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SHORT COMMUNICATION

Independent voluntary correction and savings in locomotor learning

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ABSTRACT

Humans can acquire new walking patterns in many different ways. For example, we can change our gait voluntarily in response to instruction or adapt by sensing our movement errors. Here, we investigated how acquisition of a new walking pattern through simultaneous voluntary correction and adaptive learning affected the resulting motor memory of the learned pattern. We studied adaptation to split-belt treadmill walking with and without visual feedback of stepping patterns. As expected, visual feedback enabled faster acquisition of the new walking pattern. However, upon later re-exposure to the same split-belt perturbation, participants exhibited similar motor memories whether they had learned with or without visual feedback. Participants who received feedback did not re-engage the mechanism used to accelerate initial acquisition of the new walking pattern to similarly accelerate subsequent relearning. These findings reveal that voluntary correction neither benefits nor interferes with the ability to save a new walking pattern over time.

KEY WORDS: Visual feedback, Adaptation, Motor memory, Locomotion, Split-belt walking

INTRODUCTION

When trying to master a new, unfamiliar movement pattern (e.g. playing the piano, learning to salsa dance), humans use different forms of feedback to learn the desired movement. We may seek out external feedback from an expert or simply use information gathered by our own senses. For example, we can use visual feedback (e.g. using a mirror, watching a video recording) to view our mistakes and then voluntarily modify movements to make corrections. We can also use proprioceptive feedback to sense how we move and then adapt subsequent movements when an error is made.

We recently studied how visual and proprioceptive feedback can be used simultaneously to acquire a new walking pattern (Roemmich et al., 2016). When healthy participants walked on a split-belt treadmill and viewed visual feedback of their gait symmetry, we found that they used the visual feedback to restore symmetry quickly (as has been observed previously; Malone and Bastian, 2010). However, this did not lead to lasting learning; the newly acquired pattern was not retained once the visual feedback was removed. On the contrary, participants learned the new walking pattern by using proprioception to recalibrate their walking patterns to the split-belt environment. This work showed that the nervous system can use visual and proprioceptive feedback in parallel to facilitate quick acquisition and lasting learning of a new walking pattern, respectively.

We do not yet have a good understanding of how visual and proprioceptive feedback influence locomotor learning over longer time scales. In rehabilitation, we are often interested in understanding how to facilitate 'savings' of learning so that a patient can build off of what has been learned from one therapy session to the next. Savings is a commonly studied motor learning phenomenon where a memory of the learned pattern persists over time, facilitating subsequent relearning that occurs faster than initial learning (Shadmehr and Brashers-Krug, 1997; Malone et al., 2011; Krakauer et al., 2005). Here, we aimed to understand how visual and proprioceptive feedback influence savings of a newly learned walking pattern.

Many studies in reaching and walking have proposed several mechanisms to explain savings of newly learned movement patterns (Haith et al., 2015; Herzfeld et al., 2014; Morehead et al., 2015; Malone et al., 2011; Roemmich and Bastian, 2015; Huang et al., 2011). Adaptation during reaching tasks has been dissected into implicit and explicit components. Participants improve performance by adapting to prediction error via implicit mechanisms and making voluntary (explicit) changes to their movements simultaneously (Taylor et al., 2014). One study suggested that savings of an upper extremity motor behavior can be influenced by voluntary changes in movement (Morehead et al., 2015). Yet, savings also occurs in adaptation paradigms less likely to be influenced by explicit cognitive control [e.g. eye blink conditioning (Medina et al., 2001), saccades (Kojima et al., 2004)]. It is as yet unclear how voluntary correction influences savings during a continuous, relatively automatic movement such as walking.

We studied whether voluntary changes in walking patterns driven by visual feedback influenced savings of a new walking pattern learned through proprioception-driven adaptive learning. We used behavioral data from split-belt treadmill walking to show that voluntary correction and savings occur independently in human locomotor learning. Participants used the visual feedback to acquire the new walking pattern faster; however, savings was similar whether participants adapted with or without visual feedback. This finding was consistent whether the participants adapted over a shorter (1 min) or a longer (10 min) period. In summary, visual feedback of error can drive faster acquisition of a new walking pattern but neither benefits nor interferes with savings of the new pattern.

MATERIALS AND METHODS

Participants

Forty healthy young people participated (experiment 1: n=20, 8 male/12 female; mean±s.d. age: 23±4 years; experiment 2: n=20, 8 male/12 female; mean age: 24±4 years). This sample is a subset

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from a larger cohort reported in a previous study (Roemmich et al., 2016). All participants were naive to split-belt treadmill walking, free of neurological, musculoskeletal and cardiovascular conditions, and participated in only one of the two experiments. We recorded leg dominance as the leg used to kick a soccer ball. Participants provided written informed consent in accordance with the Johns Hopkins Medicine Institutional Review Board prior to participating and were compensated for participation. All investigations were conducted according to the principles expressed in the Declaration of Helsinki.

Split-belt treadmill walking protocol

Participants walked on a custom-built split-belt treadmill (Woodway USA, Waukesha, WI, USA) with two separate belts, each driven by an independently controlled motor. We controlled the treadmill belts using custom-written code in Vizard (WorldViz USA, Santa Barbara, CA, USA). Before walking, participants stood in the middle of the treadmill with one foot on each belt. A 12 inch (30.48 cm) tall partition was placed lengthwise between the belts to prevent stepping on both belts simultaneously, but did not otherwise interfere with walking. Participants wore a safety harness suspended from the ceiling that did not provide body-weight support during walking. We informed the participants about when the treadmill was about to start or stop, but not the speed of the belts. Immediately prior to starting the treadmill, participants held on to a horizontal handrail but were instructed to release the rail and cross their arms as soon as the treadmill started moving. This may have affected stepping behavior in response to the perturbation, but was necessary to prevent blocking of the active marker set used for motion capture. While walking, the participants viewed a television screen placed directly in front of the treadmill. Depending on group assignment, this showed either visual feedback of step lengths (Roemmich et al., 2016) or a television show to discourage looking at the treadmill belts. The treadmill was stopped briefly (<1 min) between each testing block (e.g. baseline, adaptation, deadaptation, etc.).

Experimental protocols

Across all groups in both experiments, participants first walked with the belts tied without visual feedback and then with visual feedback for 2 min each (baseline). This was followed by walking with the belt speeds split in a 2:1 ratio (dominant leg at 0.7 m s^{-1} and non-dominant leg at 1.4 m s^{-1}) during an adaptation block (adaptation) with or without visual feedback of step lengths. The 2:1 split condition was introduced abruptly (at an approximate acceleration of 1.0 m s^{-2}) from a standing position. In experiment 1, adaptation was 10 min long. Demonstrated in our previous work (Roemmich et al., 2016), participants initially use the visual feedback to acquire the new walking pattern rapidly but rely less on the feedback over time as adaptation progresses; given enough time, participants learn a symmetric gait pattern with or without visual feedback. Therefore, we truncated the adaptation block to 1 min in experiment 2 so that only the group with visual feedback would acquire the symmetric pattern. In other words, we isolated the portion of the adaptation block where performance is most strongly influenced by the visual feedback to assess whether this rapid, visual feedback-driven acquisition of the new walking pattern influenced savings. After adaptation, participants in both experiments completed a washout block at the slow speed without feedback (deadaptation; 10 min), and a second adaptation block without feedback at the same belt speed configuration as the adaptation block (readaptation; 10 min). Visual feedback was not provided during re-adaptation because we know that visual step length feedback accelerates acquisition of the symmetric walking pattern via voluntary correction independently of the underlying adaptation (Roemmich et al., 2016). Therefore, if we provided visual feedback during re-adaptation and observed accelerated re-acquisition of the symmetric walking pattern, we would not be able to disentangle whether this was due to feedback-driven voluntary correction or accelerated relearning (i.e. savings). Experimental protocols are shown in Fig. 1A.

Visual feedback display

We interfaced the kinematic data with Vizard software to calculate and display step lengths at each heel-strike. Fig. 1B,C shows the feedback setup and display that were provided on a 56 inch television placed in front of the treadmill. The feedback display consisted of 16 vertically arranged virtual targets (each 10 cm wide; Roemmich et al., 2016). At right foot heel-strike, a blue circle appeared on the right half of the screen at a vertical position that represented the right step length (e.g. for a right step length of 100 cm, the blue circle would appear inside target 10 as in Fig. 1C – the circle did not move horizontally). The corresponding target number along the center of the screen also turned blue to ensure that the participant knew which target had been hit. We provided similar feedback at left foot heel-strike except the circle and target numbers were red and the circle appeared on the left half of the screen. Whenever the feedback was displayed, we asked participants to step symmetrically such that the red and blue circles appeared inside the same target with each pair of steps. Whenever the feedback of step lengths was withheld, we asked participants to walk however they felt most comfortable while they watched a television show. Importantly, the circles only updated position once the foot struck the treadmill (i.e. feedback was not online foot position feedback, but rather step length feedback).

Kinematic data collection

We collected kinematic data at 100 Hz (Optotrak Certus, Northern Digital, Waterloo, ON, Canada). Infrared-emitting active markers were placed bilaterally over the toe (fifth metatarsal head), ankle (lateral malleolus), knee (lateral femoral epicondyle), hip (greater trochanter), pelvis (iliac crest) and shoulder (acromion process). For this study, only the data from the ankle markers were used for analysis. All participants remained on the treadmill throughout the duration of the testing sessions and wore comfortable walking shoes and form-fitting clothing to reduce marker movement artifacts.

Data analysis

For experiments 1 and 2, the primary behavioral outcome measure of interest was step length asymmetry: (fast step length−slow step length)/(fast step length+slow step length). This metric adapts robustly during split-belt treadmill walking (Reisman et al., 2005). A value of zero step length asymmetry indicates symmetric stepping. We calculated step length as the distance between the ankle markers along the anterior–posterior axis at heel-strike of each leg. For experiment 1, we analyzed step length asymmetry in adaptation and readaptation across three distinct time epochs: initial (mean of the first 5 strides), late change (mean of strides 6–200) and plateau (mean of the last 30 strides). These epochs were selected to maintain consistency with our prior work (Roemmich et al., 2016). For experiment 2, we evaluated step length asymmetry during similar time epochs, but because the adaptation block was shorter, we quantified early change (mean of strides 6–30) in step length asymmetry, and the mean of the last 10 strides was used for plateau.

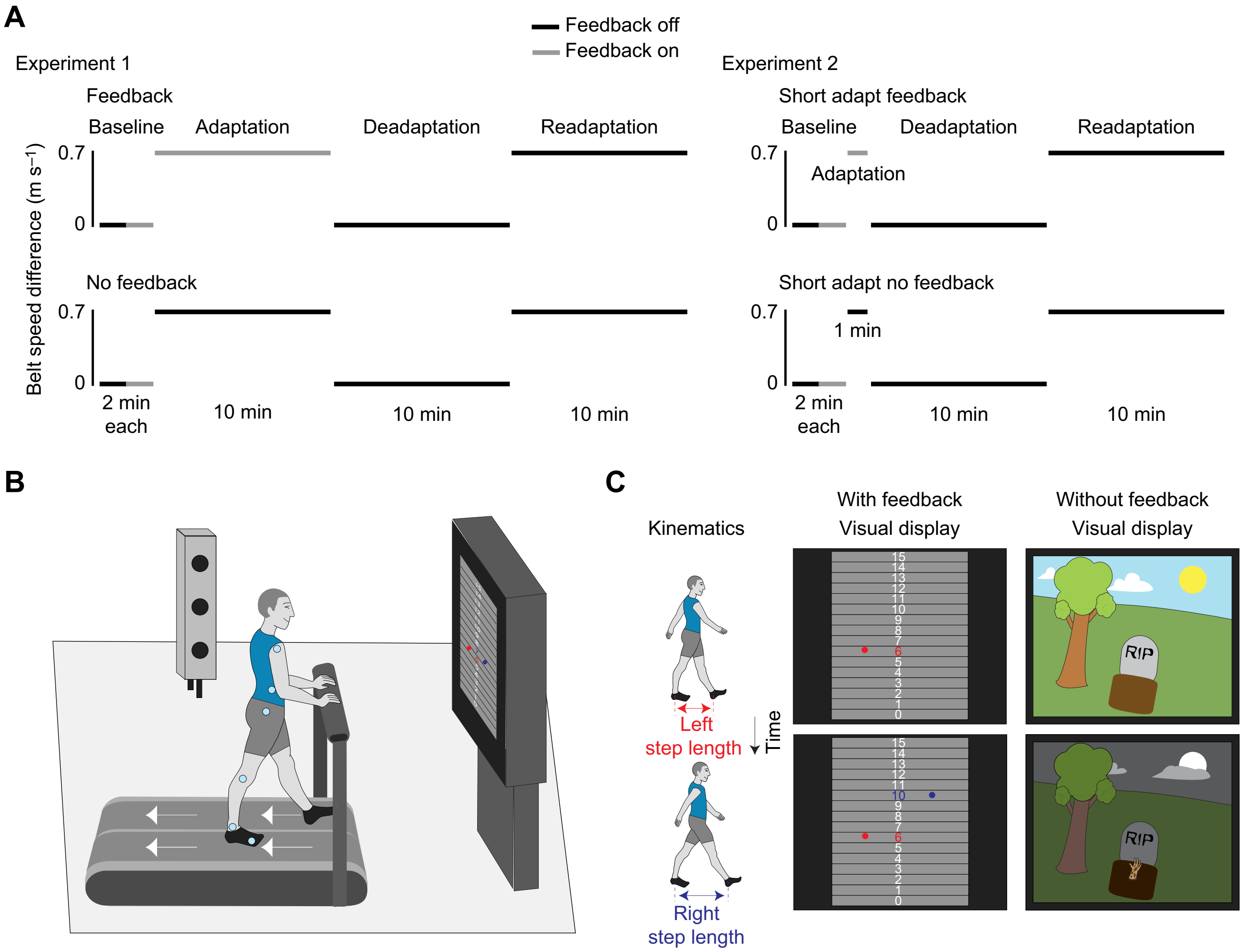

Fig. 1. Experimental protocols, laboratory set-up and visual display for experiments 1 and 2. (A) Experimental protocols for the feedback and no feedback groups in experiments 1 and 2. Gray lines indicate when visual feedback of step lengths was on, whereas black lines indicate that the feedback was off. (B) Participants walked on a split-belt treadmill while viewing visual feedback about their step lengths (as depicted), or without visual feedback and instead a television show or movie. Participant kinematics were recorded using three-dimension motion capture. (C) Example participant kinematics and corresponding visual display for experiments 1 and 2 with visual feedback (left) and without visual feedback (right). Note that the visual feedback does not indicate real-time foot position, but rather step length. That is, the distance between the ankle markers (light blue) at heel-strike. Participants in the no feedback groups watched a television show or movie during the experiments, depicted here as a cartoon demonstrating a progression of time.

For both experiments, we compared the behavior during these periods of the adaptation and readaptation blocks in the feedback and no feedback groups using a 2×2 group (feedback, no feedback)×time (adaptation, readaptation) mixed-model ANOVA (α level set to 0.05). We performed Fisher's LSD tests to compare behavior within adaptation and readaptation blocks whenever we observed a significant group×time interaction.

To assess the amount to which all groups washed out during deadaptation, we also assessed the plateau epochs (mean of last 30 strides) of the last baseline and deadaptation blocks. For both experiments, we first performed separate unpaired *t*-tests to compare baseline step length asymmetry values during walking at baseline with and without the feedback to confirm that no differences existed in baseline walking between the groups. We then performed a 2×2 group (feedback, no feedback)×time (no feedback baseline plateau, deadaptation plateau) mixed-model ANOVA to compare the degree to which learning washed out during deadaptation in each group.

RESULTS AND DISCUSSION

Experiment 1: visual feedback of error during initial learning drives rapid voluntary correction of walking patterns but does not influence savings

The goal of experiment 1 was to understand how voluntary movement correction during initial learning influences savings of the newly learned walking pattern. In other words, we wondered whether subjects would use the fast, feedback-driven correction evident during initial learning (Roemmich et al., 2016) to similarly accelerate relearning (i.e. facilitate greater savings). Fig. 2A shows the group mean time courses for the step length asymmetry throughout the paradigm for the feedback and no feedback groups. Both groups walked similarly at baseline; we observed no differences between the groups in step length asymmetry during baseline walking with (P=0.99) or without visual feedback (P=0.47). Importantly, we also observed that both groups washed out similarly by the end of deadaptation. When comparing deadaptation plateau with baseline, we observed a significant

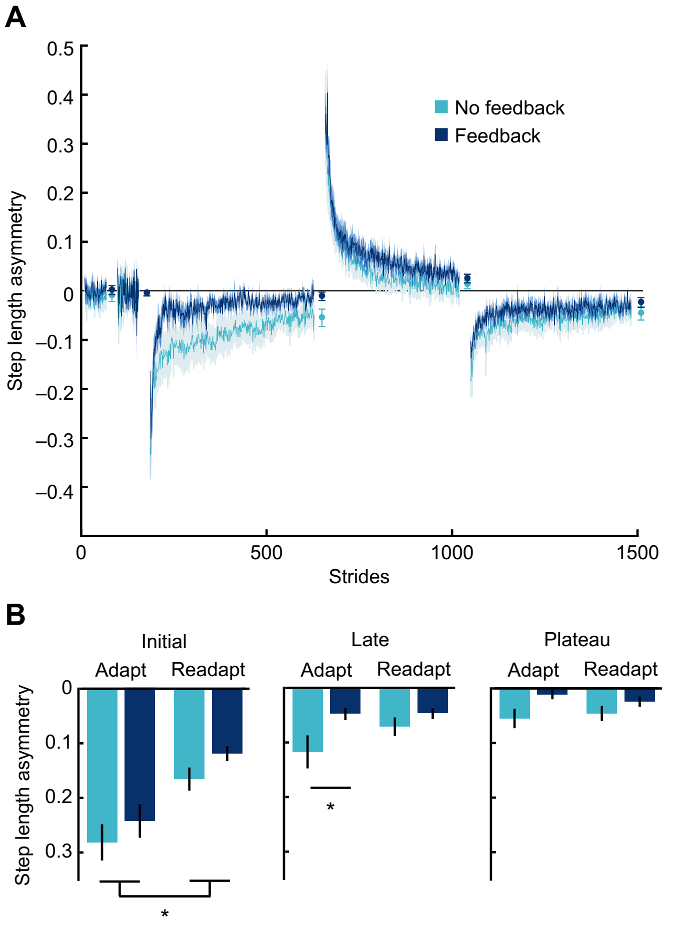

Fig. 2. Experiment 1 results. (A) Mean±s.e.m. adaptation curves across participants within the no feedback (light blue; n=10) and feedback (dark blue; n=10) groups. The curves are truncated in length to match the participant that took the fewest strides during adaptation. Data points immediately following each block of the experiment show the step length asymmetry during the plateau (mean±s.e.m. of the last 30 strides) for both groups. (B) Mean±s.e.m. of the step length asymmetry within the epochs of interest in adaptation and readaptation for both groups. Comparisons of behavior during these epochs were made using a 2×2 mixed-model ANOVA. *P<0.05.

main effect for time ($F_{1,18}$=10.7, P=0.004) but no group×time interaction ($F_{1,18}$=0.003, P=0.96).

When comparing adaptation with readaptation, the feedback and no feedback groups both showed savings in step length asymmetry during initial (mean of strides 1–5) readaptation (main effect for time: $F_{1,18}$=36.8, P<0.001; Fig. 2B), with no effect of visual feedback (group×time interaction: $F_{1,18}$=0.037, P=0.85). Similarly, savings was apparent in both groups during the late change epoch (mean strides 6–200); we observed significant decreases in step length asymmetry from adaptation to readaptation (main effect for time: $F_{1,18}$=6.9, P=0.017). We observed a significant effect of visual feedback (group×time interaction: $F_{1,18}$=6.4, P=0.021) during the late change epoch; however, *post hoc* testing revealed that this interaction was driven by differences in performance during adaptation driven by visual feedback (adaptation late change for feedback versus no feedback groups: P=0.045) and not differences in savings (readaptation late change for feedback versus no feedback groups: P=0.23). Both groups walked similarly by the end of adaptation and readaptation (i.e. plateau: mean of last 30 strides) regardless of visual feedback; we did not observe main effects of time ($F_{1,18}$=0.091, P=0.766), group ($F_{1,18}$=3.6, P=0.075) or a group×time interaction ($F_{1,18}$=3.6, P=0.073).

Experiment 2: similar savings following short adaptation despite large changes in performance driven by visual feedback

In experiment 1, the adaptation block was 10 min long. Generally, participants use the visual feedback to acquire the new walking pattern rapidly during early learning but rely less on the feedback over time as adaptation progresses (Roemmich et al., 2016). Given enough time, participants eventually learn a symmetric gait pattern with or without visual feedback. In experiment 2, we then truncated the adaptation block to 1 min so that only the group with visual feedback would acquire the symmetric pattern during adaptation. In other words, we isolated the portion of the adaptation block where performance is most strongly influenced by the visual feedback to assess whether this rapid, feedback-driven acquisition of the new walking pattern influenced savings. Excluding the length of the adaptation block, the experimental paradigm was identical to that of experiment 1 (Fig. 1A).

Fig. 3A shows the group mean time courses for the short adapt feedback and short adapt no feedback groups throughout the paradigm. Both groups showed similar step length asymmetry at baseline when walking with (P=0.09) or without (P=0.21) visual feedback. By the end of deadaptation, both groups were similarly washed out; we did not observe main effects of time ($F_{1,18}$=1.3, P=0.27) or a group×time interaction ($F_{1,18}$=1.6, P=0.22) when comparing deadaptation with baseline.

Group mean step length asymmetry during each epoch of interest is displayed in Fig. 3B. We observed savings even after only 1 min of adaptation; step length asymmetry during initial readaptation was significantly smaller in both groups as compared with initial adaptation (main effect for time: $F_{1,18}$=23.9, P<0.001), with no significant effect of visual feedback (group×time interaction: $F_{1,18}$=2.47, P=0.13). We also observed significant differences between groups in step length asymmetry during early change (mean of strides 6–30) from adaptation to readaptation (group×time interaction: $F_{1,18}$=8.7, P=0.009). However, similar to the results from experiment 1, *post hoc* analyses again demonstrated that this resulted from differences in step length asymmetry during adaptation that were driven by voluntary correction (P=0.002) rather than differences in step length asymmetry during readaptation, or savings (P=0.24). Visual feedback led to voluntary improvements in performance during 1 min of adaptation such that the step length asymmetry at plateau (mean of the last 10 strides) in the short adapt feedback group was significantly smaller than that achieved by the short adapt no feedback group (group×time interaction for plateau: $F_{1,18}$=19.0, P<0.001; *post hoc* comparison of short adapt feedback and short adapt no feedback during adaptation: P<0.001). We also observed a trend-level difference in step length asymmetry at the end of readaptation between the groups (*post hoc* comparison of short adapt feedback and short adapt no feedback during readaptation: P=0.05).

Discussion of results

In this study, we showed that savings of a newly learned walking pattern occurs independently of voluntary changes in walking during initial learning. Humans can use visual feedback to improve initial performance faster via voluntary correction; however, this does not carry over to influence subsequent relearning. Our analyses revealed that people exhibit similar savings regardless of whether

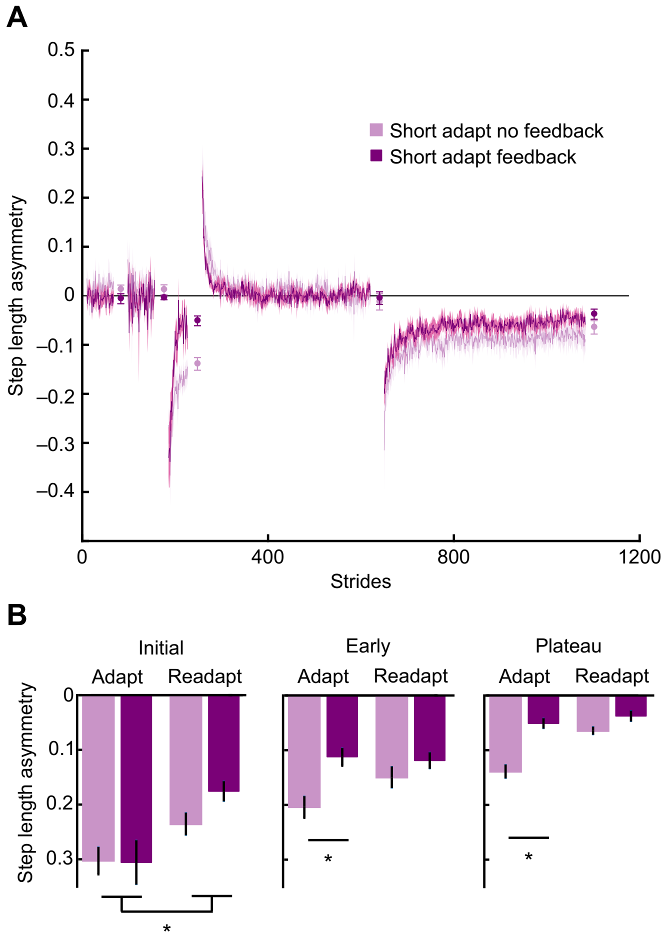

Fig. 3. Experiment 2 results. (A) Mean±s.e.m. adaptation curves across participants within the short adapt no feedback (light purple; *n*=10) and short adapt feedback (dark purple; *n*=10) groups. The curves are truncated in length to match the participant that took the fewest strides during adaptation. Data points immediately following each block of the experiment show the step length asymmetry during the plateau (mean±s.e.m. of the last 30 strides, or 10 strides of adaptation) for both groups. (B) Mean±s.e.m. of the step length asymmetry within the epochs of interest in adaptation and readaptation for both groups. Comparisons of behavior during these epochs were made using a 2×2 mixed-model ANOVA. **P*<0.05.

they receive visual feedback of movement error (i.e. step length asymmetry) during initial learning. These results indicate that voluntary correction leads to faster acquisition of a new walking pattern but neither benefits nor interferes with savings of the newly learned walking pattern.

It has become clear that voluntary changes in walking have little effect on locomotor adaptation. Adaptation proceeds uninhibited when changes in walking are voluntarily suppressed (Long et al., 2016) or accelerated (Roemmich et al., 2016). Our results extend this work to show that voluntary changes in walking during initial learning also have negligible effects on adaptive learning over longer time scales. We found that even when voluntary correction led to faster acquisition of the desired walking pattern (i.e. symmetric walking) during initial learning, participants did not appear to re-engage this mechanism to facilitate similarly accelerated changes in walking upon later exposure to the same perturbation in the absence of feedback.

Understanding how implicit (subconscious) and explicit (voluntary) learning mechanisms interact during motor adaptation has recently garnered considerable interest. Much of this work has evolved from the findings of Mazzoni and Krakauer (2006), who showed that implicit learning persists despite voluntary changes in reaching movements. More recent work showed that participants use a combination of implicit error-based learning and explicit strategy (or aiming) to improve performance on a reaching adaptation task (Taylor et al., 2014). Further work suggested that explicit contributions are also important for savings (Morehead et al., 2015) and generalization (Day et al., 2016) of reaching adaptation. Implicit and explicit learning mechanisms are more difficult to dichotomize in walking. Walking is a continuous, more automatic movement and it is unlikely that people ‘aim’ their steps when walking in environments that do not require precise stepping (e.g. walking on stepping stones or stepping over puddles). However, there does seem to be some cognitive influence on locomotor adaptation (Sawers et al., 2013). Our recent work in this area has clarified how voluntary correction and sensorimotor adaptation interact to improve behavior during locomotor learning (Roemmich et al., 2016). Specifically, we showed that these two mechanisms act independently to contribute to improvements in performance while learning a new walking pattern.

It is as yet unclear why participants do not use the same voluntary correction employed during initial learning to speed relearning when the visual feedback is removed. One explanation may be that although the voluntary correction facilitated faster restoration of step length symmetry, other features of the walking pattern may have been dissimilar to that eventually achieved through adaptation (e.g. less stable, more energetically costly). We know that this form of voluntary correction relies on visual feedback, as it was not employed when visual feedback was removed abruptly during initial learning in our prior work (Roemmich et al., 2016) and was not used to facilitate faster relearning when visual feedback was omitted in the present study. Future investigations into why the voluntary correction is not recalled during relearning may reveal important information that could be useful for understanding how to most effectively drive changes in walking patterns using visual feedback, as is often done in clinical settings.

In conclusion, here we showed that voluntary correction and savings of a newly learned walking pattern are independent. People can use external feedback to make quick, voluntary changes to their gait while simultaneously learning a new walking pattern via adaptation. However, this neither enhances nor interferes with the ability to save the adapted pattern over time. Taking advantage of voluntary correction and adaptation mechanisms simultaneously may lead to fast changes in walking that also last over extended time scales.

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Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: R.T.R.; Methodology: K.A.L., R.T.R.; Formal analysis: K.A.L., R.T.R.; Investigation: K.A.L., R.T.R.; Resources: R.T.R.; Data curation: R.T.R.; Writing - original draft: K.A.L.; Writing - review & editing: K.A.L., R.T.R.; Visualization: K.A.L.; Supervision: R.T.R.; Project administration: R.T.R.; Funding acquisition: K.A.L., R.T.R.

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Data availability

Data will be made available upon reasonable request.

References

Day, K. A., Roemmich, R. T., Taylor, J. A. and Bastian, A. J. (2016). Visuomotor learning generalizes around the intended movement. *eNeuro* **3**, e0005-16.

Haith, A. M., Huberdeau, D. M. and Krakauer, J. W. (2015). The influence of movement preparation time on the expression of visuomotor learning and savings. *J. Neurosci.* **35**, 5109-5117.

Herzfeld, D. J., Vaswani, P. A., Marko, M. K. and Shadmehr, R. (2014). A memory of errors in sensorimotor learning. *Science* **345**, 1349-1353.

Huang, V. S., Haith, A., Mazzoni, P. and Krakauer, J. W. (2011). Rethinking motor learning and savings in adaptation paradigms: model-free memory for successful actions combines with internal models. *Neuron* **70**, 787-801.

Kojima, Y., Iwamoto, Y. and Yoshida, K. (2004). Memory of learning facilitates saccadic adaptation in the monkey. *J. Neurosci.* **24**, 7531-7539.

Krakauer, J. W., Ghez, C. and Ghilardi, M. F. (2005). Adaptation to visuomotor transformations: consolidation, interference, and forgetting. *J. Neurosci.* **25**, 473-478.

Long, A. W., Roemmich, R. T. and Bastian, A. J. (2016). Blocking trial-by-trial error correction does not interfere with motor learning in human walking. *J. Neurophysiol.* **115**, 2341-2348.

Malone, L. A. and Bastian, A. J. (2010). Thinking about walking: effects of conscious correction versus distraction on locomotor adaptation. *J. Neurophysiol.* **103**, 1954-1962.

Malone, L. A., Vasudevan, E. V. and Bastian, A. J. (2011). Motor adaptation training for faster relearning. *J. Neurosci.* **31**, 15136-15143.

Mazzoni, P. and Krakauer, J. W. (2006). An implicit plan overrides an explicit strategy during visuomotor adaptation. *J. Neurosci.* **26**, 3642-3645.

Medina, J. F., Garcia, K. S. and Mauk, M. D. (2001). A mechanism for savings in the cerebellum. *J. Neurosci.* **21**, 4081-4089.

Morehead, J. R., Qasim, S. E., Crossley, M. J. and Ivry, R. (2015). Savings upon re-aiming in visuomotor adaptation. *J. Neurosci.* **35**, 14386-14396.

Reisman, D. S., Block, H. J. and Bastian, A. J. (2005). Interlimb coordination during locomotion: what can be adapted and stored? *J. Neurophysiol.* **94**, 2403-2415.

Roemmich, R. T. and Bastian, A. J. (2015). Two ways to save a newly learned motor pattern. *J. Neurophysiol.* **113**, 3519-3530.

Roemmich, R. T., Long, A. W. and Bastian, A. J. (2016). Seeing the errors you feel enhances locomotor performance but not learning. *Curr. Biol.* **26**, 2707-2716.

Sawers, A., Kelly, V. E. and Hahn, M. E. (2013). Effects of gradual versus sudden training on the cognitive demand required while learning a novel locomotor task. *J. Mot. Behav.* **45**, 405-414.

Shadmehr, R. and Brashers-Krug, T. (1997). Functional stages in the formation of human long-term motor memory. *J. Neurosci.* **17**, 409-419.

Taylor, J. A., Krakauer, J. W. and Ivry, R. B. (2014). Explicit and implicit contributions to learning in a sensorimotor adaptation task. *J. Neurosci.* **34**, 3023-3032.