Gradual mechanics-dependent adaptation of medial gastrocnemius activity during human walking

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Wellighoff MA, Bunchman AM, Dean JC. Gradual mechanics-dependent adaptation of medial gastrocnemius activity during human walking. J Neurophysiol 111: 1120–1131, 2014. First published December 11, 2013; doi:10.1152/jn.00251.2013.—While performing a simple bouncing task, humans modify their preferred movement period and pattern of plantarflexor activity in response to changes in system mechanics. Over time, the preferred movement pattern gradually adapts toward the resonant frequency. The purpose of the present experiments was to determine whether humans undergo a similar process of gradually adapting their stride period and plantarflexor activity after a change in mechanical demand while walking. Participants walked on a treadmill while we measured stride period and plantarflexor activity (medial gastrocnemius and soleus). Plantarflexor activity during stance was divided into a storage phase (30–65% stance) and a return phase (65–100% stance) based on when the Achilles tendon has previously been shown to store and return mechanical energy. Participants walked either on constant inclines (0%, 1%, 5%, 9%) or on a variable incline (0–1%) for which they were unaware of the incline changes. For variable-incline trials, participants walked under both single-task and dual-task conditions in order to vary the cognitive load. Both stride period and plantarflexor activity increased at steeper inclines. During single-task walking, small changes in incline were followed by gradual adaptation of storage-phase medial gastrocnemius activity. However, this adaptation was not present during dual-task walking, indicating some level of cognitive involvement. The observed adaptation may be the result of using afferent feedback in order to optimize the contractile conditions of the plantarflexors during the stance phase. Such adaptation could serve to improve metabolic economy but may be limited in clinical populations with disrupted proprioception.

Afferent feedback strongly influences the performance of functional movement tasks. The loss of such feedback alters the motor control strategies used to accomplish tasks ranging from single joint movements (Nougier et al. 1996) to multijoint tasks such as walking (Lajoie et al. 1996). Previous work has demonstrated the importance of afferent feedback in three distinct aspects of walking (Cronin et al. 2011a). First, afferent feedback can directly contribute to ongoing muscle activity (Nielsen and Sinkjaer 2002). Second, afferent feedback can produce predictable responses to mechanical perturbations, such as a trip (Nielsen and Sinkjaer 2002). Finally, the gait transition from stance to swing appears to be partially dependent on afferent feedback (Pearson 2008).

We have recently proposed that humans may also use afferent feedback to identify their preferred pattern of movement (Dean 2013). For a simple bouncing task, noninvasive techniques can identify the resonant frequency, at which minimal muscle activity is required to power the movement and the plantarflexors remain near-isometric while active (Dean and Kuo 2011; Takeshita et al. 2006). Altering the mechanics of this task by adding mass or stiffness predictably alters both the resonant frequency and the frequency at which humans prefer to bounce (Raburn et al. 2011). However, disrupting afferent feedback with peripheral ischemia eliminates the dependence of the preferred bouncing frequency on system mechanics (Raburn et al. 2011), suggesting the importance of afferent feedback in identifying the preferred movement pattern.

While system mechanics appear to play an important role during a simple bouncing task, humans do not immediately move at the mechanically optimal resonant frequency. Instead, humans gradually adapt their movement period and level of plantarflexor activity over time (Merritt et al. 2012). Only after a period of minutes do humans approach the resonant frequency, which corresponds to the movement pattern with minimal metabolic demand (Dean and Kuo 2011; Merritt et al. 2012). This preference for a movement pattern that takes advantage of the body’s mechanics has also been observed during human walking, in which the plantarflexors remain close to isometric for much of the stance phase, while the Achilles tendon stores and then returns energy in a “catapult-like” fashion (Ishikawa et al. 2005). When the mechanical demands of walking are altered by varying incline, this near-isometric behavior is retained for the majority of the stance phase even as plantarflexor activity changes dramatically (Lichtwark and Wilson 2006). It is not currently clear whether this mechanics-dependent change in muscle activity during walking occurs immediately in response to the altered demand or requires a period of gradual adaptation as observed during bouncing.

Adaptation toward an optimal or preferred movement pattern could be the result of either relatively high-level cognitive processing or lower-level automatic responses that do not involve cortical control. Dual-task experimental paradigms have been used extensively to investigate the automaticity of various tasks, including standing posture (Fraizer and Mitra 2008; Woollacott and Shumway-Cook 2002), walking (Grabiner and Troy 2005; Yogev-Seligmann et al. 2008), and novel movement patterns (Lang and Bastian 2002; Taylor and Thor- oughman 2008). Essentially, participants perform these motor tasks while simultaneously performing a second task with a cognitive component. Decrement in motor performance with the increased cognitive load are interpreted as evidence that the motor task requires cognitive processing. For example, the rate

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of spatial adaptation during split-belt treadmill walking experiments is reduced under dual-task conditions (Malone and Bastian 2010), suggesting the involvement of cognitive processes.

The primary goal of this project was to determine whether humans gradually adapt their movement period and plantarflexor activation patterns after a change in the mechanical demands of walking. We first quantified the effects of treadmill incline on plantarflexor muscle activity during phases of gait in which previous experiments have shown that the Achilles tendon stores and returns mechanical energy. In a subsequent experiment, we subtly altered the task’s mechanical demands by slowly changing the incline of the walking surface, with the goal of participants not becoming consciously aware of the changes. We quantified the effects of these small incline changes on muscle activity over time, with a focus on storage-phase activity that would control whether a muscle remained near-isometric as the tendon stored energy. A secondary goal of the project was to determine whether the increased cognitive load under dual-task conditions influenced the response to changes in the mechanical demands of walking.

We hypothesized that humans would gradually adapt their stride period and muscle activation patterns after a change in the mechanical demands of walking, paralleling our previous findings during bouncing. Specifically, we expected that after an increase in incline participants would gradually increase plantarflexor muscle activity over time. Conversely, after a decrease in incline, we expected that participants would gradually decrease plantarflexor muscle activity. Secondary, we hypothesized that the gradual adaptation to altered mechanical demand would be reduced under dual-task conditions as a result of the increased cognitive load.

MATERIALS AND METHODS

We conducted two treadmill walking experiments to investigate whether changes in the mechanical demands of walking caused subsequent gradual adaptation. In the first experiment, participants walked on a series of constant inclines. In the second experiment, participants walked over a varying incline under both single-task and dual-task conditions. For both experiments, participants provided informed consent, according to forms and protocols approved by the Institutional Review Board at the Medical University of South Carolina and consistent with the Declaration of Helsinki.

Experiment 1. Constant-Incline Walking

Seven young, healthy participants (4 women, 3 men; age = 28 ± 4 yr; mass = 69 ± 9 kg; height = 1.75 ± 0.09 m; mean ± SD) walked on an instrumented treadmill (Bertec, Columbus, OH) at 1.25 m/s for a series of trials. To become accustomed to walking on the treadmill, participants first walked on a 0% incline for 5 min (Zeni and Bastian 2013). Summed between the two legs, the average values of these forces are determined directly by treadmill incline, with the potential for small fluctuations from stride to stride due to movement relative to the treadmill surface. Average perpendicular force will be equal to the product of body weight and the cosine of the treadmill angle, while the average parallel force will be equal to the product of body weight and the sine of the treadmill angle. While average GRFs are constrained by treadmill incline, the pattern of instantaneous forces produced during the stance phase may vary. We quantified propulsive force as the peak parallel GRF, as has been done previously in studies of gait mechanics on inclined surfaces (Franz and Kram 2013). To quantify participants’ anteroposterior location on the treadmill, we calculated the location of the center of pressure (CoP) under the left foot at midstance (50% of the stance phase). Anteroposterior drift over time was quantified as the range of the 95% CoP confidence interval.

A primary goal of this project was to investigate changes in muscle activity during the phase of gait when the plantarflexors remain near-isometric, allowing the Achilles tendon to effectively store mechanical energy. Therefore, we calculated average EMG during a storage phase (30–65% stance phase) based on previous experiments that quantified muscle fascicle and Achilles tendon behavior during walking. After a relatively brief shortening period, the Achilles tendon lengthens from ∼10–25% of the stance phase to ∼70–80% of the stance phase (Cronin et al. 2010; Farris and Sawicki 2012; Ishikawa et al. 2005, 2007; Lichtwarck et al. 2007; Lichtwarck and Wilson 2006). The chosen storage phase range (30–65% stance phase) was relatively conservative, to ensure that the plantarflexors were clearly active at each incline and to account for the relatively brief electromechanical delay (∼20 ms) between plantarflexor activity and muscle force (Muraoka et al. 2004). This storage phase is similar to the period of near-isometric activity (15–60% stance phase) that has previously been used to investigate the immediate effects of surface incline changes on plantarflexor activity (af Klint et al. 2008, 2010). Secondarily, we also calculated average EMG during a return phase (65–100% stance phase), which will include the period during which the Achilles tendon is returning energy and the plantarflexors are actively shortening. It should be noted that this period will likely also include brief periods of tendon lengthening in some strides, as well as the final portion of the stance phase during which the plantarflexors are often inactive.

To combine data across individuals, we grouped the calculated stride period, peak parallel GRF, and muscle activity values into 5-s bins. Therefore, data were grouped into 60 bins over the course of the 5-min trials. We performed a series of two-way repeated-measures ANOVAs with interactions to determine whether the quantified gait characteristics were influenced by treadmill incline or time. The independent variables were treadmill incline (0%, 1%, 5%, or 9%) and time (bins 1–60). The dependent variables were stride period, peak parallel GRF, MG storage-phase activity, SO storage-phase activity, MG return-phase activity, and SO return-phase activity. We also performed a one-way repeated-measures ANOVA to determine whether anteroposterior drift on the treadmill was influenced by treadmill incline. For all tests, P < 0.05 was considered significant.

Experiment 2. Variable-Incline Walking

Ten young, healthy individuals (all women; age = 24 ± 1 yr; mass = 63 ± 5 kg; height = 1.68 ± 0.05 m; mean ± SD) participated in the second experiment. None of these individuals had previously partici-
of the data within these periods (see Figs. 3–7 for illustrations). A positive slope would indicate an increase in this metric over time, while a negative slope would indicate a decrease over time. Finally, we quantified the variability of each of these metrics by subtracting the best linear fit from the data and calculating the standard deviation of the residuals. Greater variability levels would indicate larger fluctuations that cannot be explained by linear changes in behavior over time.

We performed a series of two-way repeated-measures ANOVAs with interactions to determine whether treadmill incline (0° vs. 1°) or walking condition (single task vs. dual task) had significant effects on each of our metrics (stride period, peak parallel GRF, CoP location, MG storage-phase activity, SO storage-phase activity, MG return-phase activity, and SO return-phase activity). We first quantified any significant effects of treadmill incline or walking condition on the average values of these metrics. We then determined whether treadmill incline or walking condition significantly influenced the gradual adaptation of our metrics following a change in treadmill incline. Finally, we determined whether treadmill incline or walking condition had a significant effect on the variability of each of our metrics. We also performed a two-way repeated-measures ANOVA with interactions to determine whether treadmill incline or walking condition significantly influenced anteroposterior drift. Where appropriate, we performed paired t-test post hoc tests with Bonferroni corrections to account for the number of comparisons. The normality of each of these data distributions was confirmed with the Kolmogorov-Smirnov test. In all cases, $P < 0.05$ was interpreted as significant.

RESULTS

Participants varied their gait characteristics in response to changes in treadmill incline. Even when participants were not consciously aware of changes in incline, they gradually adapted their storage-phase MG activity over time. However, this gradual adaptation was not observed with the increased cognitive load present during dual-task walking.

Experiment 1. Constant-Incline Walking

Treadmill incline influenced both gait mechanics and plantarflexor muscle activity (Fig. 2). Incline had a significant main effect ($P < 0.001$) on stride period, peak parallel GRF (propulsive force), storage-phase activity for MG and SO, and return-phase activity for MG and SO. Throughout the walking trials, participants walked with longer stride periods (Fig. 2B) and larger peak propulsive forces (Fig. 2C) when walking up steeper inclines. Plantarflexor muscle activity was higher when walking up steeper inclines, as illustrated for the SO during the storage phase (Fig. 2D) and the return phase (Fig. 2E). Anteroposterior drift during trials did not vary significantly ($P = 0.94$) across inclines, with an overall average value of 21.0 cm.

Both gait mechanics and plantarflexor muscle activity changed over time. Time did not have a significant main effect

| Table 1. Participant responses to questions asked at completion of experiment 2 |
|-----------------|-------|-------|
| Did you notice a change in | Yes | No |
| The size of the dot? | 0 | 10 |
| The size of the printed words? | 0 | 10 |
| The rate at which words were presented? | 6 | 4 |
| Treadmill speed? | 1 | 9 |
| Treadmill incline? | 0 | 10 |

Question of primary interest is in italics; all other questions were distractors.
on stride period \((P = 0.10)\), but there was a significant interaction \((P < 0.001)\) between time and incline. Stride period gradually increased when subjects walked up the shallower inclines \((0–5\%)\) but gradually decreased with a 9\% incline (Fig. 2B). Similarly, time did not have a significant main effect \((P = 0.32)\) on peak propulsive force, but a significant interaction \((P = 0.012)\) between time and incline was found. Over time, peak force increased slightly at shallow inclines but decreased slightly at the steepest incline (Fig. 2C). Storage-phase and return-phase activity of both the MG and the SO were significantly influenced by a main effect of time \((P < 0.001)\) and an interaction between incline and time \((P < 0.007)\). Plantarflexor muscle activity gradually decreased over time, with larger decreases observed at steeper inclines (Fig. 2D and E).

Experiment 2. Variable-Incline Walking

Treadmill incline periodically alternated between 0\% (level walking) and a 1\% uphill incline. We quantified the effects of these small incline changes on several metrics of gait behavior: stride period, CoP location, peak propulsive force, storage-phase plantarflexor activity, and return-phase plantarflexor activity. For each of these metrics, the group averages within each 5-s bin are plotted over time in Figs. 3–7 to illustrate the effects of changes in treadmill incline.

The small changes in incline were not consciously detected by the participants. After the experiment, none of the 10 participants reported noticing a change in treadmill incline (Table 1). In contrast, six participants reported a change in the rate at which words were presented during the Stroop test, and one participant reported that the treadmill speed changed. Neither of these parameters actually changed during the experiment.

Stride period. Changes in treadmill incline did not have consistent effects on stride period (Fig. 3A). During single-task walking, stride period appeared to slightly increase over time before reaching a plateau. This pattern was not present during dual-task walking. Stride period values remained within a relatively narrow range throughout the 5-min walking trials but were slightly longer during single-task walking than during dual-task walking.

Across walking conditions, treadmill incline also did not significantly influence stride period. While the average stride period was somewhat longer when subjects walked up a 1\% incline (Fig. 3B), this difference did not reach the level of statistical significance \((P = 0.054)\). The gradual changes in stride period following an increase in treadmill incline were not significantly different \((P = 0.72)\) from the gradual changes following a decrease in treadmill incline (Fig. 3C), providing no evidence for incline-dependent gradual adaptation. Treadmill incline also did not significantly \((P = 0.79)\) influence stride period variability (Fig. 3D).

Increasing cognitive load with a dual-task walking paradigm caused participants to walk with a significantly \((P = 0.021)\) shorter average stride period (Fig. 3B). Walking condition did not significantly \((P = 0.08)\) influence the gradual adaptation...
following an incline change, despite the apparent trend for stride period to only consistently increase during single-task walking (Fig. 3C). Walking condition also did not significantly (P = 0.91) affect stride period variability (Fig. 3D).

Center of pressure. Participants’ position on the treadmill was quantified by the location of their CoP at midstance. Over the course of walking trials, participants slowly moved forward on the treadmill (Fig. 4A). Throughout the trials, participants were located farther forward during the dual-task walking condition.

The average anteroposterior location of the CoP was significantly (P < 0.0001) closer to the front of the treadmill when walking on level ground than when walking uphill (Fig. 4B). However, the direction of changes in treadmill incline did not have a significant main effect (P = 0.82) on the subsequent gradual adaptation of CoP location (Fig. 4C). While the interaction between incline and walking condition did not reach significance (P = 0.07), we observed a trend for participants to gradually move forward when walking uphill under single-task...
conditions and when walking on level ground under dual-task conditions (Fig. 4C). Treadmill incline did not significantly influence \((P = 0.98)\) the variability in CoP location (Fig. 4D). Similarly, the amount of anteroposterior drift was not significantly \((P = 0.47)\) different between inclines, with an overall average value of 20.9 cm.

Walking condition also influenced average CoP location, which was significantly \((P = 0.049)\) closer to the front of the treadmill under dual-task conditions (Fig. 4B). However, the increased cognitive load during dual-task walking did not have a significant main effect on either the gradual adaptation in CoP location \((P = 0.70); \text{Fig. 4C}\) or CoP location variability \((P = 0.20); \text{Fig. 4D}\). The amount of anteroposterior drift was also not significantly \((P = 0.07)\) influenced by walking condition.

Peak parallel ground reaction force. Forward propulsion was quantified by the peak GRF directed parallel to the treadmill belt (Fig. 5A). This peak force was higher when walking up a 1% incline than when walking on a level surface (Fig. 5B). Peak propulsive force was also consistently higher during single-task walking than during dual-task walking.

Treadmill incline influenced both the average peak propulsive force and the changes in this force over time. Average peak force was significantly \((P < 0.0001)\) higher when walking up a 1% incline than when walking on a level surface (Fig. 5C). The direction of the incline change had a significant \((P = 0.038)\) main effect on the subsequent gradual adaptation, as peak force increased to a greater extent after an increase in incline than after a decrease in incline. However, this difference was only significant during dual-task walking; during single-task walking the peak force gradually increased at both incline levels (Fig. 5D). Peak propulsive force variability was not significantly influenced \((P = 0.92)\) by treadmill incline (Fig. 5E).

Walking condition also influenced peak propulsive force. Average peak forces were significantly higher \((P = 0.038)\) during single-task walking than during dual-task walking (Fig. 5C). Walking condition did not significantly \((P = 0.71)\) influence the adaptation of peak force following incline changes (Fig. 5D). However, peak force was significantly \((P = 0.004)\) more variable during single-task walking than during dual-task walking (Fig. 5E).

Storage-phase plantarflexor activity. Storage-phase muscle activity was influenced by changes in treadmill incline, as illustrated in Fig. 6, A and B, for the MG. During single-task walking, increases in treadmill incline were followed by gradual increases in storage-phase activity. Conversely, decreases in treadmill incline were followed by gradual decreases in storage-phase activity. These gradual changes were less apparent in dual-task walking trials.

Treadmill incline influenced both average storage-phase activity and the gradual changes in this activity over time. For both MG and SO, average storage-phase activity was significantly \((P < 0.0005)\) higher when walking up a 1% incline than when walking on level ground (Fig. 6C). Gradual changes in MG storage-phase activity were also observed following a change in treadmill incline (Fig. 6D). The adaptation in MG storage-phase activity following an incline increase was significantly \((P = 0.0022)\) more positive than the adaptation following an incline decrease (Fig. 6D). However, this evi-
Fig. 6. Storage-phase plantarflexor activity was influenced by treadmill incline. A: example medial gastrocnemius (MG) activity traces during the stance phase are illustrated for a single subject, as described in Fig. 5. The timing of MG activation remained consistent, while storage-phase activity varied slightly with treadmill incline and over time. B: storage-phase MG activity is plotted over time following the format described in Fig. 3. Under single-task conditions, this activity underwent alternating periods of gradual increases and gradual decreases following changes in treadmill incline. C: for both MG and SO, storage-phase activity was higher when walking up a 1% incline. D: under single-task conditions, the adaptation of storage-phase MG activity was differentially affected by increases and decreases in treadmill incline. This effect was not as apparent for the SO or under dual-task conditions. E: storage-phase MG activity was more variable under single-task conditions than under dual-task conditions. C–E: *significant (P < 0.05) post hoc effect of incline under this walking condition, #significant (P < 0.05) main effect of walking condition.
patterns of MG activity. Treadmill incline significantly influenced plantarflexor activity during both the storage and return phases of stance. As hypothesized, a small change in treadmill incline caused subsequent gradual adaptation in MG storage-phase activity. This behavior is consistent with humans using proprioceptive feedback to adapt their muscle activation patterns during functional movement. However, the observed gradual adaptation was not present during dual-task walking, indicating that cognitive processing plays a role in the adaptation process.

Gait behavior during constant-incline walking was influenced by the mechanical demand and duration of the task. Treadmill incline had clear effects on gait mechanics and plantarflexor activity, consistent with previously reported increases in stride period (Leroux et al. 2002), peak parallel GRF (Franz and Kram 2013), and plantarflexor activity (Franz and Kram 2012; Lay et al. 2007; Leroux et al. 1999) at steeper inclines. Over the course of the 5-min trials, stride period and propulsive force changed only slightly, with the direction of this change dependent on treadmill incline. In contrast, plantarflexor activity during both the storage and return phases consistently decreased over time. The gradual decreases in plantarflexor activity without major changes in propulsion may seem counterintuitive. The ankle plantarflexors are typically considered to be a major contributor to propulsion during human walking, with model simulations suggesting a direct link between plantarflexor activation and peak anterior GRF (Neptune et al. 2004). However, this simple relationship is not maintained when walking speed is increased above the preferred speed, as anterior GRF decreases despite increases in plantarflexor activity (Neptune and Sasaki 2005). Recent ultrasound experiments have explained this finding through changes in plantarflexor contractile conditions (Farris and Sawicki 2012). Specifically, a constant level of plantarflexor activation will produce less force when the muscle is either shortening more quickly (because of the force-velocity relationship) or acting farther from the optimal length (because of the force-length relationship). Allowing a muscle to operate under favorable mechanical conditions would thus be expected to decrease the activation required for a given mechanical output.

The gradual reduction of plantarflexor activity during constant-incline walking may be explained by participants adapting their muscle activation patterns in order to optimize the contractile conditions. Humans may modulate their plantarflexor activity in order to either hold the muscle near-isometric during much of the stance phase, allowing mechanical energy to effectively be stored in the Achilles tendon, or produce force when the muscle is closer to its optimal length (because of the force-length relationship). Allowing a muscle to operate under favorable mechanical conditions would thus be expected to decrease the activation required for a given mechanical output.

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movement pattern toward the resonant frequency (Merritt et al. 2012) at which the plantarflexors are able to contract nearly isometrically (Takeshita et al. 2006). In walking, such an adaptation process would be expected to result in variable plantarflexor activation patterns but similar muscle mechanics during steady-state gait under a range of conditions. Indeed, when walking uphill or downhill, humans vary their plantarflexor activation patterns dramatically even as the MG is held near-isometric for the majority of the stance phase (Lichtwark and Wilson 2006).

Alternatively, the gradual decreases in plantarflexor activity may be caused by peripheral neuromuscular changes rather than adaptation toward a mechanical optimum. The decreased plantarflexor activity may result from a reduction in cocontraction of the ankle musculature, as commonly observed during learning of a novel movement task (Franklin et al. 2003). The present experiments did not measure dorsiflexor activity, preventing us from directly addressing this possibility. The decreases in plantarflexor activation may also be a response to increased tendon compliance, which can accompany extended periods of walking (Cronin et al. 2009, 2011b). However, these previous studies only quantified changes in musculotendon behavior after at least 30 min of walking and did not observe a significant change in muscle activity until the 20th minute, substantially longer than our 5-min trials. Finally, the decreased plantarflexor activity could be the result of altered muscle contractility caused by repeated contractions, as increases in muscle relaxation time can reduce the motor unit discharge rate required to maintain a steady muscle contraction (Bigland-Ritchie et al. 1983). Future experiments could directly discriminate between these possible explanations by using more detailed measurements of muscle activity, muscle contractile properties, and muscle mechanics (likely with ultrasound experiments as described below).

The variable-incline experiments can provide insight into the most likely explanation for the changes in plantarflexor activity over time. Our discussion is primarily focused on the MG, as changes in treadmill incline had clearer effects on the gradual adaptation of MG activity than on the adaptation of SO activity (see Fig. 6). Additionally, our MG results are more easily compared with previous investigations of the effects of incline and speed on plantarflexor mechanics (Farris and Sawicki 2012; Lichtwark and Wilson 2006), which only quantified MG behavior. After a decrease in treadmill incline during single-task walking, MG activity during both the storage and return phases gradually decreased, just as observed during constant-incline walking. However, an increase in treadmill incline was followed by a gradual increase in storage-phase activity but a decrease in return-phase activity. This mechanics-dependent behavior is consistent with participants gradually adapting their MG activation patterns during the storage phase in order to achieve more favorable contractile conditions, as steeper inclines appear to require greater MG activity in order to hold a muscle near-isometric (Lichtwark and Wilson 2006). In turn, the gradual increases in propulsive force and decreases in MG activity during push-off could be attributed to the more effective storage of mechanical energy in the lengthening Achilles tendon, as well as more favorable muscle contractile conditions. The observed mechanics-dependent changes in storage-phase activity are not as easily explained by the alternative explanations of decreased cocontraction, increased tendon compliance, or slowing of muscle relaxation time.

MG activity underwent both relatively rapid and more gradual modifications in response to changes in the mechanical demand of walking. Changes in treadmill incline caused fast, sustained changes in return-phase activity. For example, after an increase in treadmill incline, return-phase activity increased substantially within the first 5-s period and remained relatively high while subjects walked on the new incline. It is possible that these rapid changes in return-phase MG activity are necessary in order for the ankle joint to produce an appropriate level of mechanical work during late stance, which increases with surface incline (Franz and Kram 2014). The speed of this change may be explained by altered afferent feedback directly attributable to the incline. Even within a single step, changes in surface incline can elicit predictable changes in human plantarflexor activity without the need for central processing (af Klint et al. 2008, 2010). Similarly, animal studies have indicated that responses to altered inclines can occur automatically, with both descending commands and feedback gains remaining constant (Hatz et al. 2012). In contrast, our observed changes in storage-phase activity were quite gradual, either slowly increasing or decreasing depending on the direction of the treadmill incline change. Such modifications to storage-phase activity likely do not directly contribute to the production of positive muscular work, as the MG tends not to shorten until later in stance. However, appropriate levels of storage-phase MG activity may allow subsequent mechanical work to be performed more efficiently by allowing the tendon to perform positive work instead of the muscle. These results demonstrate the response to altered mechanical demands during walking is not entirely automatic but is also dependent on the gradual processing of feedback. However, the present results are unable to identify the physiological source of this gradual adaptation, which could be caused either by changes in the descending command or by changes in afferent feedback gains.

Future experiments could address this question with the use of perturbation methods that have previously been used to clarify the roles of various feedback sources during walking (Greys et al. 2007; Nielsen and Sinkjaer 2002).

While the incline-dependent adaptation of MG storage-phase activity during single-task walking was significant, its magnitude was relatively small. This is likely due in part to the small changes in treadmill incline (0–1%). Larger incline changes presumably would have increased the observed effect but would have also increased the probability of participants being consciously aware of the changes as they occurred. This might have allowed participants to consciously choose a different motor plan for accomplishing the gait task, complicating interpretation of the results. Additionally, the 55-s walking periods following a change in treadmill incline may not have been sufficient to observe the entirety of the changes in gait characteristics. A longer time period may be required to quantify the full effects of adaptation, as plantarflexor activity appeared to continue to decrease after the first minute of the constant-incline trials. However, longer trials could increase the probability of changes to tendon compliance (Cronin et al. 2009, 2011b), of fatigue, and of participants noticing the incline changes. While we may not have had sufficient time to observe the entire adaptation process, the fastest changes in our gait metrics were observed during the first minute of constant-
incline walking. Interestingly, we did not observe significant incline-dependent adaptation of stride timing, which has previously been used to quantify gait adaptation (Snaterse et al. 2011; Snyder et al. 2012). It is possible that this relatively gross measure is not sensitive to subtle changes in muscular control over the time period investigated in the present study.

Cognitive load influenced the adaptive responses to changes in treadmill incline, as well as the average gait behavior and its variability. While participants were not consciously aware of the incline changes, significant mechanics-dependent gradual adaptation of storage-phase MG activity was present during single-task walking trials. However, this significant adaptation was not present when cognitive load was increased during dual-task trials. Previous investigations of dual-task walking have largely focused on the link between cognitive load and balance (Dingwell et al. 2008; Grabiner and Troy 2005; Siu et al. 2009). The present results indicate that cognition is also involved in the adaptation to altered mechanical demands of walking. Therefore, this adaptation appears to require involvement of the brain and cannot be attributed solely to more peripheral changes in the musculotendon complex or spinal cord. Walking under dual-task conditions reduced the average stride period, consistent with the choice of a safer, more conservative gait strategy (Cappellini et al. 2010; Monsch et al. 2012). These shorter strides were accompanied by reduced peak propulsive forces and lower MG activity, relationships that have been reported previously (Martin and Marsh 1992; Sawicki and Ferris 2009). Counterintuitively, the distraction present during dual-task walking reduced variability in peak propulsion and MG activity, suggesting that the observed variability may be an indicator of humans exploring the range of possible MG activation patterns and may be important for adaptation (Stergiou and Decker 2011). Alternatively, it is possible that the periodic display of the Stroop test images (with a 1.01-s period) may have reduced variability by partially entraining participant behavior to this rhythm.

To definitively determine whether humans adapt their plantarflexor activity in order to achieve favorable contractile conditions, future experiments must measure muscle mechanics. The most likely source of such measurements will be ultrasound, which can allow the noninvasive quantification of muscle fascicle length and velocity (Cronin et al. 2011a) and could reveal whether the MG gradually behaves more isometrically over the course of the adaptation process. However, the analysis of ultrasound data can be quite time intensive, which is likely one reason why most ultrasound studies quantify muscle mechanics over only a few strides at a time. The present results allow us to make predictions about the types of changes in mechanical demand that could lead to gradual changes in altered musculotendon mechanics (i.e., incline changes), as well as the time course over which these changes may occur (at least a minute). Such predictions could justify the analysis of ultrasound data at specific time points after specific events within a well-designed walking trial.

We have previously proposed that humans may use proprioceptive feedback to drive mechanics-dependent adaptation (Dean 2013), such as that observed here for single-task walking trials. Specifically, proprioceptive feedback could be used to sense muscle velocity through Ia afferent pathways. Patterns of muscle activation could then be iteratively adjusted in order to produce near-isometric muscle behavior (Merritt et al. 2012), allowing metabolically efficient propulsion (Ishikawa et al. 2005). Adaptation may thus be beneficial not only for reductions of kinematic errors but also for improvements in metabolic economy (Finley et al. 2013). The possible use of proprioceptive feedback to sense muscle velocity suggests an important role for muscle spindles during active, cyclical movements. This process could occur in parallel with the strong influence of Golgi tendon organ feedback through Ib pathways on ongoing plantarflexor activity (af Klint et al. 2010; Grey et al. 2007; Hatz et al. 2012). While the present results are consistent with this proposal, we are unable to rule out the possibility that other sources of feedback may have played an important role in the observed adaptation. For example, while participants were unable to see the treadmill surface, they still may have used visual feedback to sense their distance from the screen in front of them and modify their gait pattern in order to remain safely on the treadmill. The significant trend during single-task walking for participants’ CoP to gradually move forward when they walked uphill could conceivably be driven by such visual feedback. Future experiments could be designed to directly test the importance of proprioceptive feedback in gradual adaptation. Specifically, ankle tendon vibration could be used to disrupt proprioceptive feedback (Courtine et al. 2001; Ivanenko et al. 2000; Verschueren et al. 2002) in order to determine whether the gradual adaptation is affected.

The ability to adapt behavior to changing mechanical demands during gait may be limited in clinical populations. For example, proprioception is often impaired after a stroke (Connell et al. 2008), likely because of a decreased ability to interpret sensory information. Feedback from proprioceptive receptors is also reduced in patients with peripheral neuropathies (van Deursen and Simoneau 1999). In these populations, the contributions of afferent feedback to ongoing muscle activity during gait may be altered (Mazzaro et al. 2005, 2007). Patients may also have a reduced ability to use afferent feedback to drive the gradual adaptation we observed in uninjured participants. If this is found to be true, then enhancing proprioceptive feedback with techniques such as white noise tendon vibration (Ribot-Ciscar et al. 2013) may hold promise for improving function, similar to the beneficial effects of foot sole vibration on balance (Priplata et al. 2006).

In conclusion, the present results provide evidence for mechanics-dependent gradual adaptation of MG activity during human walking. These results are consistent with the proposal that humans iteratively adjust their muscle activation patterns based on proprioceptive feedback, with the goal of harnessing the body’s mechanics to allow economical propulsion. However, further research will be required to differentiate between possible neural mechanisms underlying this adaptation (e.g., altered descending commands or feedback gains), quantify the adaptation magnitude and time course, and directly measure changes in musculotendon mechanics during the adaptation process. The possible role for proprioceptive feedback in the identification of economical movement patterns could have clear implications for clinical populations with disrupted sensory feedback and altered movement patterns during functional tasks.
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AUTHOR CONTRIBUTIONS
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