Muscle-specific modulation of vestibular reflexes with increased locomotor velocity and cadence

Christopher J. Dakin,1 John Timothy Inglis,1,2,3 Romeo Chua,1 Jean-Sébastien Blouin1,2,4

1School of Kinesiology, University of British Columbia, Vancouver, British Columbia, Canada; 2Brain Research Center, University of British Columbia, Vancouver, British Columbia, Canada; 3International Collaboration on Repair Discoveries, University of British Columbia, Vancouver, British Columbia, Canada; and 4Institute for Computing, Information and Cognitive Systems (ICICS), Vancouver, British Columbia, Canada

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Dakin CJ, Inglis JT, Chua R, Blouin JS. Muscle-specific modulation of vestibular reflexes with increased locomotor velocity and cadence. J Neurophysiol 110: 86–94, 2013. First published April 10, 2013; doi:10.1152/jn.00843.2012.—Vestibular information is one of the many sensory signals used to stabilize the body during locomotion. When locomotor velocity increases, the influence of these signals appears to wane. It is unclear whether vestibular signals are globally attenuated with velocity or are influenced by factors such as whether a muscle is contributing to balance control. Here we investigate how vestibular sensory signals influence muscles of the leg during locomotion and what causes their attenuation with increasing locomotor velocity. We hypothesized that 1) vestibular signals influence the activity of all muscles engaged in the maintenance of medio-lateral stability during locomotion and 2) increases in both cadence and velocity would be associated with attenuation of these signals. We used a stochastic vestibular stimulus and recorded electromyographic signals from muscles of the ankle, knee, and hip. Participants walked using two cadences (52 and 78 steps/min) and two walking velocities (0.4 and 0.8 m/s). We observed phase-dependent modulation of vestibular influence over ongoing muscle activity in all recorded muscles. Within a stride, reversals of the muscle responses were observed in the biceps femoris, tibialis anterior, and rectus femoris. Vestibular-muscle coupling decreases with increases in both cadence and walking velocity. These results show that the observed vestibular suppression is muscle- and phase dependent. We suggest that the phase- and muscle-specific influence of vestibular signals on locomotor activity is organized according to each muscle’s functional role in body stabilization during locomotion.

The vestibular system provides an essential sensory contribution to the maintenance of balance during human locomotion. When this system is impaired, locomotion can become unstable and in severe cases lead to falls (Brandt 2000). Currently, our understanding of how vestibular information is used to maintain balance during locomotion remains generalized to full-body compensatory responses resulting from electrically induced vestibular errors (Bent et al. 2004; Fitzpatrick et al. 1999, 2006). The role individual muscles play in contributing to this compensatory response remains unclear.

Research in animal models suggests that vestibular contribution to locomotor activity is modulated over the stride cycle (Matsuyama and Drew 2000; Orlovsky 1972a, 1972b). In felines, the firing rate of many vestibular neurons varies in phase with lower limb extensor muscle activity (Matsuyama and Drew 2000; Orlovsky 1972a). Correspondingly, phase-dependent vestibular influence has been reported during the stance phase of human locomotion but only in muscles acting around the ankle (Iles et al. 2007), contrasting with the widespread vestibular influence typically observed during other motor activities. Vestibular stimulation usually induces responses in all muscles engaged in balance control (Ali et al. 2003; Britton et al. 1993), which during standing results in full-body postural sway (Day et al. 1997). Compared with free standing, similar postural sway is observed during locomotion (Bent et al. 2004; Day et al. 1997; Fitzpatrick et al. 2006), implying analogous widespread vestibular influence across these two activities. Thus, in humans, a vestibular stimulus ought to result in phase-dependent responses in active postural muscles throughout the legs and hips, not simply in muscles acting around the ankle.

Vestibular signals appear to contribute to the maintenance of balance during locomotion; however, this influence wanes with increased locomotor velocity. For example, compensatory whole-body sway responses to a galvanic vestibular stimulus are attenuated during running compared with walking (Jahn et al. 2000). Similar results are observed in patients with unilateral vestibular neuritis, as they normally drift toward the affected side when walking with their eyes closed but show no drift when they run (Brandt et al. 2000; Brandt et al. 1999). In felines, vestibular afference is suppressed during walking compared with a resting posture. This feline vestibular suppression is early in processing (prior to the lateral vestibular nucleus) (Orlovsky and Pavlova 1972) and presumably leads to a general reduction in the influence of vestibular signals “downstream” from the locus of suppression. Similar attenuation in humans would manifest as a general decrease in vestibular influence in trunk and limb muscles as might be inferred from the studies of Brandt et al. (Brandt 2000; Brandt et al. 1999; Jahn et al. 2000). However, muscle-specific suppression may also contribute to the general decrease in vestibular influence, with increases in locomotor velocity depending on the functional role of the muscles. For example, as cadence increases the small moments generated by muscles at the ankle render them largely ineffective for medio-lateral balance control, and therefore foot placement plays a dominant role in medio-lateral balance control (Bauby and Kuo 2000; MacKinnon and Winter 1993; Winter 1995). Since engagement in the act of balance control appears requisite for vestibular signals to influence a muscle (Britton et al. 1993; Fitzpatrick et al. 1994; Luu et al. 2012), a
reduction in a muscle’s role in balance should be associated with a decrease in vestibular influence over that muscle. Therefore, vestibular coupling should be attenuated in the ankle muscles during faster locomotion because of their reduced role in balance control relative to other muscles in the body such as the leg abductors, which may still be required (during the swing phase for foot placement) for balance control.

Here we investigate the contribution of vestibular signals to balance during locomotion by examining both the phase-dependent modulation of vestibular coupling in muscles acting around the ankle, knee, and hip and the suppression of vestibularly evoked responses with increasing locomotor velocity and cadence. We hypothesized that 1) all muscles engaged in the control of balance during locomotion will exhibit coupling with the vestibular stimulus at defined periods in the stride cycle and 2) the magnitude of vestibulo-myogenic coupling will decrease with increases in locomotor velocity and cadence. Depending on whether the suppression of vestibular coupling is observed in all muscles or is muscle specific, we will infer whether the mechanism responsible for this suppression is global or context dependent.

METHODS

Subjects. Nine healthy subjects (height 170 ± 9 cm, mass 68 ± 13 kg; 4 women, 5 men) between the ages of 21 and 34 yr participated in this study. The experimental protocol was explained to each subject, and their written informed consent was obtained. All procedures used in this study conformed to the standards of the Declaration of Helsinki and were approved by the University of British Columbia’s clinical research ethics board.

Stimulus. Electric vestibular stimulation is the percutaneous application of a small electric current that modulates the firing rate of the vestibular nerve (Aw et al. 2008; Goldberg et al. 1982; Kim and Curthoys 2004). This type of stimulation provides an isolated vestibular signal without accompanying congruent feedback from other sensory modalities. Sensory signals caused by “external” environmental stimuli have classically been termed ex-afferent signals (von Holst and Mittelstaedt 1950), and, as such, vestibular signals induced by the stochastic vestibular stimulus will be described here as ex-afferent signals. When electric vestibular stimulation is delivered in a bipolar binaural electrode configuration with the head facing forward, the postural response is a roll response in the frontal plane (Fitzpatrick and Day 2004). In the present study the vestibular stimulus was delivered with a binaural bipolar electrode configuration with carbon rubber electrodes (9 cm²) secured over the mastoid processes with an elastic headband. Bandwidth-limited stochastic stimuli (SVS; 0–25 Hz, peak amplitude of ± 4.5 mA, root mean square 1.05 mA) lasting 305 s were created with LabVIEW software and were delivered with an isolated constant-current stimulation unit (model 2200, A-M Systems) (Dakin et al. 2007, 2010).

Test procedures. Participants walked on a treadmill, guided by a metronome, at two velocities (0.4 and 0.8 m/s) and two cadences (52 and 78 steps/min) for a total of three trial conditions (0.4 m/s at 52 steps/min, 0.4 m/s at 78 steps/min, and 0.8 m/s at 78 steps/min). The 0.4 m/s treadmill velocity replicates the velocity used by Iles et al. (2007) and Blouin et al. (2011) in their demonstration of phase-dependent vestibular responses during locomotion. The 0.8 m/s velocity was chosen to provide a 100% increase in locomotor velocity. A cadence of 52 steps/min was chosen to match that used in previous locomotor studies incorporating vestibular stimulation (Fitzpatrick et al. 1999, 2006), and the 78 steps/min cadence was chosen to provide an increase in cadence but one that is reasonably comfortable for participants to perform at the slower locomotor velocity. We did not use a full factorial design because a cadence of 52 steps/min was too slow to perform with a walking velocity of 0.8 m/s. Participants maintained their Frankfurt plane (the auriculo-orbital plane) 18° nose up from the floor by keeping a headgear-mounted laser on a target located 2 m in front of them (Cathers et al. 2005; Day and Fitzpatrick 2005; Fitzpatrick and Day 2004). The locomotor parameters and head position were chosen to maximize the amplitude of vestibulo-motor responses in the medio-lateral directions (Fitzpatrick et al. 2006; Iles et al. 2007). Periods in the stride cycle that exhibit strong vestibular responses are interpreted as times at which vestibular information is useful for medio-lateral balance control during locomotion by a given muscle. Subjects walked while being provided the stochastic stimulus for three 5-min trials at 52 steps/min and two 5-min trials at 78 steps/min, with a total of 350 strides collected per condition. Each of the cadence and velocity conditions was provided in a random order, and participants were provided rest periods between trials and at their request to avoid fatigue.

Electromyography and signal analysis. Surface electromyography (EMG) was collected from eight muscles: bilaterally from the medial gastrocnemius and from the right lateral gastrocnemius, soleus, tibialis anterior, biceps femoris, rectus femoris, and gluteus medius. Data from the medial gastrocnemius were used previously (Blouin et al. 2011) to establish the methodological framework for this study. Self-adhesive Ag/AgCl surface electrodes (Ambu Blue Sensor M) were positioned over the muscles of interest after cleaning and abrading of the skin. These muscles were chosen to provide a summary of vestibulo-motor interactions in muscle spanning the ankle, knee, and hip joints. Foot switches were fastened bilaterally to the toe and heel of the shoe and used to estimate heel strike and toe off for each stride. EMG was amplified (×5,000), band-pass filtered from 30 to 1,000 Hz (Neurolog NL-844, Digitimer), and digitized along with the vestibular stimulus and foot switches at 2 kHz (PXI-6289, National Instruments). All data were saved on a personal computer for later off-line analyses.

Correlations in both the time (cross-correlation) and frequency (coherence) domains were used to estimate the magnitude of covariance between the stimulus (SVS) and stimulus-induced modulation in muscle activity (EMG). Since a component of the variation in muscle activity is correlated with the use of “SVS” or “vestibulo-EMG coupling” to describe the relationship between the two signals. Coherence and cross-correlation between the vestibular stimulus and EMG were computed as a function of time to estimate the phase modulation between the vestibular stimulus and EMG over the gait cycle (Blouin et al. 2011). Prior to the time-dependent correlation analyses, the SVS and EMG signals were cut into strides synchronized to the right heel strike (identified by contact in the right heel switch). Right heel strike therefore serves as time zero in figures and analyses. To avoid distortion in the correlations at right heel strike, each stride was padded at the start and end with data from the previous (50%) and subsequent (50%) strides. EMG signals were also full-wave rectified, and both SVS and EMG signals were low-pass filtered (100 Hz 4th-order dual-pass Butterworth filter) and resampled at 200 Hz for data reduction.

Time-dependent coherence was estimated with a Morlet wavelet decomposition because of the nonstationarity of the EMG signal (Zhan et al. 2006), and time-dependent cross-correlations were estimated with a method described by Blouin et al. (2011). To account for stride-to-stride variability, we normalized the stride duration in time by normalizing each stride to the average stride duration across trials. Stride duration normalization was performed on the autospectra of the SVS and EMG signals, as well as their cross-spectrum, prior to estimating coherence. Mathematical derivation of the normalization and time-dependent cross-correlation procedures is presented in Blouin et al. (2011). Briefly, cross-correlations were calculated at each sample in the stride cycle, providing a window of correlation from −50 ms before to 300 ms after the stimulus at each point in the stride cycle. The time-dependent cross-correlations were then normalized to
provide values of correlation between −1 and 1 and used to identify both the timing and amplitude of the SVS-EMG coupling in all recorded muscles. By convention, anode right/cathode left currents are represented by positive vestibular signals. Therefore, a correlation of 1 indicates that anode right/cathode left currents are associated with muscle facilitation and a correlation of −1 indicates that anode right/cathode left currents are associated with an attenuation of muscle activity. For illustrative purposes, time-dependent coherence for each muscle was averaged across all subjects to provide a representation of the global behavior.

Data reduction and statistical analyses. SVS-EMG coherence was used to identify phase-dependent coupling between SVS and muscles spanning the ankle, knee, and hip joints. Significant coupling was defined in each subject as the period over the gait cycle at which SVS-EMG coherence exceeded a confidence limit set at \( P = 0.01 \) (corresponding to a confidence magnitude of 0.013). This value was chosen because it better represents an \( \alpha \)-level of 0.05 because of the bidimensional nature of these correlations. The interval over which SVS-EMG coherence exceeded this confidence limit was determined for each muscle on a subject-by-subject basis. To determine whether vestibular input to the lower leg muscles is suppressed with higher walking velocities and cadences, the maximum time-dependent coherence across all frequencies was determined for each walking condition. We chose to use coherence as our dependent variable to estimate the magnitude of vestibular-induced contribution per unit of muscle activation. Since coherence is normalized by the power in both the SVS and EMG signals, it is less sensitive to changes in EMG magnitude related to walking velocity or cadence (Nilsson et al. 1985; Yang and Winter 1985) on the magnitude of SVS-EMG coupling. Gain, on the other hand, is not normalized by the EMG signal amplitude and therefore will rise and fall with changes in EMG amplitude not related to increases or decreases in SVS-EMG coupling. After the calculation of SVS-EMG coherence, the peak value of coherence was retrieved from both the stance and swing phases of the stride cycle. Coherence values for each subject within each muscle and each stride phase were tested for normality in SPSS. Because peak coherence values were not distributed normally in some muscles we compared peak coherence within stance and swing between the two cadences and two locomotor velocities, using a Wilcoxon matched-pairs signed-rank test. The effect of cadence was determined by comparing the 0.4 m/s at 52 steps/min condition to the 0.4 m/s at 78 steps/min condition, whereas the effect of locomotor velocity was determined by comparing the 0.4 m/s at 78 steps/min and 0.8 m/s at 78 steps/min conditions. Since previous studies demonstrated a reduction in vestibular influence with increased locomotor velocity, we anticipated a reduction in SVS-EMG coupling with both increasing locomotor cadence and velocity (Brandt 2000; Brandt et al. 1999; Jahn et al. 2000). We therefore used a one-tailed Wilcoxon matched-pairs signed-rank test with \( P = 0.05 \).

RESULTS

SVS-EMG coupling is present in muscles acting around hip, knee, and ankle joints. Phase-dependent modulation of EMG was visually apparent across all participants in all conditions, and, in general, the magnitude of each muscle’s contribution varied both with cadence and walking velocity (Fig. 1).

To address our first hypothesis, we examined whether muscles spanning the ankle, knee, and hip joints exhibit phase-dependent vestibular coupling over the stride cycle. Significant SVS-EMG coupling was observed in all recorded muscles (Fig. 2), but not all subjects exhibited significant coupling in all muscles. Muscles acting around the ankle exhibited coupling only prior to and during the stance phase of the locomotor cycle, while muscles acting around the knee and hip exhibited periods of coupling throughout the gait cycle. Overall, the largest average peak SVS-EMG coherence during stance was observed in the medial gastrocnemius (0.23 ± 0.11; 0.4 m/s at 52 steps/min), while the weakest was observed in the rectus femoris (0.04 ± 0.03; 0.8 m/s at 78 steps/min). In general,

![Fig. 1. Averaged muscle activity for each of the 3 trial conditions (n = 9). Phase-dependent modulation of muscle activity is unique in each trial condition, and peak EMG tends to be highest in the 0.8 m/s-78 steps/min condition. r-MG, right medial gastrocnemius; r-LG, right lateral gastrocnemius; r-Sol, right soleus; r-TA, right tibialis anterior; r-RF, right rectus femoris; r-BF, right biceps femoris; r-GM, right gluteus medius; l-MG, left medial gastrocnemius.](http://jn.physiology.org/doi/10.1152/jn.00843.2012/fig1)
SVS-EMG coupling was present during periods when the muscles were active. However, high levels of muscle activity did not necessarily correspond to high SVS-EMG coupling. For example, the tibialis anterior exhibited a prominent increase in EMG activity just after toe off (Fig. 1), but during this time the stimulus did not appear to influence muscle activity (Fig. 2). Gluteus medius exhibited constant EMG activity during the swing phase, whereas SVS-EMG coupling prominently increased over this time period.

Significant SVS-EMG coupling in the medial gastrocnemius began at heel strike, peaking early in midstance phase and ending late in midstance. As expected, coupling in the left medial gastrocnemius was the mirrored response to the right medial gastrocnemius. The lateral gastrocnemius, in comparison, exhibited significant SVS-EMG coupling beginning in midstance and ending at toe off. The right soleus displayed a pattern distinct from the right gastrocnemius, exhibiting SVS-EMG coupling for the duration of stance phase, e.g., from heel strike to toe off, instead of only from heel strike to late midstance as in the medial gastrocnemius. In addition, the soleus appears to also have two periods of peak coherence: the first prior to midstance and the second just prior to toe off. In the anterior compartment of the leg, the tibialis anterior exhibited coupling from just prior to heel contact until early midstance.

Muscles of the thigh and hip generally exhibited patterns of coupling different from those observed in the lower leg. The rectus femoris exhibited very little SVS-EMG coupling excluding a brief period around heel strike prominent only in the 0.4 m/s at 78 steps/min condition. In contrast, the biceps femoris and gluteus medius exhibited SVS-EMG coupling during heel contact and early stance as well as at toe off. The gluteus medius also exhibited coupling during late swing phase. When SVS-EMG coupling is combined across all the muscles recorded in the right leg and the lone medial gastrocnemius from the left leg, it appears that vestibular ex-afferent signals can influence muscle activation over the entire gait cycle (Fig. 2, bottom).

During periods of significant SVS-EMG coupling each recorded muscle produced a bi- or triphasic response in the time-dependent cross-correlation. The average timing of the peaks of these responses across all recorded muscles was 59 ± 8 ms for the short-latency response and 118 ± 27 ms for the medium-latency response. At heel contact, all muscles in the right leg exhibited positive- followed by negative-going waves. In most muscles response polarity was consistent over the entire stride cycle; however, in three muscles the polarity of these responses reversed at different points in the stride cycle. The biceps femoris and tibialis anterior response polarity reversed prior to toe off (Fig. 3), and in a few subjects (n = 4) the rectus femoris response reversed at right heel contact.

**SVS-EMG coupling is attenuated during stance with increases in locomotor velocity and cadence.** To address our second hypothesis, we examined whether increases in locomotor velocity generally decreased vestibular coupling in muscles spanning the ankle, knee, and hip joints. Increasing velocity (from 0.4 to 0.8 m/s at 78 steps/min) reduced SVS-EMG coupling in nearly all muscles during the stance phase of the locomotor cycle. In particular, SVS-EMG coherence decreased in the tibialis anterior, gluteus medius, biceps femoris, and rectus femoris (Fig. 4). The soleus also exhibited a decreasing trend, but it was not statistically significant (Table 1). At the
ankle, both the tibialis anterior and left medial gastrocnemius exhibited a significant decrease in SVS-EMG coherence during stance with increased locomotor velocity.

We also examined whether increases in locomotor cadence decrease SVS-EMG coupling in muscles acting around the ankle because of their reduced role in frontal plane balance control. Across all recorded muscles, reductions in vestibulomuscle coupling due to cadence were only observed during the stance phase of the locomotor cycle (Fig. 4). Indeed, both the medial gastrocnemius (bilaterally) and tibialis anterior exhibited decreases in SVS-EMG coherence during stance with increases in cadence (Fig. 4; Table 2). However, SVS-EMG coherence did not decrease in all muscles acting around the ankle. The soleus exhibited a decreasing trend that was non-significant, and the lateral gastrocnemius demonstrated no sign of decreased vestibulo-motor coupling. At the hip and knee SVS-EMG coherence also decreased in both the biceps femoris and glutaeus medius, with no significant change in the rectus femoris.

**DISCUSSION**

The first aim of this study was to identify whether vestibular ex-afferent signals exhibit widespread phase-dependent influence over muscle activity across the ankle, knee, and hip joints during locomotion. We found that vestibular ex-afferent-like signals can contribute to the control of balance at any point in the stride cycle; however, the influence of these signals on the individual muscles is dependent on the phase of the stride cycle. Each muscle recorded exhibited its own pattern of coupling with the vestibular stimulus over the stride cycle. The second aim of this study was to determine whether muscles acting around the ankle experienced the greatest decline in vestibular sensitivity because of their reduced role in frontal plane balance control. In contrast, we observed decreases in vestibular sensitivity in muscles acting around all three joints with increases in cadence and velocity. This effect was primarily observed during stance and was absent in the lateral gastrocnemius and soleus. Ultimately, this study has provided the first in-depth examination of the phase-dependent influence of vestibular signals during human locomotion and has shown that vestibular influence can be selectively suppressed at higher locomotor velocities or cadences.

**Phasic modulation of vestibular responses is ubiquitous in lower limbs.** Phase-dependent modulation of vestibular input to limb muscles has been observed in both animals and humans (Iles et al. 2007; Matsuyama and Drew 2000; Orlovsky 1972a, 1972b). One of our objectives was to revisit this phasic modulation in humans and determine whether it is more widespread than had been initially reported in humans (Iles et al. 2007). We observed SVS-EMG coupling in all measured muscles, suggesting widespread influence of vestibular ex-afferent signals over the locomotor cycle. Our findings extend those of Iles et al. (2007), who observed responses only in muscles distal to the knee, with the observation of phase-dependent vestibular coupling in rectus femoris, biceps femoris, and glutaeus medius. Presumably, the differences in findings between these two studies are due to the stimulus format and advantages related to the analysis approach (Blouin et al. 2011). Overall, the observation of widespread phasically modulated vestibulo-muscle interactions is congruent with the whole-body postural response to electric vestibular stimulation typically observed (Ali et al. 2003; Day et al. 1997) and the broad excitatory influence of vestibular signals on extensor muscles observed in felines (Orlovsky 1972b). These results indicate that compensatory actions to a vestibular perturbation are dependent on the phase of the locomotor cycle.

The form of compensation of a vestibular perturbation is a generalized whole-body response (Day et al. 1997), and therefore it is not surprising that SVS-EMG coupling is widespread in muscles of the lower limbs during locomotion. Despite the limited number of muscles examined here, it is clear that vestibular ex-afferent signals can influence gait over the entire stride cycle. However, this influence may not be uniform in magnitude across the entire gait cycle. Our data suggest that the largest net response to a vestibular stimulus occurs early during the stance phase of the locomotor cycle. This observation mirrors those of Bent et al. (2004), who found that postural deviation to vestibular stimulation during locomotion was largest when the stimulus was provided at heel strike. Presumably, the differences in findings between these two studies are due to the stimulus format and advantages related to the analysis approach (Blouin et al. 2011). Overall, the observation of widespread phasically modulated vestibulo-muscle interactions is congruent with the whole-body postural response to electric vestibular stimulation typically observed (Ali et al. 2003; Day et al. 1997) and the broad excitatory influence of vestibular signals on extensor muscles observed in felines (Orlovsky 1972b). These results indicate that compensatory actions to a vestibular perturbation are dependent on the phase of the locomotor cycle.

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ably, the timing of these vestibular responses is tied to two important factors: the activity level and mechanical effect of the muscle. Vestibular stimulation induces relatively small muscle responses that are usually not large enough to induce activity in a quiescent muscle on its own (Fitzpatrick et al. 1994). These responses are therefore likely to be observed in muscles already active and absent in muscles not active, such as the soleus during swing phase. Second, whether or not the mechanical action of the active muscle aids in compensation of a virtual roll perturbation induced by SVS likely plays a major role in determining the timing or presence of these responses. Presumably the pathways activated by the vestibular stimulus have evolved to provide effective compensation to vestibular perturbations. Therefore SVS-EMG coupling is likely strongest during periods when muscles can compensate for the vestibular perturbation, similar to what occurs when muscles respond to a mechanical perturbation (Misiaszek 2006).

Vestibular signals may modify thrust, medio-lateral placement of the foot, and double support to contribute to locomotor stability. SVS-EMG coupling in the gluteus medius, in particular, suggests that compensation for a vestibular-induced roll in the frontal plane is conducted not only by thrust provided by the muscles acting around the ankle (Iles et al. 2007) but also through an abduction action of the leg just prior to and following heel contact. This observation corresponds well with the proposed role of both the abductors and adductors in frontal plane stabilization during locomotion (MacKinnon and Winter 1993; Winter 1995). SVS-gluteal EMG coherence prior to heel contact supports the purported role of medio-lateral placement of the foot as a primary mechanism for frontal plane stabilization during locomotion (Bauby and Kuo 2000; Donelan et al. 2004; Kuo 1999; Redfern and Schumann 1994). However, the additional periods of SVS-EMG coupling during stance phase suggest that medio-lateral placement of the foot is not the only

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Fig. 4. Change in coherence across trial conditions. For each subplot, compare columns A and B for the effects of cadence and B and C for velocity. Both cadence and locomotor velocity reduced peak coherence. The reduction in peak coherence was most prominent during the stance phase of the stride cycle and was observed in all muscles except soleus and lateral gastrocnemius. Gray dots indicate each subject’s mean, and black dots indicate the group mean. Error bars indicate SD. *Statistically significant decreases in coherence ($P < 0.05$).
mechanism contributing to frontal plane stability. The primary period of gluteus medius coupling with the vestibular stimulus was immediately after heel strike during the double support phase. This period of heightened SVS-EMG coherence loosely corresponds in time with increased coupling in the tibialis anterior, soleus, and medial gastrocnemius, suggesting that these muscles become important for compensation for frontal plane vestibular perturbations during the double support phase and leading into thrust generation. When examined across all muscles, the vestibular stimulus appears to have a relatively continuous influence over the stride cycle, signifying that some combination of thrust control, lateral placement of the foot, and adjustment of body motion during double support is exploited to maintain stability in the presence of a vestibular perturbation in the frontal plane.

Vestibular influence on muscle activity can reverse over stride cycle. The functional mapping between the vestibular signals and the corresponding response also appears to vary across the stride cycle in some muscles. At right heel contact, all recorded muscles in the right leg exhibit a negative medium-latency response indicating a reduction in muscle activity in response to anode right/cathode left stimuli. Near right toe off and during swing, the biceps femoris, tibialis anterior, and rectus femoris experience periods in which the polarity of the medium-latency response flips, exhibiting a positive medium-latency response (Fig. 3). This behavior is similar to nonvestibular reflex reversals that have been observed previously both in animals (Akay and Buschges 2006; DiCaprio and Clarac 1981; Fossberg et al. 1977) and in human muscle responses to sural and tibial nerve stimulation (Duyens et al. 1990, 1992; Yang and Stein 1990). In these studies, reflex reversals were thought to be caused by peripheral sensory feedback or central pattern generators modifying input to the muscle at different phases of the stride cycle. Similar mechanisms could modify vestibular-induced responses in the muscle through actions of the cerebellum on neurons in the vestibular nuclei (lito and Yoshida 1964; Orlovsky 1972a; Walberg and Jansen 1961) and through the local spinal circuitry since there are many indirect vestibular connections to motor neurons (Davies and Edgley 1994; Hsu et al. 2012; Hultborn et al. 1976; Iles and Pisini 1992; Pierrot-Deseilligny and Burke 2005). Coincidentally, the pattern of response reversal to vestibular stimuli observed in the tibialis anterior closely resembles responses in the same muscle to sural and tibial nerve stimulation, which in humans has been suggested to result from the actions of a central pattern generator (Duyens et al. 1990, 1992). This explanation would fit some of these data, as reversals in both the tibialis anterior and biceps femoris occur during the stance phase of the locomotor cycle and not during an event producing an abrupt change in peripheral sensory feedback, such as toe off or heel contact. In contrast, responses in the rectus femoris reversed at heel strike, suggesting that reversal could result from load-related peripheral feedback. Regardless of the potential source of these reversals, it is clear that vestibular influence is modulated in both its timing of influence and, in some muscles, its polarity over the stride cycle.

Vestibular influence is selectively suppressed with increases in both cadence and locomotor velocity. In some lower limb muscles SVS-EMG coupling decreased as locomotor velocity and/or cadence increased. This result parallels previous studies (Brandt 2000; Brandt et al. 1999; Jahn et al. 2000) that observed a decrease in vestibular-related heading error in both patients with acute unilateral vestibulopathy and subjects administered galvanic vestibular stimulation while running com-

<table>
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<tr>
<th>Summary of coherence values and statistical tests: comparison of velocity</th>
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<tbody>
<tr>
<td><strong>Table 1.</strong></td>
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<td><strong>Stance</strong></td>
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</tr>
<tr>
<td>4 m/s</td>
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<td>-----------------------------------------------</td>
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<tr>
<td>r-MG 0.16 ± 0.12</td>
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<tr>
<td>i-MG 0.18 ± 0.10</td>
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<tr>
<td>r-LG 0.14 ± 0.10</td>
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<tr>
<td>r-GM 0.10 ± 0.04</td>
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<tr>
<td>r-Sol 0.19 ± 0.12</td>
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<tr>
<td>r-BF 0.10 ± 0.08</td>
</tr>
<tr>
<td>r-TA 0.11 ± 0.08</td>
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<tr>
<td>r-RF 0.08 ± 0.04</td>
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<tr>
<th>Swing**</th>
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<tr>
<td>4 m/s</td>
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<tr>
<td>0.07 ± 0.04</td>
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<tr>
<td>0.06 ± 0.03</td>
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<td>0.06 ± 0.02</td>
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<td>0.13 ± 0.05</td>
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<td>0.08 ± 0.04</td>
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<td>0.14 ± 0.09</td>
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<td>0.09 ± 0.06</td>
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Coherence values are means ± SD.

Coherence values are means ± SD.

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pared with walking. In contrast to previous studies, attenuation of vestibular influence was selective, as both the soleus and lateral gastrocnemius exhibited no significant decrease in vestibular coupling. Furthermore, the reduction in SVS-EMG coherence also appears to depend on the phase of the stride cycle, as SVS-EMG coherence was primarily reduced during stance. Both the gluteus medius and biceps femoris exhibit a reduction in SVS-EMG coherence with increasing velocity and cadence during stance but appear uninfluenced during swing. The combined muscle- and phase-specific attenuation implies that responses to vestibular efferent signals may not experience a general “downregulation” at the tested walking velocities but rather muscle-specific suppression or inhibition. While suppression of vestibular influence was not isolated to muscles acting around the ankle as initially hypothesized, the general reduction in vestibular influence during stance and the absence of attenuation in biceps femoris and lateral gastrocnemius during swing are consistent with vestibular influence being modulated by the muscle’s role in balance control at higher velocity or cadence. As reported previously, it appears that as locomotor velocity increases the control of frontal plane stability is increasingly mediated through changes in foot placement as opposed to active stabilization at the ankle, knee, and hip during stance. This change in the source of stabilization should result in a decrease in vestibular coupling in these muscles during stance and maintained vestibular coupling in muscles that are active and contribute to limb placement during swing. This is precisely what is observed in both the biceps femoris and the gluteus medius, both of which show a reduction in coherence during stance and maintenance of coherence during swing. In contrast, the varying SVS-EMG coherence between muscles, such as the lack of effect in the soleus and lateral gastrocnemius, indicates that the attenuation in vestibular coupling varies depending on the muscle examined and may ultimately reflect functional differences between these muscles.

**Conclusions.** We have shown that vestibular efferent input to lower limb muscles is modulated phasically across the locomotor cycle. These signals modify muscle activation in muscles acting across the hip, knee, and ankle joints over the entire stride cycle and are selectively suppressed with higher walking velocities and cadences. Together these findings demonstrate the widespread and phase-dependent influence of vestibular efferent signals on muscle activation for the purpose of balance stabilization during locomotion in humans.

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**DISCLOSURES**

No conflicts of interest, financial or otherwise, are declared by the author(s).

**AUTHOR CONTRIBUTIONS**

Author contributions: C.J.D., J.T.I., R.C., and J.-S.B. conception and design of research; C.J.D. analyzed data; C.J.D. and J.-S.B. interpreted results of experiments; C.J.D. prepared figures; C.J.D. drafted manuscript; C.J.D., J.T.I., R.C., and J.-S.B. edited and revised manuscript; C.J.D., J.T.I., R.C., and J.-S.B. approved final version of manuscript; J.-S.B. performed experiments.

**REFERENCES**


