude and directional biases were present in both the TVib and vision occlusion conditions. TVib caused shifts in both accuracy and precision of movement endpoint. As well, variability analyses showed that participants were most affected by TVib in the directional axis at 75% of the movement, even in the presence of vision. These findings suggest that proprioception is important when controlling the late parts of movement, regardless of visual feedback availability.
The Assessment of Multisensory Control Processes Using Altered Proprioception
Coupled with Online Vision Manipulations

Introduction

Sensory information is necessary to ensure safe and efficient navigation, as well as efficient limb-object interactions. To complete an accurate voluntary action, an estimation of the body in space is needed. The estimation is used to plan desired movement kinematics to execute the movement properly (Graziano, 1999; Sober & Sabes, 2003; van Beers et al., 1999). Vision is one of the most important senses used to create this estimation, however people are constantly incorporating other sensory modalities, such as proprioception, to help improve interactions with the environment.

The central nervous system (CNS) relies more on visual sensory information for movement planning and execution than any other sense (e.g., Poser, Nissen, & Klien, 1976). Although, limb position can be estimated using proprioceptive information (see below), vision of the limb still represents a very reliable and useful source of information when planning a movement (Carlton, 1981; Heath, 2005). When available, vision is used efficiently to complete accurate upper-limb reaching movements (e.g., Hay, Pick, & Ikeda, 1965). Vision is also important for the online control of goal-directed movements (e.g., Khan & Franks, 2003). More particularly, the use of visual feedback is thought to occur during the deceleration phase of reaching movements, after the limb has reached its peak velocity (see Elliott, Hansen, Grierson, Lyons, Bennett, & Hayes, 2010). Thus, visual feedback is gathered after movement initiation and
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processed in order to prepare for any necessary trajectory amendments to be made from the original estimation.

Goal-directed arm movements are controlled by impulse control (i.e., planning) and current control processes (e.g., Woodworth 1899; Elliott, Helsen, & Chua 2001). The initial impulse phase of movement is where the movement plan is executed during the early stages of movement, while the current control phase is when corrections are made to this motor plan when deviations occur. Thus, it is important to focus on the time spent after peak velocity during a trajectory to infer the use of online feedback (e.g., Elliott et al., 2001). Although more corrections have been observed when movements were made with eyes open, significant amount of corrections can still be observed when movements are performed with the eyes closed (Elliott, Carson, Goodman & Chua, 1991). Elliot and colleagues reported these observations, suggesting that when vision is degraded, participants “may depend more on kinesthetic feedback to control their movements” (pp. 407). Such observation implies that other sensory modalities than vision may be contributing to the online control of movement, such as proprioceptive feedback from the moving limbs. Yet, evidence on the use of proprioception for goal-directed behaviors remains scarce relative to the visuomotor regulation literature.

Before initiating a voluntary arm movement, the CNS must identify sensory information from both the position of the upper-limb, as well as the information regarding the location of the desired target (Gardner & Johnson, 2013). While information regarding the spatial target location is best identified with visual information, the location of hand position requires both the use of visual feedback (e.g., Prablanc, Echallier, Komilis, & Jeannerod, 1979), as well as feedback from proprioceptive afferent signals (e.g., Bagesteiro, Sarlegna & Sainburg, 2006). Once both these sources of information are relayed and integrated at the CNS, a motor plan can be generated to
properly and efficiently execute the movement (e.g., Rossetti et al., 1995). However the individual contributions of each sensory modality is not fully understood.

The discrete influences of proprioception and vision on the online control of a goal-directed movement have been studied extensively. People are more accurate pointing to an intended target when they have vision and proprioception available to them, than when one of the modalities is disrupted. What is not clear, however, are the online relative contributions from each sensory modality, to control ongoing limb trajectories. It is well known that visual feedback is important in motor planning, however visual processing times have been reported to be around 190 ms (Keele & Posner, 1968) (cf. 100 ms: Carlton, 1982). More recently, Elliott and colleagues (2010) describe a model incorporating multiple processes for the online control of action. The authors suggested that when planning a rapid goal-directed movement, both sensory and motor representations are formed along with the subsequent consequences of movement. The motor plan can be compared to the initial impulse as early as prior to or at peak acceleration, where initial impulse regulation occurs along with the acquisition of visual and proprioceptive information. In the presence of visual feedback, limb-target regulation begins and continues until the movement is completed. The current study aims to assess the individual and combined contributions of vision and proprioception to impulse regulation and limb-target regulation processes.

Proprioceptive sensation and movement have been studied for over a century (Sherrington 1900), yet it is not fully understood how proprioceptive information is integrated during the control of a goal-directed task. As muscles lengthen, proprioceptive afferent information is sent to the CNS regarding both static and dynamic limb positioning. Specifically, muscle spindle afferents send information regarding the stretch of a desired muscle (Gardner &
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Johnson, 2013). If the limb appears to be in an undesirable location via proprioceptive information, movements are initiated to correct for any positional discrepancy. Proprioception has been observed to contribute to the late online control of a goal-directed action (e.g., Cordo, Gurfinkel, Bevan, & Kerr, 1995; Redon, Hay, & Velay, 1991). Particularly, proprioceptive feedback during movement is important in the control of muscle forces and torques (Ghez, Gordon, Ghilardi, Christakos, & Cooper, 1990), as well as the compensation to initial planned movement errors (i.e., online control).

In a study done by Bageistero et al. (2006), the relative influences of proprioception and vision during movement were evaluated to identify the contributions of each sensory modality on a goal directed movements. The authors employed a virtual location of the target to create a proprioceptive mismatch between where the participant saw the cursor to be and where the participant felt their hand to be. The cursor was displaced relative to the actual limb position. Participants were unaware of the discrepancy, which was observed when asked about the displacement after the procedure was over. Acceleration profiles were used to analyze which sensory system guided which parts of the movement trajectory (see Bagesteiro et al., 2006 for full analyses). It was found that proprioception, or the trials when the hand was displaced, affected the peak velocity of movement towards the target that was further away, while the accurate target location had no effect. The authors suggested that proprioception must have been used to implement online corrections to complete the movement. Alternatively, the authors concluded that movement-planning mechanisms predominantly rely on visual information. As such, Bagesteiro and colleagues suggested that while vision is required for planning the distance of movement, online corrections might rely to a greater extent on proprioception during movement (Bagesteiro et al., 2006). It must be noted that the trials in this study were completed in the absence of vision of the limb.
To investigate the use of vision and proprioception relative to hand position movement, Rossetti, Desmurget and Prablanc (1995) also studied the use of feedback in a visual-proprioceptive mismatch task using visual prismatic perturbations. Participants were required to point in the absence of vision to a target that was displaced to the right or not. Specifically, if vision was the only sensory modality involved, the endpoint error should be proportionate to the magnitude of displacement. The authors found that movement endpoint in the target-displaced condition showed partial corrections of the target bias (Rossetti et al., 1995). Specifically, the shift in endpoint was only one third the magnitude of the displacement. In this instance, proprioceptive information was likely used to control the position of the limb at movement start, to alleviate the mismatch caused by the visual displacement. Rossetti and colleagues (1995) subsequently suggested that it may not be individual contributions, but rather vision and proprioception may be fused to create and execute motor plans.

The works of Bageistero et al. (2006) and Rossetti et al. (1995) investigated the contribution of vision or proprioceptive information, respectively, using a visual or proprioceptive-visual mismatch. However, the authors did not manipulate proprioceptive information per se. Thus, it is hard to accept the conclusions about vision and proprioception without investigating the individual sensory contributions separately. More specifically, the authors were able to make conclusions about visual feedback, but could only make inferences about the contribution of proprioceptive feedback. Alternatively, there are more direct ways of perturbing proprioceptive information, including muscle tendon vibration.

Muscle tendon vibration alters proprioceptive feedback in the static (e.g., Goodwin et al., 1972), passive (e.g., Cordo et al., 1995) and dynamic limb positions (e.g., Capaday & Cooke, 1981; Inglis & Frank, 1990). Goodwin and his colleagues (1972) vibrated the stationary upper-
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limb leading to the sensation of extension occurring in the vibrated muscle, and attributed this
phenomenon to the heightened discharging of the muscle spindle afferents embedded in muscle.

More specifically, vibration of the biceps brachii muscle causes undershooting in an extension
movement, while vibration of the triceps brachii muscle produces and undershooting in a flexion
movement (Goodwin et al., 1972; Capaday & Cooke, 1981). Muscle tendon vibration can
perturb voluntary movement if presented constantly over several continuous movements, but also
when activated throughout the entirety of a single goal-directed movement (Capaday & Cooke,

Redon, Hay and Velay (1991) employed tendon vibration during a voluntary goal-
directed movement in both the absence and presence of vision to investigate the proportions of
movement affected by tendon vibration. Initially, the authors asked participants to perform
movements to one of four targets (40 cm amplitude). The movements were controlled and
performed for 200, 500 or 800 ms with tendon vibration activated throughout the entire
movement. Participants exhibited a leftward endpoint bias (i.e., undershooting) in all vibration
conditions, which was found at a greater degree in the 800 ms condition relative to the 500 and
200 ms conditions. In a follow-up experiment, the movement time was held constant at 800 ms
while vibration was presented for different durations (200, 400 or 600 ms), beginning from the
start of movement. These conditions were also compared with the 800 ms results from the first
experiment. This allowed the authors to compare vibration effects of an 800 ms movement with
vibration on for 25, 50, 75 and 100% of the movement time. Similarly, there were no differences
in constant error in either the 200, 400 or 600 ms conditions. Alternatively, they were all
different than the bias from the 800 ms condition. A third experiment was then employed using
200 ms of vibration in either a 200 ms movement (all vibration) or during an 800 ms movement
(only the first or last 200 ms vibration). The largest leftwards bias was found in the 800 ms
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condition when vibration was employed for the last 200 ms of movement. These results altogether contribute to the idea that muscle tendon vibration does certainly induce a directional bias during movement when employed over one muscle, but also that proprioceptive information is crucial during the online control of movement. The final experiment supplements the knowledge that proprioception is used to regulate the online control, especially during the later or final stages of voluntary movements.

The shifts in endpoint distribution seen in studies employing tendon vibration imply that proprioception contributes to the online control of movement (Goodwin et al., 1972; Sittig et al., 1987; Cordo et al., 1995; Capaday & Cook, 1981). Similarly, as previously discussed, results have shown that when vision is available during movement, endpoint accuracy is improved (Lemay & Proteau, 2001), indicating that visual feedback is as well very important during movement. Models of multisensory integration indicate that sensory modalities are weighted differently depending on their relative contributions to the current task (Ernst & Banks, 2002). This idea is in line with the results of Rossetti et al., (1995), who stated that different senses are used to control different aspect of movement. As well, when one modality becomes unavailable, it can be assumed others will be relied upon to a certain extent (Sober & Sabes 2003). However, we are still uncertain as to which sensory modality is most important during different portions of a goal directed movement. The current study intended to further investigate this multisensory integration dilemma by having participant perform a goal-directed movement with both visual and proprioceptive feedback directly perturbed. This was done using muscle tendon vibration and liquid crystal goggles (Milgram, 1987).

One limitation to employing tendon vibration during a goal-directed action is the possibility of eliciting a tonic vibration reflex (TVR: Eklund & Hagbarth, 1966). TVR occurs
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when muscle spindle afferents are over stimulated due to vibration stimulation combined with
natural firing patterns. This leads to the subsequent relaxation of the antagonist muscles (Elkund & Hagbarth, 1966). Thus, the current study employed a between-trial tendon vibration protocol, to avoid the effects of the TVR.

The previous literatures that investigated both sensory modalities typically employed a visual-proprioceptive mismatch to assess the individual involvement of visual and proprioceptive feedback. The current study used a direct perturbation of the proprioceptive system (i.e., tendon vibration) coupled with direct occlusion to the visual system (liquid-crystal goggles). Moreover, this study employed tendon vibration simultaneously to both the biceps brachii and the triceps brachii muscles before the initiation of movement, to avoid involuntary muscle activation (i.e., TVR).

A previous study performed recently has shown that using between-trial dual-muscle tendon vibration on a perceptual limb-matching task has the ability increase the variability of movement endpoint. The experiment was performed using a slow voluntary movement towards a proprioceptive target and without the use of vision. The current study tested the ability for muscle tendon vibration to perturb proprioceptive feedback during a rapid voluntary movement, coupled with trials with and without vision.

It was hypothesized that consistent with the previous experiment, between-trial dual-muscle tendon vibration would cause increased endpoint variability in the absence of vision. Due to previous conclusions regarding the dominance of visual feedback, it was also hypothesized that the effects of vibration perturbations on endpoint precision and accuracy would decrease when vision was given throughout the movement. If proprioception is most important during the online control phase of movement or during the time after peak velocity, it was expected that
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during this time, tendon vibration would cause increased deviations in movement position
variability. Alternatively, during the vibration trials when vision was available it was expected to
see a decline in this variability, due to the ability to appropriately compare online visual and
proprioceptive information discrepancies to the motor plan and make appropriate corrections
(Elliott et al., 2010). It was also hypothesized based on the previous study that directional biases
would not be exhibited due to the use of both biceps and triceps tendon vibration. The results
intend to corroborate the current literature regarding tendon vibration assessments as well as add
to the knowledge of visual-proprioceptive integration during movement.

Methods

Seventeen participants (mean age: 23.4 years old) from the University of Toronto
community completed the protocol. All participants were right-handed and right-eye dominant
and were naïve to the purpose of the experiment. Participants performed 50 goal-directed
movements to a target located 30 cm away from a home position. The participants were seated in
front of a table (60 cm in height) equipped with a custom built aiming console (see Figure 2.1).
The movements were performed without any head or joint constraints. The console contained a
light emitting diode (LED) below a translucent surface, so the LED could only be seen if
illuminated. A piece of black Velcro (1 cm square) placed on top of the translucent surface
defined the home position. The tactile surface allowed participants to place their finger on the
home location because vision was not available between trials. Under the board surface was also
a piezoelectric buzzer (Mallory Sonalert Products Inc., Model SC628, tone frequency of 2900
Hz). The buzzer was used to alert the participant about the start and end of each trial. The finger
of the participant was tracked using an Optotrak Certus (Northern Digital Inc.) motion tracking
system. This system monitors Infrared Emitting Diodes (IRED), which was placed on the tip of
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the participant’s index finger of their right hand during the protocol. The primary movement axis was defined as the amplitude of movement, and the secondary axis was referred to as the direction axis (see Figure 2.1). The direction axis was located perpendicular to the primary movement axis.

Figure 2.1. Overview of the experimental set up. The participant was seated with one vibrator over the distal biceps tendon and one over the triceps tendon. Vibrators and goggles were worn throughout the experiment. The board was angled at 50 degrees to the midline of the participant, and the participant had their chest pressed against the chest rest of the chair.

Two high intensity tendon vibrators (Dynatronic VB100, excursion 0.5 mm, 100 Hz, 30 mm in diameter, 75 mm in length, 125 g) were placed on the distal biceps brachii and distal triceps brachii muscle tendons of the participant’s right arm. The tendon vibrators were affixed
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with athletic polyurethane foam wrap (i.e., 7 cm in width) to ensure proper placement with minimal shifting. Additionally, participants wore liquid crystal goggles (PLATO, Translucent Technologies, Inc.), which occluded vision when desired.

The familiarization phase consisted of ten trials, with the goggles remaining open and the vibrators off. These trials were to allow the participant to get familiar with the experimental movement time bandwidth (i.e., 290-400 ms). Such a bandwidth was used to avoid speed-accuracy trade-offs (Fitts, 1954). The participants were told to move their limb as accurately as possible within the time bandwidth to the green target location, after hearing the signaling beep. If the participant performed the movement in more than 450 ms, they were told to focus more on speed and the familiarization trial was repeated. All participants exhibited longer than desired movement times at least once and no more than four times, during the familiarization trials. In contrast, no participants exhibited initial movements faster than 290 ms. The experimental blocks were performed when the participant could perform 10 movements in the appropriate bandwidth time.

After the familiarization phase was completed, two blocks of twenty trials were completed, one with vibration the other without vibration. The order of the blocks was counter-balanced across participants. Prior to the block of vibration trials, the tendon vibrators were activated for sixty seconds before the first trial. Also, the vibrators were turned on for 5 seconds, prior to each subsequent trial. The five-second intermittent activations were to ensure the aftereffects of vibration did not diminish over the procedure, without having to present it during the actual movement. The trial began immediately following the 5 seconds of vibration. On each trial, participants had a 1-second preview of the environment, thus there was always this delay between vibration offset and the actual start of movement, thus avoiding the effects of TVR.
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Between the two blocks of trials, a 10-minute resting period was employed to wash out any post-stimulation effects of the vibration. All participants were given the resting period regardless of vibration block order, to control for temporal effects.

During each block, there were 10 vision and 10 no-vision trials, presented in a pseudo-random fashion, with the limitation of not presenting the same vision condition more than 2 times in a row. In the vision condition trials, the participant had vision throughout the entire movement, until movement end, when the velocity of the limb fell below the movement threshold (0.03 m/s) for three consecutive samples. In the no-vision conditions, vision was removed as soon as the limb velocity rose above 0.03 m/s for three consecutive samples. This temporal marker was also defined in both vision conditions as movement start.

Movement profiles were recorded for each individual trial in order to calculate a velocity profile. Movement time was calculated as the collected end time minus the collected start time. The maximum limb velocity reached for each trial (PV) was recorded and calculated based on the difference between 2 consecutive samples. From PV, the amount of time spent to reach PV was calculated from movement start (TtPV), as well as the time spent after PV was reached until movement end (TaPV). In order to evaluate the amount of online and offline control during each trial, the standard deviation of limb position was calculated at 25%, 50%, 75% and 100% (movement end) of movement time (Kahn et al., 2006). The extraction was done in both the primary (i.e., amplitude) and secondary (i.e., direction) movement axes. During data collection, the primary axis was labeled Y, and the secondary axis was labeled X (see Figure 2.1).

Two participants were removed from the data set due to collection errors, as the Optotrack camera did not capture the IRED marker throughout most of the movements. Additionally, a proportion of trials from the remaining participants were removed (i.e., 4%) due
to collection errors, again due to lost markers during a portion of the movement. All calculated kinematic and endpoint error values were then reviewed and any value that was 2.5 or more standard deviations away from the mean was discarded as well (i.e., 2.6% of all trials for all participants). SPSS statistical software (IBM, Version 21) along with Microsoft Excel Processing (2011, Version 14.4.4), were used for all data sorting and analysis processing.

To analyze all bias and variability endpoint data, a 2 Vision (vision, no-vision) by 2 Vibration (no-vibration, vibration) analyses of variance (ANOVA) design was used. The ANOVAs were performed on each axis (i.e., amplitude and direction) for both constant and variable error values. Constant error was defined as the directionality of error from the target while variable error was defined as the standard deviation of endpoint position. The same analysis was also used to analyze the following kinematic variables: movement time, time to peak velocity, peak velocity and time after peak velocity. Mauchly’s test of sphericity was used to validate each ANOVA analysis, however there were no violations in any of the significant results. Tukey’s HSD values were used to assess differences for all significant interactions found.

To breakdown the trajectory, the portions of movement where online corrections are known to take place were isolated and analyzed. In order to assess the relative online control of each sensory system, a standard deviation (SD) analysis was performed on the movement conditions at different parts of the movement (Khan et al., 2006). The SD’s of finger position were calculated at 25%, 50%, 75% and 100% of movement time in each experimental condition to track the consistency of the trajectory across the movement. In the primary and secondary axes, a 4 Movement Proportion (25%, 50%, 75%, 100%) by 2 Vision (vision, no vision) by 2
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Vibration (no vibration, vibration) ANOVA was performed to investigate the variability of finger position at different parts of the trajectory.

Results

In the primary movement axis (Y), the ANOVA of constant error (CE) revealed a main effect of vibration, $F(1,14)=5.5$, $p<.05$, as participants undershot the target more in the non-vibration condition than in the vibration condition. The analysis also revealed a main effect of vision, $F(1,14)=9.4$, $p<.01$, indicating that participants undershot the target more in the absence of vision than when they had vision of the trajectory. The interaction between these factors was not significant, $F(1,14)=0.1$, $p=.73$. Table 2.1 includes the constant error values for each experimental condition in the primary movement axis and Figure 2.2 displays the main effects of the ANOVA.

In the secondary movement axis (X), the ANOVA on the CE values revealed a main effect of vibration, $F(1,14)=6.3$, $p=.03$, indicating that participants displayed a smaller rightward bias (i.e., away from the participant) in the presence of vibration. The analysis also revealed a main effect of vision, $F(1,14)=34.8$, $p<.01$, as participants exhibited a rightward bias in the absence of vision. The interaction between these factors was not significant, $F(1,14)=0.1$, $p=.72$. Table 2.1 contains the CE values for each experimental condition in the secondary movement axis and Figure 2.3 displays the main effects of the ANOVA.
Figure 2.2. Bar graph displaying the average Constant Error in the Primary Axis (Y axis), separated by vision conditions (vision and no vision), and by vibration conditions (vibration and no vibration).

Figure 2.3. Bar graph displacing the average Constant Error in the Secondary Axis (X axis), separated by vision conditions (vision and no vision), and by vibration conditions (vibration and no vibration).
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Table 2.1 Constant Error in primary and secondary movement axes

<table>
<thead>
<tr>
<th></th>
<th>No-Vibration</th>
<th>Vibration</th>
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</thead>
<tbody>
<tr>
<td></td>
<td>Vision</td>
<td>No-Vision</td>
</tr>
<tr>
<td><strong>Primary Axis</strong></td>
<td>-2.48 (4.3)</td>
<td>-10.89 (10.7)</td>
</tr>
<tr>
<td><strong>Secondary Axis</strong></td>
<td>0.36 (2.5)</td>
<td>5.48 (4.9)</td>
</tr>
</tbody>
</table>

Note: Value of the mean between subjects with the standard deviation in brackets.

The ANOVA on variable error (VE) data of endpoint in the primary axis (Y) revealed no main effect of vibration, $F(1,14)=1.9$, $p=.19$, while vision yielded a significant effect, $F(1,14)=27.7$, $p<.01$. Participants exhibited greater endpoint variability in the absence of vision than when they could see their limb trajectory (see Figure 2.4). Again, no significant interactions were found between vision and vibration, $F(1,14)=1.9$, $p=.19$. Table 2.2 presents the VE values for each experimental condition in the primary axis and Figure 2.4 displays the main effects of the ANOVA.

The ANOVA revealed a significant effect of both vibration, $F(1,14)=9.1$, $p<.01$ and vision, $F(1,14)=5.0$, $p<.05$, in the secondary axis. Participants were more variable in secondary axis endpoint position in both the presence of vibration and when vision was taken away. Again, the interaction between these factors was not significant, $F(1,14)=2.1$, $p=.17$. Table 2.2 contains all the VE endpoint data, while Figure 2.5 displays the main effects of the ANOVA on the VE data, in the secondary axis. Despite the fact that no interaction was found, the within vision differences were tested.
Figure 2.4. Bar graph displacing the average Variable Error in the Primary Axis (Y axis), separated by vision conditions (vision and no vision), and by vibration conditions (vibration and no vibration).

Figure 2.5. Bar graph displacing the average Variable Error in the Secondary Axis (X axis), separated by vision conditions (vision and no vision), and by vibration conditions (vibration and no vibration).
Table 2.2 Variable error in primary and secondary movement axes

<table>
<thead>
<tr>
<th></th>
<th>No-Vibration</th>
<th>Vibration</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Vision</td>
<td>No-Vision</td>
</tr>
<tr>
<td><strong>Primary Axis</strong></td>
<td>5.83 (1.5)</td>
<td>8.11 (2.6)</td>
</tr>
<tr>
<td><strong>Secondary Axis</strong></td>
<td>4.16 (1.1)</td>
<td>4.32 (1.4)</td>
</tr>
</tbody>
</table>

Note: Value of the mean between subjects with standard deviation in brackets

The 4x2x2 ANOVA performed on the standard deviation of finger position in the primary axis, revealed a main effect of movement proportion, $F(3,42)=29.6$, p<.01. A post-hoc analysis (HSD=10.4 mm) was performed on the main effect of movement proportion revealing the greatest variability in finger position occurred at 50% across all conditions (see Figure 2.6). Variability at 50% of movement time was greater than at all other movement time percentages. Also, the lowest amount of variability was at 100% of the movement, which was significantly lower than 25%, 50% and 75% of movement time. The ANOVA also revealed a main effect of vibration, $F(1,14)=6.8$, p<.05, indicating that participants were more variable in their movements when vibration was present (see Figure 2.7). This was true regardless of vision condition. Table 2.3 contains the individual means for the variability within each proportional movement time, across both vision and vibration conditions.
Figure 2.6. Line graph showing the standard deviation of finger position at various movement proportion times in the primary movement axis. Variability was significantly higher at 50% than all other conditions and significantly lower at 100% than all other conditions.

Figure 2.7. Bar graph showing significant difference in trajectory variability between vibration conditions in the primary movement axis.
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Table 2.3. Standard deviation of limb position at various portions of movement time in the primary axis

| Variability of the limb position (mm) in the primary axis at various portions of movement time |
|-----------------------------------------------|-----------------------------------------------|
|                                | No-Vibration |               | Vibration |               |
|                                | Vision       | No-Vision     | Vision     | No-Vision     |
| 25%                            | 12.7         | 13.8          | 18.9       | 15.7          |
| 50%                            | 21.8         | 24.0          | 28.2       | 29.6          |
| 75%                            | 11.9         | 14.6          | 19.4       | 18.4          |
| 100%                           | 6.0          | 8.1           | 6.0        | 10.4          |

*Bold* denoted significantly different values from all other movement time proportion conditions

The 4x2x2 ANOVA was performed on the variability of finger position in the secondary axis revealed a main effect of movement proportion, $F(3,42)=16.3$, $p<.01$, and vibration, $F(1,14)=14.3$, $p<.01$. A post-hoc analysis (HSD=2.2 mm) of the movement proportion times reveals that the variability of finger position was different between all points during the movement trajectory (i.e., 25% vs. 50%, 50% vs. 75%, & 25% vs. 75%), as shown in Figure 2.8. The main effect of vibration revealed that participants were more variable in their finger positioning when vibration was presented between trials (see Figure 2.9). Consistent with the primary movement axis, there was no main effect of vision, $F(1,14)=0.2$, $p=.13$. Alternatively, in the secondary axis, there was a significant movement proportion by vibration interaction, $F(3,42)=3.8$, $p<.05$. Post-hoc testing (HSD=1.7 mm) revealed that variability in the secondary axis was greater 75% of the movement than at all other movement time percentages (see Figure 2.10). The ANOVA also revealed a significant time by vision interaction, $F(3,42)=4.91$, $p<.01$, and
however, post-hoc analysis (HSD=1.1 mm) revealed significant differences but none of the differences were meaningful (see Figure 2.11). Table 2.4 contains the individual means for the variability within each proportional movement time across both vision and vibration conditions.

Table 2.4. Standard deviation of limb position at various portions of movement time in the secondary axis

| Variability of limb position (mm) in the secondary axis at various portions of movement time |
|---------------------------------|---------------------------------|---------------------------------|---------------------------------|
|                                   | No-Vibration Vision             | No-Vision Vision                | Vibration Vision                |
| 25%                              | 3.43                            | 3.26                            | 3.77                            | 3.03                            |
| 50%                              | 4.67                            | 4.20                            | 6.20                            | 4.80                            |
| 75%                              | 5.60                            | 5.06                            | 7.21                            | 7.09                            |
| 100%                             | 4.33                            | 4.31                            | 5.01                            | 5.72                            |

*Bold* denoted significantly different values from all other movement time % conditions

Figure 2.8. Line graph showing the standard deviation of finger position at various movement proportion times in the secondary movement axis. Variability was significantly higher at 75% than all other conditions.
Figure 2.9. Bar graph showing significant difference between vibration conditions in the secondary movement axis.

Figure 2.10 Time by Vibration interaction on the standard deviation of finger position in the secondary axis
The ANOVA on movement time (MT) revealed a main effect of vision, $F(1,14)=6.3$, $p<.05$, where participants took more time to complete their movements in the presence of vision (see Figure 2.12). The analysis revealed no main effect of vibration, $F(1,14)=2.3$, $p=.15$, as well as no interaction between the factors, $F(1,14)=1.2$, $p=.30$ (see Figure 2.12).

Figure 2.11 Time by Vision interaction on the standard deviation on finger position in the secondary axis

Figure 2.12. Box and whisker plots of Movement Time (MT) as a function of vision condition for each vibration condition.
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The ANOVA for Peak Velocity (PV) revealed no significant effects, as there was no difference in the maximum values reached in any of the experimental conditions: Vibration: $F(1,14)=1.4, p=.26$; Vision: $F(1,14)=.05, p=.83$; Vibration X Vision: $F(1,14)=1.9, p=.19$. The same ANOVA investigating time to peak velocity (TtPV) showed no significant differences between any of the experimental conditions as well: Vibration: $F(1,14)=0.0, p=.97$; Vision: $F(1,14)=3.3, p=.10$; Vibration X Vision: $F(1,14)=1.2, p=.30$. Alternatively, the same ANOVA on time after peak velocity (TaPV) revealed a significant main effect of both vibration, $F(1,14)=11.4, p<.01$, and vision, $F(1,14)=9.4, p<.01$. Participants exhibited longer TaPV when they had vision throughout the movement (M=198.1 ms; SD=28.4) than when vision was removed at movement onset (M= 183.2 ms; SD=26.6). Similarly, participants had longer TaPV when there was no vibration presented between trials (M=193.8 ms; SD=30.2) than during the vibration block (M=187.5 ms; SD=26.4). No interactions between these factors were found, $F(1,14)=0.39, p=.54$. All kinematic ANOVA results are displayed in Figure 2.13.
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A. Figure 2.13. Box and whisker plots of A) Time to Peak Velocity (TtPV), B) Average Peak Velocity reached across all conditions and C) Average Time After Peak Velocity separated by both vision conditions and vibration conditions.
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Discussion/Conclusion

The purpose of the current study was to further investigate the relative contributions of vision and proprioception to the online control of goal-directed movements. Participants were asked to perform a simple voluntary goal-directed reaching task (30 cm in amplitude). Proprioceptive and visual feedback was manipulated to determine the contribution of these sensory modalities to the control of ongoing movement. Because the task was the same for all trials, limb trajectory differences should be a direct result of movement control processes.

Accuracy

In both the primary and secondary axis, there was significant effect of both vibration and vision for the constant error. In the secondary movement axis, when vibration was introduced and vision withdrawn, participants exhibited a directional biases, away from their body. Also, as expected, participants undershot the target in the primary axis in the absence of vision (e.g., Elliott et al. 2001). However, the opposite occurred in the primary movement axis as participants undershot target more when vibration was off.

In terms of the effects of tendon vibration, the simultaneous biceps and triceps stimulation can explain these conflicting results. Typically, studies using tendon vibration that stimulate one muscle at a time, reporting that vibration creates the sensation that a muscle is longer than it really is (Goodwin et al., 1972; Capaday & Cooke 1981). Also during movement, vibration typically has the greatest effects on the muscle that is lengthening (Capaday and Cooke, 1981; Inglis & Frank, 1990). However, when muscle tendon vibration is presented before a movement, the opposite effects may occur where the vibrated muscle appears shorter due to a desensitization, or fatigue of the muscle spindle afferents (Ribot-Ciscar et al., 1998). The current
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study used dual-muscle and between-trial tendon vibration, which may mean that each muscle was perturbed approximately to the same extent. As a result, the lengthening muscle (i.e., the biceps muscle in this case) controlling the location of the limb, had reduced sensitivity from vibration aftereffects, which would in turn yield the sensation that the muscle is shorter than it is. Such a mechanism can explain the larger movement amplitude in the primary axis. Alternatively, the triceps may have some influence on limb position sense, even as the shortening muscle.

Precision

It was hypothesized that vibration would have an effect on the endpoint in the primary axis, which was not found. It was also hypothesized that variability of finger position would be highest during the deceleration phase of movement. The results however, show that in the primary movement axis, participants were most variable at 50% of movement time. This finding is inline with the work of Elliott et al. (2010), who suggested that impulse regulation mechanisms should take place before amendments for limb-target regulation.

Additionally, vision yielded no significant effects on precision in the primary axis during the trajectory. The comparable results between vision conditions in the primary movement axis may be due to uncertainty of visual feedback availability. When participants were presented with trials in which they did not know the type of visual feedback, it is possible that they adopt a ‘worst-case’ scenario strategy where the initial motor plan is prepared as if no vision was going to be provided (Elliott et al., 2004). Due to the inclusion of randomized visual conditions, participants were likely planning their movements as if vision would not be given, which explains why the trajectory variability differences were only observed at movement end.
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In the secondary axis of movement, participants were more variable in the presence of vibration throughout the trajectory. At movement endpoint, variability was increased in the secondary axis both during vibration blocks and in the absence of vision. Vibration caused significantly more variability of finger position 75% into the movement, in the secondary axis. As previously mentioned, this result is in line with previous literature (e.g., Redon et al., 1991), as participants were likely making corrections in the form of directional sub-movements during the deceleration phase of movement (Elliott et al., 2001). Taken together with the primary axis results, it can be suggested that early online regulation may be useful for the amplitude component of movement, where late online regulation takes into account the direction of movement.

Planning versus Online Control

Due to the methods and the nature of this repetitive task, participants may have adopted pre-planning strategies in order to complete their movements. Regardless of the vibration or vision condition, participants were given a 1 second preview of the environment before the go signal (as well as after tendon vibration ended in the vibration block). Thus, increased planning mechanisms may have been a result of these blocked vibration trials, where participants knew when the vibration would be happening. Although the participants were unaware of the effects of vibration, it is possible they anticipated movement perturbations simply because the use of vibration is not typical. They may have led participants to rely on more heavily visual cues to plan the movement (Ernst & Banks, 2002). The maximum-likelihood estimation (MLE) model explains how the CNS minimizes variability by weighting the most reliable sensory information more than unreliable sensory information (Ernst & Banks, 2002). Based on the blocked vibration conditions, it could be expected that participants plan differently to compensate for the
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 proprioceptive perturbations. Also, when vision was available, participants had the ability to compare visual and proprioceptive signals about limb position. As a result, during the first few trials in the vibration block, perhaps the CNS recognized that the proprioceptive information was not reliable, enticing the participant to make better planning choices on the upcoming trials in the same block.

Markers at the beginning of movement have been associated with motor programming and planning, while kinematic variability towards the end of movement have been associated with online control (Elliott et al., 2001; Kahn & Franks (2003). Consistent with Khan and Franks (2003) as well as Khan et al. (2006), it was important in the current study to break down the variability of position not only at the end of movement, but throughout various stages of the trajectory to understand the mechanisms of online control. Thus, the standard deviation of finger position was calculated within each of the four movement time percentage combinations across participants to try and separate the phases of control. In the secondary movement axis, the standard deviation of finger position at 25% and 50% of movement time did not differ between the vibration conditions, however at 75% of movement there was a significant increase in variability. At that point in the movement, the participant was thought to be in the current control phase, and thus actively making corrections, which fits well into the well-known two-component model of movement (Woodworth 1899; Elliott et al., 2001). Similarly, in the secondary axis, on top of the significant main effect of vibration, there was also an interaction effect between vibration and proportion of movement, as well as vision and proportion of movement. Contrast testing confirmed that the significant differences were also late in the movement (75% of movement time). Thus, it can be hypothesized that people are taking advantage of the online sensory feedback to make corrections to their initial impulse movements. Additionally, the increased variability during the vibration block indicates that participants were likely relying
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specifically on proprioceptive feedback late in the movement, to make corrections to their trajectory. Thus is can be concluded that in the secondary axis, proprioceptive feedback in relied upon late in a movement. This finding is in line with previous research, where proprioception is used to make corrections late in a goal-directed movement (Redon et al., 1991; Rossetti et al., 1995).

Another reason to think participants showed a reliance on online control mechanisms lies in the variability of the primary axis both during the trajectory and at movement endpoint. There was no effect of vibration on the endpoint variability in the primary axis, however vibration did affect the movement throughout the trajectory. Thus at some point in the trajectory between 75% of movement time and movement end (i.e., 100%), participants were able to reduce the variability in finger position. Also, participants were most variable overall during the trajectory in the primary axis at 50% of movement time, regardless of vibration or vision condition. In the current study time to peak velocity occurred on average at 137 ms into the trajectory, which was before 50% of movement time (i.e., on average at 164 ms into the trajectory). Based on Elliott et al. (2010), it can be assumed that participants were already using online sensory feedback to control movement. If sensory processing time begins at peak velocity, then it is likely that the most amount of variability in the primary axis occurs just after, at a time where the feedback is being used and corrections being made. Thus, in the primary movement axis, it can be concluded that vibration has the ability to increase variability of a movement trajectory, but not affect the endpoint precision. Again, one argument for this result could be due to the blocked vibration trials, where participants could have been relying on motor planning by using visual cues from the environment preview.
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The most notable result revealed by this analysis was that in both movement axes, the main effect of vibration uncovers the idea that muscle tendon vibration has the ability to increase the variability during movement regardless of the vision condition. Thus, even when given full vision of the reaching environment, participants were still more variable across the movement in the primary axis, and late in the movement in the secondary axis.

Vibration also affected the amount of time spent completing the movement after reaching peak velocity (TaPV). TaPV increased when vibration was presented between trials, meaning participants spent more time during the online control phase of action (i.e., Woodworth, 1899; Elliott et al., 2001). This finding also indicates the use of proprioceptive sensory information late in the movement. Similarly, TaPV was decreased in the absence of vision, which was accompanied by shorter movement times. This also may be indicative of people using the sensory feedback when available to complete the movement as accurately as possible, having appropriate feedback to correct for any initial planning errors. In the absence of vision, visual feedback is unavailable so participants did not need to spend extra time decelerating their movements.

In a neurophysiological sense, studies recording single neurons from monkeys can help to confirm our behavioral findings. The premotor cortex in monkeys is where visual, tactile and proprioceptive information integrate. Graziano (1999) studied the responses of single neurons in the premotor cortex while a monkey was subjected to moving visual stimuli as well as four different arm proprioceptive feedback conditions, two with vision of the arm and two without vision of the arm. When the monkey could see both the arm and visual stimuli, the visual receptive fields were anchored to the location of the arm such that there was increased contralateral activity when the visual stimulus moved directly over the arm location.
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Remarkably, the same results are found when vision of the arms was removed. The receptive fields remained to be highly activated when the visual stimulus moved over the arm, even when the monkey could not see their arm. Graziano was able to conclude that neurons in the premotor cortex are influenced by arm position and has influences on both vision and proprioception. These results are indicative that afferent information from both vision and proprioception converge in to a single signal, in order to create an appropriate perception (Graziano, 1999). This idea helps to further explain why vision and proprioceptive are so highly integrated during a rapid goal-directed movement.

Overall the results from this study are a two-fold. Firstly, the current experiment was able to demonstrate that between-trial dual-muscle tendon vibration before a movement has the potential to perturb the proprioceptive feedback during a subsequent movement, while allowing the avoidance of the TVR effects. Secondly, there is now evidence to show that during the later stages of a voluntary movement, disrupted proprioceptive information has the ability to create variability of endpoint in the directional movement axis. Additionally, in this movement axis, vibration has the ability to create variability throughout the trajectory of movement. The latter finding may indicate that with tendon vibration taking place before movement, people are unable to fix their initial motor errors or plan their movement using inaccurate proprioceptive information. We also replicated the contribution of proprioceptive information during the later stages of movement. Particularly, participants in the current study exhibited changes to trajectory variability after dual-muscle tendon vibration, even in the presence of vision. Future implications from this work may help to further investigate the implications if proprioceptive disruption on movement with the hopes to investigate ways to rehabilitate those with chronic sensory loss.
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5 Integrated Discussion and Conclusion

The purpose of the present study was to determine the potential for between-trial dual-muscle tendon vibration to alter limb-position sense, and its ability to assess the relative contributions of vision and proprioception during goal-directed action. Although it is common to employ tendon vibration to evaluate the use of proprioceptive feedback (e.g., Goodwin et al., 1972; Capaday & Cooke, 1981) and visual occlusion to evaluate the use of visual feedback (e.g., Elliott et al., 2010), the current study combined both types of manipulations to understand the relative contribution of each sensory modality to the online control of voluntary upper-limb reaches. The innovative tendon vibration between trials (see Manuscript 1) likely avoided to elicit the tonic vibration reflex (i.e., Eklund & Hagbarth 1966). Additionally, both muscles were vibrated to alleviate directional biases (e.g., Roll & Vedel, 1982). Based on the current observations, it can be argued that the decreased sensitivity caused by between-trial tendon vibration (Rogers et al., 1985; Ribot-Ciscar et al., 1998) introduced variability into the central nervous system and subsequently caused deviations across the movement trajectory, including endpoint positioning. Even with the conscious awareness of tendon vibration and in the presence of vision, participants could not overcome positioning variability during the reaching trajectory. Each of the above observations can be explained through different mechanistic justifications that will be discussed in the following sections.

5.1 Position Sense

The results from this study help to confirm the influence of tendon vibration aftereffects (e.g., Ribot-Ciscar et al., 1998). Ribot-Ciscar and colleagues describe the shortening illusion after tendon vibration as a decrease in perception of proprioceptive information due to desensitization of the muscle spindle afferents. In turn, the CNS is unable to detect the accurate change in length or rate of change in length of the vibrated muscle. In both of the current experiments, participants performed movements with increased variability when vibration was applied and shut off before the movement began. Thus, the proprioceptive perturbations used before movement did in fact reduce the reliability in limb position sense during the movements.

The first experiment had participants perform a contralateral remembered limb-positioning task. Between-trial dual-muscle tendon vibration reduced the position sense of the
vibrated arm, which influenced the control of the contralateral non-vibrated matching arm. The effect was seen through increases in the endpoint variability, even in the absence of a directional bias. In the vibration trials, participants reported uncertainty in their ability to appropriately match their limbs to the target location. Due to the nature of the first experiment, participants had time to contemplate the accuracy of the movement of the non-vibrated arm, which may have led to ambiguous estimations. The temporal advantage may have allowed the participant to receive more sensory information as they were positioning their matching limb. However, the targets obtained by the position of the right arm was held at a constant time, so it is possible that not limiting time moving the left limb decreased endpoint precision as compared to when movement time was restricted. One the other hand, restricting the movement time of the left hand would have limited the participant to a single movement, allowing less time for sensory feedback, and thus probably decreasing variability in the endpoint distribution. Nonetheless, the novel tendon vibration method used was likely causing the positional uncertainty. These results are similar to Rogers et al. (1985), who found that after vibrating either the biceps or triceps muscle for 60 seconds at 100 Hz, larger positional errors occurred when matching the non-vibrated arm in the absence of vision.

In the second experiment, we saw the potential for between-trial dual-muscle tendon vibration aftereffects to alter the proprioceptive feedback use during a rapid goal-directed movement with the ipsilateral arm. Participants had more variability in finger endpoint positioning when vibration was applied, both during and at the end of movement. Participants were affected by the tendon vibration in both vision conditions and in both axes of movement. The inclusion of a full vision condition to a vibration task was novel to this area of research. Taken together, we can conclude with confidence that employing tendon vibration before a movement has the ability to disrupt the use of proprioceptive feedback when executing a subsequent movement.

5.1.1 Post-vibration central responses

In the current study, vibration was applied to both the biceps brachii and triceps brachii muscles simultaneously. The implications of vibrating the muscle afferent fibers need to be considered to understand not only the peripheral changes to the muscle spindles, but the central processing responses.
When vibrating skeletal muscle, the post vibration effects are similar to those seen after a maximum voluntary contraction, which is the activity of the vibrated muscle remains activated after vibration cessation (Roll et al., 1980). However, these effects were not observed when two antagonistic muscles were vibrated (Gilhodes et al., 1992). Thus, the activity patterns of the post-vibrated muscle seem to differ when vibration is applied to two muscles, asymmetrically. These activity patterns have been confirmed by the studies revealing that afferent firing rates are not increased after vibration (Ribot-Ciscar et al., 1991) and can return to static levels as soon as vibration is removed (Roll & Vedel, 1982). Although no added firing rates were observed in these studies, the afferent nerves may be desensitized to the change in length of muscles. Thus, the differences may be attributable to asymmetric responses of sensorimotor integration and not a direct response of the afferent fibers themselves.

Peripherally altering afferent firing has also been shown to modulate primary motor cortex excitability (e.g., Ridding et al., 2000). It has been hypothesized that vibration of upper-limb skeletal muscle causes changes in motor cortex excitability (Naito, Ehrsson, Geyer, Zilles, & Roland, 1999). To further explore corticospinal excitability of vibration, Lapole et al. (2014) used transcranial magnetic stimulation (TMS) to explore motor evoked potentials (MEPs) created with and without vibration of the Achilles tendon. The authors wanted to observe how afferent discharges differ the activity of synergist muscles (i.e., gastrocnemius and soleus), as well as antagonist muscles (i.e., tibialis anterior). Results reveal that vibration-induced MEPs were higher than the MEPs observed in the non-vibration condition, suggesting increased corticospinal excitability with vibration. In contrast, there were no changes in MEPs between vibrations conditions of the non-vibrated tibialis anterior. Thus, there were no sign of antagonist inhibition. The results suggest vibration may alter the communication between the sensory and motor cortices (Lapole et al., 2014), although the effects may be only relative to the vibrated muscle. However, there have been no conclusions regarding corticospinal activity when two antagonist muscles are simultaneously vibrated. As mentioned previously, the post stimulation of vibration is alleviated when both muscles are vibrated together (Gilhodes et al., 1992), so perhaps different activations of the motor cortex arise during simultaneous vibration as well. Additionally, vibration has been shown to have little effect on motor neurons that are fired at saturation, suggesting that vibration may not add to the firing activity of an active muscle (see Fuglevand, Lester, & Johns, 2014). Taken together, as there is evidence that peripherally
vibrating a muscle can cause changes to activity patterns in the motor cortex, there is also evidence to show that simultaneous vibration has different effects on the CNS than the vibration of a single muscle. It is thus possible that vibrations from the current study significantly altered motor cortex excitability although it will require further investigations to confirm.

5.2 Motor Control

5.2.1 Motor Planning

In the second experiment, trials in the presence of vision exhibited longer movement times, as well as longer time spent after peak velocity. Participants also spent more time after peak velocity in the vibration trials. Participants were likely using the extra time to ensure they were accurately moving their limb to the target, while amending any errors of the initial impulse movement (e.g., Elliott et al., 2010). There were, however, no differences in the average reached peak velocity or time taken to reach peak velocity between any of the vision trials or the vibration condition blocks. Such a result may indicate that between-trial dual-muscle tendon vibration did not particularly impact motor planning that much.

Alternatively, based on the study design, participants may have opted to plan their movements differently when they knew tendon vibration was occurring. Because it was possible to preview both the limb position and the environment before movement, perhaps participants used this visual information to create a reliable motor plan. However, tendon vibration was presented before movement, indicating that planning with the use of proprioceptive feedback was probably not reliable to begin with. Consequently, if motor planning was enriched, initial impulses may have been altered. Although vision of the limb is dominant when creating a motor plan (e.g., Heath et al., 2005), proprioceptive feedback has also been shown to be important to motor planning (Ghez et al., 1990). Participants may have planned their movements using accurate visual and noisy proprioceptive information, causing early deviations, which may have been corrected prior to or at 50% of the movement time.

5.2.2 Online Control

Movement of the upper-limb requires more than the control of the biceps and triceps brachii muscles, thus it is possible that proprioceptive feedback from other arm muscles contributed to the original efference copy. In Elliott et al. (1991), the authors noted that
participants were able to make small amendments early in a movement, even in the absence of vision, which could explain why the current study saw the most variability of finger position at 50% of movement in the primary movement axis. Similarly, another mechanism for control is the ability to compare very early sensory information from the movement with the expected efference copy created and stored in the CNS. Early amendments that rely on efference copy comparisons have been seen to occur in the absence of sensory feedback (Angel & Higgins, 1969), or before the time of visual and proprioceptive processing. Again, the information may have come from multiple proprioceptive receptors allowing the CNS to recognize discrepancies. This forward processing may also help to explain why the variability of movement was highest halfway through the movement and then decreased towards the end.

Tendon vibration elicited the most salient differences for the online control of goal-directed reaches. In the first experiment, participants were given unlimited time to complete their movement towards the target location. Therefore, there was a definite opportunity to consciously control the action, even in the absence of vision. Yet, from this experiment alone, it is difficult to make temporal inferences about the use of proprioceptive feedback.

Alternatively, in the second experiment movement time was limited because the participants were instructed to move ‘as accurately as possible’ to the target location, within the provided movement time bandwidth. The maximum movement time of any condition observed was 408 ms. Additionally, in the second experiment the participants saw the target location on every trial. The greatest variability of finger position induced by tendon vibration across all trials was seen during the final stages of movement (75% of movement time) in the secondary axis. Such variability was thus observed during the deceleration or the time where online control is deemed to be taking place (e.g., Elliott et al., 2001).

There is clear evidence that proprioception is used online and has influences on the control of movement, regardless of other contributions. Our results are consistent with the results from Redon and colleagues (1991) who found that muscle tendon vibration was as effective method of perturbing movement during the final stages as it was when presented during the whole movement. In the study of Redon et al. (1991), results showed that movement was affected most during the last 200 ms of an 800 ms movement, which translates to about the final 25% of movement time or 75% into the movement. The current results also found movement to
be the most variable at 75% of movement time in the secondary axis. More interestingly, the participants in the current study did not seem to attempt to minimize the effect of the visual perturbation by increasing speed of movement, as peak velocity was constant in all conditions. Previous evidence has shown that people will exhibit slower movements when they know vision will not be available (Elliott et al., 2004), while this was not the case for the current study. Slower movement times in the presence of vision may be a result of the participants attempting to utilize visual feedback when no movement time bandwidth are employed. This can also be confirmed by the observation of better accuracy and precision in the presence of vision in both the primary and secondary movement axes.

One argument as to why visual feedback did not appear to contribute to the control of action is that participants may not have been relying on vision at all during the current task in the second experiment. In 2006, Hansen and colleagues conducted a study to investigate how goal-directed movements are prepared and executed based on the information about vision and target location. The authors had participants create movements to a specified target, however the availability of visual information was given on only a portion of the trials. The results confirm that when there is uncertainty about visual information people prepare for the ‘worst-case’ and execute more pre-planned movements, or may not have relied on visual feedback as much as possible (Hansen et al., 2006). In the current study, no differences in movement variability were found between vision conditions at any point during the flight in both the presence and absence of vibration, potentially having all movement prepared for an open-loop control strategy. Participants in the current study may have adopted this ‘worse-case’ strategy, making it difficult to make straightforward conclusions about the use of vision during the task.

5.2.3 Multisensory Integration

Firstly, it must be reiterated that multisensory integration strategies cannot be compared between the two current experiments. One reason is due to the temporal demands of the task, while another reason is due to the spatial target demands of the task. The first experiment used a proprioceptive target, while the second experiment had participants aim to a visual target. Bernier et al. (2007) tested whether target location is encoded through proprioceptive or visual cues before movement. The authors probed this theoretical question using visual prismatic shifting, and only found differences when movements were perturbed with a visual target. The results led the authors to conclude that distinct sensorimotor transformations are dependent on
the type of target location, and vision is important when planning movement to a visual target, while proprioception is important while planning movements to a proprioceptive target.

Increases in variability can be mechanistically attributed to increased noise in the relay of information from the peripheral nervous system (PNS) to the CNS. The Maximum Likelihood Estimation (MLE) model would suggest that the vibration induced a decrease in reliability, causing a shift in the use of proprioceptive feedback, (Ernst & Banks, 2002). The MLE model gives the least weight to the sensory system with the most variability. However, when integrating noisy sensory information, the CNS has the ability to use the most appropriate information to complete a task. According to the model, we could expect no effect of vibration in the vision condition, as visual feedback would be most relied on. However, it was clear the proprioceptive information was not completely ruled out based on the conflicting biases in both the primary and secondary axes. Moreover, this was particularly evident in the second experiment when increases in the variability of movement were seen during vision trials in the vibration block. The participant was always consciously aware of the vibration trials and could have strategized for an abnormal the use of proprioceptive information. Yet, the central nervous system still seemed to incorporate proprioceptive information to implement trajectory amendments. The results support a weighted information model (e.g., MLE), opposed to insisting on one dominant sensory system controlling various aspects of movement.

In some trials, visual information was present throughout the entire trial and previous research has documented that the effect of muscle tendon vibration is diminished (Lackner & Taublieb, 1984) or nonexistent (Capaday & Cooke, 1981) when presented with full vision. Thus, in the tendon vibration block of the current study, it was expected that participants would be able to use vision to compensate for the variability caused by the vibration. However, this was not observed, as variability was significantly larger during different phases of movement with tendon vibration presented between trials. Participants were unable to rectify the discrepancy between visual and proprioceptive information, even when using visual feedback. Another explanation for this may also be due to the visual adoption of the ‘worst-case’ discussed in the section above, where participants executed movements as if visual feedback was not available.

The current findings also relate to the ongoing conflict regarding open versus closed control loop systems. Closed loop control is when sensory information is used during movement
to control and guide the trajectory (Adams 1971), while open loop control relies on a precise motor plan or program to control movement with little or no online feedback (Plamondon & Alimi, 1997). Currently, literature attempting to investigate the debate focuses on manipulating visual processing feedback times at various portions of the movement (e.g., Keele & Posner, 1968; Beggs & Howarth, 1970). Alternatively, there are not many studies that involve the manipulation of proprioception to study online control systems, and the subsequent relative time during movement it is of most importance. Yet, there is extensive literature discussing the important of proprioception to the control of upper-limb movements (e.g., McCloskey & Prochazka, 1994). The current study intended to use a combination of both visual and proprioceptive manipulations to investigate the roles of each sensory modality on the online control of movement. The findings complement the existing work of both visual (Carlton, 1992; Elliott et al., 2001) and proprioceptive (Redon et al. 1990), suggesting a closed-loop system even with minimal time available to use incoming sensory information. This was seen through the previous discussed increases in variability during the phases of online control.

5.3 Early versus Late Control

The theory that visual information is used for planning and proprioceptive information is used for online control has been seen many times in literature (Rossetti et al., 1995; Bagiesterio et al., 2006). The current study can help to affirm the idea that proprioception is important for online control, but no novel conclusions about vision can be made. The study simply affirmed that in the absence of vision, people exhibit a decrease in accuracy and precision of movement.

Alternatively, the current study can lend knowledge regarding amplitude versus direction control. The current results show that amendments to the primary axis were made early in the movement, while amendments to the direction axis were made late in the movement. While Bagiesterio et al., (2006) reported that vision is important for planning movement amplitude; perhaps this early control is responsible for correcting deviations to the amplitude as a result of rapid visual processing time. Alternatively, late control, which is controlled by proprioceptive feedback (Bagiesterio et al., 2006), may be crucial to the direction component of the movement. Perhaps central control processes handle task demands by monitoring movement vectors. Amendments made to a motor plan, thus may first occur to correct amplitude or distance, followed by corrections to the direction or angle. These spatial differences may simply be a
result of the demands of the task, having the accurate amplitude as the most relevant goal, where directional accuracy is a secondary objective. The axes used in the second experiment were in Cartesian coordinates although they were not deemed to represent a coordinate system used by the CNS. Still, they could be used to make inferences about various control mechanisms. Overall the present data still represents evidence that control mechanisms for the amplitude and direction of a voluntary movement may occur through different processes.

5.4 Implications

Through this study, a better understanding of how between-trial dual-muscle tendon vibration creates variability in the proprioceptive system has been gained. The implications from the current research can be directly concerned with the sensory deprived populations, specifically regarding their rehabilitation. Using between-trial vibration can help to alleviate the effects of the TVR and help researchers to understand movements in the absence of proprioceptive feedback. The current work helps to confirm that after a short bout of tendon vibration, the sensitivity of the muscle spindles afferents are likely reduced, causing the actual stretch in muscle to not be picked up the CNS, creating the illusion that the previously vibrated muscle is shorter than it really is. This finding supports the potential for tendon vibration to be used as an assessment tool for diagnosing sensory deprivations.

One aspect to consider when using tendon vibration as a diagnostic tool is the age of the population who may need proprioceptive assessments. Hay, Bard, Fleury and Teasdale (1996), were interested in how age affects our ability to adapt to changes in vision and proprioception during a simple postural control task. The authors used muscle tendon vibration coupled with liquid-crystal goggles to manipulate feedback. The elderly population was tested and compared to a young-adult population. As expected, the elderly participants were more affected in the absence of vision. The authors suggested that older adults may rely more on visual inputs to control posture, or that their proprioceptive abilities are simply less efficient. Thus, an ageing population may not be as effected by tendon vibration, if the reliance of proprioceptive feedback natural diminished with age.
5.5 Limitations

It is important to note the limitations of the current study. The number of trials used in each experiment was small in comparison to typical motor control studies. Experiment 1 only had 10 vibrations trials, while Experiment 2 had 20. This was purposefully done to reduce the potential adaptations of tendon vibration on movement strategies. However, it was not possible to gather enough information regarding the kinematics of movement (e.g., velocity profile variables) to see significant effects of online control strategies through this way. In future studies, experiments should include more trials with possibly more time for rest in between.

Although there were differences in endpoint precision between the no-vibration and vibration blocks in Experiment 1, some sources of variability must be addressed to recognize the reproducibility of the study design. First, it must be noted that the vibrated muscles are bi-articulate and cross not only the elbow joint but the shoulder joint as well. Thus, it is possible that the movements may not have been 100% about the elbow. Small movements created at the shoulder joint may have introduced variability, especially for Experiment 2. Second, the measurements of the left arm in Experiment 1 were taken from the middle finger whereas the elbow of the right arm created the targets. Depending on the size and length of the arm of the participant, it is possible the location of the arm on the angle chart and the actual position in degrees at the elbow may have been exposed to small discrepancies. However, as previously mentioned, the first experiment was created with the potential to be easily reproduced (e.g., in a clinical setting), so it is important to recognize such potential sources of variability.

Another limitation to the current study is the lack of counterbalancing trials during Experiment 1. Each participant performed both the non-vibration and vibration trials in this specific order. This was done because of the minimal trials used and time constraints for the inclusion of a drown-out period for vibration. Order of treatments has the ability to affect behaviour, fatigue, or learning, however due to the short duration of the experiment, these factors were most likely not affected. If learning patterns arose, participants should have increased performance measures during the second block. Alternatively, the results revealed that participants performed with less precision during the second block, affirming the effects of tendon vibration. Regardless, to rectify this problem, future study should incorporate counterbalancing blocks.
The current study also used blocked vibration trials in the second experiment. In this case, the participant may have been able to identify that proprioceptive information was not reliable and adopt visual feedback planning strategies. The current results, however, showed that this might not have been the case, as vibration had an effect of movement even in the presence of vision. Future studies should investigate similar effects using a randomized vibration paradigm to see if similar results can be obtained. Alternatively, as previously discussed, the current study used randomized vision conditions which may have led participants to always behave as if they were performing an action in the absence of vision (e.g. Hansen et al., 2006), limiting the ability to conclude visual feedback effects. Alternatively, future directions should include blocked vision conditions to allow better comparison between visual feedback conditions.

5.6 Conclusion

The purpose of this thesis was to investigate the ability of dual-muscle between-trial tendon vibration aftereffects to alter limb position sense and evaluate the contributions of vision and proprioception to the online control of a voluntary goal-directed movement. Initially, a limb-matching task was employed to evaluate the ability of tendon vibration before a movement to cause significant variability in position sense error. After observing the significant differences in variability between vibrated and non-vibrated trials, similar methods were applied to a goal-directed movement task. In this second experiment, participants performed the task in one block of trials with no vibration and one block of trials with vibration between each trial. Additionally, the availability of vision was randomized to make inferences about online sensory modulations. As expected, vibration trials created more variability in the online control of movement. Differences were seen both in the primary and secondary axes of movement. Even in the presence of vision, participants showed greater error in in the primary movement axis, implying that they were unable to overcome the added noise in the proprioceptive system. Movement time as well as time after peak velocity were both shortened (i.e., participants moved faster) in the presence of either tendon vibration or in the absence of visual feedback. From these increased kinematic variables, we can conclude people were attempting to use the sensory feedback available to them during the online control phase of movement. Altogether, people rely predominantly on vision to create a motor plan especially for the amplitude of movement, while proprioceptive and visual information remain important in the control of direction of movement. Moreover, even when participants were aware they would be receiving disrupted proprioceptive
feedback (i.e., blocked vibration trials), it appeared they somewhat relied on the feedback anyways. This may be indicative of natural control patterns, or rather the central nervous system will always incorporate all incoming afferent information, even when weighted differently (e.g., MLE model, Ernst & Banks, 2002). Nevertheless, the results from the thesis have applied knowledge from the motor control literature to investigate the aftereffects of dual-muscle between-trial tendon vibration during movement. Although we have seen the ability for tendon vibration to induce variability, future studies should be employed to further test kinematic modifications. If it is possible to discover how people adapt to movement deficiencies caused by sensory deprivation, we can help to design rehabilitation techniques for those with chronic sensorimotor deficits.
References


movements from kinematic data. *Neuroscience and Biobehavioral Reviews, 30*, 1106–1121.


Appendices
Appendix A

**Brief Neurological Questionnaire**

How often do you experience the following?

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<thead>
<tr>
<th></th>
<th>Never</th>
<th>Seldom</th>
<th>Often</th>
</tr>
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<tbody>
<tr>
<td>Headaches</td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Light-headed or dizziness</td>
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<tr>
<td>Numbness or tingling</td>
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<tr>
<td>Tremor</td>
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<td>Paralysis</td>
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<td>Convulsions or seizures</td>
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<tr>
<td>Stroke</td>
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<td>Sensory impairment</td>
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Appendix B

Hand Dominance Test

Hand dominance test (adapted from Oldfield, 1971)

Please indicate which hand you would use for the following activities:

- Writing
  - □ right
  - □ left

- Throwing
  - □ right
  - □ left

- Scissors
  - □ right
  - □ left

- Toothbrush
  - □ right
  - □ left

- Drawing
  - □ right
  - □ left