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Proprioceptive feedback contributes to the adaptation toward an economical gait pattern

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ABSTRACT

Humans generally prefer gait patterns with a low metabolic cost, but it is unclear how such patterns are chosen. We have previously proposed that humans may use proprioceptive feedback to identify economical movement patterns. The purpose of the present experiments was to investigate the role of plantarflexor proprioception in the adaptation toward an economical gait pattern. To disrupt proprioception in some trials, we applied noisy vibration (randomly varying between 40–120 Hz) over the bilateral Achilles tendons while participants stood quietly or walked on a treadmill. For all 10 min walking trials, the treadmill surface was initially level before slowly increasing to a 2.5% incline midway through the trial without participant knowledge. During standing posture, noisy vibration increased sway, indicating decreased proprioception accuracy. While walking on a level surface, vibration did not significantly influence stride period or metabolic rate. However, vibration had clear effects for the first 2–3 min after the incline increase; vibration caused participants to walk with shorter stride periods, reduced medial gastrocnemius (MG) activity during mid-stance (30–65% stance), and increased MG activity during late-stance (65–100% stance). Over time, these metrics gradually converged toward the gait pattern without vibration. Likely as a result of this delayed adaptation to the new mechanical context, the metabolic rate when walking uphill was significantly higher in the presence of noisy vibration. These results may be explained by the disruption of proprioception preventing rapid identification of muscle activation patterns which allow the muscles to operate under favorable mechanical conditions with low metabolic demand.

1. Introduction

Minimization of metabolic energy expenditure is often cited as a primary goal of human walking (Alexander, 2002), but the mechanisms used to identify economical movement patterns are unclear. Prescribing non-preferred step lengths or widths causes an increase in metabolic rate (Donelan et al., 2001; Minetti et al., 1995; Umberger and Martin, 2007; Zarrugh and Radcliffe, 1978), indicating a preference for economical gait patterns. When humans self-select their gait characteristics, the preferred gait pattern is influenced by the mechanical context, such as gait speed or surface incline (Leroux et al., 2002; Minetti et al., 1995). However, the new preferred gait pattern does not arise immediately after a change in mechanical context. Instead, humans gradually adapt their gait pattern over tens of seconds, possibly driven by direct minimization of metabolic expenditure (O′Connor and Donelan, 2012; Pagliara et al., 2014; Snaterse et al., 2011).

We recently proposed that adaptation toward an economical movement pattern may also involve proprioception (Dean, 2013). Proprioceptive feedback can provide information about muscle contraction characteristics (e.g. muscle velocity and force) which are closely linked to metabolic demand (Griffin et al., 2003; Ryschon et al., 1997). Integrating this mechanical information into an estimate of metabolic cost may allow faster identification of an economical movement pattern, as the time course of proprioceptive feedback is substantially faster than the known pathways for direct metabolic feedback (Ainslie and Duffin, 2009; Kaufman and Hayes, 2002; Starr et al., 1981).

During walking, proprioception may help humans effectively take advantage of body mechanics to produce economical propulsion. The plantarflexors, important contributors to gait propulsion, remain near-isometric for much of the stance phase while the Achilles tendon stores mechanical energy (Cronin et al., 2010; Farris and Sawicki, 2012; Ishikawa et al., 2005; Lichtwark and

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Wilson, 2006). The subsequent return of this stored energy allows strong push-off forces without requiring metabolically costly high-velocity muscle contractions (Farris and Sawicki, 2012; Lichtwark and Wilson, 2006). This musculotendon behavior persists when walking on moderate inclines or declines, despite large changes in plantarflexor activation (Lichtwark and Wilson, 2006). Humans could conceivably generate this behavior by monitoring muscle spindle feedback and adjusting plantarflexor activation to hold the muscle near-isometric.

The roles of proprioceptive feedback during functional tasks can be investigated using tendon vibration. Muscle spindles are particularly sensitive to vibration, which the nervous system interprets as muscle lengthening (Goodwin et al., 1972; Roll and Vedel, 1982). The onset of Achilles tendon vibration during standing posture causes posterior sway, a response to the illusion of anterior sway induced by increased plantarflexor spindle feedback (Eklund et al.,1972; Ivanenko et al., 2000; Kavounoudias et al., 1999). During walking, the effects of continuous Achilles tendon vibration are less apparent (Courtine et al., 2001; Ivanenko et al., 2000; Verschueren et al., 2002), possibly because humans ignore the constant vibratory background signal while monitoring the superimposed natural sensory signal (Courtine et al., 2001). Applying noisy, unpredictable vibration may more effectively reduce the accuracy of available proprioceptive feedback.

The purpose of this experiment was to test whether adaptation toward an economical gait pattern is influenced by disruption of plantarflexor proprioceptive feedback. We disrupted proprioception by applying noisy vibration over the Achilles tendons, and quantified walking behavior in response to a small change in surface incline. We hypothesized that noisy vibration would delay or reduce the adaptation to the new mechanical context, increasing metabolic expenditure.

2. Methods

2.1. Participants

Ten young, healthy individuals (8 female, 2 male; age = 24 ± 2 yr; mass = 64 ± 9 kg; height = 1.68 ± 0.07 m; mean ± s.d.) participated in this experiment. All participants provided informed consent, using forms and protocols approved by the Institutional Review Board at the Medical University of South Carolina and consistent with the Declaration of Helsinki.

2.2. Vibration characteristics

During some trials, noisy vibration was applied to the bilateral Achilles tendons using small, eccentrically weighted motors (35 g; 35 mm × 20 mm × 18 mm outer dimensions) strapped approximately 4 cm above the ankle joint (Floyd et al., 2014). The vibration characteristics varied randomly over time, between 40 Hz vibration (0.18 mm amplitude) and 120 Hz vibration (0.31 mm amplitude). Previously, the low end of this frequency range had no effect on an ankle movement matching task, with the effect of vibration increasing with higher frequencies across this range (Floyd et al., 2014). Therefore, the effects of the applied vibration varied over time, and were not predictable.

2.3. Standing posture trials

Participants completed three 90 s trials in which they stood on a force plate (Bertec; Columbus, OH) with their eyes closed, arms crossed, and feet positioned parallel and as close together as possible without touching. Noisy vibration was off for the first 30 s, turned on for the next 30 s, and turned off for the final 30 s. Trials were separated by 2 min of rest.

Ground reaction force and moment data were collected from the force plate at 1000 Hz, and low-pass filtered at 3 Hz. While previous studies have investigated whether constant frequency vibration influences average standing posture (Eklund et al., 1972; Ivanenko et al., 2000; Kavounoudias et al., 1999), our focus was on whether noisy vibration increased postural sway by reducing the accuracy of available proprioceptive feedback. Therefore, we calculated anteroposterior CoP speed, a measure of postural sway (Jeka et al., 2004), as the absolute value of the time derivative of anteroposterior CoP position. For each participant, the average CoP speed was calculated across all three trials for the 30 s periods before vibration, during vibration, and after vibration.

2.4. Walking trials

Participants performed a series of treadmill (Bertec; Columbus, OH) walking trials at 1.25 m/s. Participants wore a harness attached to an overhead rail which did not support body weight, but would have prevented a fall in case of a loss of balance. Participants first performed a 10 min trial in order to become accustomed to treadmill walking (Zeni and Higginson, 2010). Participants then completed four 10 min trials in which the treadmill incline slowly (over 7 s) increased to 2.5% at the 5 min mark. Incline changes were not visually apparent to participants, as they were instructed to keep their vision focused forward, the metabolic cart mask (see below) obstructed their vision of the treadmill belt, and this treadmill provides users with no visual feedback of their performance (e.g. speed, incline). After completion of the 10 min walking trial, the treadmill was returned to level before the treadmill belt was stopped. All walking trials were separated by 5 min of rest.

While the vibration device was worn for all trials, noisy vibration was continuously applied to the bilateral Achilles tendons in only two of the walking trials. To account for any effects of trial order, vibration was applied in the first and third trials for 5 participants, and in the second and fourth trials for the other 5 participants. Participants were assigned to these groups in alternating order. To determine whether participants were consciously aware of changes in treadmill incline, they were asked a series of questions in random order after the experiment (see Table 1).

The locations of active LED markers (Phase Space; San Leandro, CA) placed on the left and right heels were sampled at 120 Hz, with their calculated anteroposterior velocities used to identify heel-strike and toe-off events (Zeni et al., 2008). Stride period was calculated as the time between consecutive right heel-strike events. Breath-by-breath oxygen consumption and carbon dioxide production were measured using a metabolic cart (Cosmed; Rome, Italy), and metabolic rate was calculated using a standard equation (Brockway, 1987). Metabolic rate was normalized by body mass, and the metabolic rate during a 6 min quiet standing trial was subtracted. Surface electromyographic (EMG) electrodes (Motion Lab Systems; Baton Rouge, LA) over the bilateral medial

Table 1
Participant responses to questions asked at completion of the walking trials. The question regarding treadmill slope was of primary interest. All other questions were distractors.

Did you notice	Yes	No
The motor on your left ankle vibrating in any trials?	10	0
The motor on your right ankle vibrating in any trials?	10	0
Changes in the speed of the treadmill in any trials?	1	9
Changes in the slope of the treadmill in any trials?	0	10