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Punishment feedback enhances visually-guided locomotor adaptation

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ABSTRACT

Reward and punishment reinforcement feedback has been shown to influence initial learning and re-learning of upper extremity motor tasks, but the influence on lower extremity motor learning is unknown. The objective of this study was to examine the effects of reinforcement feedback (reward and punishment) on the learning process of asymmetrical gait on a novel 'virtual' split-belt paradigm, that alters visual target speed on one side to induce an asymmetrical gait pattern. Twenty-seven healthy young adults (20.44 ± 2.50 yrs) walked on an instrumented treadmill with real-time visual feedback of the toe position and stepping targets. During adaptation, the visual targets moved slower on one side while the treadmill speed was equal between sides. The control group received no scores, while the reward group received increasing scores and the punishment group received decreasing scores when the toe was within and beyond 4 cm from the center of the target, respectively. Participants came back after 24 ± 2 hours and completed the same paradigm for a re-learning assessment. Participants adapted and demonstrated aftereffects in error symmetry, step length symmetry, and step time symmetry with the 'virtual' split-belt paradigm during both initial- and re-exposure. Reinforcement feedback did not influence initial adaptation or de-adaptation, but punishment group demonstrated faster spatial re-adaptation compared to Reward and Controls. Our results on the differential effect of punishment and reward are consistent with previously reported upper-extremity studies. Together, this study points to a potential novel paradigm that utilizes visual feedback to address gait asymmetry.

NEW & NOTEWORTHY

This is the first study to examine the effect of a ‘virtual’ split-belt paradigm, and to examine the effect of reward and punishment reinforcement feedback on lower extremity locomotor learning task. We have found that healthy young adults are able to adapt both spatial and temporal gait measures with the paradigm, and that punishment reinforcement feedback specifically influences the spatial re-learning on locomotor error-based adaptation task.

KEYWORDS

Locomotion, adaptation, visuomotor, reinforcement feedback

INTRODUCTION

Walking must be constantly monitored and adjusted to the immediate environment by the nervous system to prevent the loss of balance. Although the task of walking on flat surfaces for healthy humans is largely an automatic action that does not require conscious thought to control (Choi et al., 2016; Malone & Bastian, 2010) walking can be voluntarily controlled by changing step length (i.e. foot placement) in response to visual cues perceived in the environment (Maeda et al. 2017). This is especially important when walking across uneven terrains that require careful stepping.

When there are discrepancies between visual feedback and perceived proprioception, this can result in motor adaptation. For example, when real-time visual biofeedback of a specific gait parameter (e.g. knee flexion angle) is altered, this can induce adaptation in the specific gait parameter and show aftereffects (Cherry-Allen et al. 2018; Chunduru et al. 2019; Kim and Krebs 2012; Kim et al. 2015; Statton et al. 2016). With altered visual feedback of step length on one side, previous studies have demonstrated that participants gradually adapt to an asymmetrical step length, and that this asymmetry persists even with the visual feedback removed (Kim and Krebs 2012; Kim et al. 2015). Interestingly, when compared to split-belt treadmill walking adaptation, the aftereffect in step length asymmetry with the visual distortion is longer (Chunduru et al. 2019). This provides opportunities for the development of novel visually-guided interventions that can target specific gait kinematics with prolonging aftereffects tailored towards specific clinical population needs.

When healthy humans learn to adapt to a specific learning pattern, this can be re-learned at a faster rate, even after de-adaptation following the initial adaptation (Huang et al. 2011; Malone et al. 2011). In a visuomotor locomotor task with prism glasses, healthy young participants re-learn walking pattern faster and retain the information for at least one year after the initial training (Maeda et al. 2018). To our knowledge, this has not been investigated with visually-guided locomotor learning that presents real-time feedback of kinematics, such as foot trajectory during walking. Investigating the re-learning of novel interventions is important for future applications in the rehabilitation therapy settings, where interventions are presented a multitude of times.

One way to alter the effectiveness of interventions that involve visual feedback is by the introduction of operant conditioning. Human behavior has been known to respond to positive (additive) reinforcement stimuli (i.e. reward) to increase a certain behavior and to positive punishment stimuli to decrease a certain behavior (Daw et al. 2002). Previously, it was speculated that motor adaptation is an implicit process which is insensitive to the effects of reward and punishment feedback (Mazzoni and Krakauer 2006; Shadmehr and Krakauer 2008). However, recent studies have shown that motor adaptation requires descending control from the cortex (Barthelemy et al. 2011; Sato and Choi 2019) and responds to reward and punishment feedback, but the effects are task specific (Abe et al. 2011; Galea et al. 2015; Song et al. 2020; Wachter et al. 2009). In an upper extremity sequence learning task, punishment feedback led to better performance while reward feedback led to greater learning (Wachter et al. 2009), whereas in a motor skill learning task, there were no immediate differences in learning with the punishment or reward feedback (Abe et al. 2011). In error-based visuomotor upper extremity tasks, punishment feedback has shown to accelerate learning during initial adaptation (Galea et al. 2015; Song et al. 2020). This suggests that punishment may be useful to enhance initial acquisition in motor tasks, however, the effect seems to be specific to error-based learning.

Reward and punishment feedback have also been demonstrated to play a role in re-learning. With an upper extremity error-based motor task, punishment accelerated re-learning rates, while reward feedback increased retention of the learned motor task (Galea et al. 2015; Quattrocchi et al. 2017; Quattrocchi et al. 2018). The increase in retention with rewarded feedback was also observed in an study that used sequence learning (Abe et al. 2011). This suggests that reward feedback enhances retention irregardless of the type of motor task, unlike the initial learning acquisition phase. Therefore, reward and punishment feedback may be useful to implement in visually-guided therapeutic interventions for efficient motor recovery. However, the effects of reward and punishment on lower extremity locomotor adaptation with visual distortion is not known.

The objective of this study is to examine the effects of reinforcement feedback (reward and punishment) on the learning process of asymmetrical gait on a novel ‘virtual’ split-belt paradigm, which alters visual target speed on one side to induce an asymmetrical gait pattern. We explored our objective with three participant groups: (1) control group who received no reinforcement feedback, (2) reward group who received increasing scores for an accurate step, and (3) punishment group who received decreasing scores for inaccurate steps. The specific aims were: (1) To examine whether spatial and temporal gait asymmetry can be adapted and stored through a 'virtual' split-belt paradigm, (2) to examine the effects of reinforcement feedback on the acquisition of asymmetrical gait pattern, and (3) to examine the effects of reinforcement feedback (on the re-learning of asymmetrical gait pattern. We hypothesized that (1) all groups will adapt and de-adapt to asymmetrical step lengths and step times with the 'virtual' split-belt paradigm, and based on upper extremity visually-guided motor learning studies that (2) punishment group will demonstrate faster learning in the asymmetrical gait pattern compared to the reward group during initial learning (Galea et al. 2015; Song and Smiley-Oyen 2017), and that (3) the punishment group will demonstrate faster re-learning compared to the reward group (Galea et al. 2015).

METHODS

Participants

Twenty-seven healthy young adults (13 male, 14 females) ages 18 to 30 years old (20.44 ± 2.50 yrs) participated in this study. We excluded participants with any history of neurological or orthopedic impairments, with less than 20/30 vision, with any color blindness, and with a leg length difference greater than 2 centimeters. All participants gave informed written consent before the study in accordance with the protocol approved by the Institutional Review Board of the University of Massachusetts Amherst. None of the participants had prior experience walking on a split-belt treadmill.

Experimental Paradigm

Participants walked on a split-belt treadmill (Bertec, Columbus, Ohio, USA) that has two separate belts for each leg with a screen placed in front of the treadmill. Throughout the experiment, participants walked with the two treadmill belts at the same speed (i.e. tied-belt condition). The speed of the treadmill was based on each participants' leg length (m), from the greater trochanter to the lateral malleolus for each leg and averaged between limbs. Step length (m) for the visuomotor task was determined as two-thirds of the leg length, and the speed of the treadmill and visuomotor task was determined as 1.33 x step length (speed (m/s) = step length (m) x cadence (constant variable: 1.33 = 90 steps/60 seconds)). A cadence of 90 steps/minute has been determined as a comfortable cadence for participants performing a similar visuomotor task in a different study (Choi et al. 2016).

A screen in front of the treadmill was used to project the visuomotor task. Real-time position of the toe was projected on the screen as a blue dot (Figure 1A). Based on the calculated step lengths and speed of the treadmill, red square targets were projected on the screen when the leg is in swing phase (Figure 1B). For the visuomotor locomotor task, visuomotor gain (i.e. the ratio of the relationship between the screen and treadmill space) was altered. When the visuomotor gain was set as 1.0, the ratio between the treadmill and screen space was equal so that the speed at which the targets move down was the same as the treadmill speed. When the visuomotor gain was set to 0.9, the relationship between the screen and treadmill space was decreased, and as a result, the target speed on the screen was decreased compared to the treadmill speed. In the lower gain condition, the participants had to step with greater step lengths to hit the target.

The study consisted of two sessions, 24 ± 2 hrs apart. Each session consisted of 5 conditions, all at the participant-specific set treadmill speed with tied-belt treadmill (Figure 1C): (1) Familiarization, where participants first walked on the treadmill with no visuomotor task for 5 minutes, (2) Pre-slow condition, where participants walked with the visuomotor task with symmetrical low visuomotor gain (0.9:0.9) for 300 steps, (3) Pre-fast condition, where participants walked with the visuomotor task with symmetrical 1.0:1.0 visuomotor gain, (4) Split-visuomotor adaptation, where participants walked with the visuomotor task with 1.0 visuomotor gain on one side and 0.9 visuomotor gain on the other for 450 steps, and (5) Split-visuomotor de-adaptation, where participants walked with symmetrical 1.0:1.0 visuomotor gain for 450 steps. From here on forward the leg on the 1.0 visuomotor gain during adaptation is referred to the ‘fast’ leg and the leg on the 0.9 visuomotor gain during adaptation is referred to the ‘slow’ leg. The fast and slow leg side was randomized between participants.

Participants were randomly placed into one out of three groups for the visuomotor task: (1) Control, (2) Reward, or (3) Punishment. In the control group (n = 9, Age: 21.4 ± 3.5 years; Table 1) participants did not receive any external feedback on the knowledge of results during all of the conditions with the visuomotor task. In the reward group (n = 9, Age: 20.4 ± 1.9 years) participants received positive external feedback on the knowledge of results during the adaptation condition on both day 1 and day 2. In the punishment group (n = 9, Age: 19.4 ± 1.4 years) participants received negative external feedback on the knowledge of results during the adaptation condition on both day 1 and day 2. For the reward group, the score on the top-right corner of the screen counted up by one from zero and the dot representing the toe position turned green for each successful step (less than 4 cm of the center of the target). For the punishment group, the score on the top-right corner of the screen counted down by one from 2000, and the dot representing the toe position turned red for each unsuccessful step (greater than 4cm from the center of the target).

Data collection

Lower limb kinematics were recorded at 100 Hz using a 4-camera Oqus system (Qualysis, Gothenburg, Sweden). Reflective markers were placed on the 5th metatarsal (big toe) of each foot. Ground reaction force data was collected from the force plate under each treadmill belt. Force data was sampled at 1000 Hz and synchronized with kinematics data using Qualisys Track Manager (Qualisys, Goöteborg, Sweden).

Data pre-processing

Data processing and analysis was performed using custom software written in MATLAB (Mathworks, Natick, MA). Ground reaction force data was low-pass filtered (3rd order Butterworth) with a 15 Hz cut-off frequency. Heel-strike and toe-off times on each leg were identified when the vertical ground reaction force crossed a threshold of 10 N. Time of heel-strike and toe-off was visually inspected, and manually corrected if necessary, by marking them on kinematic trajectories.

Gait adaptation measures

Kinematic measures quantified for each condition include step length, step time, and double support time. Step length was calculated as the anterior-posterior distance between the toe markers at time of heel strike. Step time was calculated as the time between consecutive heel strike. For the conditions that included the visuomotor task, error (not absolute) was also quantified as the distance between the target to the marker; a negative error would indicate undershooting and a positive error would indicate overshooting of limb trajectory in relation to the target.

Locomotor adaptation was determined by calculating stride-by-stride changes in error, step length, and step time (Choi et al. 2009; Reisman et al. 2005). Fast and slow step length corresponds to when the leading leg is on the 1.0 or 0.9 visuomotor gain side, respectively, at heel strike. Similarly, fast and slow step time corresponds to when the leading leg is on the 1.0 or 0.9 visuomotor gain side, respectively, at heel strike. Error symmetry was defined as the difference between limbs (fast leg – slow leg). Step length, and step were defined as the normalized difference between legs:

$$Asymmetry = \frac{Fast\ leg - Slow\ leg}{Fast\ leg + Slow\ leg}$$

Changes in locomotor symmetry during the visuomotor task were assessed based on averaged values over the first 30 strides of each baseline conditions (pre-slow, pre-fast), and four time periods during adaptation and de-adaptation: (1) initial (first 5 strides), (2) early change (Stride number 6-30), (3) late change (Stride number 31-100) and (4) plateau phase (last 30 strides). The difference between exposure was assessed as the first exposure on the first day – the second exposure on the second day.

Statistical analysis

For baseline conditions, group differences were examined with one-way ANOVAs for pre-slow and pre-fast. In addition, one-sample t-tests were used to examine if there was significant asymmetry (perfect symmetry = 0 in all symmetry variables) during the baseline conditions.

For initial adaptation and de-adaptation, changes in spatiotemporal gait symmetry were compared using sphericity-assumed two-way mixed measures ANOVAs to determine the main effects of time (Initial, early change, late change, and plateau phase) and group (Controls, Reward, and Punishment), and their interaction for each symmetry variable.

To examine exposure difference for adaptation and de-adaptation, a sphericity-assumed two-way repeated measures ANOVA was used to determine main effect of exposure, main effect of time (Initial, early change, late change, and plateau phase), and exposure x time interaction effect for each group. To examine between group differences in exposure differences, exposure difference (first – second exposure) were compared with a sphericity-assumed two-way mixed measures ANOVAs to determine the main effects of time (Initial, early change, late change, and plateau phase) and group (Controls, Reward, and Punishment), and their interaction for each symmetry variable.

For all repeated and mixed-measured ANOVAs, separate ANOVAs were performed for adaptation and de-adaptation walking conditions. If the assumption of sphericity was violated and Greenhouse-Geisser epsilon was less than 0.75, the Greenhouse-Geisser correction was used to report the ANOVA results. All statistical analyses were performed on SPSS 23.0 (IBM, Armonk, NY), and all significant differences were established at $p < 0.05$.

RESULTS

Kinematic adaptation with the visuomotor task

Participants adapted error symmetry (Table 2; Figure 2A-B; $F(1.48, 35.47) = 44.48$, $p < 0.001$), step length symmetry (Figure 2C-D; $F(1.68, 40.34) = 73.75$, $p < 0.001$), and step time symmetry (Figure 2E-F; $F(3, 72) = 14.98$, $p < 0.001$), but there was no group differences (Error symmetry: $F(2, 24) = 1.62$, $p = 0.219$; SL symmetry: $F(2, 24) = 0.27$, $p = 0.768$; ST symmetry: $F(2, 24) = 0.37$, $p = 0.696$) nor an time x group interaction effect (Error symmetry: $F(2.96, 35.47) = 0.74$, $p = 0.535$; SL symmetry: $F(3.36, 40.34) = 0.53$, $p = 0.687$; ST symmetry: $F(6, 72) = 0.54$, $p = 0.779$).

Error symmetry at initial phase during adaptation was more positively asymmetrical (in which the fast leg overshot the target more than the slow leg) compared to early ($p < 0.001$, 95% confidence interval for difference (CI) = [19.16, 51.28]), late ($p < 0.001$, 95% CI = [29.48, 61.17]) and plateau phase ($p < 0.001$, 95% CI = [28.07, 67.53]). Error symmetry during early phase was significantly more positively asymmetrical compared to late ($p = 0.002$, 95% CI = [3.11, 17.10]) and plateau phase ($p = 0.003$, 95% CI = [3.47, 21.69]). Error symmetry between late and plateau phase was not significantly different ($p = 1.00$, 95% CI = [-5.01, 9.97]).

During adaptation, participants gradually stepped with larger step lengths on the slow side compared to the fast side (negative asymmetry). Step length symmetry at initial phase during adaptation was more symmetrical compared to early ($p < 0.001$, 95% CI = [0.05, 0.11]), late ($p < 0.001$, 95% CI = [0.07, 0.12]) and plateau phase ($p < 0.001$, 95% CI = [0.07, 0.13]), and step length symmetry at early phase was significantly more symmetrical compared to late ($p = 0.004$, 95% CI = [0.01, 0.03]) and plateau phase ($p = 0.012$, 95% CI = [0.004, 0.04]). Step length symmetry between late and plateau phase was not significantly different ($p = 1.00$, 95% CI = [-0.01, 0.02]).

Participants gradually stepped with longer step times on the fast leg compared to the slow leg (positive asymmetry). Step time symmetry at initial phase during adaptation was more symmetrical compared to early ($p = 0.010$, 95% CI = [-0.04, -0.01]), late ($p < 0.001$, 95% CI = [-0.05, -0.02]) and plateau phase ($p < 0.001$, 95% CI = [-0.07, -0.02]). There was no evidence of difference between early and late ($p = 0.438$, 95% CI = [-0.03, 0.01]), early and plateau ($p = 0.07$, 95% CI = [-0.04, 0.001]), and late and plateau phase ($p = 1.00$, 95% CI = [-0.03, 0.01]).

Kinematic de-adaptation with the visuomotor task

During de-adaptation, participants altered error symmetry. Participants initially overshot with the slow limb (Table 3; Figure 3A-B; $F(1.85, 44.29) = 42.31$, $p < 0.001$). In addition participants altered step length symmetry (Figure 3C-D; $F(1.96, 47.14) = 72.67$, $p < 0.001$), and step time symmetry during de-adaptation (Figure 3E-F; $F(1.95, 46.72) = 27.40$, $p < 0.001$), but there was no group differences (Error symmetry: $F(2, 24) = 0.26$, $p = 0.776$; SL symmetry: $F(2, 24) = 0.02$, $p = 0.980$; ST symmetry: $F(2, 24) = 1.21$, $p = 0.317$) nor a time x group interaction effect (Error symmetry: $F(3.69, 44.29) = 2.02$, $p =$

0.112; SL symmetry: $F(3.93, 47.14) = 2.34$, $p = 0.080$; ST symmetry: $F(3.89, 46.72) = 0.69$, $p = 0.602$).

Post-hoc comparisons showed that error symmetry, step length symmetry, and step time symmetry at initial phase was significantly different compared to early, late and plateau phase, and early phase was significantly different compared to late and plateau phase, but late and plateau phases were not different from each other (p-values and confidence intervals are provided in Table 4).

Re-adaptation with the visuomotor task

For adaptation in Controls, there was a main effect of exposure in error symmetry and step length symmetry, but not for step time symmetry (Table 5; Figure 4A,D,G; Error symmetry: $F(1,8) = 6.62$, $p = 0.033$; SL symmetry: $F(1,8) = 6.62$, $p = 0.033$; ST symmetry: $F(1,8) = 0.53$, $p = 0.488$). Error symmetry in Controls during adaptation in first exposure was more asymmetrical compared to the second exposure ($p = 0.033$; 95% CI = [0.46, 8.39]), and step length symmetry was less asymmetrical in first exposure compared to second exposure ($p = 0.033$; 95% CI = [0.001, 0.020]), indicating faster learning in the spatial measures in Controls. Similarly, in Punishment there was a significant main effect of exposure in error symmetry and step length symmetry, but not for step time symmetry (Figure 4C,F,I; Error symmetry: $F(1,8) = 16.37$, $p = 0.004$; SL symmetry: $F(1,8) = 12.92$, $p = 0.007$; ST symmetry: $F(1,8) = 0.20$, $p = 0.664$). in contrast, there was no evidence of a main effect of exposure for adaptation in Reward (Figure 4B,E,H; all p's > 0.750), and there was no evidence of a exposure x time interaction effect for any of the groups for all symmetry measures (all p's > 0.150).

Similar to adaptation during initial exposure, there was a main effect of time during adaptation for all groups for all conditions (p-values and confidence intervals are provided in Table 6).

For adaptation, there was a group effect in exposure difference in error symmetry and step length symmetry, but not for exposure difference in step time symmetry (Figure 5A,C,E; Error symmetry: $F(2, 24) = 4.42$, $p = 0.023$; SL symmetry: $F(2, 24) = 3.93$, $p = 0.033$; ST symmetry = $F(2, 24) = 0.06$, $p = 0.945$). The exposure difference was consistent across adaptation phases in all three symmetry measures (Error symmetry: $F(1.74, 41.78) = 0.481$, $p = 0.481$; SL symmetry: $F(1.94, 46.62) = 0.48$, $p = 0.616$; ST symmetry: $F(3, 72) = 0.02$, $p = 0.995$). There was no evidence of an interaction effect for any symmetry measures (Error symmetry: $F(3.48, 41.78) = 0.82$, $p = 0.508$; SL symmetry: $F(3.89, 46.62) = 0.31$, $p = 0.864$; ST symmetry: $F(6, 72) = 0.55$, $p = 0.768$).

Post-hoc comparisons revealed that the punishment group presented with less error asymmetry and more step length asymmetry during day 2 compared to day 1 (positive exposure difference in both error and step length symmetry). Exposure difference during adaptation in error symmetry and step length symmetry was larger in punishment compared to reward (Error symmetry: $p = 0.022$, 95% CI = [1.81, 27.79]; SL symmetry: $p = 0.029$, 95% CI = [0.002, 0.05]). Spatial exposure difference during adaptation in Controls was not significantly different compared to Reward (Error symmetry: $p = 0.924$, 95% CI = [-7.73, 18.24]; SL symmetry: $p = 0.546$, 95% CI = [-0.01, 0.04]) and Punishment (Error symmetry: $p = 0.212$, 95% CI = [-22.53, 3.45]; SL symmetry: $p = 0.497$, 95% CI = [-0.04, 0.01]).

In contrast to adaptation, in de-adaptation there was no evidence of a main effect of exposure in all groups for all symmetry measures (Table 7; Figure 6; all p's > 0.100). In Controls there was a significant exposure x time interaction effect for error symmetry and step length symmetry, but not step time symmetry (Error symmetry: $F(3,24) = 3.93$, $p = 0.021$; SL symmetry: $F(3,24) = 5.24$, $p = 0.006$; ST symmetry: $F(3,24) = 0.93$, $p = 0.444$). Reward and Punishment did not show a significant day x time interaction effect during de-adaptation (all p's > 0.400). There was a main effect of time during de-adaptation for all groups for all conditions (p-values and confidence intervals are provided in Table 8).

For exposure difference in de-adaptation, there was no evidence of an effect of time (Figure 5B,D,F; Error symmetry: $F(2.05, 49.11) = 2.56$, $p = 0.086$; SL symmetry: $F(1.96, 46.93) = 3.42$, $p = 0.042$, but post-hoc comparisons all $p > 0.05$ with Bonferroni corrections; ST symmetry: $F(1.96, 46.99) = 0.10$, $p = 0.898$), nor an effect of group (Error symmetry: $F(2, 24) = 0.81$, $p = 0.456$; SL symmetry: $F(2, 24) = 0.82$, $p = 0.452$; ST symmetry: $F(2, 24) = 2.13$, $p = 0.141$), nor an interaction effect in all three symmetry measures (Error symmetry: $F(4.09, 49.11) = 1.28$, $p = 0.291$; SL symmetry: $F(3.91, 46.93) = 1.84$, $p = 0.138$; ST symmetry: $F(3.92, 46.99) = 0.94$, $p = 0.450$).

Discussion

Healthy young adults adapted and demonstrated aftereffects in error symmetry, step length symmetry, and step time symmetry with a 'virtual' split-belt paradigm with unequal stepping target visuomotor gains. Reinforcement feedback did not influence initial adaptation or de-adaptation with the paradigm, but punishment group demonstrated faster spatial re-adaptation compared to reward and control groups.

'Virtual' split-belt can induce changes in kinematic symmetry with robust aftereffects

Our results demonstrated that healthy young adults adapted both step lengths and step time symmetry with robust aftereffects even after the visual targets were brought back to the symmetrical visuomotor gain. This is in line with previous studies that have demonstrated that when visual feedback of target step length is altered on one side, healthy young adults gradually adapt to an asymmetrical step length (Kim and Krebs 2012; Kim et al. 2015) and with studies that observed altered gait pattern in virtual environments (Lamontagne et al. 2007; Prokop et al. 1997). With our visual feedback, we aimed to recreate a virtual treadmill environment instead of the previously used bars to indicate step lengths (Kim and Krebs 2012; Kim et al. 2015) or specific joint kinematics (Cherry-Allen et al. 2018; Statton et al. 2016), to examine if healthy young adults adapt spatial and/or temporal gait measures to visual targets at uneven speeds between sides. This way, the visual paradigm more closely resembles the split-belt adaptation treadmill where participants are not restricted to one gait parameter to learn an asymmetrical pattern.

The robust aftereffect that we observed in our participants suggests that the new gait pattern attained during adaptation using sensory information is stored in the nervous system. The neural control of locomotion that integrates visual, proprioceptive and vestibular feedback is complex and requires both spinal and supraspinal input (Hinton et al. 2020; Takakusaki 2017), which makes pinpointing the location of the stored information difficult. However, in cats, it has been shown that cortical control, especially the posterior parietal cortex for planning of limb trajectory and motor cortex for execution of motor commands are important for visually guided gait (Drew and Marigold 2015). Although we can expect that quadrupedal and bipedal locomotion require different neural mechanisms, cortical control is likely to play important role in visuomotor locomotor adaptation, unlike split-belt proprioception-driven locomotor adaptation that is does not critically dependent on cortical control (Reisman et al. 2007).

Reward and punishment reinforcement feedback does not influence initial locomotor visuomotor learning

In our study, control participants who received no score on their stepping (i.e. implicit learning condition) was able to adapt their gait to achieve the asymmetrical gait pattern. This is in line with other paradigms such as the split-belt locomotor adaptation (Reisman et al. 2005; Sato and Choi 2019) and implicit visuomotor paradigms (French et al. 2018; Kim and Krebs 2012) that people are able to adapt their gait even without instructions on how to do so.

We demonstrated that reward and punishment reinforcement feedback does not influence initial locomotor adaptation with the visuomotor paradigm. This finding is in contrast to upper extremity studies that demonstrated punishment feedback to accelerate initial learning in error-based tasks (Galea et al. 2015; Song et al. 2020), which may suggest that although visuomotor locomotor adaptation likely requires more cortical control compared to split-belt adaptation, the visuomotor locomotor adaptation is more implicit compared to upper-extremity tasks. Is it important to note though, French and colleagues (2018) have seen success in accelerating visually-guided locomotor adaptation with instructional external feedback. There are other studies that have supported the use of individualized feedback to enhance initial locomotor learning (Hussain et al. 2013; Rendos et al. 2020; Roemmich et al. 2016), suggesting that merely providing correct/incorrect feedback is not enough, but individualized feedback is needed to enhance initial visuomotor locomotor learning.

Punished reinforcement feedback may influence locomotor visuomotor re-learning

In our study, the reinforcement feedback group with punished feedback demonstrated faster spatial learning on the second day. Specifically, the punishment group learned spatial asymmetry faster compared to the reward group. This is in line with findings of Galea and colleagues (2015), who observed faster re-adaptation in punished feedback groups in an upper-extremity error-based adaptation task. Our findings supplement the reinforcement feedback literature that reward and punishment feedback have differential effects on motor learning (Abe et al. 2011; Galea et al. 2015; Quattrocchi et al. 2018; Song et al. 2020; Wachter et al. 2009).

Punished reinforcement feedback may have only influenced re-learning due to the differential neural processes underlying the initial learning and re-learning process (Galea et al. 2011; Hadipour-Niktarash et al. 2007). Motor cortex activation in humans does not affect adaptation, but improved retention (Galea et al. 2011), suggesting dissociable neural mechanisms underlying initial learning and re-learning. Punishment feedback has been reported to alter activity in the anterior cingulate cortex (Holroyd and Coles 2002) which is functionally connected (Paus 2001; Wang et al. 2001; Williams et al. 2004) and in anatomical proximity to the primary motor cortex. This may suggest that punishment feedback during initial learning may influence cortical plasticity in the motor cortex which is reflected in the faster spatial re-learning.

Limitations

A limitation of our paradigm is that we did not have monetary associations with our reinforcement feedback paradigm. Scores increased or decreased by 1 for the reward and punishment groups, respectively, which may not have been enough motivational incentive for participants. Although more robust effect is expected to be observed with monetary associations (Ohgami et al. 2006), previous studies with increasing and decreasing scores for reward and punishment have successfully seen effects in upper-extremity motor learning (Nikooyan and Ahmed 2015). Furthermore, our future goal is to apply the findings to enhance interventions in rehabilitation, and the monetary reward or punishment would not be feasible in clinic. Therefore, we decided that for the purposes of this study we will examine and report on the effects of rewarded and punished feedback with no monetary associations.

Conclusions

With a ‘virtual’ split-belt paradigm that projected stepping targets with altered visuomotor gain on one side, we demonstrated that healthy young adults are able to adapt and de-adapt both spatial and temporal gait asymmetry. Reward and punishment reinforcement feedback did not influence initial learning with the paradigm, which suggests that correct/incorrect feedback is not enough to improve visuomotor locomotor learning. However, punished reinforcement feedback led to faster spatial re-adaptation compared to reward and control groups. Together, this points towards a possible visually-guided locomotor paradigm to restore gait symmetry.

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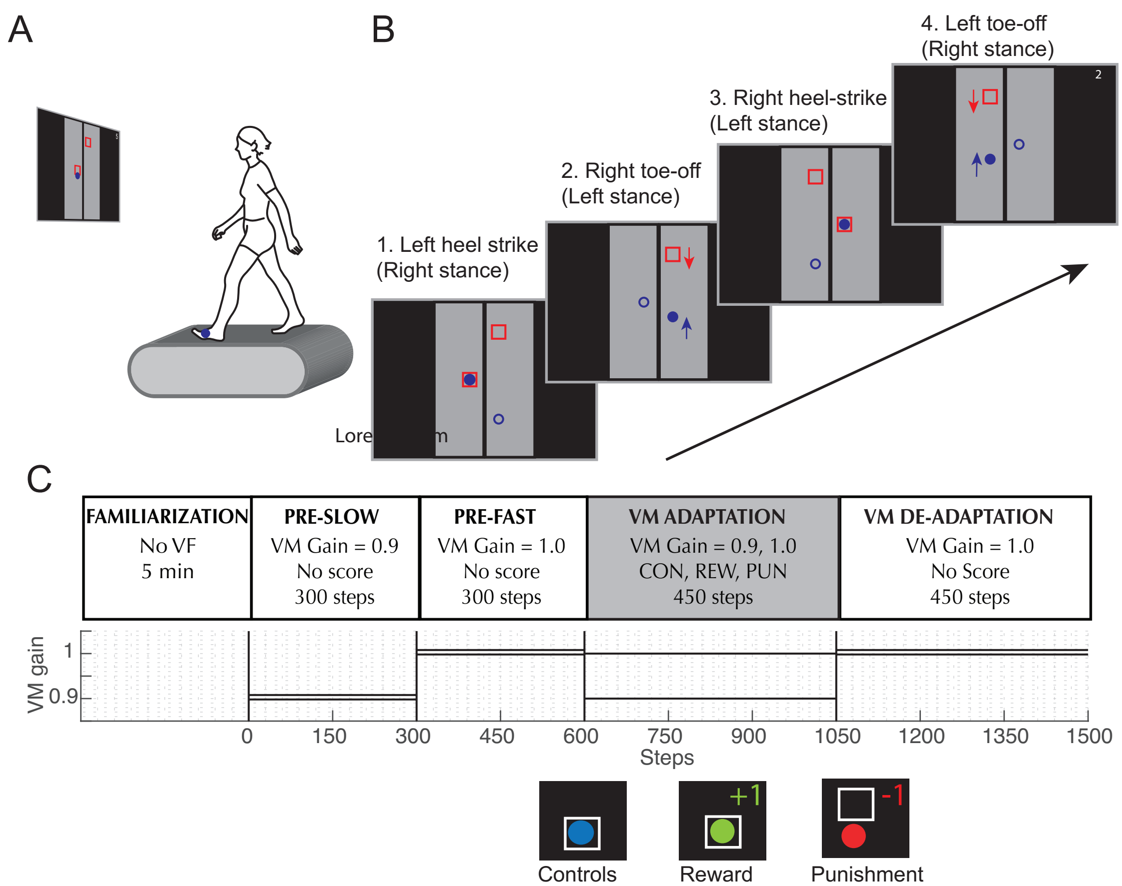

Figure 1. Experimental methods. A. Experimental setup. Participants walked with a screen in front of the treadmill, with a reflective marker on the 5th metatarsal. During the visuomotor walking task, the real-time position of the toe was projected on the screen as a blue dot. B. Progression of visuomotor task. Real-time toe location during the swing phase of gait will be displayed as a solid blue dot on the screen. Red boxes represent the target that will be displayed on the screen. Empty blue circles represent the position of the toe on the opposite (stance) leg (not visible to the participant). Red and blue arrows indicate which direction the target and toe location will move (respectively) and will not be displayed on the screen. C. Experimental paradigm. Double lines indicate when visuomotor gain will be equal for both left and right treadmill belts. Singular lines indicate the visuomotor gain for each right and left side during the visuomotor adaptation condition. During the adaptation period, the feedback that the participants see will be different for the control, reward and punishment groups. Reward and Punishment saw scores go up and down if the toe marker is within and outside of 4 cm from the center of the target, respectively.

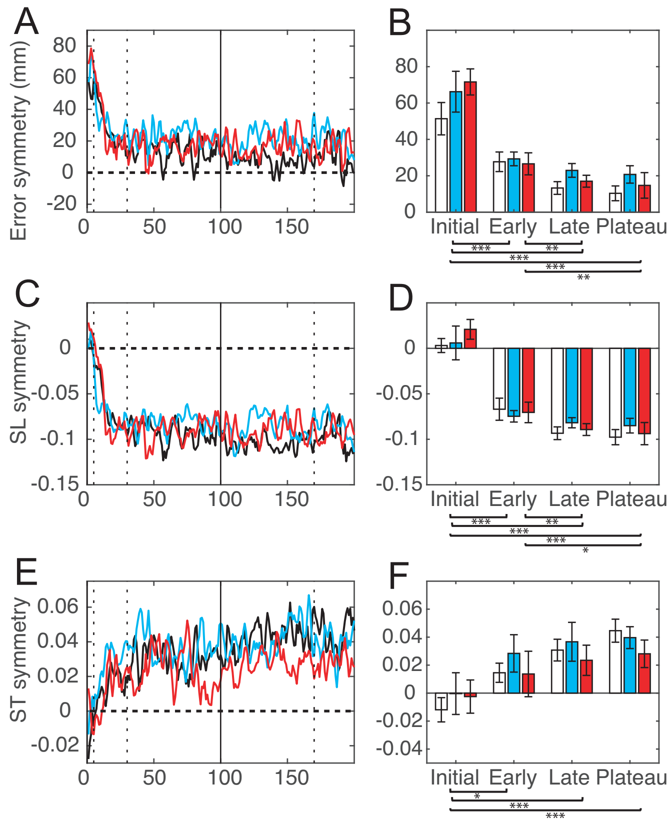

Figure 2. Adaptation with the visuomotor task on the first day in error symmetry (A-B), step length (SL) symmetry (C-D), and step time (ST) symmetry (E-F). A, C, E. Stride-by-stride changes during the first 100 and last 100 strides during adaptation are plotted with moving average of 3 strides. Vertical dotted line are lines at stride 5, 30, and 170, and coincides with the bar graph phases. Horizontal dotted line at 0 indicates perfect symmetry. B, D, F. Kinematic symmetry changes at initial (strides 1-5), early (strides 6-30), late (strides 31-100) and plateau (last 30 strides). Error bars are standard error bars. In black = Controls; In blue = Reward; In red = Punishment; ***: p < 0.001; **: p = 0.001-0.009; *: p = 0.010-0.049.

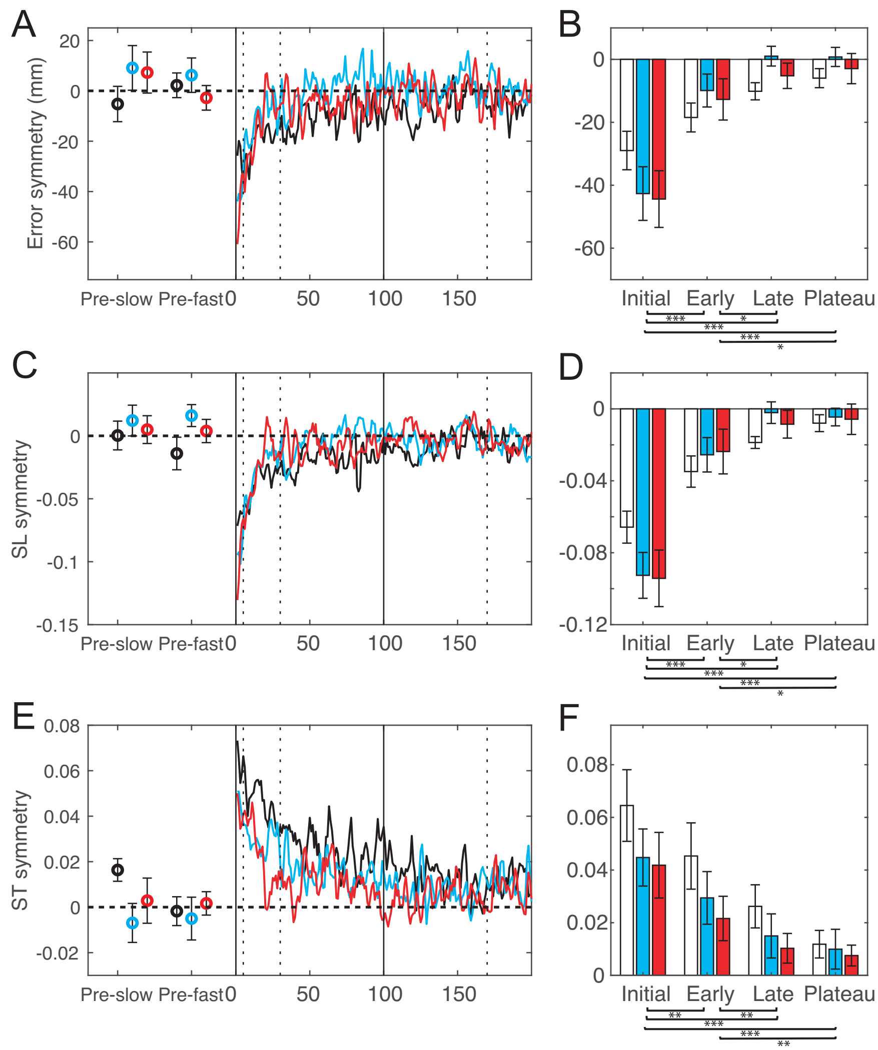

Figure 3. Baseline conditions and de-adaptation with the visuomotor task on the first day in error symmetry (A-B), step length (SL) symmetry (C-D), and step time (ST) symmetry (E-F). A, C, E. Average of first 30 strides of baseline conditions with standard error and stride-by-stride changes during the first 100 and last 100 strides during de-adaptation are plotted with moving average of 3 strides. Vertical dotted line are lines at stride 5, 30, and 170, and coincides with the bar graph phases. Horizontal dotted line at 0 indicates perfect symmetry. B, D, F. Kinematic symmetry changes at initial (strides 1-5), early (strides 6-30), late (strides 31-100) and plateau (last 30 strides). Error bars are standard error bars. In black = Controls; In blue = Reward; In red = Punishment; ***: $p < 0.001$; **: p = 0.001-0.009; *: p = 0.010-0.049.

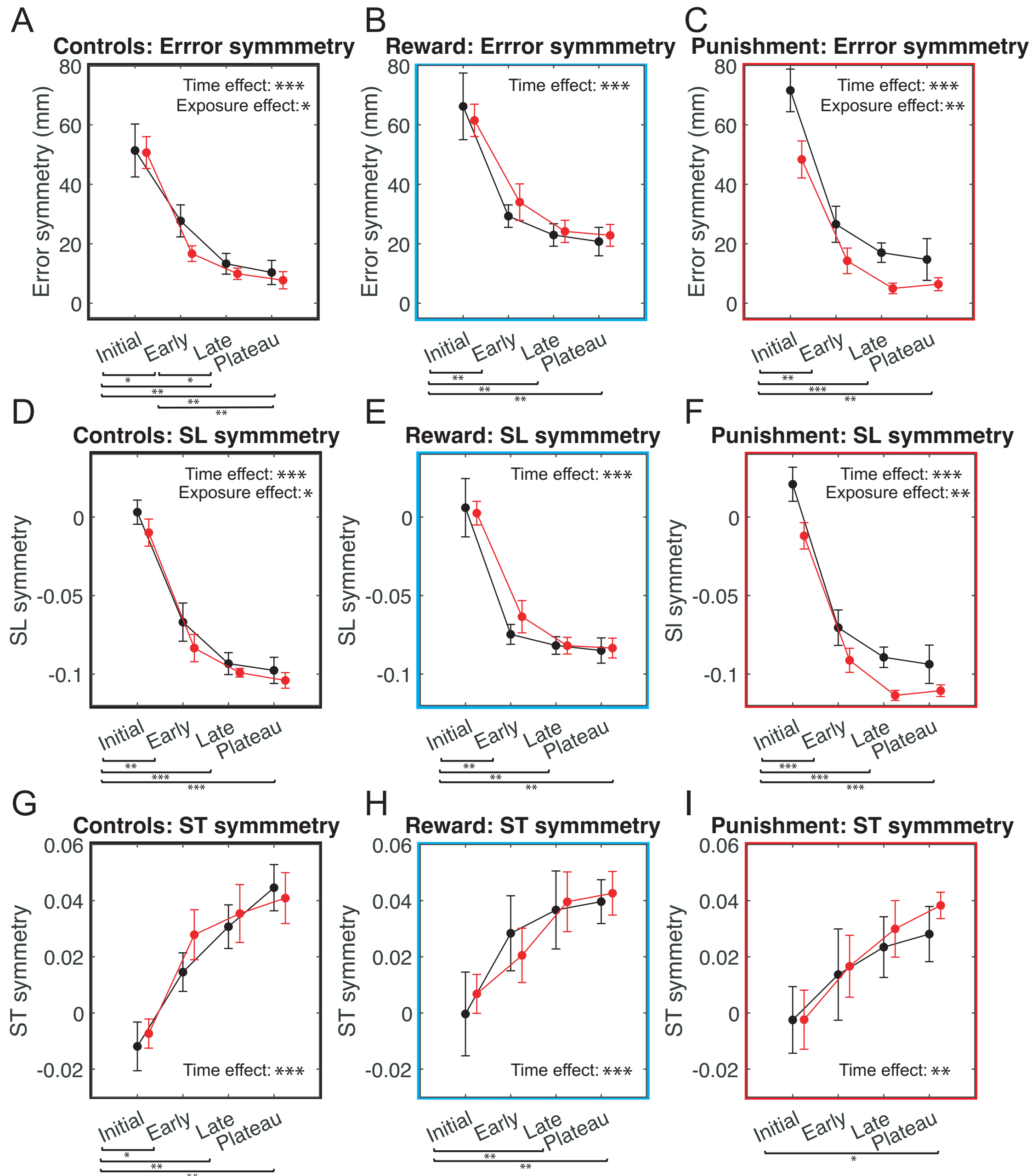

Figure 4. First and second exposure during adaptation in error symmetry (A-C), step length (SL) symmetry (D-F), and step time (ST) symmetry (G-I). Kinematic symmetry changes at initial (strides 1-5), early (strides 6-30), late (strides 31-100) and plateau (last 30 strides). 0 indicates perfect symmetry. In black = first day. In red = second day. Outlined in black = Controls; Outlined in blue = Reward; Outlined in red = Punishment. ***: $p < 0.001$; **: $p = 0.001$-0.009; *: $p = 0.010$-0.049.

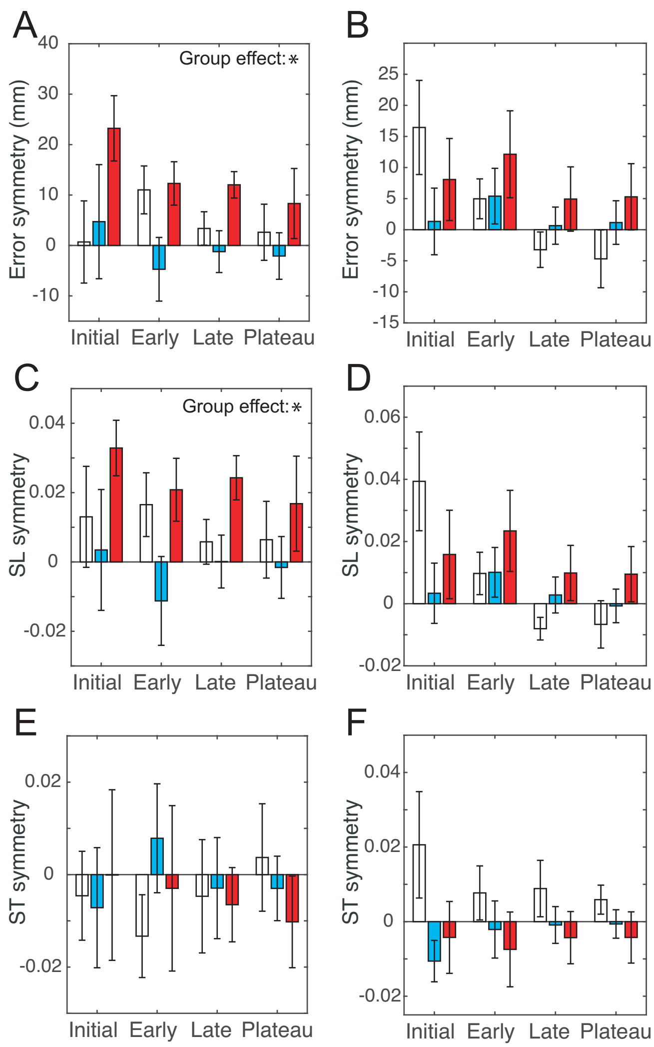

Figure 5. Exposure difference in in error symmetry (A-B), step length (SL) symmetry (C-D), and step time (ST) symmetry (E-F) for adaptation (A, C, E) and de-adaptation (B, D, F). Difference (first – second exposure) at initial (strides 1-5), early (strides 6-30), late (strides 31-100) and plateau (last 30 strides). Error bars are standard error bars. In black = Controls; In blue = Reward; In red = Punishment; *: p = 0.010-0.049.

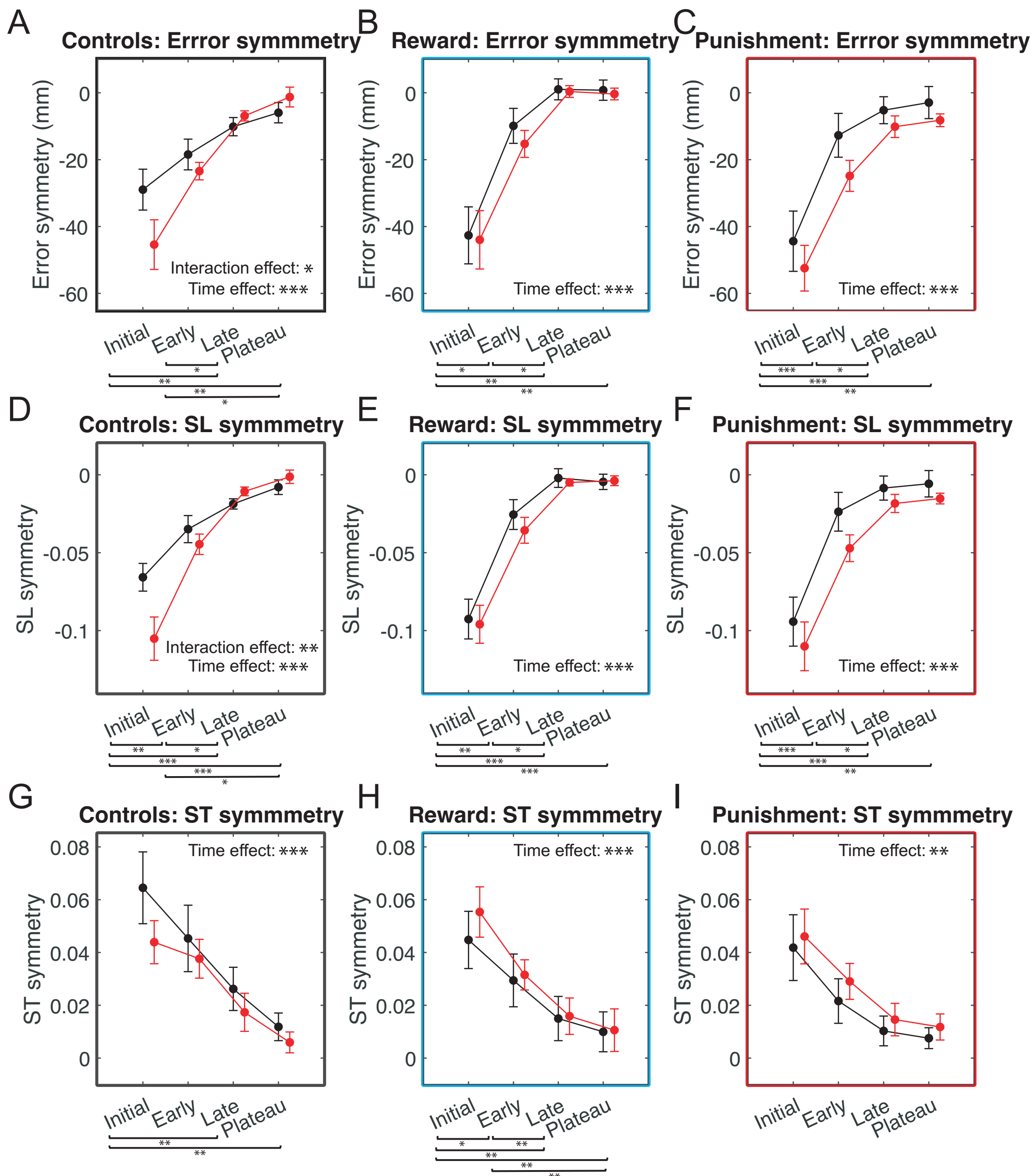

Figure 6. First (in black) and second exposure (in red) during de-adaptation in error symmetry (A-C), step length (SL) symmetry (D-F), and step time (ST) symmetry (G-I). Kinematic symmetry changes at initial (strides 1-5), early (strides 6-30), late (strides 31-100) and plateau (last 30 strides). 0 indicates perfect symmetry. ***: p < 0.001; **: p = 0.001-0.009; *: p = 0.010-0.049.

	Controls (n = 9)	Reward (n = 9)	Punishment (n = 9)
Age (years)	21.4 ± 3.5	20.4 ± 1.9	19.4 ± 1.4
Sex (F:M)	5:4	4:5	5:4
R dominant leg	7	6	9
Leg length (cm)	80.7 ± 6.5	81.2 ± 8.3	83.0 ± 5.8
Step length (cm)	54.1 ± 4.5	54.4 ± 3.8	55.7 ± 3.8
VM task speed (m/s)	0.72 ± 0.06	0.72 ± 0.07	0.74 ± 0.05

Table 1. Participant demographics.

		Controls	**Reward**	**Punishment**
Error symmetry (mm)	Initial	51.38 ± 26.69	66.22 ± 33.64	71.59 ± 21.51
	Early	27.69 ± 16.15	29.29 ± 11.33	26.56 ± 18.18
	Late	13.27 ± 10.5	22.95 ± 11.34	17 ± 9.81
	Plateau	10.34 ± 12.19	20.73 ± 14.35	14.71 ± 21.09
SL Symmetry	Initial	0.003 ± 0.023	0.006 ± 0.056	0.021 ± 0.033
	Early	-0.067 ± 0.036	-0.075 ± 0.019	-0.07 ± 0.034
	Late	-0.093 ± 0.021	-0.082 ± 0.017	-0.089 ± 0.02
	Plateau	-0.098 ± 0.025	-0.085 ± 0.024	-0.094 ± 0.037
ST symmetry	Initial	-0.012 ± 0.026	0 ± 0.045	-0.002 ± 0.036
	Early	0.015 ± 0.021	0.028 ± 0.04	0.014 ± 0.049
	Late	0.031 ± 0.023	0.037 ± 0.042	0.023 ± 0.032
	Plateau	0.045 ± 0.025	0.04 ± 0.023	0.028 ± 0.029

Table 2. Mean and standard deviation for adaptation on the first day.

		Controls	Reward	Punishment
Error symmetry (mm)	Pre-slow	-5.23 ± 21.04	9.12 ± 26.62	7.27 ± 24.46
	Pre-fast	2.22 ± 14.69	6.22 ± 20.51	-2.77 ± 14.66
	Initial	-28.97 ± 18.34	-42.64 ± 25.56	-44.39 ± 27.03
	Early	-18.46 ± 13.78	-9.89 ± 15.7	-12.72 ± 19.66
	Late	-10.14 ± 8.18	1.02 ± 9.41	-5.21 ± 12.09
	Plateau	-5.96 ± 9.09	0.78 ± 9.10	-2.93 ± 14.39
SL Symmetry	Pre-slow	0.0003 ± 0.034	0.012 ± 0.037	0.005 ± 0.033
	Pre-fast	-0.014 ± 0.039	0.016 ± 0.026	0.004 ± 0.028
	Initial	-0.066 ± 0.027	-0.093 ± 0.038	-0.094 ± 0.047
	Early	-0.035 ± 0.026	-0.026 ± 0.029	-0.024 ± 0.037
	Late	-0.019 ± 0.010	-0.002 ± 0.018	-0.009 ± 0.023
	Plateau	-0.008 ± 0.014	-0.005 ± 0.015	-0.006 ± 0.025
ST symmetry	Pre-slow	0.016 ± 0.015	-0.007 ± 0.026	0.003 ± 0.03
	Pre-fast	-0.002 ± 0.019	-0.005 ± 0.028	0.002 ± 0.015
	Initial	0.065 ± 0.041	0.045 ± 0.033	0.042 ± 0.037
	Early	0.045 ± 0.038	0.029 ± 0.030	0.022 ± 0.025
	Late	0.026 ± 0.025	0.015 ± 0.025	0.01 ± 0.017
	Plateau	0.012 ± 0.016	0.01 ± 0.023	0.008 ± 0.012

Table 3. Mean and standard deviation for baseline conditions and de-adaptation on the first day.

	Bout 1	Bout 2	p-value	95% Confidence interval for difference
Error Symmetry	Initial	Early	< 0.001	[-35.21, -14.74]
		Late	< 0.001	[-46.12, -21.66]
		Plateau	< 0.001	[-49.84, -22.09]
	Early	Late	0.024	[-16.97, -0.86]
		Plateau	0.022	[-20.79, -1.19]
	Late	Plateau	1.000	[-7.65, 3.51]
SL symmetry	Initial	Early	< 0.001	[-0.08, -0.04]
		Late	< 0.001	[-0.09, -0.06]
		Plateau	< 0.001	[-0.10, -0.06]
	Early	Late	0.011	[-0.03, -0.003]
		Plateau	0.011	[-0.04, -0.004]
	Late	Plateau	1.00	[-0.01, 0.006]
ST symmetry	Initial	Early	0.005	[0.01, 0.03]
		Late	< 0.001	[0.02, 0.05]
		Plateau	< 0.001	[0.02, 0.06]
	Early	Late	0.002	[0.01, 0.03]
		Plateau	0.002	[0.01, 0.04]
	Late	Plateau	0.159	[-0.002, 0.02]

Table 4. Bonferroni post-hoc tests for main effect of time during de-adaptation on the first day. SL = Step length; ST = Step time.

		Controls	Reward	Punishment
Error symmetry (mm)	Initial	50.69 ± 16.07	61.51 ± 16.33	48.37 ± 18.68
	Early	16.68 ± 7.89	34.01 ± 18.41	14.26 ± 12.89
	Late	9.9 ± 5.71	24.17 ± 11.23	4.98 ± 5.33
	Plateau	7.73 ± 8.69	22.83 ± 11.03	6.39 ± 6.56
SL Symmetry	Initial	-0.01 ± 0.026	0.002 ± 0.023	-0.012 ± 0.025
	Early	-0.083 ± 0.026	-0.063 ± 0.031	-0.091 ± 0.023
	Late	-0.099 ± 0.008	-0.082 ± 0.016	-0.114 ± 0.010
	Plateau	-0.104 ± 0.015	-0.083 ± 0.019	-0.111 ± 0.011
ST symmetry	Initial	-0.007 ± 0.016	0.007 ± 0.021	-0.002 ± 0.032
	Early	0.028 ± 0.027	0.021 ± 0.029	0.017 ± 0.033
	Late	0.035 ± 0.031	0.04 ± 0.032	0.03 ± 0.030
	Plateau	0.041 ± 0.027	0.043 ± 0.023	0.038 ± 0.014

Table 5. Mean and standard deviation for adaptation on the second day.

	Bout 1	Bout 2	Controls		Reward		Punishment	
			p-value	95% Confidence interval for difference	p-value	95% Confidence interval for difference	p-value	95% Confidence interval for difference
Error Symmetry	Initial	Early	0.037	[1.65, 56.05]	0.006	[10.07, 54.36]	0.001	[20.21, 58.94]
		Late	0.001	[17.48, 61.41]	0.003	[15.38, 65.23]	<0.001	[28.96, 69.02]
		Plateau	0.002	[18.11, 65.88]	0.007	[12.33, 71.84]	0.001	[22.25, 76.61]
	Early	Late	0.032	[0.85, 20.35]	0.106	[1.36, 17.54]	0.191	[-3.20, 22.03]
		Plateau	0.008	[3.66, 22.64]	0.181	[-3.18, 22.92]	0.692	[-9.56, 29.27]
	Late	Plateau	0.728	[-2.57, 7.57]	1.000	[-7.46, 11.02]	1.000	[-10.69, 11.58]
SL symmetry	Initial	Early	0.001	[0.04, 0.11]	0.002	[0.03, 0.11]	< 0.001	[0.06, 0.11]
		Late	< 0.001	[0.08, 0.11]	0.001	[0.04, 0.13]	< 0.001	[0.07, 0.14]
		Plateau	< 0.001	[0.08, 0.12]	0.003	[0.04, 0.14]	< 0.001	[0.06, 0.15]
	Early	Late	0.060	[-0.001, 0.04]	0.178	[-0.004, 0.03]	0.114	[-0.004, 0.05]
		Plateau	0.055	[-0.001, 0.05]	0.305	[-0.01, 0.04]	0.494	[-0.02, 0.06]
	Late	Plateau	0.679	[-0.004, 0.01]	1.000	[-0.01, 0.02]	1.000	[-0.02, 0.02]
ST symmetry	Initial	Early	0.032	[-0.06, -0.003]	0.084	[-0.05, 0.002]	0.469	[-0.05, 0.01]
		Late	0.002	[-0.07, -0.02]	0.003	[-0.06, -0.01]	0.109	[-0.06, 0.01]
		Plateau	0.002	[-0.08, -0.02]	0.008	[-0.07, -0.01]	0.018	[-0.07, -0.01]
	Early	Late	1.000	[-0.04, 0.02]	0.095	[-0.03, 0.002]	1.000	[-0.04, 0.02]
		Plateau	0.106	[-0.05, 0.004]	0.172	[-0.04, 0.005]	0.381	[-0.05, 0.01]
	Late	Plateau	0.890	[-0.03, 0.01]	1.000	[-0.03, 0.02]	1.000	[-0.03, 0.02]

Table 6. Bonferroni post-hoc tests for main effect of time during adaptation. SL = Step length; ST = Step time.

		Controls	Reward	Punishment
Error symmetry (mm)	Pre-slow	-9.1 ± 19.46	5.45 ± 12.2	-9.41 ± 13.67
	Pre-fast	1.94 ± 13.94	6.63 ± 15.47	-6.02 ± 8.18
	Initial	-45.41 ± 22.27	-43.97 ± 26.19	-52.46 ± 20.48
	Early	-23.43 ± 7.86	-15.29 ± 12.09	-24.85 ± 13.89
	Late	-6.91 ± 4.54	0.38 ± 5.25	-10.14 ± 9.69
	Plateau	-1.27 ± 8.87	-0.37 ± 5.27	-8.22 ± 5.72
SL Symmetry	Pre-slow	-0.0173 ± 0.019	0.003 ± 0.021	-0.006 ± 0.018
	Pre-fast	0.007 ± 0.014	0.008 ± 0.031	-0.002 ± 0.014
	Initial	-0.105 ± 0.042	-0.096 ± 0.037	-0.11 ± 0.047
	Early	-0.045 ± 0.02	-0.036 ± 0.025	-0.047 ± 0.026
	Late	-0.011 ± 0.008	-0.005 ± 0.007	-0.018 ± 0.017
	Plateau	-0.001 ± 0.013	-0.004 ± 0.009	-0.015 ± 0.01
ST symmetry	Pre-slow	0.014 ± 0.016	0.006 ± 0.033	0.013 ± 0.020
	Pre-fast	0.003 ± 0.020	0.005 ± 0.024	0.003 ± 0.024
	Initial	0.044 ± 0.024	0.055 ± 0.029	0.046 ± 0.031
	Early	0.038 ± 0.022	0.032 ± 0.017	0.029 ± 0.020
	Late	0.017 ± 0.022	0.016 ± 0.021	0.015 ± 0.018
	Plateau	0.006 ± 0.012	0.011 ± 0.024	0.012 ± 0.015

Table 7. Mean and standard deviation for baseline conditions and de-adaptation on the second day.

	Bout 1	Bout 2	Controls		Reward		Punishment	
			p-value	95% Confidence interval for difference	p-value	95% Confidence interval for difference	p-value	95% Confidence interval for difference
Error Symmetry	Initial	Early	0.150	[-36.80, 4.31]	0.020	[-56.63, -4.80]	<0.001	[-40.52, -18.75]
		Late	0.005	[-47.98, -9.35]	0.003	[-71.67, -16.65]	<0.001	[-60.14, -21.35]
		Plateau	0.007	[-57.39, -9.76]	0.002	[-69.41, -17.61]	0.002	[-67.83, -17.88]
	Early	Late	0.027	[-23.51, -1.33]	0.015	[-23.91, -2.67]	0.036	[-21.56, -0.65]
		Plateau	0.012	[-30.74, -3.91]	0.074	[-26.65, 1.06]	0.105	[-28.62, 2.19]
	Late	Plateau	0.099	[-10.56, 0.74]	1.000	[-8.06, 9.05]	1.000	[-9.47, 5.26]
SL symmetry	Initial	Early	0.004	[-0.08, -0.02]	0.002	[-0.10, 0.03]	<0.001	[-0.09, -0.04]
		Late	<0.001	[-0.10, -0.04]	<0.001	[-0.13, -0.05]	<0.001	[-0.13, -0.05]
		Plateau	<0.001	[-0.12, -0.04]	<0.001	[-0.13, -0.06]	0.001	[-0.14, -0.04]
	Early	Late	0.018	[-0.05, -0.004]	0.015	[-0.05, -0.01]	0.041	[-0.04, -0.001]
		Plateau	0.012	[-0.06, -0.01]	0.063	[-0.06, 0.001]	0.089	[-0.053, 0.003]
	Late	Plateau	0.157	[-0.02, 0.003]	1.000	[-0.01, 0.01]	1.000	[-0.02, 0.01]
ST symmetry	Initial	Early	0.981	[-0.02, 0.04]	0.033	[0.001, 0.04]	0.134	[-0.004, 0.04]
		Late	0.005	[0.01, 0.05]	0.002	[0.02, 0.06]	0.057	[-0.001, 0.06]
		Plateau	0.004	[0.02, 0.08]	0.004	[0.02, 0.07]	0.054	[-0.001, 0.07]
	Early	Late	0.097	[-0.003, 0.04]	0.009	[0.004, 0.03]	0.085	[-0.001, 0.03]
		Plateau	0.053	[-0.001, 0.07]	0.006	[0.01, 0.03]	0.082	[-0.002, 0.03]
	Late	Plateau	0.288	[-0.006, 0.03]	0.109	[-0.001, 0.01]	1.000	[-0.01, 0.01]

Table 8. Bonferroni post-hoc tests for main effect of time during de-adaptation. SL = Step length; ST = Step time.