Explicit and implicit locomotor learning in individuals with chronic hemiparetic stroke

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Abstract (250 words max)

Motor learning involves both explicit and implicit processes that are fundamental for acquiring and adapting complex motor skills. However, stroke may damage the neural substrates underlying explicit and/or implicit learning, leading to deficits in overall motor performance. While both learning processes are typically used in concert in daily life and rehabilitation, no gait studies have determined how these processes function together after stroke when tested during a task that elicits dissociable contributions from both. Here, we compared explicit and implicit locomotor learning in individuals with chronic stroke to age- and sex-matched neurologically intact controls. We assessed implicit learning using split-belt adaptation (where two treadmill belts move at different speeds). We assessed explicit learning (i.e., strategy-use) using visual feedback during split-belt walking to help individuals explicitly correct for step length errors created by the split-belts. The removal of visual feedback after the first 40 strides of split-belt walking, combined with task instructions, minimized contributions from explicit learning for the remainder of the task. We utilized computational modeling to determine the individual contributions of explicit and implicit processes to overall behavioral change. The computational and behavioral analyses revealed that, compared to controls, individuals with chronic stroke demonstrated deficits in both explicit and implicit contributions to locomotor learning, a result that runs counter to prior work testing each process individually during gait. Since post-stroke locomotor rehabilitation involves interventions that rely on both explicit and implicit motor learning, future work should determine how locomotor rehabilitation interventions can be structured to optimize overall motor learning.

New and noteworthy (75 words max):

Motor learning involves both implicit and explicit processes, the underlying neural substrates of which could be damaged by after stroke. While both learning processes are typically used in concert in daily life and rehabilitation, no gait studies have determined how these processes function together after stroke. Using a locomotor task that elicits dissociable contributions from both processes and computational modeling, we found evidence that chronic stroke causes deficits in both explicit and implicit locomotor learning.

53 ***Introduction***

54 Motor learning, the ability to acquire and maintain motor skills with practice (Schmidt
55 and Lee 2005), involves both explicit and implicit processes. Explicit learning, as in strategy
56 formation and use, is critical for skill acquisition because it provides the means for fast,
57 flexible changes in movements (Bond and Taylor 2015; Huberdeau et al. 2019; Roemmich
58 and Bastian 2018). Implicit processes keep movements finely calibrated in the face of
59 changes to the body or environment (Bond and Taylor 2015; Krakauer et al. 2019; Mazzoni
60 and Krakauer 2006; Roemmich and Bastian 2018). While both explicit and implicit processes
61 typically work in concert when learning complex motor skills, stroke may damage the neural
62 substrates underlying either component (or both), leading to deficits in overall motor
63 learning. Since motor learning is foundational to rehabilitation of individuals post-stroke, and
64 since explicit and implicit learning are often used concurrently (Roemmich et al. 2016;
65 Taylor and Ivry 2011, 2012), it is important to determine if individuals post-stroke have
66 impairments in one or both processes when assessed during the same motor task.

67 Explicit learning, sometimes referred to as "voluntary correction" (Roemmich et al.
68 2016) or "cognitive strategies" (Taylor and Ivry 2011), involves consciously directing
69 specific changes in movement patterns. For example, a patient may consciously increase their
70 step length in response to a clinician's verbal instructions. Explicit learning plays a critical
71 role in skill acquisition and motor memory for neurologically intact individuals, and is
72 hypothesized to be mediated primarily in prefrontal cortex (Krakauer et al. 2019; McDougle
73 et al. 2016; Taylor and Ivry 2014). We assume this process is driven by target error, the
74 difference between a movement outcome and the task goal (French et al. 2018; Mazzoni and
75 Krakauer 2006; Taylor and Ivry 2012). A key feature of this process is that it can be
76 volitionally "switched" on or off in response to context or instructions (Bond and Taylor
77 2015; French et al. 2018; Wood et al. 2020, 2021). Explicit learning can be used during gait

in both neurologically intact individuals and those post-stroke by providing visual feedback and specific task instructions (French et al. 2021b, 2021a; Hussain et al. 2013). When tested in isolation during locomotion, individuals post-stroke do not demonstrate impairments in explicit learning (French et al. 2021a, 2021b).

Sensorimotor adaptation is an implicit motor learning process that is essential for maintaining well-calibrated movements in response to ever-changing environments and body states. Sensorimotor adaptation, which we refer to here as "implicit adaptation", is driven by sensory prediction error, the difference between the actual and expected sensory consequences of a motor command, and mediated in large part by the cerebellum (Krakauer et al. 2000; Morton and Bastian 2006; Shadmehr et al. 2010; Shadmehr and Mussa-Ivaldi 1994; Tseng et al. 2007). During gait, implicit adaptation can be elicited using a split-belt treadmill where the belts under each limb move at different speeds (Dietz et al. 1994). This perturbation initially produces asymmetric gait patterns (e.g., step length asymmetries) which are slowly recalibrated back to baseline asymmetry levels (Malone et al. 2012; Reisman et al. 2005). The hallmark of implicit adaptation is the storage of the adapted stepping pattern when the belts return to the same speed, termed an "implicit aftereffect" (Reisman et al. 2005). When tested in isolation during locomotion, individuals with non-cerebellar stroke adapt to a similar magnitude as neurologically intact participants by the end of learning, but they do so at a slower rate (Malone and Bastian 2014; Reisman et al. 2007; Savin et al. 2013; Tyrell et al. 2014).

While explicit learning and implicit adaptation are typically used simultaneously to learn new skills in everyday life, including rehabilitation practice, they are mostly studied individually during gait (French et al. 2018; Hussain et al. 2013; Reisman et al. 2005; Wood et al. 2020, 2021). This may be because when they are studied within the same task, it can be difficult to dissociate the individual contributions of each process to overall behavior

103 (Cherry-Allen et al. 2018; Long et al. 2016; Malone and Bastian 2010; Roemmich et al.
104 2016). A study in young neurotypical adults accomplished this using visual feedback to
105 induce explicit learning that helped correct the step length errors produced by the split-belt
106 treadmill (Roemmich et al. 2016). They found explicit learning improved performance during
107 split-belt walking compared to a group that did not receive feedback. However, the implicit
108 aftereffects (measured without visual feedback) were similar between groups, indicating
109 explicit learning did not impact the recalibration of motor commands (i.e., implicit
110 adaptation). Thus, the authors concluded that, within the same locomotor learning task, while
111 explicit learning improves overall performance, implicit adaptation proceeds despite
112 involvement from explicit learning in individuals with intact neurologic systems. Critically, it
113 is unclear to what degree explicit learning versus implicit adaptation is impaired in
114 individuals post-stroke when assessed in a task requiring dissociable contributions from both.

115 While explicit learning and implicit adaptation are broadly intact after stroke when
116 assessed individually during gait, it is unknown if this holds when they are combined in the
117 same task. Only two studies, both in reaching movements, have attempted to tackle this
118 question, but with mixed results (Binyamin-Netser et al. 2023; Taylor and Ivry 2014),
119 indicating more work is necessary to determine if there are deficits in these learning
120 processes when assessed within the same task. This is a critical gap because gait
121 rehabilitation post-stroke involves a combination of explicit learning and implicit adaptation
122 (e.g., a patient may explicitly try to increase step length based on their therapist's instructions
123 while simultaneously implicitly adapting to small movement-related errors). Therefore,
124 determining how each is impaired, when occurring together in the same task, has important
125 implications for how rehabilitation of locomotor tasks should be optimally structured.

126 The purpose of this study was to determine if individuals with chronic, hemiparetic
127 stroke demonstrate impaired explicit learning and/or implicit adaptation during a locomotor

task involving dissociable contributions from both processes. We accomplished this through a combination of behavioral testing and computational modeling. Since explicit learning involves cognitive processes (French et al. 2021a; McDougle et al. 2016; Taylor and Ivry 2014) that are often impaired in stroke (Barker-Collo and Feigin 2006), we hypothesized that individuals with stroke would demonstrate impaired explicit learning compared to controls. Additionally, because the rate of implicit adaptation on the split-belt treadmill is slow but the magnitude is intact in persons post-stroke (Reisman et al. 2007; Savin et al. 2013; Tyrell et al. 2014) we hypothesized that individuals with stroke would demonstrate similar levels of implicit adaptation as controls.

Materials and methods

Participants

We recruited 21 (10 Female) individuals with one prior unilateral, stroke to participate in this study and 18 (9 Female) healthy age- and sex-matched control participants. Individuals with stroke were included if they were between 18 and 85 years old, had a single unilateral hemiparetic stroke (confirmed by an MRI or CT scan) more than 6 months prior, and were able to walk without assistance from another person. Individuals with stroke were excluded if they had evidence of cerebellar stroke, other neurologic diagnoses aside from stroke, inability to walk outside of the home prior to stroke, pain limiting walking, neglect, or significant aphasia. Control participants were excluded if they had any conditions that might limit their walking or motor learning, any neurologic conditions, or uncorrected vision or hearing loss. All individuals provided written informed consent prior to participating and the study was approved by the University of Delaware Institutional Review Board.

150 Experimental design

151 To determine if individuals with stroke have impaired explicit learning or implicit
152 adaptation during a locomotor learning task that requires contributions from both processes,
153 we combined the split-belt adaptation paradigm with real-time visual feedback, similar to a
154 previous study (Figure 1A; Roemmich et al. 2016). Participants performed 4 phases of
155 treadmill walking: Baseline, Practice, Adaptation, and De-adaptation (Figure 1B). During
156 Baseline and Practice, both the treadmill belts moved at the same speed. During the Baseline
157 phase, no visual feedback was provided on the screen and individuals were told to "walk
158 comfortably". The Practice phase served to introduce participants to the visual feedback
159 (details below). Step length targets first appeared at each participant's baseline step length for
160 90 seconds, at which point, they were verbally oriented to the feedback and instructed to
161 practice changing their step lengths by stepping both above and below the targets. For the
162 next 30 seconds, the step length targets shifted 10 cm longer for the limb taking the longer
163 baseline step and 10 cm shorter for the limb taking the shorter baseline step. This allowed
164 participants to practice hitting targets that were not their baseline step lengths. The targets
165 shifted back to the baseline step lengths for the final 60 seconds of the Practice phase and
166 individuals were asked to "walk comfortably".

167 During the Adaptation phase (8 minutes), the fast belt speed was set at the fastest
168 overground gait speed (constrained between 0.6 and 1.0 m/s), and the slow belt moved at half
169 the speed of the fast belt, producing a 2:1 speed ratio (Charalambous et al. 2018; Tyrell et al.
170 2014). For all participants, the limb that took the longer step during the Baseline phase was
171 placed on the fast belt. This perturbation produces a large asymmetry of the left and right step
172 lengths (defined as the distance between two feet at heel strike), and is corrected on a stride-
173 by-stride basis through implicit adaptation (Charalambous et al. 2018; Reisman et al. 2005,
174 2007). Lastly, participants performed a De-adaptation phase (8 minutes) where they were

175 instructed to “walk comfortably”, and both belts moved at the same speed as the Baseline
176 phase (i.e., the slow belt speed) so that we could measure the size of the implicit aftereffect,
177 our measure of the total magnitude of implicit adaptation.

178 To assess explicit learning, defined as the ability to consciously correct for errors
179 between a movement outcome and the task goal, we provided visual feedback of the left and
180 right step lengths during the first 40 strides of the Adaptation phase. The real-time visual
181 feedback was displayed on a vertically orientated LCD television screen placed 100 cm in
182 front of the treadmill (Figure 1A; Size: 123.3 x 71.1 cm; Sony Tokyo, Japan). The Motion
183 Monitor software (Innovative Sports Training Inc., Chicago, IL, USA) was used to display
184 the visual feedback during the experiment. The feedback consisted of a target grid of 12
185 possible step lengths, each 10 cm in height. This grid had a 1:1 correspondence with the
186 actual step length. The left and right step length feedback was displayed as a red and blue
187 foot, respectively. Each foot was presented in the center of the row corresponding to that step
188 length window, and appeared as soon as heel strike was detected, then disappeared once the
189 subsequent swing phase began. The target right and left step lengths during the Adaptation
190 phase were set at each participant’s left and right baseline step lengths, denoted by
191 highlighting the corresponding row of the grid. Participants were instructed to “hit the
192 targets” when the feedback was visible. Therefore, because the targets were set at baseline
193 step length, the feedback guided participants to voluntarily correct the step length asymmetry
194 induced by the split-belt treadmill via explicit learning.

195 The key manipulation that allowed us to assess the magnitude of explicit learning was
196 to turn off the feedback after the first 40 strides of Adaptation and instruct participants to
197 “walk comfortably”. Here, we relied on the flexibility of explicit learning, assuming it could
198 be voluntarily “switched off”, leaving no residual aftereffects (Bond and Taylor 2015;
199 McDougle and Taylor 2019; Wood et al. 2020). Meaning, after the instructions and removal

of feedback, only implicit adaptation remained. Thus, our measure of the total magnitude of explicit learning was the difference between the step length behavior when the feedback was on and when it was first turned off (Roemmich et al. 2016).

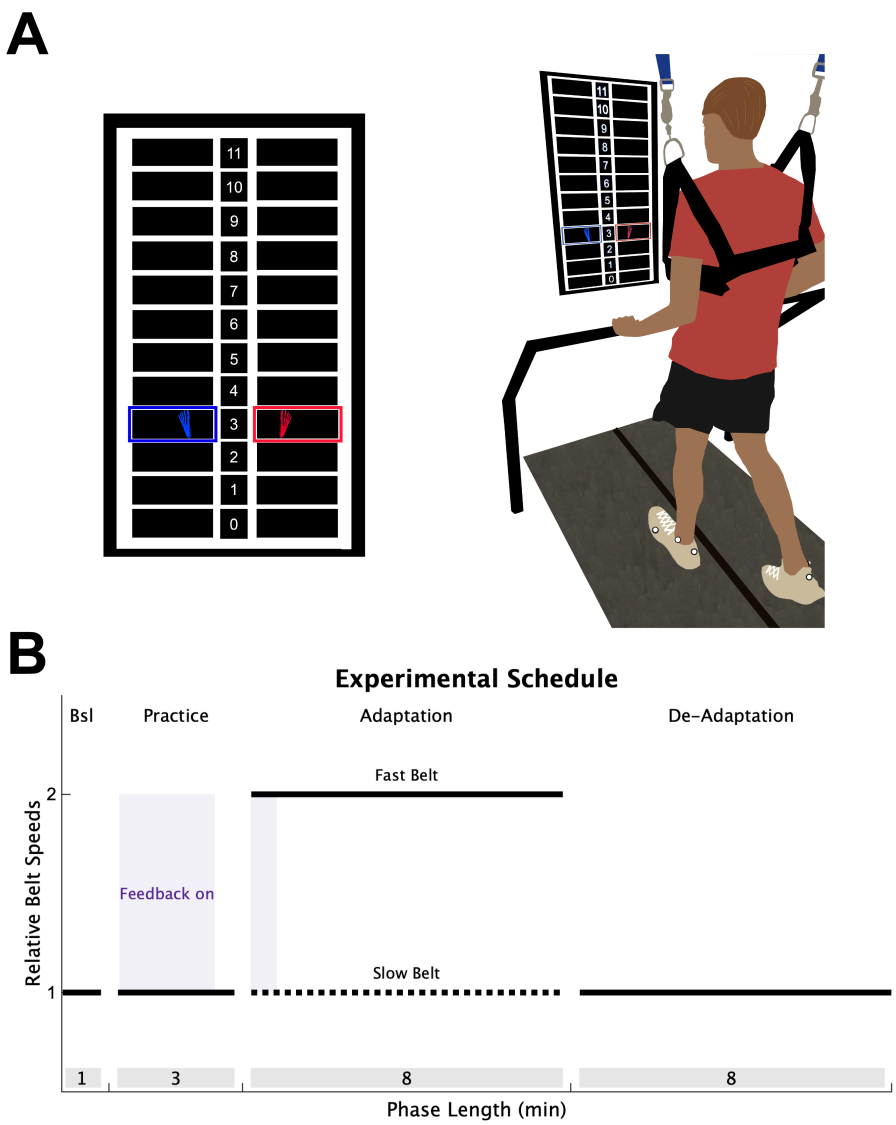

Figure 1 Experimental Design. (**A**) Individuals walked on a split-belt treadmill with a vertically mounted television screen in front of them. The visual feedback was a grid of 12 different step lengths, each 10 cm in height. The step length feedback was represented on the screen as blue (left) and red (right) feet that appeared on the screen as soon as heel strike was detected and disappeared once toe off was detected. **(B)** All participants completed 4 walking phases: 1) A Baseline (Bsl) phase of normal walking where no feedback was on the screen; 2) A Practice phase where individuals were introduced to the visual feedback while walking (purple shading); 3) An Adaptation phase where the slow belt (dotted black line) moved at

half the speed of the fast belt (solid black line), with feedback activated during only the first 40 strides (purple shading); 4) A De-adaptation phase where the belts returned to the same speed. The length of each phase (in minutes) is displayed in the grey shading at the bottom of the figure.

Data collection

During all phases of treadmill walking, individuals wore a ceiling mounted harness (that did not provide body weight support) and held a handrail to prevent falls. Additionally, we monitored heart rate (Polar, Kempele, Finland) for safety, and determined perceived exertion using the Borg Rate of Perceived Exertion (RPE) scale after each walking phase. If participants exceeded >80% their age-predicted max heart rate, the treadmill was stopped, and the participant was provided with a seated rest break until their heart rate recovered. However, no included participants needed the treadmill to stop during any of the walking phases.

Participants walked on a dual belt treadmill that captured kinetic data through two force plates, one under each belt, at 1000 Hz (Bertec, Columbus, OH, USA). Kinematic data were captured and recorded at 100 Hz using a Vicon MX40, 8-camera motion capture system, and time-synchronized with the kinetic data in Nexus software (v2.8.2, Vicon Motion Systems, Inc., London, UK). We used a custom marker set with seven retroreflective markers, one for each heel, lateral malleolus, and fifth metatarsal head, and the left medial malleolus.

Data analysis

Step length, calculated in real-time using motion capture and the Motion Monitor, was defined as the anterior-posterior distance between the two ankle markers at heel strike. Heel strike was determined in real time using the following criteria: 1) The velocity of the heel

markers changed from positive to negative; 2) a ground reaction force > one-third of the participants body weight detected through the treadmill force plate; and 3) no forces were detected through that same belt 4 ms prior to the detected step length.

The remainder of the data were analyzed with custom written MATLAB scripts (vR2022a, Mathworks, Natick, MA, USA). Step lengths were used to calculate step length asymmetry on each stride (s):

$$step\ length\ asymmetry_{[s]} = \frac{fast\ step\ length_{[s]} - slow\ step\ length_{[s]}}{fast\ step\ length_{[s]} + slow\ step\ length_{[s]}} * 100\% \qquad (1)$$

Thus, values of 0 indicate perfect symmetry between the fast and slow step lengths, while values further from 0 indicate greater asymmetry. We baseline corrected this measure by subtracting the mean step length asymmetry during the Baseline phase from each stride in the experiment for each individual. We removed outlier step length asymmetry strides, defined as any step length asymmetry exceeding 3x the interquartile range of that participant's step length asymmetry (mean percent removed [min max] stroke = 0.14% [0.0 0.39]; control = 0.92% [0.0 2.32]). We also removed the first stride of each phase to account for treadmill acceleration.

We used step length asymmetry data to calculate an Adaptation Index for each individual for each stride (s; Charalambous et al. 2018; Mawase et al. 2014; Roemmich et al. 2016):

$$Adaptation\ Index_{[s]} = \frac{step\ length\ asymmetry_{[s]} - \ condition * perturbation}{|perturbation|} \qquad (2a)$$

$$condition\ = \begin{cases} 1, if\ belts\ are\ split \\ 0, if\ belts\ are\ tied \end{cases} \qquad (2b)$$

$$perturbation = \begin{cases} min(step\ length\ asymmetry), if\ condition_{[s]} = 1 \\ max(step\ length\ asmmyetry), if\ condition_{[s]} = 0 \end{cases} \qquad (2c)$$

The min and max step length asymmetries used to determine the perturbation in equation 2c were calculated only within the first 10 strides of each respective phase (Charalambous et al. 2018). Thus, during the Adaptation phase, an Adaptation Index of 0 represents the minimum step length asymmetry (i.e., the max perturbation), and 1 indicates the perturbation has been fully corrected. The reverse is true during the De-adaptation phase.

To test our hypotheses, we averaged Adaptation Index during 4 key timepoints of interest: 1) Feedback On: the final five strides of the feedback being on during Adaptation, 2) Feedback Off: the first five strides immediately after the feedback was turned off during Adaptation, 3) End Adaptation: the last five strides of Adaptation, and 4) Implicit Aftereffect: the first five strides of De-adaptation. Our hypothesis for explicit learning was tested by comparing Feedback On (implicit adaptation plus explicit learning), to Feedback Off (implicit adaptation only). Larger differences between Feedback On and Feedback Off indicate greater explicit learning. We assessed the interaction between group (stroke vs control) and time (Feedback On vs Feedback Off) as our primary behavioral measure testing for impaired explicit learning in the stroke group. A secondary behavioral measure of explicit learning was between group differences during Feedback On, as this reflected the ability of individuals to use the visual feedback during implicit adaptation. Our primary behavioral measure to assess implicit adaptation, defined as the recalibration of step lengths caused by the split-belt treadmill, was comparing the Implicit Aftereffect between groups (Reisman et al. 2005; Shadmehr and Mussa-Ivaldi 1994). A secondary behavioral measure of implicit adaptation was a between groups comparison at End Adaptation.

Computational modeling

Since the behavioral analysis only provides a brief (i.e., 5 strides) and somewhat arbitrary window into explicit learning and implicit adaptation, we used a computational

model to characterize each learning process. This approach allowed us to map the underlying learning processes and their subcomponents onto each participant's behavior. Specifically, we fit the model to individual data to obtain a unique set of parameter values for each participant. Since these parameters represent specific aspects of explicit and implicit learning, we can make inferences regarding the function of these underlying learning components (Charalambous et al. 2018; Mawase et al. 2014; Roemmich et al. 2016). Then, we compared the individual learning processes (i.e., model parameters) between the stroke and control groups.

This "voluntary correction" model was previously used to capture explicit and implicit learning in this paradigm (Roemmich et al. 2016), and the implicit adaptation component of the model can successfully capture split-belt adaptation behavior in individuals with stroke (Charalambous et al. 2018). The computational modeling used here followed that of Roemmich and colleagues which defines the Adaptation Index (x) on each stride (s) as the sum of both explicit learning ($x_{explicit}$) and implicit adaptation ($x_{implicit}$):

$$x_{[s]} = x_{explicit[s]} + x_{implicit[s]} \tag{3}$$

Both processes correct for the same error ($\text{error}_{[s]} = \text{perturbation}_{[s]} - x_{\text{implicit }[s]}$), where the perturbation = 1 during Adaptation and 0 during De-adaptation. Explicit learning is only active when the feedback is on:

$$x_{explicit[s+1]} = \begin{cases} B_{explicit} * error_{[s]}, & if\ feedback\ is\ on \\ 0, & if\ feedback\ is\ off \end{cases} \tag{4}$$

The free parameter, $B_{explicit}$, represents the learning rate for explicit learning as it is the proportion of error that is explicitly corrected from one stride to the next (i.e., higher values indicate faster learning). The implicit adaptation process has dual components, fast and slow,

305 and is active throughout the Adaptation and De-adaptation phases (Roemmich et al. 2016;
306 Smith et al. 2006):

307 $$x_{implicit[s]} = x_{fast[s]} + x_{slow[s]} \quad (5a)$$

308 $$x_{fast[s+1]} = A_{fast}x_{fast[s]} + B_{fast}error_{[s]} \quad (5b)$$

309 $$x_{slow[s+1]} = A_{slow}x_{slow[s]} + B_{slow}error_{[s]} \quad (5c)$$

310 Implicit learning has four free parameters. The learning rates, B_{fast} and B_{slow}, represent the
311 proportion of the error that is implicitly corrected from one stride to the next, and the
312 retention rates, A_{fast} and A_{slow}, represent the proportion of the current adapted state that is
313 retained. The fast process quickly learns from errors, but also quickly forgets, while the slow
314 process takes longer to learn from errors but retains longer (Smith et al. 2006).

315 Model fitting and model comparison

316 We fit the voluntary correction model to each participant's Adaptation Index data
317 during the Adaptation and De-adaptation phases using MATLAB's fmincon function, setting
318 the objective function as the sum of squared errors between the model output (x) and the data.
319 All parameters were constrained between 0 and 1. Additionally, we constrained the fast-
320 learning rate, B_{fast}, to be at least 5 times higher than the slow learning rate, B_{slow}; and the slow
321 retention rate, A_{slow}, was constrained to be greater than the fast retention rate, A_{fast}
322 (Roemmich et al. 2016; Smith et al. 2006). To ensure stable fits, we initialized the implicit
323 process parameters to the same values (Charalambous et al. 2018; Roemmich et al. 2016;
324 Smith et al. 2006) based on a prior locomotor adaptation study in individuals with stroke
325 (Charalambous et al. 2018): $A_{fast} = 0.92$, $B_{fast} = 0.03$, $A_{slow} = 0.996$, $B_{slow} = 0.004$. The
326 explicit parameter was initialized at uniformly random values between 0 and 1. To improve
327 the stability of the $B_{explicit}$ parameter, we performed 10 initializations for each participant. We

calculated model fits (r^2) using a bootstrapping procedure. We resampled with replacement the Adaptation and De-adaptation data 1000 times for each group, fitting the model to the bootstrapped samples. We report the mean and 95% confidence intervals of these r^2 values. We also calculated the r^2 of individual fits and report these the supplemental results, below.

To ensure that we did not overfit the data with the five-parameter, voluntary correction model, we also fit two simpler models to the data. For the single-rate model, the motor output (x; i.e., Adaptation Index) is the result of a single process that has two parameters B, the learning rate, and A the retention rate (Smith et al. 2006; Thoroughman and Shadmehr 2000):

$$x_{[s+1]} = A\, x_{[s]} + B\, error_{[s]} \tag{6}$$

Additionally, we fit a four-parameter, dual-rate model to the data (Charalambous et al. 2018; Roemmich et al. 2016; Smith et al. 2006). This dual-rate model represents motor output (x; i.e., Adaptation Index) as the sum of a fast and slow process. This model is equivalent to the implicit process in the voluntary correction model (equations 5a-c). Thus, neither alternative model includes a voluntary correction, or explicit learning component. We compared fits of the three different models using Akaike Information Criterion (AIC). We used a model recovery analysis to confirm that AIC was better than BIC at distinguishing between the three models for the current experiment (Wilson and Collins 2019).

Statistical analysis

For our Bayesian statistical analysis, we assumed the Adaptation Index data at each timepoint of interest (Feedback On, Feedback Off, End Adaptation, Implicit Aftereffect) was sampled from a normal distribution, with a mean which depended on both within subject (i.e., time) and between subject (i.e., group) parameters as well as an interaction parameter. We confirmed a normal distribution was a reasonable assumption for our data by observing

352 favorable model comparison results against a student's t distribution. We estimated the
353 posterior distribution for these means (and all the statistical model parameters) using Bayes
354 rule, combining the evidence from our data with our prior assumptions about each parameter.
355 The prior distributions for the between and within subject effects were set as a wide normal
356 distribution centred on 0, and the prior for the standard deviation was set as a wide, positive-
357 valued uniform distribution. Thus, our prior assumptions only served to make our inferences
358 more conservative and did not bias the posterior. We estimated the joint posterior distribution
359 in Python v4.3.0 using the PyMc 4 library (Salvatier et al. 2016) and the bayes-toolbox
360 Python package (Kim 2023). We used Markov Chain Monte Carlo sampling to sample from
361 joint posterior distribution 10,000 times with 2,000 tuning samples. We performed posterior
362 predictive checks to ensure that the posterior samples accurately represented the data
363 (Kruschke 2014; McElreath 2016).

364 This procedure allowed us to report the full range of credible differences between the
365 groups along with the probability of a difference, given our data. To accomplish this, we
366 compared the posterior distributions of between group differences which are presented as
367 histograms representing the full distribution of possible differences based on the data we
368 collected. For each posterior distribution, we report the mean and 95% high density interval
369 (HDI), defined as the narrowest span of credible values that contain 95% of the distribution
370 (Kruschke 2014). The HDI can be interpreted as the true value falling between this range
371 with 95% certainty. We also report the probability of a difference as a percentage of posterior
372 distribution samples on one side of zero (e.g., $p_{difference}$ = 94.7%).

373 ***Results***

374 Of the 21 individuals recruited to participate in the stroke group, we removed 4 from
375 the analysis due to an inability to properly complete the task (n=3) or follow instructions

(n=1). Average participant characteristics for each group are displayed in Table 1. In Figure 2, we display the mean, baseline-corrected step length asymmetry data during the Adaptation and De-adaptation phases for both groups. For ease of group comparisons, we present our primary analyses using the Adaptation Index. We note that similar results were obtained when using step length asymmetry index, with no impact on any of our inferences.

	Stroke Group (n=17)	Control Group (n=18)
Age (years)	64.5 ± 10.2	64.8 ± 9.6
Sex	9M / 8F	9M / 9F
Time since stroke (months)	71.0 ± 49.1	
Side of brain lesion	7R/10L	
Self-selected (overground) walking speed (m/s)	0.92 ± 0.27	1.33 ± 0.28
Fastest (overground) walking speed	1.29 ± 0.38	1.81 ± 0.22
Fast treadmill belt speed	0.94 ± 0.12	1.00 ± 0
Lower Extremity Fugl Meyer	25.41 ± 6.27	

Table 1 Group characteristics. Demographic and clinical characteristics of participants. All continuous variables are represented as mean ± 1 SD. (F = female, M = male, R = right, L = left)

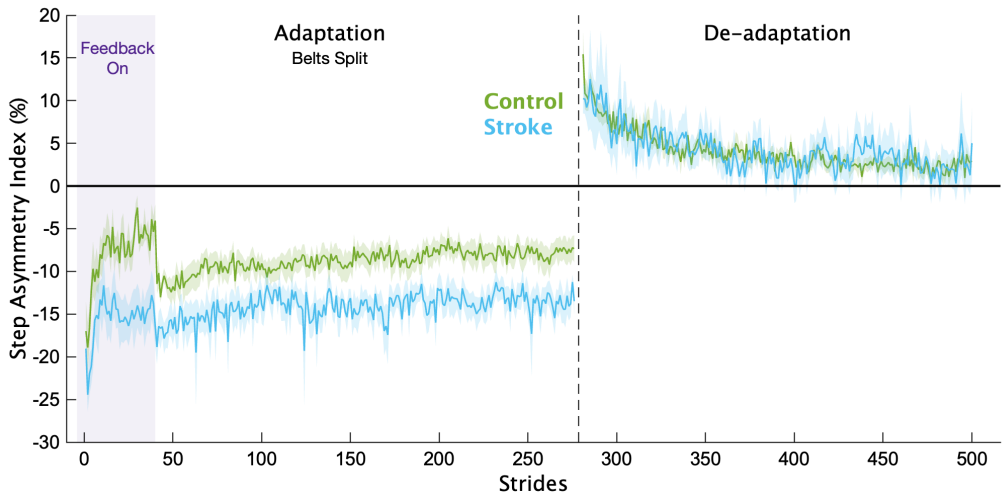

Figure 2 Step length asymmetry. Mean baseline-corrected step length asymmetry for each group for the Adaptation and De-adaptation phases. Purple shading is the time when the feedback was on. The vertical dashed line separates the Adaptation and De-adaptation phases. Each phase was truncated to the participant with the shortest phase for visualization purposes. Shading represents ±1 SEM.

In Figure 3, we display the mean Adaptation Index data and key timepoints of interest for each group. First, we determined if individuals with stroke had impairments in explicit learning (Figure 3B). Based on our instructions and previous work (Roemmich et al. 2016), we assumed participants used explicit learning only while the feedback was on during the Adaptation phase. Therefore, explicit learning magnitude was characterized as the difference in Adaptation Index between Feedback On and Feedback Off. This difference was larger for the control group (mean interaction effect [95% HDI] = 0.09 [-0.05 0.25], $p_{difference}$ = 88.2%), providing evidence that the individuals with stroke had diminished explicit learning compared to controls. Additionally, individuals in the stroke group were less able to use the visual feedback during Adaptation compared to controls (Figure 3C), with much lower Adaptation Index values during Feedback On (mean group difference = 0.23 [0.11 0.34], $p_{difference}$ = 100.0%). Combined, these results point to impairments in explicit learning in individuals with stroke compared to controls.

Next, we determined if individuals with stroke had impaired implicit adaptation by comparing the size of the implicit aftereffect (Figure 3D). The control group demonstrated larger implicit aftereffects compared to the stroke group (group difference = 0.10 [-0.02 0.21], $p_{difference}$ = 94.3%), providing evidence that individuals with stroke have impaired implicit adaptation compared to controls. Additionally, we found large and reliable differences between the groups at End Adaptation (group difference = 0.17 [0.07 0.28], $p_{difference}$ = 99.9%). Overall, the behavioral results indicate that impairments may exist in both explicit learning and implicit adaptation.

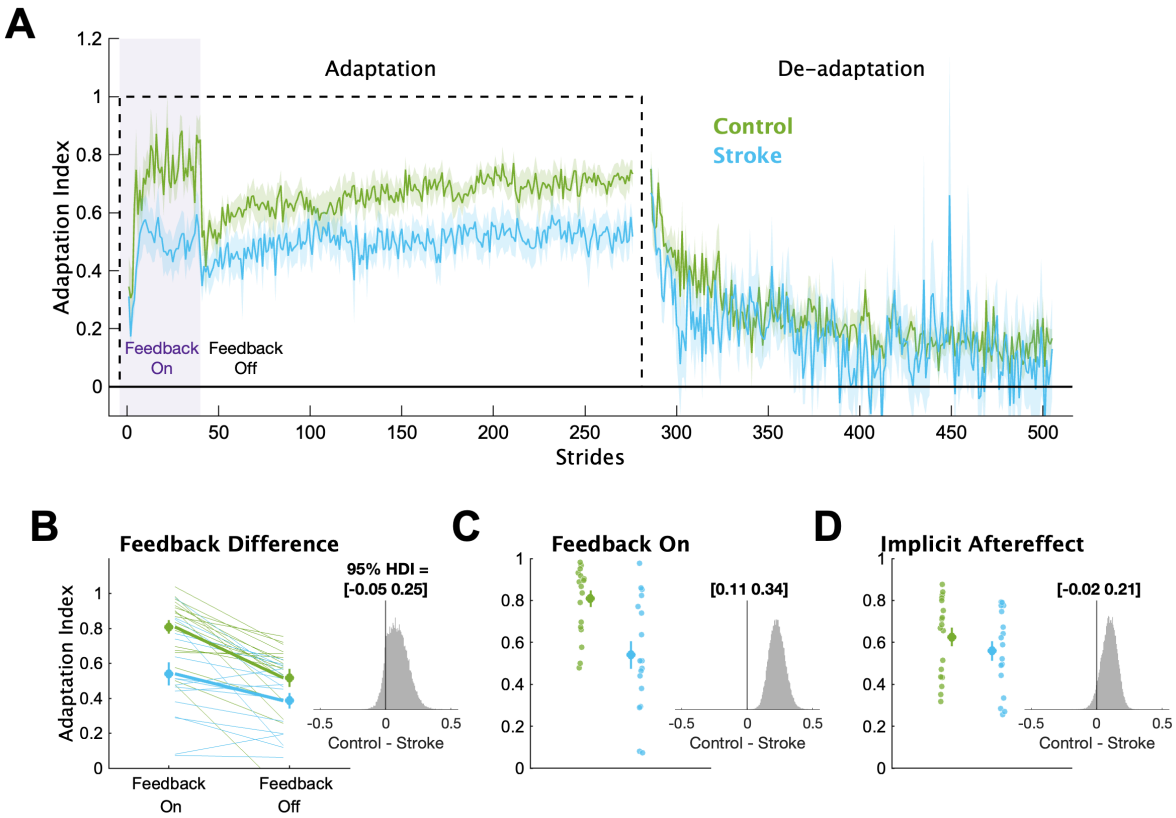

Figure 3 Adaptation Index. (**A**) Group averaged Adaptation Index data for the Adaptation and De-adaptation phases. The dashed line represents the walking period when the belts were split (i.e., the perturbation). Purple shading represents the time when the feedback was turned on. For visualization purposes, data for each phase were truncated to the individual with least number of strides. Solid lines represent group means, shading represents ±1 SEM. (**B**) Group and individual data for the Feedback On and Feedback Off timepoints. Thick lines represent the group average slopes. **(C)** Group and individual data for the Feedback On timepoint. **(D)** Group and individual data for the Implicit Aftereffect timepoint. For panels B-D, large circles and error bars represent the group means ±1 SEM and smaller dots represent individuals. The insets display a histogram of the posterior distribution for the between group differences. The black vertical line in the histogram is there to aid visualization of the credibility of a between group difference (i.e., how much of the posterior probability distribution is on one side of zero). We report the 95% HDI regarding the range of credible effect sizes above the insets of the posterior distributions.

To provide a more complete picture of how each individual learning process contributed to overall adaptation, we applied a series of computational models to the data. The voluntary correction model, specifically, allowed us to map each individual's behavior to explicit learning and implicit adaptation processes (Figure 4; see supplemental Figures S1-S2 for individual fits). This model fit the bootstrapped data well (stroke group mean r^2

[bootstrapped 95% CI] = 0.70 [0.11 0.89]; control group = 0.90 [0.81 0.95]). The model fits to the stroke group's behavior were more variable as compared to the control group, which is not surprising given that stroke participants tend to be more heterogeneous than age-matched controls. Nevertheless, the overall quality of fits to both groups was high. Importantly, we confirmed that the voluntary correction model had better (lower) AICs then both the single rate and the dual rate model for both the stroke (single rate AIC difference mean [95% HDI] = 111 [54 167], $p_{difference}$ = 100.0%; dual rate AIC difference = 36 [-20 89], $p_{difference}$ = 89.9%) and control groups (single rate AIC difference = 281 [226 336], $p_{difference}$ = 100.0%; dual rate AIC difference = 89 [35 142]; $p_{difference}$ = 99.9%), indicating that the voluntary correction model accurately characterizes learning on this task without overfitting. As the single- and dual-rate state-space models do not include a voluntary correction process, these results also support our assumption that explicit learning contributed to behavioral change specifically when visual feedback was on.

Comparing the individual parameters from the voluntary correction model allowed us to determine the specific components of learning that were impaired. The learning rate parameter for explicit learning, $B_{explicit}$, served as a measure of each individual's explicit learning ability, with higher values indicating faster explicit learning (Figure 4C). The stroke group had much smaller $B_{explicit}$ values compared to the control group (group difference = 0.23 [0.06 0.40], $p_{difference}$ = 99.5%), providing strong support for the hypothesis that explicit learning is impaired in individuals with stroke compared to controls. Next, we examined the four implicit adaptation process parameters (Figure 4F-G). While there was evidence of differences between groups for most parameters, the magnitude of differences for three of the four were near zero (group differences: A_{slow} = 0.00 [-0.00 0.01], $p_{difference}$ = 87.7%; B_{slow} = 0.00 [-0.00 0.00], $p_{difference}$ = 68.2%, B_{fast} = 0.01 [-0.01 0.03], $p_{difference}$ = 84.7%). In contrast, there was a marked difference in the retention rate for the fast state (A_{fast} group difference =

0.09 [-0.04 0.24], $p_{difference}$ = 92.6%). Thus, it appears that individuals with stroke, as a group, have a specific impairment in their ability to retain what was learned by the fast implicit adaptation process. In sum, the results of our computational modeling provided strong support for the hypothesis that explicit learning is impaired post-stroke and revealed that the retention rate for the fast state could underlie slower implicit adaptation in stroke.

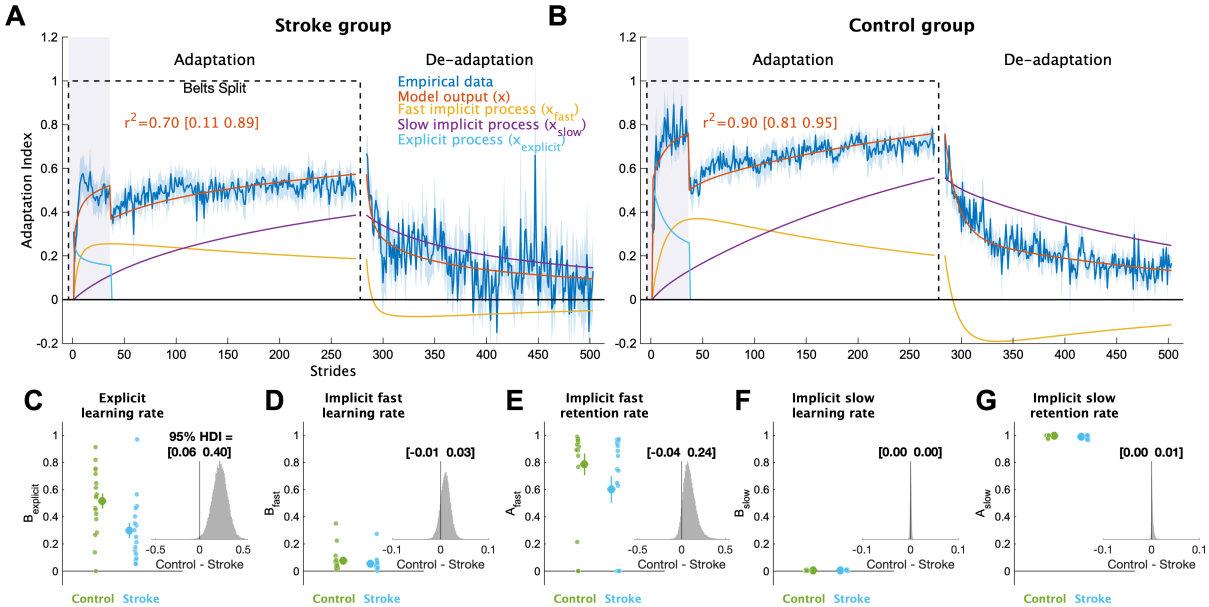

Figure 4 Computational model results. Mean model fits to bootstrapped samples plotted against the empirical data for the **(A)** stroke group and **(B)** control group. See supplemental Figures 1 and 2 for the model fits for each individual participant. Purple shading represents the time when the feedback was turned on. For visualization purposes, data for each phase were truncated to the individual with least number of strides. Shading represents ±1 SEM **(C-G)** Model parameter values for each group. Large circles and error bars represent the group means ±1 SEM and smaller dots represent individuals. The insets are histograms of the posterior of the between groups difference (contrast) in parameter values. We report the 95% HDI regarding the range of credible effect sizes above the insets of the posterior distributions. Note the scale of the x-axis varies for these inset plots.

Discussion

In the current study, we examined explicit learning and implicit adaptation within the same locomotor learning task in individuals with chronic, hemiparetic stroke. We combined a behavioral manipulation and computational modeling to determine the presence, and

481 potential degree, of impairment in both learning processes. The majority of work in
482 locomotor learning and stroke has primarily studied implicit adaptation (Betschart et al. 2017;
483 Charalambous et al. 2018; Reisman et al. 2007; Savin et al. 2013; Tyrell et al. 2014), with
484 less attention paid to explicit learning (French et al. 2021b, 2021a). While some gait studies
485 have examined both processes in the same task (Cherry-Allen et al. 2018; Day et al. 2019;
486 Moore et al. 2022; Mutha et al. 2011; Schaefer et al. 2009), only two studies in reaching have
487 attempted to discern their individual contributions to overall motor learning (Binyamin-
488 Netser et al. 2023; Taylor and Ivry 2014). To our knowledge, the current study is the first to
489 assess explicit and implicit motor learning within the same task in individuals with chronic
490 stroke using both behavioral manipulations and computational modeling. While our sample
491 size is relatively small, our results provide strong evidence that stroke impairs explicit
492 learning and the rate of implicit adaptation during a locomotor task that elicits dissociable
493 contributions from both processes. This has important implications for the design of
494 locomotor learning tasks in post-stroke rehabilitation because many interventions involve
495 both explicit and implicit components.

496 Explicit learning is impaired in chronic stroke

497 We found that individuals with chronic, hemiparetic stroke have impairments in
498 explicit learning in a locomotor task involving both explicit learning and implicit adaptation.
499 Individuals with stroke had a smaller change in behavior compared to controls after the visual
500 feedback, intended to drive and support explicit learning, was removed. Additionally, the
501 computational modeling revealed significantly slower explicit learning in individuals with
502 stroke.

503 While there are few prior studies assessing both explicit learning and implicit
504 adaptation in the same task after stroke, one experiment in reaching showed that individuals

with lateral prefrontal cortex (LPFC) lesions demonstrate impairments in explicit learning (Taylor and Ivry 2014). This and other work raises the possibility that cognitive processes such as working memory or general cognition in reaching studies (Anguera et al. 2011; Binyamin-Netser et al. 2023; Seidler et al. 2012; Vandevoorde and Orban de Xivry 2020), and fluid cognition in gait (French et al. 2021a) contribute to explicit motor learning, but more work is required to determine the specific contribution of cognition to explicit learning in stroke.

Contrary to the current findings, prior work in reaching (Binyamin-Netser et al. 2023) and gait (French et al. 2021b, 2021a) observed no differences in explicit learning in individuals with stroke compared to controls. However, the studies in gait used a primarily explicit task without a split-belt perturbation, likely making the task easier, which could reduce the ability to detect explicit learning deficits in stroke. The reaching study dissociated explicit learning and implicit adaptation using visual cues (the color and shape of a cursor). It is possible that either this manner of distinguishing between explicit and implicit processes or the broader inclusion criteria for their stroke group can account for the differences between their findings and those of the current study. Similar to Taylor and Ivry (Taylor and Ivry 2014), we provided clear instructions and removed all visual feedback to ensure explicit learning was "switched off", and provided a narrower range of inclusion criteria, potentially explaining why our results were more consistent with theirs. Still, it is critical to determine if the manner of eliciting explicit learning (a specific type of cue or instruction) impacts the ability to use this process in stroke given its ubiquity in rehabilitation settings.

<u>Slower implicit adaptation in stroke is due to worse retention of the fast process</u>

Contrary to our hypothesis, we found evidence that implicit adaptation is impaired after stroke. The stroke group demonstrated smaller implicit aftereffects and a lower plateau

529 at the end of the Adaptation phase indicating a smaller overall magnitude of implicit
530 adaptation. Prior studies in locomotor adaptation after stroke indicate that the overall
531 magnitude of implicit adaptation is similar to controls, but the rate is slower (Malone and
532 Bastian 2014; Reisman et al. 2007; Savin et al. 2013; Tyrell et al. 2014). Therefore, the
533 slower rate of adaptation in stroke, combined with the relatively short Adaptation phase in the
534 current study (8 minutes compared to 10-15 minutes in the prior studies), could have
535 prevented us from observing asymptotic adaptation.

536 While it may seem that the visual feedback interfered with implicit adaptation for the
537 stroke group, prior work in young individuals with intact neurologic systems demonstrate that
538 visual feedback used to either help or hinder performance during split-belt walking does not
539 change the total magnitude of implicit adaptation (Long et al. 2016; Malone and Bastian
540 2010; Roemmich et al. 2016). Additionally, individuals with stroke can successfully adapt to
541 the split-belt treadmill while also explicitly learning to change a separate gait parameter (knee
542 flexion angle) using visual feedback (Cherry-Allen et al. 2018). Therefore, it is unlikely that
543 explicit learning itself hindered implicit adaptation in the current study since implicit
544 adaptation proceeds in spite of explicit learning, and even worsens performance in some
545 cases (Mazzoni and Krakauer, Taylor and Ivry 2011), across reaching and walking paradigms
546 (Mazzoni and Krakauer 2006; Roemmich et al. 2016), including in stroke (Binyamin-Netser
547 et al. 2023; Cherry-Allen et al. 2018; Taylor and Ivry 2014).

548 The computational modeling utilized in this study provides insight into why the
549 learning rate of implicit adaptation was impaired in stroke in this task. The voluntary
550 correction model incorporates a dual-rate model of adaptation which frames implicit
551 adaptation as the combination of a fast state and a slow state (Smith et al. 2006). These states
552 represent updates to an internal model, a prediction of the sensory consequences of
553 movement, that could occur either in the cerebellum or motor cortex (Smith et al. 2006). One

554 theory suggests that the motor cortex is responsible for retention of the adapted state while
555 the cerebellum is responsible for learning (Galea et al. 2011; Li et al. 2001). Thus, damage to
556 motor cortices or possibly its outputs could explain poor retention of the fast process in
557 individuals with stroke. Alternatively, the fast process has been closely linked to explicit
558 learning during visuomotor rotation tasks (Krakauer et al. 2019; Taylor and Ivry 2014).
559 However, to date there is no evidence of contributions from explicit learning to standard
560 split-belt adaptation (i.e., without additional visual feedback; Charalambous et al. 2018;
561 Mawase et al. 2014; Roemmich et al. 2016). Another possibility is that the fast state
562 represents a reactive balance element that is sensitive to environmental changes (Mariscal et
563 al. 2023). Future studies are required to dissociate between these potential explanations.

564 ***Conclusion***

565 Motor learning involves multiple processes, both explicit and implicit, that work
566 together to improve overall task performance. We found that individuals with chronic stroke
567 have impairments in explicit learning and implicit adaptation during a locomotor task that
568 elicits dissociable contributions from both. These findings are important because of the
569 potential application to post-stroke rehabilitation, which often combines different forms of
570 learning in a single task. To improve outcomes, future work should determine how locomotor
571 rehabilitation interventions can be structured to target these deficits and optimize overall
572 motor learning.

573

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580 ***Disclosures***

581 The Authors declare that there is no conflict of interest.

582 ***Author Contributions***

583 JMW, DSR, HEK Conceived and designed research; HW, LF, JMW performed experiments;
584 JMW analyzed data; JMW, ET, SMM, DSR, HEK interpreted results of experiments; JMW
585 prepared figures; JMW drafted manuscript; All authors edited and revised manuscript; All
586 authors approved final version of manuscript.

587

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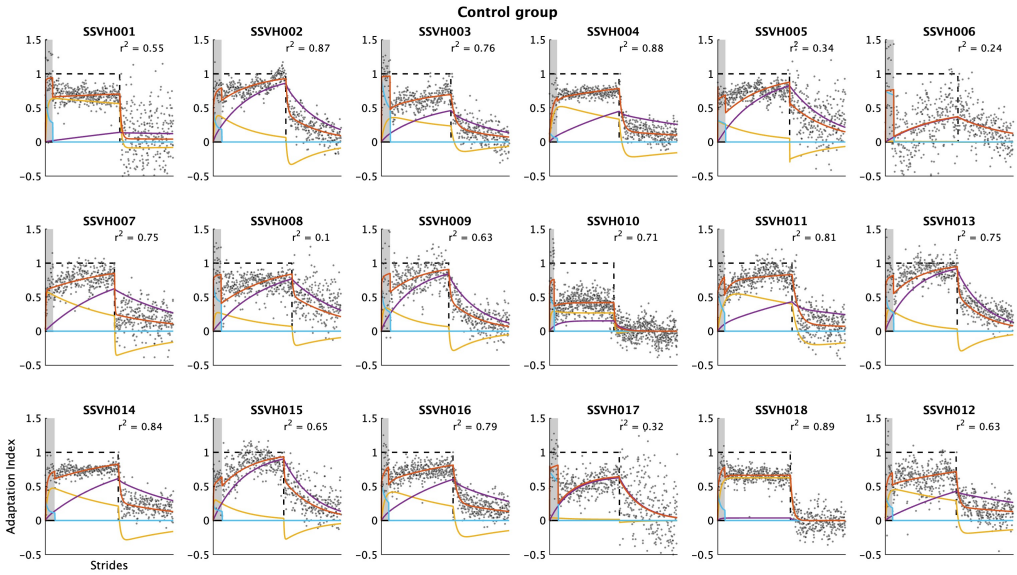
Supplemental material

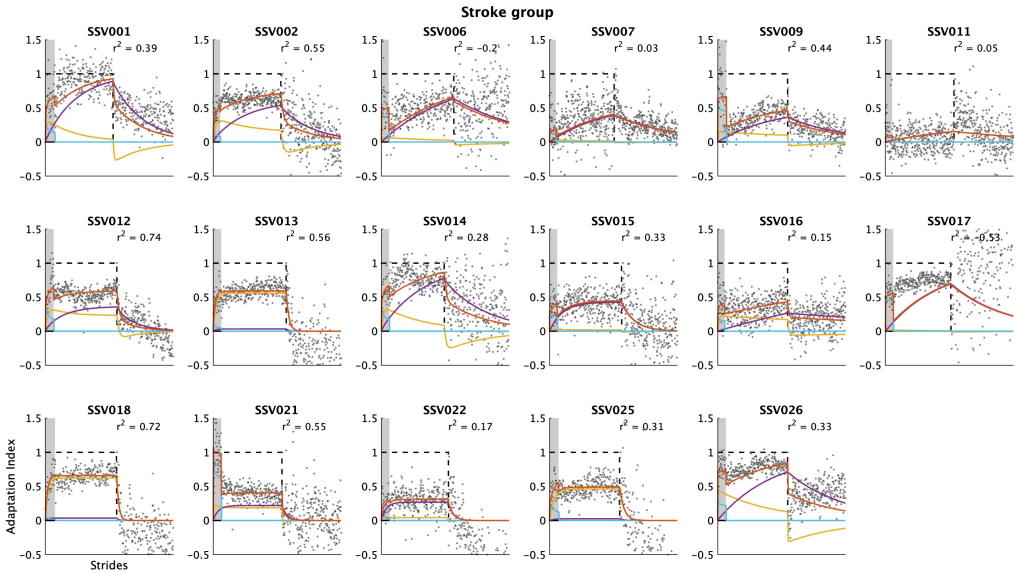
Explicit and implicit locomotor learning in individuals with chronic hemiparetic stroke.

Authors: Jonathan M. Wood, Elizabeth Thompson, Henry Wright, Liam Festa, Susanne M. Morton, Darcy S. Reisman, and Hyosub E. Kim

Supplemental Figures: Individual model fits



Supplemental Figure S1 Individual model fits for the control group. The voluntary correction model was fit to each participant's Adaptation Index data in the control group (n=18). Black dots represent the participant's Adaptation Index on that stride and the black dashed line represents the perturbation (which equals one during the Adaptation phase and 0 during De-adaptation phase). The red function represents the model's motor output (x), the light blue function (active only when the feedback is turned on – denoted by the gray shading) represents the explicit component ($x_{explicit}$), and the yellow and purple functions represent the fast (x_{fast}) and slow (x_{slow}) components of the implicit process, respectively.



Supplemental Figure S2 Individual model fits for the stroke group. The voluntary correction model was fit to each participant's Adaptation Index data in the stroke group (n=17). Black dots represent the participant's Adaptation Index on that stride and the black dashed line represents the perturbation (which equals one during the Adaptation phase and 0 during De-adaptation phase). The red function represents the model's motor output (x), the light blue function (active only when the feedback is turned on – denoted by the gray shading) represents the explicit component ($x_{explicit}$), and the yellow and purple functions represent the fast (x_{fast}) and slow (x_{slow}) components of the implicit process, respectively.