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Gradual training reduces practice difficulty while preserving motor learning of a novel locomotor task

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ABSTRACT

Motor learning strategies that increase practice difficulty and the size of movement errors are thought to facilitate motor learning. In contrast to this, gradual training minimizes movement errors and reduces practice difficulty by incrementally introducing task requirements, yet remains as effective as sudden training and its large movement errors for learning novel reaching tasks. While attractive as a locomotor rehabilitation strategy, it remains unknown whether the efficacy of gradual training extends to learning locomotor tasks and their unique requirements. The influence of gradual vs. sudden training on learning a locomotor task, asymmetric split belt treadmill walking, was examined by assessing whole body sagittal plane kinematics during 24 hour retention and transfer performance following either gradual or sudden training. Despite less difficult and less specific practice for the gradual cohort on day 1, gradual training resulted in equivalent motor learning of the novel locomotor task as sudden training when assessed by retention and transfer a day later. This suggests that large movement errors and increased practice difficulty may not be necessary for learning novel locomotor tasks. Further, gradual training may present a viable locomotor rehabilitation strategy avoiding large movement errors that could limit or impair improvements in locomotor performance.

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1. Introduction

There exists an abundance of motor learning strategies (Schmidt & Lee, 2005) that can be used to make practice more difficult. Such an approach to training has been consistently shown to improve motor learning despite decrements in initial performance (Christina & Bjork, 1991; Schmidt & Bjork, 1992; Schmidt & Lee, 2005). Practice difficulty can also be manipulated by controlling the rate at which the task requirements of a motor skill are introduced during training. Specifically, practice difficulty can be increased by using a sudden training strategy whereby task requirements are abruptly introduced and then maintained throughout practice, an approach which results in large movement errors (Criscimagna-Hemminger, Bastian, & Shadmehr, 2010). Alternatively, practice difficulty can be reduced by using a gradual training strategy which incrementally introduces task requirements over the course of a practice session, resulting in small movement errors which often go unnoticed by the learner (Criscimagna-Hemminger et al., 2010).

The detection of large movement errors by the cerebellum (Morton & Bastian, 2006; Shadmehr, Smith, & Krakauer, 2010), and subsequent correction by the motor system is thought to be critical to sensorimotor motor learning as it drives the adaptation of movement strategies and the acquisition of motor skills (Lisberger, 1988; Rumelhart, Hinton, & Williams, 1986; Tseng, Diedrichsen, Krakauer, Shadmehr, & Bastian, 2007) by updating an internal model of the interaction between the limb and the environment (Wolpert & Ghahramani, 2000). Thus, the more challenging sudden training and its large movement errors has been proposed as a means to increase practice difficulty and enhance motor learning by cueing the nervous system to make movement corrections in response to large movement errors (Reisman, Bastian, & Morton, 2010). However, a number of studies in which participants practiced visually distorted or physically perturbed reaching tasks have demonstrated that upon removal of the perturbation, individuals who received gradual training exhibited a slower rate of decay of the adapted reaching pattern, taking longer to reestablish unperturbed reaching movements; an indication that these individuals adapted to the novel reaching tasks more thoroughly than those who received sudden training (Buch, Young, & Contreras-Vidal, 2003; Criscimagna-Hemminger et al., 2010; Huang & Shadmehr, 2009; Kagerer, Contreras-Vidal, & Stelmach, 1997; Taylor, Wojaczynski, & Ivry, 2011).

Beyond short term adaptive responses, novel reaching skills practiced using gradual training are retained as well or better than those using sudden training (Klassen, Tong, & Flanagan, 2005), and appear to generalize to conditions that differ from those of original practice better than after sudden training (Malfait & Ostry, 2004). This suggests that gradual rather than sudden training results in superior motor learning. Thus it would appear that sudden training and large movement errors may not be necessary for motor learning. Therefore, gradual training may be an effective rehabilitation strategy for retraining populations where large movement errors could present substantial challenges, altering what movement strategies are selected to perform the task and how well they are learned. Additionally, not all individuals are responsive to sudden training (Criscimagna-Hemminger et al., 2010; Musselman, Patrick, Vasudevan, Bastian, & Yang, 2011; Reisman et al., 2010).

To date only one study has examined the influence of gradual versus sudden training on locomotor tasks (Torres-Oviedo & Bastian, 2012). In this study of short term adaptations, gradual training resulted in a slower rate of decay of an adapted locomotor pattern, while sudden training induced greater initial adaptation to the novel locomotor task (Torres-Oviedo & Bastian, 2012). It remains unknown whether the efficacy of gradual training demonstrated for the delayed retention and transfer of novel upper extremity reaching tasks (Klassen et al., 2005; Malfait & Ostry, 2004) generalizes to the delayed retention and transfer of locomotor skills and their unique requirements. A better understanding of whether and how gradual versus sudden training influences the acquisition of locomotor skills may be particularly important to locomotor rehabilitation, especially considering the emergence of powered prosthetic and exoskeleton technology. Given the rapid rate of technological advancement in the field of prosthetics and orthotics (Grill, 2007), the development of appropriate training strategies will be essential to ensure the most effective and widespread application of these devices among individuals with locomotor impairments.

The objective of this study was to determine whether gradual versus sudden training influenced how well a novel locomotor task was learned. This was accomplished by examining whole body sagittal plane kinematics during training and 24 hour retention or transfer performance of a novel locomotor task, asymmetric split belt treadmill walking (Dietz, Zijlstra, & Duysens, 1994). We hypothesized that despite reduced practice difficulty, gradual training would result in equivalent or superior motor learning as assessed by 24 hour retention or transfer performance of the novel locomotor task.

2. Methods

2.1. Recruitment

Thirty-two participants from the general population of adults without impairment were recruited and distributed randomly among the experimental groups ($n = 8$ per group). Inclusion criteria were age between 18 and 50, and the ability to walk continuously for 20 minutes on a treadmill without assistance. Exclusion criteria were medical conditions, assessed by self report, which could result in impaired gait or sensory loss, including significant musculoskeletal, neurologic, or cardiopulmonary conditions and any previous split belt walking experience. Testing of this population allows for a controlled assessment of gradual versus sudden training for learning locomotor tasks prior to their implementation in rehabilitation protocols for individuals with locomotor impairments. Local Institutional Review Boards approved all protocols. Informed consent was obtained from each participant prior to enrollment. Demographic factors including age, height, mass, gender, self-selected walking speed (SSWS) and limb dominance were recorded. SSWS was calculated from the average time over four trials required to walk a known distance of 19.63 m, while limb dominance was assessed by self report of preferred kicking leg (Kramer & Balsor, 1990).

2.2. Experimental protocol

All participants were asked to practice the same novel locomotor task, asymmetric split belt treadmill walking, where one leg is driven at a faster velocity than the other leg (Dietz et al., 1994). This task was chosen because it is a novel locomotor task that provides an established experimental paradigm for examining sensorimotor learning (Bastian, 2008), a process that is critical to locomotor rehabilitation.

Two training strategies were explored in the current study, gradual and sudden training. During sudden training, the novel locomotor task (split belt treadmill walking) was introduced via a single abrupt change in belt velocity. The belt under the dominant leg was accelerated at 5.0 m/s^2 to reach a velocity of 1.4 m/s (2:1 walking) between heel strikes. 2:1 walking was then maintained for the remainder of training, 720 consecutive strides. Similar to protocols using perturbed reaching tasks (Klassen et al., 2005; Malfait & Ostry, 2004), the gradual training cohort was introduced to split belt treadmill walking using incremental steps. Each of these steps consisted of 20 strides, over which the dominant leg belt speed was increased by 0.02 m/s using an acceleration of 0.001 m/s^2. This continued until the dominant leg belt velocity reached 1.4 m/s (2:1 walking), a transition which took 700 strides (35 blocks of 20 strides). Twenty additional 2:1 walking strides were then performed during gradual training to ensure that the number of strides taken over the course of training were the same for each cohort, 720. The magnitude of the velocity changes and the acceleration were chosen to minimize the detection of each incremental change and represent the lower limits of the treadmill controls.

Prior to training, a 15-min treadmill acclimation phase, during which participants walked at a controlled velocity of 0.7 m/s on a Bertec split belt instrumented treadmill (Bertec, Columbus, OH), was provided to promote gait consistency (Zeni & Higginson, 2010). The same controlled walking speed (0.7 m/s) was used for each participant to ensure that identical velocity changes were used during subsequent phases of the experiment for all participants. This provided each participant with the same training experience, strengthening the internal validity of our protocol. Following treadmill acclimation, an additional 20 strides at 0.7 m/s were performed to characterize baseline walking performance. Participants were then randomly allocated to one of four cohorts: (1) gradual training and retention testing, (2) sudden training and retention testing, (3) gradual training and transfer testing, or (4) sudden training and transfer testing. Noise cancelling earphones and custom eyewear were worn throughout the experiment to control acoustic feedback from treadmill motors and visual feedback from treadmill belts. All participants were given the same instructions: maintain or restore a comfortable, rhythmic walking pattern. Participants were naïve to the novel locomotor task, split belt treadmill walking, and to their allocation to gradual or sudden training. A handrail in front of the treadmill was made available, although participants were encouraged to use it only as needed.

Retention and transfer tests were performed 24 hours post training to allow sufficient time for stabilization and consolidation of motor memories created during training (Luft, Buitrago, Ringer, Dichgans, & Schulz, 2004; Muellbacher et al., 2002). Prior to retention or transfer testing the next day, all participants were given 5 minutes to reacclimatize to the treadmill at 1:1 walking. The retention test consisted of the same 2:1 walking task performed during training, with the exception that all participants experienced a sudden reintroduction during retention testing. Retention testing allowed us to assess how the durability or recall of the locomotor strategy practiced the previous day was affected by gradual versus sudden training. Transfer testing consisted of a modification of the original locomotor task practiced during training, wherein the dominant leg belt speed was three times that of the non-dominant leg belt, 2.1 m/s (3:1 walking). Similar to retention, a sudden reintroduction of the novel locomotor task was used during transfer testing. This branch of the experiment allowed us to assess the flexibility of the locomotor strategy, the degree to which it could be produced in a different environment from which it was originally practiced. Retention and transfer tests consisted of 400 strides.

2.3. Data collection

Fifty-seven reflective markers, 14 mm in diameter were placed bilaterally on the participants' bony landmarks, using an accepted whole-body marker set (Sawers & Hahn, 2012). Throughout all phases of the protocol, three-dimensional marker coordinate data were collected at 120 Hz using a 12 camera Vicon MX motion capture system (Vicon, Oxford, UK) and synchronized with ground reaction force (GRF) data collected from the treadmill force platforms (Bertec, Columbus, OH) at 1200 Hz for gait event detection.

2.4. Data analysis

Raw three dimensional marker coordinate data were filtered (4th order Butterworth filter with 5 Hz low pass cutoff frequency) (Winter, 2009) and combined with participant specific anthropometric data adapted from the initial work of Dempster (Winter, 2009) to build a 15 segment whole body model in Visual 3D (C Motion, Germantown, MD) (Sawers & Hahn, 2012). Whole body center of mass (COM) position was calculated using the weighted sum of all body segments, with 15 segments representing the whole body: head neck, trunk, pelvis, upper arms, forearms, hands, thighs, shanks, and feet.

The Sagittal Inclination Angle (SIA), a measure of limb endpoint control relative to the whole body COM, was chosen as the metric of locomotor performance. It was defined as the angle formed by a vector from the COM to the lateral malleolus with respect to the vertical in the sagittal plane (Chen & Chou, 2010),

$$\theta = \sin^{-1}\left(\frac{\vec{J}_{\text{ankle to COM}} \times \vec{J}_{\text{vertical}}}{|\vec{J}_{\text{ankle to COM}}|}\right)$$

where $\vec{J}_{\text{ankle to COM}}$ is the vector from the ankle (lateral malleolus) to the whole body COM in the sagittal plane, and J_{vertical} is the unit vector of the vertical. The SIA was chosen as the metric for locomotor performance on the basis of previous biomechanical (Griffin, Main, & Farley, 2004; McMahon & Cheng, 1990), neurophysiological (Bosco, Eian, & Poppele, 2005; Bosco, Poppele, & Eian, 2000; Bosco, Rankin, & Poppele, 1996), and behavioral (Chang, Auyang, Scholz, & Nichols, 2009; Lacquaniti, Le Taillanter, Lopiano, & Maioli, 1990) studies which have shown that whole limb function is an important characteristic of locomotion, specifically with respect to the whole body COM (Balasubramanian, Neptune, & Kautz, 2010; Redfern & Schumann, 1994; Winter, McFadyen, & Dickey, 1991). Furthermore, the SIA excludes any effects of body height (Lee & Chou, 2006), making it suitable for inter-individual comparisons. A similar metric has also been shown to demonstrate adaptive qualities during split belt treadmill walking (Reisman, Block, & Bastian, 2005). Using custom MATLAB™ (MathWorks, Natick, MA) code, discrete values for the SIA were calculated on a stride by stride basis at ipsilateral heel strike for the fast (dominant) and slow (non dominant) legs. The standard deviation (*SD*) of the SIA was then calculated for each 20 stride bin during baseline walking, training, retention and transfer phases of the experiment. The *SD* reflects the amount of variability in the movement pattern (Stergiou, 2004). The amount of uncertainty in a movement pattern is a useful metric for assessing recovery of sensorimotor control (Bauby & Kuo, 2000) as it reflects the challenge or difficulty of a locomotor task (Bauby & Kuo, 2000; Donelan, Shipman, Kram, & Kuo, 2004; Owings & Grabiner, 2004b). A reduction in uncertainty is thought to result from efficient execution of that movement pattern (Stergiou & Decker, 2011) and to be indicative of the amount of learning that has occurred (Marteniuk, 1976). A measure of movement uncertainty also provides a more universal and less biased approach to the assessment of motor learning as it does not presume that there is an ideal kinematic movement strategy that all individuals should conform to, nor does it penalize individuals who later elect to perform the motor skill with a movement strategy that differs from initial training, a scenario likely to present itself during transfer testing. Therefore, in this study, motor learning was operationally defined as the extent to which the amount of uncertainty in the SIA during retention (2:1 walking) or transfer (3:1 walking) was restored to baseline 1:1 walking levels.

To determine whether gradual versus sudden training influenced how well the novel locomotor task was learned, we calculated the Average Uncertainty Residual (AuR) of the SIA for the fast (dominant) and slow (non dominant) legs during training, retention and transfer. The AuR was defined as the mean difference in the SIA uncertainty (*SD*) between baseline 1:1 walking (20 strides) and each of the training, retention and transfer bins (20 strides). The lower the AuR, the closer the amount of uncertainty in the movement pattern to that of baseline 1:1 walking. During training, a lower AuR indicates less difficulty or challenge presented by the locomotor task. During retention or transfer, a lower AuR can be further interpreted as greater learning of the novel locomotor task.

2.5. Statistical analysis

To evaluate the influence of the between-subjects effect of training strategy on practice difficulty and motor learning, we examined the influence of a single independent variable, training strategy, with two levels, gradual and sudden, on two dependent variables, the fast leg and slow leg Average Uncertainty Residual (AuR) of the SIA during the Training phase (to assess practice difficulty) and the Retention or Transfer phase (to assess motor learning), using multivariate analysis of variance (MANOVA) (*1-sided test*,$\alpha = .05$) for each data set (training, retention and transfer). To examine whether practice difficulty and motor learning varied by leg within each training strategy, paired *t*-tests (*2-sided*,$\alpha = .05$) were performed to compare the AuR between the fast and slow legs within each training strategy during training, retention and transfer. One-sided tests were selected when a sound rationale based upon pilot data was available to reasonably propose the expected direction of difference. All statistical tests were conducted using SPSS (V.19; SPSS, Inc., Chicago IL).

3. Results

All recruited participants ($n = 32$) participated in the complete study (Table 1). During the training phase, the one-way MANOVA revealed a significant multivariate main effect for training strategy (Hotelling's T = 0.606, $F(2,29.00) = 8.781$, $p = .001$). Given the significance of the overall test, univariate effects were examined. Training strategy was found to have a statistically significant between-subjects effect on both the fast leg Average Uncertainty Residual (AuR), $F(1,30) = 16.595$, $p < .0001$; and slow leg AuR, $F(1,30) = 6.605$, $p = .015$, such that the AuR of the Sagittal Inclination Angle (SIA) for fast and slow legs were significantly larger for the sudden versus the gradual training cohort (Figs. 1 and 2; Table 2). Paired *t*-tests during the training phase revealed a significant within-subject effect of leg for both training strategies. The AuR of the fast leg was found to be significantly lower than that of the slow leg for both training strategies (gradual training, $p = .04$; sudden training, $p = .04$) (Table 2).

Table 1
Participant demographics.

Cohort		Height (m)	Mass (kg)	Age (years)	Sex[a]	SSWS (m/s)	Dominant Leg[b]
Gradual Retention ($n = 8$)	Mean (*SD*)	1.73 (*0.10*)	67 (*12*)	33 (*8*)	4M, 4F	1.44 (*0.13*)	8 R, 0 L
	Range	1.60–1.85	54–89	24–50		1.23–1.67	
Sudden Retention ($n = 8$)	Mean (*SD*)	1.71 (*0.13*)	74 (*17*)	31 (*6*)	5M, 3F	1.41 (*0.16*)	8R, 0L
	Range	1.51–1.85	49–103	25–43		1.13–1.63	
Gradual Transfer ($n = 8$)	Mean (*SD*)	1.79 (*0.07*)	76 (*12*)	28 (*5*)	7M, 1F	1.42 (*0.10*)	7R, 1L
	Range	1.65–1.88	56–91	23–36		1.25–1.51	
Sudden Transfer ($n = 8$)	Mean (*SD*)	1.67 (*0.12*)	67 (*9*)	28 (*4*)	2M, 6F	1.43 (*0.17*)	7R, 1L
	Range	1.52–1.85	55–83	24–36		1.12–1.70	

[a] M = Male; F = Female.
[b] R = Right; L = Left.

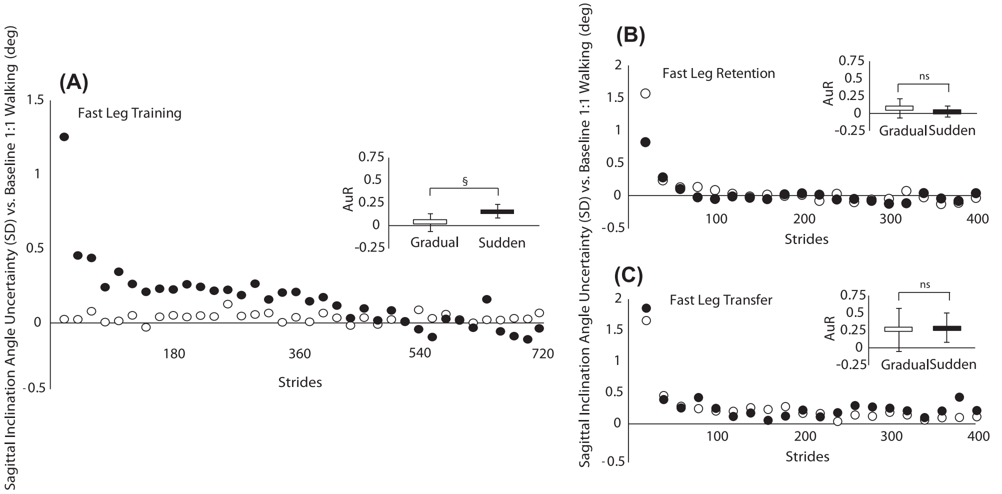

Fig. 1. Sagittal plane COM ankle angle uncertainty (*SD*) of the fast (dominant) leg with respect to Baseline Walking for the Gradual (○) and Sudden Training (●) cohorts during (A) Training, (B) Retention, and (C) Transfer. Each data point represents the average uncertainty over 20 strides with respect to Baseline Walking. Inset is the resulting Average Uncertainty Residual (AuR) with error bars equal to ±1*SD*. (A) The AuR of the fast leg during Training was significantly larger during sudden vs. gradual training $(p < .0001)^{\S}$. The amount of uncertainty in the fast leg COM ankle angle during Training was significantly greater than during Baseline Walking for Sudden $(p < .0001)^{\infty}$, but not Gradual Training. No significant differences in the AuR of the fast leg were found between Gradual and Sudden Training during (B) Retention or (C) Transfer.

During the retention and transfer phases, the one-way MANOVAs did not reveal a significant multivariate main effect for training strategy during retention (Hotelling's T = 0.934, $F(2, 13.00) = 0.463$, $p = .640$), or transfer (Hotelling's T = 0.498, $F(2, 13.00) = 3.238$, $p = .072$). Given the lack of significance of the overall test, univariate effects were not examined during retention or transfer. Paired *t*-tests during retention revealed a significant within-subject effect of leg following sudden training (Table 2). The AuR of the fast leg was found to be significantly less than that of the slow leg ($p = .021$). Paired *t*-tests during transfer revealed a significant within-subject effect of leg following gradual training (Table 2). The AuR of the fast leg was found to be significantly less than that of the slow leg ($p = .017$). While not statistically significant, the AuR of the fast leg showed a trend of being consistently less than that of the slow leg during retention following gradual training and during transfer following sudden training (Table 2).

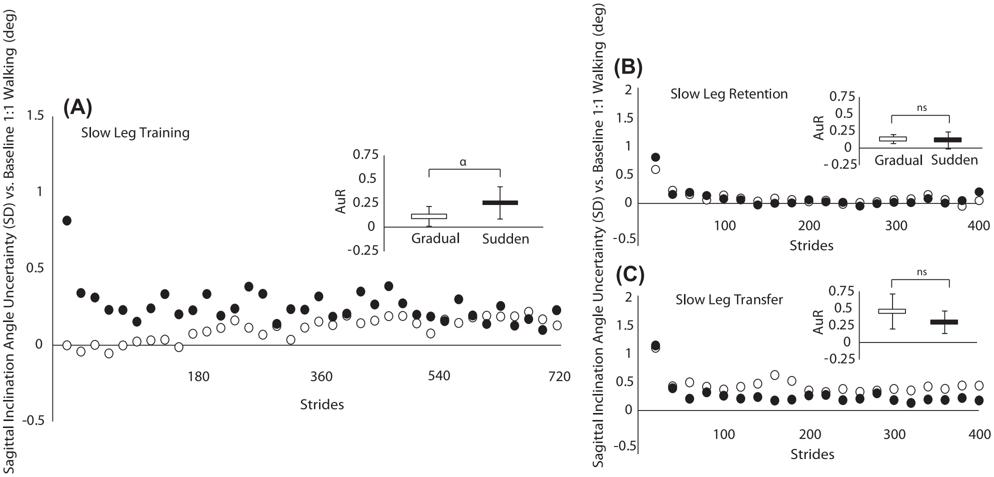

Fig. 2. Sagittal plane COM ankle angle uncertainty (*SD*) of the slow (non dominant) leg with respect to Baseline Walking for the Gradual (○) and Sudden Training (●) cohorts during (A) Training, (B) Retention, and (C) Transfer. Each data point represents the average uncertainty over 20 strides with respect to Baseline Walking. Inset is the resulting Average Uncertainty Residual (AuR) with error bars equal to ±1*SD*. (A) The AuR of the fast leg during Training was significantly larger during sudden vs. gradual training ($p = .015$)[α]. The amount of uncertainty in the slow leg COM ankle angle during Training was significantly greater than Baseline Walking for both Sudden ($p < .0001$)[∞], and Gradual Training ($p = .04$)[∞]. No significant differences in the AuR of the fast leg were found between Gradual and Sudden Training during (B) Retention or (C) Transfer.

Table 2
The sagittal inclination angle (SIA) Average Uncertainty Residual (AuR) of the slow and fast legs during Training, Retention and Transfer phases.

Phase	Sudden Training Cohort		Gradual Training Cohort	
	Fast Leg AuR (*SD*)	Slow Leg AuR (*SD*)	Fast Leg AuR (*SD*)	Slow Leg AuR (*SD*)
Training	0.1676 (0.07)[§,*]	0.2556 (0.17)[α,*]	0.0371 (0.10)[§,♦]	0.1138 (0.13)[α,♦]
24 hr Retention	0.0326 (0.08)[*]	0.1542 (0.08)[*]	0.0830 (0.14)	0.1405 (0.06)
24 hr Transfer	0.2960 (0.21)	0.3022 (0.16)	0.2276 (0.25)[♦]	0.4685 (0.25)[♦]

[§] Represents the univariate effect for training strategy on the fast leg AuR during the Training Phase ($p < .0001$).
[α] Represents the univariate effect for training strategy on the slow leg AuR during the Training Phase ($p = .015$).
[*] Represents a comparison of fast and slow leg AuR within Sudden Training with $p = .04$.
[♦] Represents a comparison of fast and slow leg AuR within Gradual Training with $p = .04$.

4. Discussion

4.1. Overview

This study sought to determine whether gradual versus sudden training influenced how well a novel locomotor task was learned. The Average Uncertainty Residual (AuR) of the Sagittal Inclination Angle (SIA) was calculated to quantify the amount of uncertainty in the whole-body sagittal plane movement pattern during training, retention or transfer with respect to baseline walking, and infer the difficulty of training and the degree of motor learning. During sudden training the AuR of the fast and slow legs were significantly larger than during Gradual Training, while the AuR of the slow leg was significantly larger than that of the fast leg within each training strategy (Figs. 1 and 2; Table 2). This suggests that Sudden Training was significantly more difficult than Gradual Training and that regardless of training strategy, acquisition of the slow leg whole-body sagittal plane kinematic pattern was more difficult than that of the fast leg.

During retention and transfer testing, the AuR of the fast and slow legs were found to be equivalent between the gradual and sudden cohorts (Figs. 1 and 2; Table 2). This suggests that despite more specific and challenging training for the sudden cohort on day one, both training strategies resulted in equivalent motor learning of the complex locomotor task when assessed by delayed retention and transfer, suggesting that large movement errors are not necessary for learning a novel locomotor task and that gradual training may represent a viable locomotor rehabilitation strategy. Additionally, the gradual and sudden cohorts both exhibited a lower AuR for the fast than the slow leg during retention and transfer testing. However, this difference was only statistically significant during transfer testing of the gradual cohort and retention testing of the sudden cohort. This suggests that whole-body sagittal plane kinematic patterns of the fast leg were learned better than those of the slow leg, but only significantly so during transfer testing for the gradual cohort, and retention testing of the sudden cohort.

4.2. Effect of gradual vs. sudden training on practice difficulty

These results corroborate previous findings (Criscimagna-Hemminger et al., 2010; Kagerer et al., 1997; Klassen et al., 2005; Kluzik, Diedrichsen, Shadmehr, & Bastian, 2008; Malfait & Ostry, 2004; Torres-Oviedo & Bastian, 2012) that gradual training is significantly less difficult than sudden training. Thus despite the additional performance requirements associated with a locomotor task (i.e., balance control, whole body support, maintenance of forward progression), gradual training appears equally capable of reducing the difficulty associated with practicing novel reaching or locomotor tasks. Given that a fundamental trait of gradual training is its ability to reduce movement errors and task difficulty during practice; this is an important step when considering whether gradual training may apply to locomotor rehabilitation.

To date, the only other study that has examined the influence of gradual versus sudden training on practice difficulty of a novel locomotor task focused on measures of locomotor symmetry (Torres-Oviedo & Bastian, 2012). While yielding valuable insight, the assessment of symmetry, where values for each leg are combined, may overlook important functional differences between each leg. Specifically, the present study found that regardless of whether gradual or sudden training was used, the difficulty of the novel locomotor task during training was significantly greater for the slow than the fast leg (Table 2). These findings may be particularly relevant to locomotor rehabilitation as the changes experienced by the fast and slow legs during split-belt treadmill walking may model those of unilateral locomotor impairments such as lower limb loss or stroke. For example, the fast leg on the treadmill during 2:1 walking and the paretic or amputated leg undergo changes to their state or condition (i.e., increased belt velocity; limb loss or paresis) as well as changes in performance requirements. Conversely, the slow leg during 2:1 walking and the unimpaired contralateral leg of an individual who has suffered a lower limb loss or stroke only undergoes a change in performance requirements, not state or condition (i.e., belt velocity does not change and the leg has no level of impairment). Based on this analogy and our results, it can be inferred that during locomotor rehabilitation, individuals with unilateral locomotor impairments may experience significant difficulty not only with re-learning the dynamics of the impaired leg, but perhaps more so with the contralateral unimpaired leg. While this hypothesis may have clinical relevance for the staging and focus of locomotor rehabilitation of common unilateral locomotor impairments such as lower limb loss or stroke, it may be better tested by decreasing rather than increasing the speed of one leg while the other remains at a more traditional self-selected or controlled walking speed.

4.3. Effect of gradual vs. sudden training on delayed retention and transfer performance

To date, the influence of gradual versus sudden training on delayed retention and transfer performance has been limited to the assessment of novel upper extremity reaching tasks (Klassen et al., 2005). Klassen et al. (2005) examined the influence of gradual versus sudden training on the retention of two novel reaching tasks. In both, participants were asked to make a reaching movement from a constant starting position to targets located 15 cm radially from the start position in the horizontal plane. In one task, participants had to adapt their reaching behavior to a visuomotor rotation of their hand position, while in a second, participants had to adapt their reaching behavior to a perturbing force that was directed perpendicular to the direction of the hand velocity vector during each reaching trial. Upon re-testing participants a day later, they found that for the visuomotor reaching task, gradual and sudden training resulted in equivalent levels of performance, while for the perturbed reaching task, gradual training resulted in superior performance compared to sudden training (Klassen et al., 2005). From these results the authors concluded that gradual training is capable of producing equivalent or superior retention and thus learning of novel reaching tasks. Our results support those of equivalent retention found by Klassen et al. (2005), but not those of superior retention, suggesting that the ability of gradual training to produce equivalent retention generalizes from upper extremity to locomotor tasks, but not the ability to produce superior retention.

Using a similar force perturbation reaching task, Malfait and Ostry (2004) examined the degree to which a gradual versus sudden introduction of the perturbing force during training influenced how well participants could transfer the acquired reaching pattern across different configurations of the same arm. In the present study we found that gradual and sudden training resulted in equivalent transfer of the novel locomotor pattern, however Malfait and Ostry (2004) reported that transfer of the novel reaching task to a different arm configuration (i.e., a different shoulder position) was greater following gradual than sudden training (Malfait & Ostry, 2004). While this discrepancy could be due to inherent differences between constrained reaching tasks and complex locomotor tasks, it is more likely due to methodological differences. Where we had gradual and sudden cohorts perform an equivalent number of trials (i.e., strides), participants in Malfait and Ostry (2004) who were allocated to the sudden cohort performed 30 reaching trials, while those allocated to the gradual training cohort performed over five times as many, 160 reaching trials. This difference in the volume of training likely favored transfer in the gradual cohort, regardless of any underlying differences between gradual and sudden training. Additionally, the transfer of the novel reaching pattern was only assessed over the first few trials of transfer testing, potentially only capturing the initial response to the perturbing force, and missing the true dynamics of the learned reaching pattern. Given these methodological differences, it would seem likely that the true influence of gradual versus sudden training on the delayed transfer of novel motor skills is one of equivalent transfer performance, rather than superior transfer performance.

While gradual training appears to make locomotor performance during practice less difficult, results from the present study indicate that the ability of gradual training to produce superior delayed retention or transfer does not appear to generalize from upper extremity to locomotor tasks. This may be due to the greater difficulty and degrees of freedom associated with locomotor versus constrained reaching tasks. However, the capacity of gradual training to produce an equivalent degree of motor learning as sudden training, while significantly reducing the difficulty of practice, should be favorably considered when weighing its potential utility to locomotor rehabilitation.

4.4. Potential mechanisms for equivalent durability and flexibility

One possible explanation for how gradual and sudden training result in equivalent motor learning of a novel locomotor task despite such disparate training experiences is that during gradual training, participants may have re-weighted the available feedback used to modify their locomotor pattern during training. For every motor command two forms of consequences are produced, a sensory consequence, and a reward consequence (Izawa & Shadmehr, 2011). The sensory consequence is based upon feedback from our sensory organs regarding the sensory outcome of the movement, and forms the basis of the sensory prediction error, a critical component of motor skill adaptation (Tseng et al., 2007). The reward consequence provides a subjective measure of the utility or usefulness of the motor commands, and forms the basis of the reward prediction error (Izawa & Shadmehr, 2011). Both sensory and reward prediction errors contribute to the acquisition of a motor skill, however, the weight they are assigned can vary. When sensory prediction errors are minimized, a greater reliance may be placed on reward prediction error to drive the modification of the movement pattern during practice (Izawa & Shadmehr, 2011). Given that gradual training reduced practice difficulty in the present study, and has been previously shown to reduce movement errors and thus the size of sensory prediction errors (Criscimagna-Hemminger et al., 2010), the gradual training cohort may have relied more on the reward prediction error, compensating for any discrepancy in the availability of sensory prediction errors (Izawa & Shadmehr, 2011). Such a strategy would allow the gradual cohort to maintain a level of motor learning equivalent to the sudden cohort despite the absence of any appreciable sensory prediction error.

Alternatively, the gradual and sudden training cohorts may have acquired the novel locomotor task using different mechanisms, implicit and explicit learning respectively. While we did not set out to test whether gradual or sudden training promoted motor learning through implicit or explicit processes, anecdotal reports from the participants suggested that gradual training did support motor learning through implicit processes. Specifically, the majority of the participants receiving gradual training were unable to accurately describe the number of velocity changes that occurred in the fast belt, and frequently mischaracterized the increase in the dominant leg belt velocity as "the non-dominant leg slowing down", or "the treadmill inclining". This demonstrates an inability to accumulate explicit rules regarding task performance despite acquisition of the motor skill, a characteristic of implicit learning (Masters, 1992). This was in direct opposition to the sudden training cohort who accurately described the locomotor task, "dominant leg faster than the non-dominant leg". Additionally, another motor learning strategy, 'errorless learning' (Maxwell, Masters, Kerr, & Weedon, 2001), which shares many features with gradual training, has been reported to promote implicit over explicit learning for a variety of motor skills (Masters, MacMahon, & Pall, 2004; Orrell, Eves, & Masters, 2006; Poolton, Masters, & Maxwell, 2005). While implicit and explicit processes may be used in parallel to learn a motor skill (Gentile, 1998), it seems likely that the gradual training cohort relied more on implicit processes.

4.5. Clinical implications

These findings may have implications for future clinical research and treatment strategies. As prosthetic and orthotic technology evolves to include devices which restore physiological levels of joint power (Herr, 2009; Herr & Grabowski, 2012), effective motor learning strategies should be developed in parallel to ensure the safe and efficient application of this technology (Grill, 2007). As a starting point, consideration ought to be given to how powered movements generated by emerging powered prosthetic and exoskeleton technology should be "turned on" or restored during training. Given the ability of gradual training to promote equivalent learning of a locomotor task with much less difficulty than sudden training, a gradual restoration of powered movement may afford patients who would otherwise not be considered candidates for advanced prosthetic and orthotic technology (due to multiple co-morbidities or mobility restrictions) the opportunity to learn to use and benefit from such devices. Additionally, as gradual training avoids major perturbations and thus the need to produce an immediate response, a gradual restoration of powered movement may allow individuals to determine the most efficient way to integrate these external sources of joint power into their neuromuscular pattern, minimizing proximal and contralateral compensations.

4.6. Limitations

While the use of a treadmill was essential to conducting this study, several aspects of its use may have influenced the results. The lack of optic flow associated with walking on a treadmill may have increased variability of the foot trajectories. However, the amount of variability has been reported to be equivalent between treadmill and overground walking (Owings & Grabiner, 2004a), therefore the lack of optic flow may not influence gait variability. While the use of a slower baseline walking speed was justified to prevent 2:1 and 3:1 walking speeds from becoming excessive, the slower walking speed may have increased medial lateral COM motion (Orendurff et al., 2004) during baseline walking. The 15 minute acclimation period was intended to reduce the influence of both of these concerns. We chose to calculate the amount of uncertainty in the sagittal plane movement pattern over 20 stride bins. While some debate exists as to whether this is a sufficient number of strides to capture the amount of uncertainty during locomotion (Owings & Grabiner, 2003), 20 stride bins were used because those were the increments over which the velocity of the fast treadmill belt was increased during gradual training. Extending the length of those bins would have made training longer, possibly inducing fatigue and confounding the results.

While many other variables have been used to assess locomotor performance during split-belt treadmill walking (Dietz et al., 1994; Reisman et al., 2005; Yang, Lamont, & Pang, 2005) data from the present study suggest that the AuR adequately represents the performance of this novel motor task during Training, Retention and Transfer. In quantifying split-belt walking performance with the AuR it can be observed that the time required for performance to plateau, or return to a near Baseline 1:1 Walking level during Training was longer than in other studies that have used different kinematic, temporal-spatial or EMG variables (specifically the fast leg AuR (Fig. 1A). This would suggest that these other variables may underestimate the time required to establish steady-state performance and alter any inference regarding adaptation and motor learning. Therefore, the AuR may provide a more robust assessment of performance and thus motor learning. Additionally, the tendency of the AuR to change in response to task demands and return to Baseline 1:1 Walking levels suggests that the AuR adequately captures changes in locomotor performance.

4.7. Future work

This work examined whether gradual versus sudden training influenced how well a novel locomotor task was learned by assessing one aspect of locomotor behavior, variability of whole-body sagittal plane kinematics. Given the possibility that the same whole-body sagittal plane kinematic movement pattern could be produced through a number of different individual segment angle combinations, additional research is required to examine how the whole-body kinematic pattern was produced. Specifically, future research should examine whether the magnitude or timing of joint or segment angle contributions to whole-body sagittal plane kinematics are affected by training strategy, and whether different kinetic or neuromuscular patterns are used to perform locomotor tasks as a function of training strategy. This may provide insight into whether different motor learning strategies encourage compensation or recovery of motor function. Additionally, the ability of gradual versus sudden training to influence other critical features of successful locomotion such as lateral balance control, cognitive demand and movement efficiency deserve further examination.

4.8. Conclusion

This study found that when assessed by delayed retention and transfer, gradual training resulted in equivalent motor learning of the novel locomotor task as sudden training, despite less difficult and less specific practice on day one, demonstrating that large movement errors may not be necessary for motor learning. In light of these results it would appear that gradual training provides a means to learn locomotor tasks with greater ease than sudden training. This characteristic may directly benefit locomotor rehabilitation, where large movement errors may limit or impair improvements in locomotor performance.

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