Reward timing matters in motor learning

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Abstract

Reward can improve motor learning and the consolidation of motor memories. Identifying the features of reward feedback that are critical for motor learning is a necessary step for successful integration into rehabilitation programs. One central feature of reward feedback that may affect motor learning is its timing – that is, the delay after which reward is delivered following movement execution. In fact, research on associative learning has shown that short and long reward delays (*e.g.*, 1 and 6 s following action execution) activate preferentially the striatum and the hippocampus, respectively, which both contribute with varying degrees to motor learning. Given the distinct functional role of these two areas, we hypothesized that reward timing could modulate how people learn and consolidate a new motor skill. In sixty healthy participants, we found that delaying reward delivery by a few seconds influenced motor learning dynamics. Indeed, training with a short reward delay (*i.e.,* 1 s) induced slow, yet continuous gains in performance, while a long reward delay (*i.e.,* 6 s) led to initially high learning rates that were followed by an early plateau in the learning curve and a lower endpoint performance. Moreover, participants who successfully learned the skill with a short reward delay displayed overnight consolidation, while those who trained with a long reward delay exhibited an impairment in the consolidation of the motor memory. Overall, our data show that reward timing affects motor learning, potentially by modulating the engagement of different learning processes, a finding that could be exploited in future rehabilitation programs.

Keywords

Motor learning, motor skill learning, memory consolidation, reward, motivation, reinforcement learning, timing.

1. Introduction

When delivered following well-executed movements, reward can boost motor learning [1–4] and the consolidation of motor memories [5]. This observation has raised hope for rehabilitation, where reward is regarded as a promising means to magnify the positive effects of practice on motor control [6–10]. Yet, this branch of research is only burgeoning, and a current challenge in the field is to identify the features of reward feedback that may be critical for motor learning.

Recent studies have started to tackle this issue, showing that the magnitude [1], the valence [2] and the stochasticity [11] of reward feedback bear all a decisive impact on motor learning. Another key feature of reward feedback that may directly affect motor learning is its timing – that is, the delay after which reward is delivered following movement execution. As such, previous studies have shown that reward prediction error signals, which are key for reward-based learning, are not only modulated by the value of the reward but also depend on the timing at which it is delivered [12–14]. Moreover, converging lines of evidence from neuroimaging and electroencephalographic studies indicate that different brain structures – known to be involved with varying degrees in motor learning – exhibit activity changes in response to reward feedback depending on its timing. Indeed, in associative learning tasks, short reward delays (*e.g.*, provided 1 s following action execution) activate a fronto-striatal network, while long reward delays (*e.g.*, 6 s following execution) evoke changes in the activity of the hippocampus primarily [15,16]. Further, Parkinson's disease and ADHD patients, both known to exhibit striatal dysfunction [17], are impaired in learning action-outcome associations based on short reward delays [15,18,19], while amnesic patients with damage to the hippocampus are unable to learn associations with long reward delays [20]. Altogether, these findings

indicate that the processing of reward preferentially engages striatum- or hippocampus-centred networks depending on the timing at which it is delivered.

The striatum and the hippocampus show varying contributions during motor learning and consolidation [21–24], which are thought to underlie the operation of distinct learning processes [25,26]. Hence, it is sensible to assume that reward may boost different motor learning processes – potentially relying on the striatum or the hippocampus – depending on the timing at which it is delivered. Notably, previous studies on reward-based motor learning have only exploited short reward delays, preventing one to test this hypothesis directly. Here, we tested this idea by evaluating the performance of sixty healthy participants in a skill learning task [1], where reward was delivered either at a short or at a long delay following movement execution. We found that delaying reward delivery by a few seconds influenced the dynamics of learning. Indeed, training with a short reward delay induced slow, yet continuous gains in performance, while a long reward delay led to initially high learning rates that were followed by an early plateau in the learning curve and a lower endpoint performance. Moreover, participants who successfully learned the skill with a short reward delay displayed overnight consolidation, while those who trained with a long reward delay exhibited an impairment in the consolidation of the motor memory. Altogether, the present results provide evidence that reward timing can strongly influence motor learning, a finding that could be exploited in future rehabilitation protocols.

2. Results

Sixty healthy participants practiced a pinch-grip force task over two consecutive days. Participants were required to hold a pinch grip transducer in their right hand and to squeeze it as quickly as possible in order to move a cursor displayed on a computer screen in front of them, from an initial position to a fixed target [1] (**Figure 1A**). The force required to reach the target ($Target_{Force}$) corresponded to 10 % of the individual maximum voluntary contraction (MVC). In most of the trials (90 %), participants practiced the task with very limited sensory feedback: the cursor disappeared when the generated force reached half of the $Target_{Force}$ (see STAR Methods for more details on the task). To learn the task, subjects were provided with six Training blocks (T1 to T6; 40 trials each; *i.e.*, total of 240 training trials; **Figure 1B**) in which they received reinforcement feedback (*i.e.*, indicating Success or Failure) associated to a monetary reward. Success on the task was determined based the Error, defined as the absolute force difference between the $Target_{Force}$ and the exerted force [5,27].

In different groups of participants, we varied the delay between the end of the movement period and the delivery of the reward during the Training blocks. As such, $Group_{Short}$ subjects trained with a short reward delay (*i.e.,* 1 s) while participants of the $Group_{Long}$ performed the task with a long reward delay (*i.e.,* 6 s). The total duration of the trials was kept constant by modulating the inter-trial interval (ITI; 6 s in $Group_{Short}$ and 1 s in $Group_{Long}$). Before, immediately and 24 hours after training, all participants performed Test blocks with no reward, a short reward delay (1 s) and a short ITI (1 s). Notably, the groups were comparable for a variety of features including Pre-training success rates, difficulty of the task, force required, sensitivity to reward and

punishment, fatigue and final monetary gains (**Figure 1C**, **Table 1**). Altogether, this design allowed us to investigate the specific effect of reward timing on motor learning and consolidation.

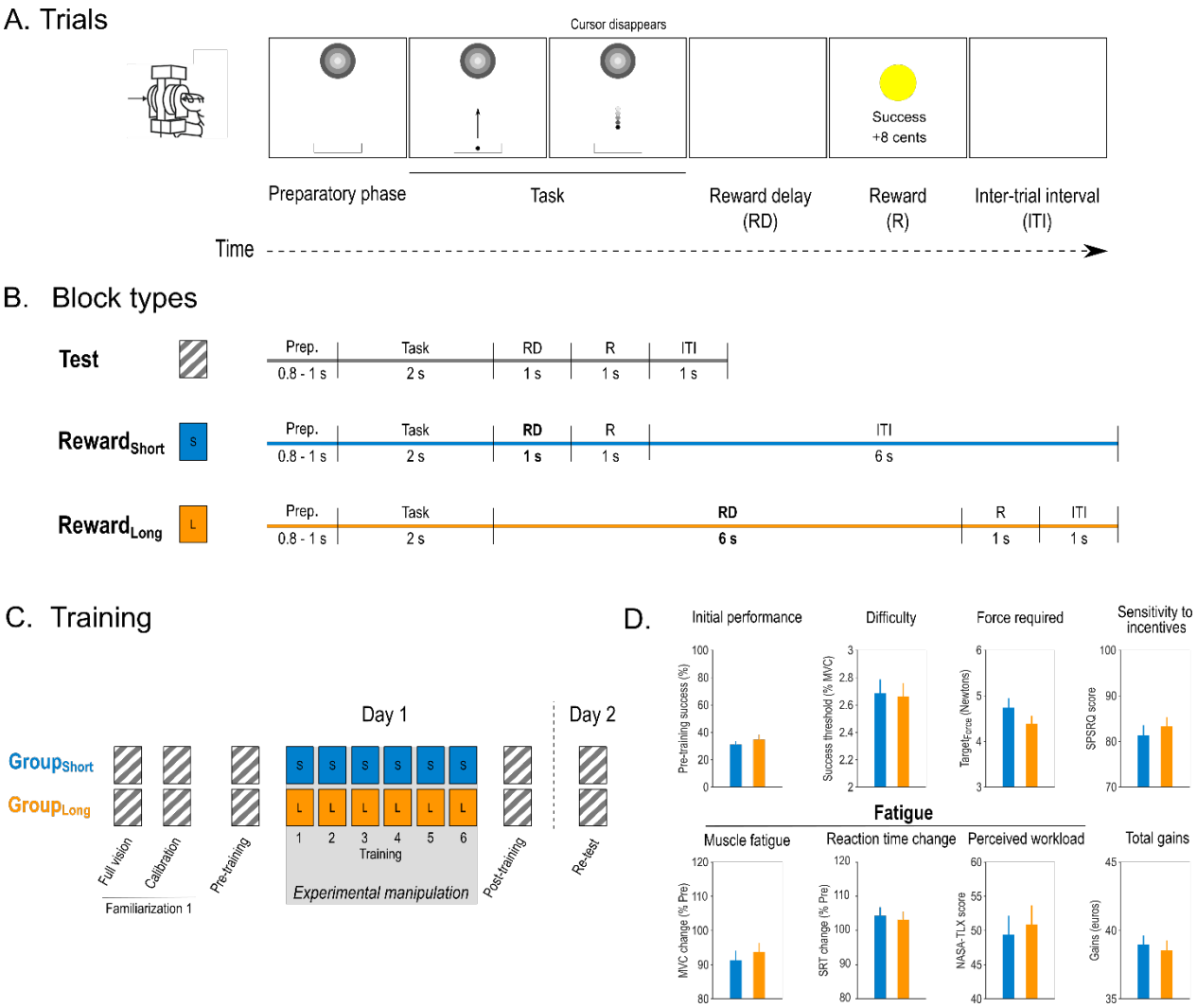

Figure 1. Motor skill learning task. A. Time course of a trial in the motor skill learning task. Each trial started with the appearance of a sidebar and a target. After a variable preparatory period (0.8-1s), a cursor appeared in the sidebar, playing the role of a "Go" signal. At this moment, participants were required to pinch the force transducer to bring the cursor into the target as quickly as possible and maintain it there until the end of the task (2 s). Notably, on most trials, the cursor disappeared halfway towards the target (as displayed here). Then, after a delay, a reward (R) appeared consisting in a reinforcement feedback and a monetary reward (a successful trial is shown here). Trials ended with an inter-trial interval (ITI). **B. Durations in the different block types.** Reward delays (RD) and ITIs were manipulated. Test blocks included a short reward delay (1 s), a short ITI (1 s) and no monetary reward (*i.e.,* only reinforcement). Reward$_{Short}$ and Reward$_{Long}$ blocks included monetary rewards and were performed with a short (1 s) and long (6 s) reward delay, respectively. The total duration of the trials was kept constant between Reward$_{Short}$

and $Reward_{Long}$ by varying the ITI. **C. Training procedure.** On Day 1, all participants performed two familiarization blocks in a Test blocks condition. The first one involved full vision of the cursor while the second one provided only partial vision and served to calibrate the difficulty of the task on an individual basis (See STAR Methods). Then, Pre- and Post-training Test blocks assessments were separated by 6 blocks of training in the condition corresponding to each individual group ($Reward_{Short}$ for $Group_{Short}$, $Reward_{Long}$ for $Group_{Long}$). Day 2 consisted in a short re-familiarization (5 trials with full vision, not represented) followed by a Re-test assessment (1 Test block). **D. Control analyses.** $Group_{Short}$ and $Group_{Long}$ were comparable for a variety of factors including initial performance, task difficulty, required force to reach the target, sensitivity to reward and punishment (as assessed by the SPSRQ questionnaire), muscular and cognitive fatigue and final monetary gains (see also Table 1).

Training with long reward delays induces an early plateau in learning and a reduction of endpoint performance

As a first step, we evaluated performance on the task by computing the average success rate per $Training_{Block}$ (T1 to T6). To compare the learning process between the groups, we performed a two-way ANOVA, with $TRAINING_{BLOCK}$ and $GROUP_{TYPE}$ as within- and between-subject factors, respectively. Overall, participants of both groups significantly improved their success rates over training (main effect of $TRAINING_{BLOCK}$: Greenhouse-Geisser [GG]-corrected $F_{(3.56, 206.77)} = 6.01$; $p < 0.001$, partial $\eta^2 = 0.094$; **Figure 2A**). Most importantly, the improvement in success rate over the blocks depended on the $Group_{Type}$, as revealed by a significant $TRAINING_{BLOCK}$ x $GROUP_{TYPE}$ interaction (GG-corrected $F_{(3.56, 206.77)} = 2.69$; $p = 0.038$, partial $\eta^2 = 0.044$; **Figure 2A**). As such, in $Group_{Short}$, performance only started to improve significantly at T4 relative to T1 (T4 vs. T1: $p = 0.044$; T5 vs T1: $p = 0.030$; T6 vs T1: $p < 0.001$) and kept improving in late $Training_{Blocks}$ (T6 vs T3: $p < 0.001$; T6 vs T4: $p = 0.034$; T6 vs T5: $p = 0.051$). In contrast, $Group_{Long}$ improved early on (*i.e.*, T2 vs T1: $p < 0.001$) but then stopped improving quickly during training, with the success rate at T2 being not different from the success rate at any of the following $Training_{Blocks}$ (all $p > 0.37$). Interestingly, post-hoc tests further revealed that endpoint performance (*i.e.*, success rate at T6)

158 was significantly lower in $Group_{Long}$ than in $Group_{Short}$ ($p = 0.047$; **Figure 2B**). Conversely, success
159 rates at all other $Training_{Blocks}$ were comparable between the two groups (all $p > 0.22$; **Figure 2A**).
160 Altogether, these findings suggest that reward timing can influence the dynamics of motor learning.
161 More specifically, it appears that training with long reward delays is associated with an early
162 plateau in learning and a related reduction of endpoint performance.

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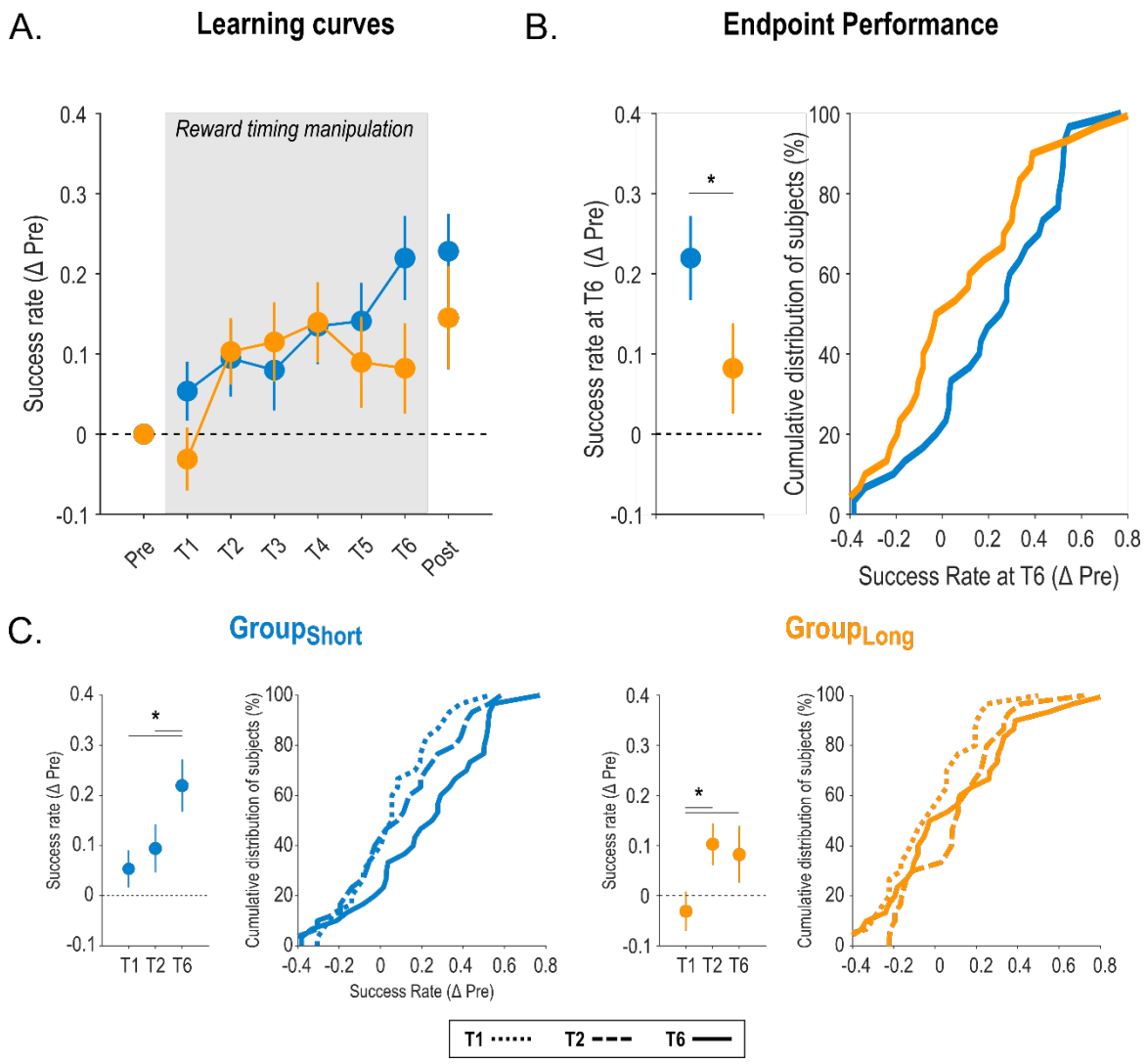

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165 **Figure 2. Effect of reward timing on motor skill learning. A. Learning curves**. Proportion of successful
166 trials (expressed as a difference with the individual Pre-training success rate) is represented across practice
167 for the two experimental groups (blue: $Group_{Short}$, orange: $Group_{Long}$). The grey shaded area highlights the

blocks concerned by the reward timing manipulation. The remaining blocks were Test blocks. **B. Endpoint performance**. Average success rates in the end of the training period (i.e., measured at T6) in the two groups (left panel) and the corresponding cumulative distributions of the data (right panel). **C. Learning dynamics.** Average success rates observed at T1 (dotted line), T2 (dashed line) and T6 (solid line) and the corresponding cumulative distributions for $Group_{Short}$ (left) and $Group_{Long}$ (right panel). Performance improved very early in $Group_{Long}$ (i.e., between T1 and T2) and then plateaus while it improved later in $Group_{Short}$. Note that performance at T1 was not different between the groups (all $p > 0.21$). *: significant difference ($p<0.05$). Data are represented as mean ± SE.

An important aspect of our experimental design is that we increased the duration of the ITI in $Group_{Short}$ relative to $Group_{Long}$ (6 s and 1 s, respectively; **Figure 1B**), in order to match the total duration of the trials in both groups despite differences in reward timing. To verify that such manipulation did not impact learning in our task, we added in the analysis another group of participants, who trained with a short reward delay (0.5 s) and an intermediate ITI (3 s; $Group_{Short\text{-}PastStudy}$, n = 30; from [1]). We reasoned that, if differences in learning dynamics were truly driven by differences in reward timing but not by differences in ITI duration, learning in $Group_{Short\text{-}PastStudy}$ should be similar than in $Group_{Short}$, and therefore different than in $Group_{Long}$. Consistently, post-hoc tests run on the $TRAINING_{BLOCK}$ x $GROUP_{TYPE}$ interaction (GG-corrected $F_{(3.78, 328.92)} = 2.84$; $p = 0.0020$, partial $\eta^2 = 0.061$) showed (1) no difference at any $Training_{Blocks}$ between $Group_{Short\text{-}PastStudy}$ and $Group_{Short}$ (all $p > 0.23$) and (2) a trend for a difference in endpoint performance when comparing $Group_{Short\text{-}PastStudy}$ and $Group_{Long}$ (*i.e.*, $p = 0.049$ and 0.053 at T5 and T6, respectively), similarly as when comparing $Group_{Short}$ and $Group_{Long}$ (**Supplementary Figure 1**). Hence, these results confirm that a change of a few seconds in ITI duration does not impact motor learning, as previously reported [28], implying that the differences in learning dynamics observed in groups exposed to short and long reward delays did not result from differences in ITI duration but rather from actual differences in reward timing.

To evaluate total learning we computed success rates at Post-training, which was performed in a Test block setting in both groups. Overall, success rates increased by 22.8 ± 4.69 % in $Group_{Short}$, and 14.5 ± 6.42 % in $Group_{Long}$ with respect to Pre-training. Interestingly, success rates at Post-training were significantly different from 0 in $Group_{Short}$ despite Bonferroni correction (cutoff for significance: $p = 0.025$; $t_{(29)} = 4.87$, $p < 0.001$), indicative of a significant improvement in performance with respect to Pre-training. In contrast, success rates at Post-training were not significantly different from 0 in $Group_{Long}$ after Bonferroni correction ($t_{(29)} = 2.26$, $p = 0.031$). However, a t-test on these data did not show any significant difference between the $Group_{TYPES}$ ($t_{(58)} = 1.05$; $p = 0.30$). Hence, reward timing only induced a subtle change in total learning that did not reach significance when comparing directly the groups.

Results of the first analysis suggest that reward timing influenced the dynamics of the learning process with long reward delays being associated with a fast improvement of performance quickly followed by a plateau. To confirm this, we aimed at directly quantifying the learning rates for early and late phases of training ($Training_{Early}$ and $Training_{Late}$, corresponding to T1-T3 and T4-T6, respectively). To do so, for each subject and each training phase, we split the data into 12 bins of 10 trials, computed the average success rate for each bin and then performed linear regressions over the bins for each $Training_{Phase}$ (*i.e.*, 12 bins per $Training_{Phase}$; **Figure 3A**). The slopes of the linear fits (*i.e.*, expressed in ΔSuccess rate per bin of trials) were exploited as a proxy of the learning rate at a given $Training_{Phase}$ (**Figure 3B, C**). A two-way ANOVA did not show any main effect of the factor $TRAINING_{PHASE}$ ($F_{(1, 58)} = 2.80$; $p = 0.10$, partial $\eta^2 = 0.046$), nor any effect of $GROUP_{TYPE}$ on the learning rates ($F_{(1, 58)} = 0.14$; $p = 0.71$, partial $\eta^2 = 0.0023$). Interestingly though, we found a strong $TRAINING_{PHASE}$ x $GROUP_{TYPE}$ interaction on these data ($F_{(1, 58)} = 9.13$; $p = 0.0037$, partial $\eta^2 = 0.14$; **Figure 3A, B, C**). This interaction was driven by the fact that learning

rates were comparable across training phases in $Group_{Short}$ ($p = 0.34$), while they were significantly lower at $Training_{Late}$ than at $Training_{Early}$ in $Group_{Long}$ ($p = 0.0016$; **Figure 3B, D, E**). Consistently, learning rates were higher in $Group_{Short}$ than in $Group_{Long}$ at $Training_{Late}$ ($p = 0.017$). This tended to be the opposite at $Training_{Early}$ ($p = 0.061$). Notably, intercepts of the linear fits were not significantly different between the groups, neither at $Training_{Early}$ ($t_{(58)} = 1.07$, $p = 0.29$), nor at $Training_{Late}$ ($t_{(58)} = -1.33$, $p = 0.19$), indicating that between-group differences in learning rates could not be accounted for by differences in initial performance. Hence, this analysis confirms that training with short reward delay induces slow, yet continuous gains in performance, while long reward timings engender large initial learning rates that then drop significantly, indicative of a plateau in learning. Overall, the data show that reward timing impacts learning dynamics during a motor training.

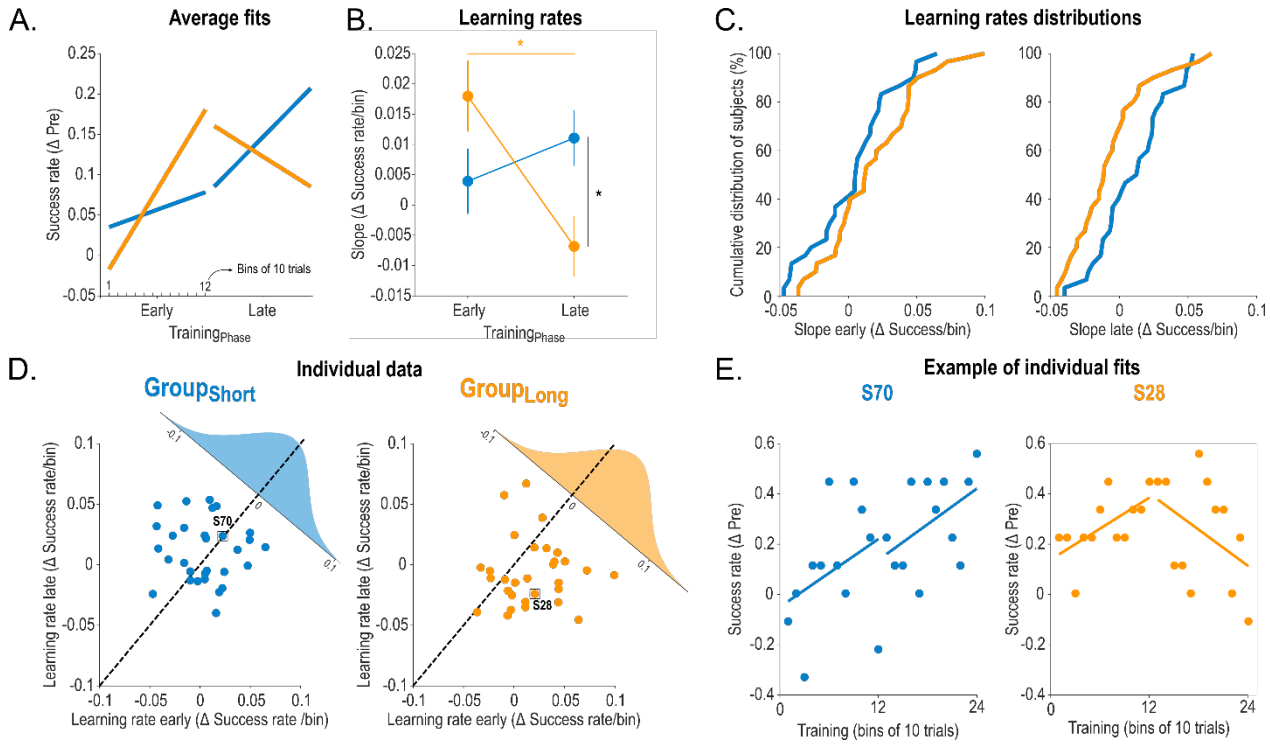

Figure 3. Effect of reward timing on learning rates. **A. Average fits**. Average fits for $Group_{Short}$ (blue) and $Group_{Long}$ (orange) obtained through linear regression on each subject's binned success data (expressed as a difference from Pre-Training) at early and late phases of training. **B. Learning rates.** The slope of the individual fits – expressed as a delta of success rate per bin on the y-axis – was exploited as a proxy of the learning rate for early and late phases of training. Note the significant $TRAINING_{BLOCK}$ x $GROUP_{TYPE}$ interaction which was driven by the fact that while learning rates were stable in $Group_{Short}$, they were initially high in $Group_{Long}$ and dropped significantly at $Training_{Late}$ (orange star). Moreover, learning rates at $Training_{Late}$ were significantly lower in $Group_{Long}$ than in $Group_{Short}$ (black star). **C. Learning rates distributions.** Cumulative distributions of the group data for early (left panel) and late (right panel) learning phases. **D. Individual learning rates.** Scatter plot representing each subject's learning rate for early (x-axis) vs late (y-axis) $Training_{Phases}$. The group distributions of the change in learning rates ($Training_{Early}$ – $Training_{Late}$) are also represented (upper right corner of each plot). Note the shift in $Group_{Long}$ below the identity line reflecting the higher learning rates at $Training_{Early}$ than at $Training_{Late}$. **E. Example of individual fits.** Binned success rates and the corresponding linear fits are represented for an exemplar subject of $Group_{Short}$ (left) and $Group_{Long}$ (right). *: significant difference ($p<0.05$). Data are represented as mean ± SE.

Training with long reward delay impairs overnight skill consolidation

As a last step, we investigated the impact of the reward timing experienced during training on Day 1 on overnight consolidation of the skill (*i.e.*, on Day 2). Because this analysis was focused on the consolidation of a learned motor skill, we only included participants who demonstrated learning on Day 1 (n = 22 and 18 in $Group_{Short}$ and $Group_{Long}$, respectively). To evaluate consolidation, we performed a two-way ANOVA on the normalized success rates obtained at Post-training of Day 1 and at Re-test of Day 2 (*i.e.*, both performed in a Test block setting) with $TEST_{BLOCK}$ and $GROUP_{TYPE}$ as within and between-subjects factors, respectively. The ANOVA showed a significant effect of $TEST_{BLOCK}$ ($F_{(1, 38)} = 5.44$; $p = 0.025$, partial $\eta^2 = 0.13$): success rates were on average smaller in the Re-test block on Day 2 than in the Post-training block on Day 1. However, this effect was mostly driven by the $Group_{Long}$, in which performance deteriorated overnight. As such, the ANOVA also revealed a $TEST_{PHASE}$ x $GROUP_{TYPE}$ interaction ($F_{(1, 38)} = 5.77$; $p = 0.021$, partial $\eta^2 = 0.13$). While performance was comparable between learners of the two groups at Post-training on Day 1 ($p = 0.65$), success rates were significantly reduced on Day 2 relative to Day 1 in $Group_{Long}$ ($p = 0.0028$), but remained stable from one day to another in

Group$_{Short}$ (p = 0.95). This indicates that delaying rewards on Day 1 impaired consolidation of the motor skill on Day 2. Overall, our results support the view that short or long reward delays support qualitatively different motor learning processes during training, leading to different consolidation of the skill.

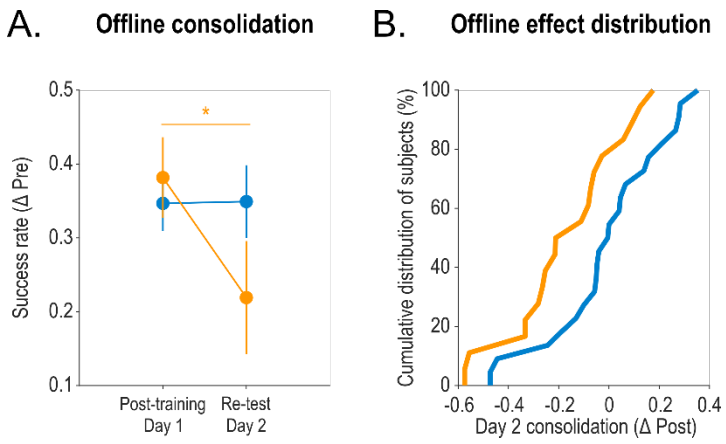

Figure 4. Effect of reward timing on overnight consolidation of the motor skill. **A. Offline consolidation of the motor skill.** Proportion of successful trials (expressed as a difference with the individual Pre-training success rate) at Post-training (Day 1) and Re-test (Day 2). Both assessments were Test blocks. This analysis only considered participants who demonstrated skill learning on Day 1 (n = 22 and 18 in Group$_{Short}$ and Group$_{Long}$, respectively). Notably, a significant TEST$_{PHASE}$ x GROUP$_{TYPE}$ interaction showed that while Group$_{Short}$ participants performed comparably well in Post-training and Re-test, demonstrating offline consolidation of the skill, this process was altered in Group$_{Long}$. **B. Offline effect distribution.** Cumulative distributions of the offline effect (Success rate in Day 2 – Success rate in Post-training) for each Group$_{Type}$

3. Discussion

Previous studies have shown that reward timing can influence the response of brain structures involved in reward processing during associative learning [12–15,20]. Inspired by these neurophysiological findings, we asked whether reward timing can also influence how people learn and consolidate a new motor skill. We found that delaying reward delivery by a few seconds influences motor learning dynamics: training with a short reward delay induced slow, yet continuous gains in performance, while a long reward delay allowed high initial learning rates that were followed by an early plateau in the learning curve and a lower endpoint performance. Moreover, among participants who successfully learned the skill, those who trained with a short reward delay displayed overnight consolidation, while those who learned the task with a long reward delay exhibited an impairment in the consolidation of the motor memory. Overall, our findings show that reward timing can influence how the brain learns and consolidates new motor skills.

The differences in learning dynamics observed in subjects trained with short and long reward delays may indicate that reward boosted processes presenting different temporal dynamics. As such, a prevalent view in the field is that motor learning entails the operation of distinct processes, with either slow (*i.e.,* developing over a few trials) or fast (*i.e.,* developing over tens/hundreds of trials) temporal dynamics [29]. The slow process is characterized by both a low learning rate and a sluggish forgetting of the acquired behaviour and is thought to reflect implicit learning [28,30]. In contrast, the fast process entails both a high learning rate and a quick forgetting of the new behavior and supports the explicit learning of new motor behaviors [28,30]. The nature of our task did not allow us to evaluate the relationship between reward timing and the relative contribution of implicit and

297 explicit learning. Still, people who trained with a short reward delay exhibited learning dynamics
298 that presented a low learning rate and a clear overnight consolidation – reminiscent of the slow
299 process, while those who trained with a long reward delay exhibited a high initial learning rate and
300 an overnight forgetting of the motor memory – evocative of the fast process. Based on these results,
301 one may suggest that short reward delays preferentially facilitate the slow (implicit) process, while
302 long reward delays may favour the fast (explicit) learning process, accentuating their respective
303 contribution to subjects' improvements, an interesting issue for future investigation.

304 Interestingly, neurophysiological data also support the latter interpretation. Indeed, the
305 striatum – which is preferentially recruited by short reward delays [15] – exhibits slow changes in
306 activity over the course of motor learning [25,26] and, relatedly, was shown to be central for slow,
307 implicit learning [31–33]. Conversely, the hippocampus – which is mostly recruited by long reward
308 delays – usually exhibits a fast increase in activity in the early phase of learning that wanes later
309 on [25,26]. In this line, the hippocampus was evidenced to be central for fast, explicit learning [34].
310 Altogether, these elements suggest that the different learning dynamics observed in individuals
311 training with short and long reward delays could result from the fact that these delays recruit the
312 striatum and the hippocampus, respectively, shaping thus their activity and boosting preferentially
313 the slow and fast processes in which those structures are mostly involved. Further
314 neurophysiological work is required to test this hypothesis directly.

315 The impairment of motor consolidation observed in subjects who trained with a long reward
316 delay also suggests that the strength of learning was altered in these participants. As such, efficient
317 reward-based motor learning relies on the mapping between somatosensory sensations (*e.g.*,
318 elicited by the generated force in the present task) and the associated reward [1,35,36], and
319 somatosensory working memory is known to decay quickly following movement execution, after

320 only a few seconds [37,38]. Hence, it is possible that delaying reward delivery blunted the
321 reinforcement of somatosensory working memory [38], explaining the limited learning and
322 consolidation observed in the subjects of $Group_{Long}$. Another, potentially complementary
323 interpretation is that rewards delivered after a long delay are temporally discounted and perceived
324 as subjectively less valuable relative to when the delay is short [39,40]. If this is true, the reduction in
325 subjective value in $Group_{Long}$ may have contributed to reducing the beneficial effect of reward on
326 offline memory consolidation [41]. Altogether, these elements indicate that the temporal contingency
327 between a movement and the ensuing reward is a decisive aspect of reward-based motor learning.

328 Beyond reward timing, another feature that could have altered motor learning in the present
329 study is the post-reward delay – *i.e.*, the delay between reward delivery and the execution of the
330 subsequent movement (referred to as ITI in the *Results* section, above). However, our data suggest
331 that post-reward delay did not affect motor learning in the present study. Indeed, subjects of
332 $Group_{Short}$ and of $Group_{Short\text{-}PastStudy}$, which trained with a short reward delay but with different ITIs,
333 displayed very similar learning (Supplementary Figure 1). This finding is in line with the idea that
334 motor learning remains largely unaffected by the ITI duration (even for ITIs of 30 s; [28]).

335 In conclusion, our data indicate that the timing at which reward is delivered during motor
336 training alters the dynamics of learning and the consolidation of the new motor memory. Research
337 is now required to gain further knowledge as to the brain networks involved in these time-
338 dependent effects of reward on motor learning as well as to characterize the relative contribution
339 of implicit and explicit learning processes to these effects. Such knowledge would prove useful for
340 the design of future reward-based rehabilitation programs, in which reward timing may be
341 individualized depending on the brain networks and learning processes affected in specific
342 populations of patients [15,20].

4. Methods

4.1. Participants

A total of sixty right-handed healthy volunteers participated in the present study (46 women, 23.7 ± 0.3 years old; mean ± SE). Data from a previous group of thirty participants was also re-analyzed [1] (20 women, 23.9 ± 0.43 years old). Handedness was determined via a shortened version of the Edinburgh Handedness inventory [42]. None of the participants suffered from any neurological or psychiatric disorder, nor were they taking any centrally-acting medication. All participants gave their written informed consent in accordance with the Ethics Committee of the Université Catholique de Louvain (approval number: 2018/22MAI/219) and the principles of the Declaration of Helsinki. Subjects were financially compensated for their participation. Finally, all participants were asked to fill out a French adaptation of the Sensitivity to Punishment and Sensitivity to Reward Questionnaire (SPSRQ [43,44]) and a NASA Task Load Index questionnaire (NASA-TLX [45]).

4.2. Motor skill learning task

Participants were seated approximately 60 cm in front of a cathode-ray tube screen (refresh rate: 100 Hz) with their right forearm positioned at a right angle on the table. The task was developed on Matlab 7.5 (the Mathworks, Natick, Massachusetts, USA) exploiting the Psychophysics Toolbox extensions [46,47] and consisted in a previously described force modulation task [1]. Briefly, the task required participants to squeeze a force transducer (Arsalis, Belgium) between the index and the thumb to control a cursor displayed on the screen. Increasing the force

365 exerted resulted in the cursor moving vertically and upward. Each trial started with a preparatory
366 period in which a sidebar appeared at the bottom of the screen and a target at the top (**Figure 1A**).
367 After a variable time interval (0.8 to 1 s), a cursor popped up in the sidebar, indicating the start of
368 the movement period. Participants had to pinch the transducer to move the cursor as quickly as
369 possible from the sidebar to the target and maintain it there for the rest of the movement period,
370 which lasted 2 s. The level of force required to reach the target ($Target_{Force}$) was individualized for
371 each participant and set at 10 % of maximum voluntary contraction (MVC). Notably, squeezing
372 the transducer before the appearance of the cursor was considered as an anticipation and therefore
373 led to the interruption of the trial. Anticipation trials were discarded from further analyses. At the
374 end of each trial, a binary reinforcement feedback was presented to the subject (yellow or blue
375 circle for success or failure, respectively).

376

377 **4.3. Sensory and reinforcement feedbacks**

378 We provided only limited visual feedback to the participants in order to increase the impact
379 of the reinforcement feedback on learning [48]. As such, on 90 % of the trials, the cursor disappeared
380 shortly after the start of the movement period: it became invisible as soon as the generated force
381 became larger than half of the $Target_{Force}$ (*i.e.,* 5 % of MVC). Conversely, the remaining trials (10
382 % of the trials) provided a continuous vision of the cursor (full vision trials). Full vision trials were
383 not considered in the analyses.

384 As mentioned above, each trial ended with the presentation of a binary reinforcement
385 feedback, indicating success or failure. Success on the task was determined based on the Error,
386 defined as the absolute force difference between the $Target_{Force}$ and the exerted force [5,27]. The Error

387 was first computed for each frame refresh from 0.15 s to the end of the trial (*i.e.,* providing 185
388 data points at 100 Hz), then averaged across the data points for each trial [27], and expressed in
389 percentage of MVC. This indicator of performance allowed us to classify a trial as successful or
390 not based on an individualized success threshold (see below). When the Error on a given trial was
391 below the threshold, the trial was classified as successful, and when it was above the threshold, the
392 trial was considered as failed. Hence, task success depended on the ability to approximate the
393 $Target_{Force}$ as quickly and as accurately as possible.

394

395 **4.4. Reward timing manipulation**

396 The protocol involved Training and Test blocks (see *Experimental protocol*, below). During
397 Training blocks, reinforcement feedbacks were associated with a reward of 8 cents on successful
398 trials, and failed trials led to 0 cent. Importantly, in two block types, we manipulated the timing at
399 which the reinforcement feedback, and therefore the associated reward, was delivered after the
400 movement period (**Figure 1A**). Indeed, the reward was displayed after either a short or a long delay
401 – that is, 1 or 6 s following the movement period in $Reward_{Short}$ and $Reward_{Long}$ blocks, respectively
402 (see [15,20] for the use of similar delays in decision-making tasks). In order to keep the total duration
403 of the trial constant in these two block types, inter-trial intervals (ITI, which followed reward
404 occurrence) were set to 6 and 1 s in the $Reward_{Short}$ and the $Reward_{Long}$ blocks, respectively. Finally,
405 we re-analyzed data from a previous study [1], in which the training blocks involved a short reward
406 delay timing (0.5 s) and an intermediate ITI (3 s; $Reward_{Short\text{-}PastStudy}$ blocks). The latter analysis
407 allowed us to test for the reproducibility of the effects of training obtained in the $Reward_{Short}$ block.

In the Test blocks, reinforcement feedback occurred 1 s after the movement period, involved an ITI of 1 s, and was not associated with any reward.

4.5. Motor skill learning protocol

Subjects were tested on two consecutive days (Day 1 and Day 2; **Figure 1C**). On Day 1, we first measured the individual MVC to calculate the $\text{Target}_{\text{Force}}$. Notably, MVCs and simple reaction times (SRT) were measured before and after the training blocks to assess potential fatigue related to the training (see **Data processing and statistical analyses**). Participants then performed 2 blocks of Familiarization, in a Test block setting. The first Familiarization block comprised 20 full vision trials. Subsequently, all blocks were composed of a mixture of partial vision trials (90 % of total trials) and full vision trials (10 % of total trials), as described above. The second Familiarization block involved 40 trials and allowed us to determine baseline performance to calibrate the difficulty of the task for the rest of the experiment (Calibration block; please see [1] for details on the Calibration procedure).

Following Familiarization, participants performed 320 trials divided in 8 blocks. All subjects started and ended the session with the realization of a Test block of 40 trials, allowing us to evaluate initial performance and total learning (*i.e.*, Pre- and Post-training blocks, respectively). In between, 6 Training blocks (T1 to T6) of 40 trials were performed by the participants (see **Figure 1B**). During the Training blocks, individuals were split into 2 separate groups depending on the type of training blocks they performed. As such, $\text{Group}_{\text{Short}}$ and $\text{Group}_{\text{Long}}$ trained with $\text{Reward}_{\text{Short}}$ and $\text{Reward}_{\text{Long}}$ blocks, respectively. The group trained with $\text{Reward}_{\text{Short-PastStudy}}$ blocks was referred to as $\text{Group}_{\text{Short-PastStudy}}$. Comparing performance between the groups during the training period allowed us to test the effect of reward timing on the learning dynamics.

Day 2 was realized 24 hours later. Subjects performed the task again with the same $Target_{Force}$ and success threshold. This assessment was composed of 5 full vision trials followed by a Test block of 40 trials (Re-test) and allowed us to assess the effect of reward timing on skill consolidation.

4.6. Data processing and statistical analyses

Statistical analyses were carried out with Matlab 2018a (the Mathworks, Natick, Massachusetts, USA) and Statistica 10 (StatSoft Inc., Tulsa, Oklahoma, USA). In the case of independent samples t-tests and Analysis of Variance (ANOVA), we verified the homogeneity of the variances systematically and non-parametric tests were used when variances were non-homogeneous. All data were systematically tested for the sphericity assumption using Maunchley's tests. The Greenhouse-Geisser (GG) correction was used for sphericity when necessary. Post-hoc comparisons were conducted using the Fisher's LSD procedure. The significance level was set at $p \leq 0.05$, except in the case of correction for multiple comparisons (see below).

4.6.1. Motor skill learning

As a first step, we tested the impact of reward timing on motor performance during each block of Test and Training block. We quantified for each subject the percentage of successful trials (*i.e.*, the success rate) for each block and then normalized the data according to individuals' initial performance by subtracting the success rate values measured at Pre-training from the values obtained in every block. To evaluate the impact of reward timing on success rates across training, we performed a two-way ANOVA with $GROUP_{TYPE}$ ($Group_{Short}$ and $Group_{Long}$) and

453 $TRAINING_{BLOCK}$ (T1 to T6) as between- and within-subjects factors, respectively. Then, to
454 evaluate the effect of the ITI's duration on motor learning, we replicated this analysis with the
455 inclusion of the $Group_{Short\text{-}PastStudy}$.

456 As a second step, we aimed at evaluating how reward timing influenced learning rates
457 during the task. To do so, we split the data into 24 non-overlapping bins of 10 trials, computed the
458 success rate for each bin and normalized the data according to individuals' initial performance, as
459 done in the first analysis. The bins were then separated into two equal parts (*i.e.*, of 12 bins each)
460 depending on whether they belonged to the early or to the late phase of training ($Training_{Early}$ and
461 $Training_{Late}$ phases, corresponding to T1-T3 and T4-T6, respectively). Finally, we performed linear
462 regressions on these data and extracted the slope of the fits for the $Training_{Early}$ and the $Training_{Late}$
463 phases of the $Group_{Short}$ and the $Group_{Long}$. The slope values – exploited here as a proxy of the
464 learning rate – were compared using a two-way ANOVA with $GROUP_{TYPE}$ ($Group_{Short}$ and
465 $Group_{Long}$) and $TRAINING_{PHASE}$ ($Training_{Early}$ and $Training_{Late}$) as between- and within-subjects
466 factors, respectively.

467 Finally, we tested for any effect of reward timing on total learning, by comparing the
468 success rates of the three groups at Post-training, using a one-way ANOVA with the factor
469 $GROUP_{TYPE}$ ($Group_{Short}$, $Group_{Long}$ and $Group_{Short\text{-}PastStudy}$). Further, in order to test the statistical
470 significance of total learning within each group, we conducted two single sample t-tests on Post-
471 training success rate, against a constant value of 0 (Bonferroni-corrected at $p \leq 0.025$).

472

473 **4.6.2. Motor skill consolidation**

474 A second goal of the study was to evaluate the effect of reward timing on skill consolidation.
475 For this analysis, we thus considered participants who demonstrated skill learning on Day 1
476 ($Success_{Post\text{-}training} - Success_{Pre\text{-}training} > 0$). This step not only allowed us to exclude non-learners but
477 also to compare consolidation in groups that exhibited a similar learning on Day 1 (*i.e.*, a similar
478 success rate at Post-training). 40 participants were considered in this analysis (22 and 18 in
479 $Group_{Short}$ and $Group_{Long}$, respectively). We compared the success rate data through a two-way
480 ANOVA with $GROUP_{TYPE}$ ($Group_{Short}$ and $Group_{Long}$) and $TEST_{BLOCK}$ (Post-training and Day 2)
481 as between- and within-subjects factors, respectively.

482

483 **4.7. Group features, initial performance and fatigue**

484 As a control, we verified that the $Group_{Short}$ and the $Group_{Long}$ were comparable in terms of
485 age, success threshold, $Target_{Force}$, sensitivity to reward and to punishment (*i.e.,* as assessed by the
486 SPSRQ questionnaire), initial performance (*i.e.,* at Pre-training) and received monetary gains. As
487 displayed in **Table 1**, independent sample two-tailed t-tests performed on these data did not reveal
488 any significant differences between the groups (see also **Figure 1C**).

489 We also assessed if potential motor and cognitive fatigue generated by Day 1 training was
490 different between the groups [49,50]. To do so, we expressed MVCs, and SRTs obtained after training
491 (MVC_{POST} and SRT_{POST}) in percentage of the values measured initially (MVC_{PRE} and SRT_{PRE}). We
492 also assessed the perceived workload after training through the NASA-TLX questionnaire.
493 Notably, these data did not differ between the groups (**Table 1**), suggesting that motor and
494 cognitive fatigue were not responsible for the effect of reward timing on motor learning.

	$Group_{Short}$ (n = 30)	**$Group_{Long}$ (n = 30)**	**t-value**	**p-value**
Age (in years)	22.8 ± 0.58	23.0 ± 0.52	-0.26	0.80
Gender (number of females)	22	24	/	/
Success Threshold (% MVC)	2.7 ± 0.01	2.7 ± 0.01	0.18	0.86
$Target_{Force}$ (Newtons)	4.74 ± 0.21	4.39 ± 0.17	1.32	0.19
Sensitivity to reward and punishment (score)	82.0 ± 2.32	83.3 ± 2.04	-0.43	0.67
Pre-training success rate	31.0 ± 2.61	34.9 ± 3.62	-0.86	0.39
Monetary Gains (euros)	39.0 ± 0.64	38.5 ± 0.73	0.45	0.66
Muscle fatigue (MVC_{POST} in % of MVC_{PRE})	91.3 ± 2.83	93.7 ± 2.67	-0.62	0.54
Simple Reaction Time change (SRT_{POST} in % of SRT_{PRE})	104.35 ± 2.51	103.21 ± 2.32	0.33	0.74
Perceived workload (NASA-TLX score)	49.4 ± 2.74	50.89 ± 2.79	-0.39	0.70

Table 1. Group features, initial performance and fatigue in the three experimental groups (mean ± SE). The 2 last columns provide the results of independent samples t-tests.

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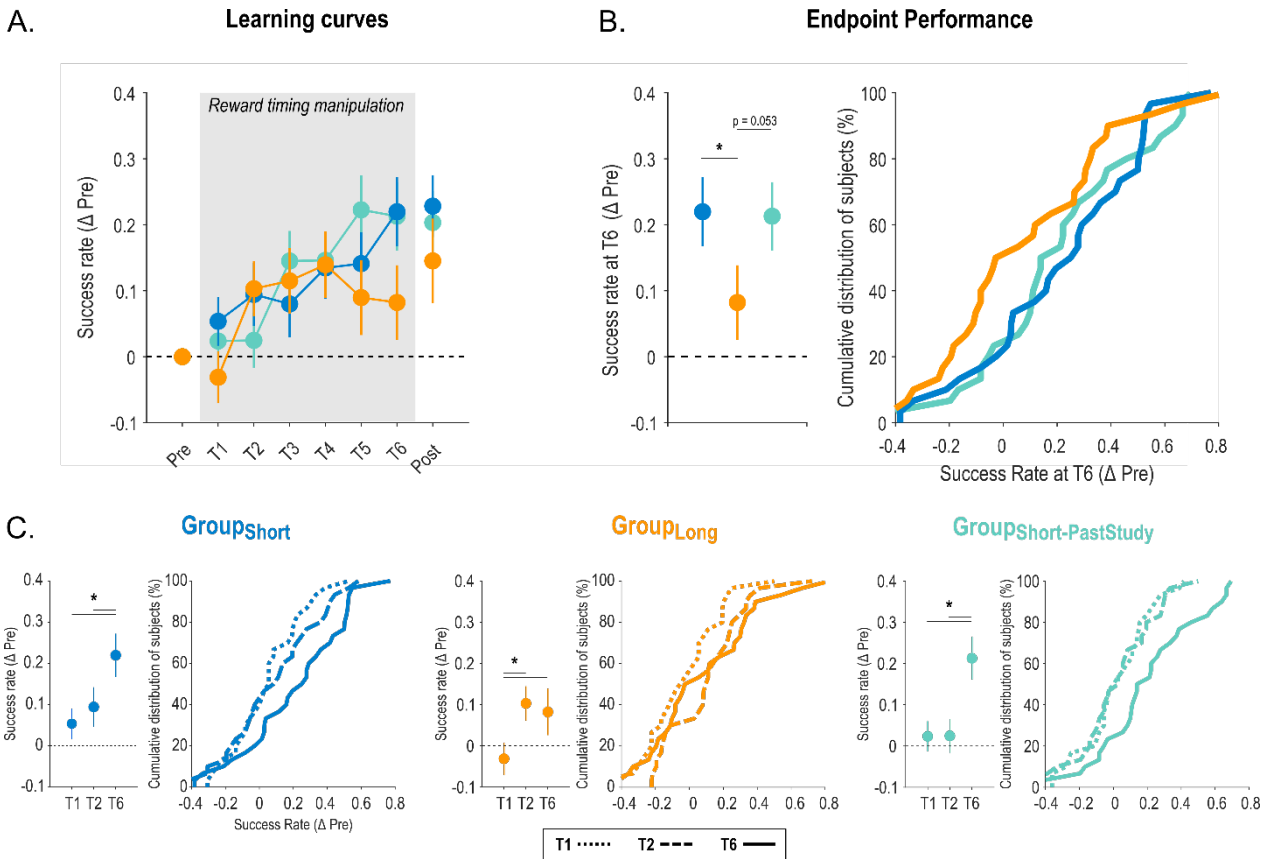
Competing interests

The authors declare no conflict of interest.

Data and code availability

Data used in this study are available upon request (contact: pierre.vassiliadis@uclouvain.be) and will be freely available at the time of publication via an open-access data sharing repository (https://osf.io).



Supplementary Figure 1. Effect of reward timing on motor skill learning with the inclusion of $Group_{PastStudy}$. **A. Learning curves**. Proportion of successful trials (expressed as a difference with the individual Pre-training success rate) is represented across practice for the three experimental groups (blue: $Group_{Short}$, orange: $Group_{Long}$, turquoise: $Group_{Short\text{-}PastStudy}$). The grey shaded area highlights the blocks concerned by the reward timing manipulation. The remaining blocks were Test blocks. Note the similarity in the learning curves of $Group_{Short}$ and $Group_{Short\text{-}PastStudy}$ despite the difference in ITI. **B. Endpoint performance**. Average success rates in the end of the training period (i.e., measured at T6) in the three groups (left panel) and the corresponding cumulative distributions of the data (right panel). **C. Learning dynamics.** Average success rates observed at T1 (dotted line), T2 (dashed line) and T6 (solid line) and the corresponding cumulative distributions for $Group_{Short}$ (left), $Group_{Long}$ (middle) and $Group_{Short\text{-}PastStudy}$ (right panel). Performance improved very early in $Group_{Long}$ (i.e., between T1 and T2) and then plateaus while it improved later in $Group_{Short}$ and $Group_{Short\text{-}PastStudy}$. Note that performance at T1 was not different between the groups (all $p > 0.21$). *: significant difference ($p<0.05$). Data are represented as mean ± SE.

References

1. Vassiliadis, P. *et al.* Reward boosts reinforcement-based motor learning. *iScience* **24**, 102821 (2021).

2. Galea, J. M., Mallia, E., Rothwell, J. & Diedrichsen, J. The dissociable effects of punishment and reward on motor learning. *Nat Neurosci* **18**, 597–602 (2015).

3. Chen, X., Holland, P. & Galea, J. M. The effects of reward and punishment on motor skill learning. *Curr. Opin. Behav. Sci.* **20**, 83–88 (2017).

4. Dhawale, A. K., Smith, M. A. & Ölveczky, B. P. The Role of Variability in Motor Learning. *Annu. Rev. Neurosci.* **40**, 479–498 (2017).

5. Abe, M. *et al.* Reward improves long-term retention of a motor memory through induction of offline memory gains. *Curr. Biol.* **21**, 557–562 (2011).

6. Vassiliadis, P. & Derosiere, G. Selecting and executing actions for rewards. *J. Neurosci.* **40**, 6474–6476 (2020).

7. Therrien, A. S., Wolpert, D. M. & Bastian, A. J. Effective Reinforcement learning following cerebellar damage requires a balance between exploration and motor noise. *Brain* **139**, 101–114 (2016).

8. Vassiliadis, P., Derosiere, G. & Duque, J. Beyond Motor Noise : Considering Other Causes of Impaired Reinforcement Learning in Cerebellar Patients. *Eneuro* **6**, 1–4 (2019).

9. Quattrocchi, G., Greenwood, R., Rothwell, J. C., Galea, J. M. & Bestmann, S. Reward and punishment enhance motor adaptation in stroke. *J. Neurol. Neurosurg. Psychiatry* jnnp-2016-314728 (2017). doi:10.1136/jnnp-2016-314728

10. Therrien, A. S., Statton, M. A. & Bastian, A. J. Reinforcement Signaling Can Be Used to

548 Reduce Elements of Cerebellar Reaching Ataxia. *Cerebellum* (2020). doi:10.1007/s12311-
549 020-01183-x

550 11. Dayan, E., Averbeck, B. B., Richmond, B. J. & Cohen, L. G. Stochastic reinforcement
551 benefits skill acquisition. *Learn. Mem.* **21**, 140–142 (2014).

552 12. Fiorillo, C. D., Newsome, W. T. & Schultz, W. The temporal precision of reward
553 prediction in dopamine neurons. *Nat. Neurosci.* **11**, 966–973 (2008).

554 13. Kobayashi, S. & Schultz, W. Influence of reward delays on responses of dopamine
555 neurons. *J. Neurosci.* **28**, 7837–7846 (2008).

556 14. Klein-Flügge, M. C., Hunt, L. T., Bach, D. R., Dolan, R. J. & Behrens, T. E. J. Dissociable
557 Reward and Timing Signals in Human Midbrain and Ventral Striatum. *Neuron* **72**, 654–
558 664 (2011).

559 15. Foerde, K. & Shohamy, D. Feedback timing modulates brain systems for learning in
560 humans. *J. Neurosci.* **31**, 13157–13167 (2011).

561 16. Peterburs, J., Kobza, S. & Bellebaum, C. Feedback delay gradually affects amplitude and
562 valence specificity of the feedback-related negativity (FRN). *Psychophysiology* **53**, 209–
563 215 (2016).

564 17. Mehler-Wex, C., Riederer, P. & Gerlach, M. Dopaminergic dysbalance in distinct basal
565 ganglia neurocircuits: Implications for the pathophysiology of parkinson's disease,
566 schizophrenia and attention deficit hyperactivity disorder. *Neurotox. Res.* **10**, 167–179
567 (2006).

568 18. Gabay, Y., Shahbari-Khateb, E. & Mendelsohn, A. Feedback Timing Modulates
569 Probabilistic Learning in Adults with ADHD. *Sci. Rep.* **8**, 1–11 (2018).

570 19. Weismüller, B. *et al.* Effects of feedback delay on learning from positive and negative
571 feedback in patients with Parkinson's disease off medication. *Neuropsychologia* **117**, 46–
572 54 (2018).

573 20. Foerde, K., Race, E., Verfaellie, M. & Shohamy, D. A role for the medial temporal lobe in
574 feedback-driven learning: Evidence from amnesia. *J. Neurosci.* **33**, 5698–5704 (2013).

575 21. Schendan, H. E., Searl, M. M., Melrose, R. J. & Stern, C. E. An fMRI study of the role of
576 the medial temporal lobe in implicit and explicit sequence learning. *Neuron* **37**, 1013–1025
577 (2003).

578 22. Doyon, J. & Benali, H. Reorganization and plasticity in the adult brain during learning of
579 motor skills. *Curr. Opin. Neurobiol.* **15**, 161–167 (2005).

580 23. Fernández-Seara, M. A., Aznárez-Sanado, M., Mengual, E., Loayza, F. R. & Pastor, M. A.
581 Continuous performance of a novel motor sequence leads to highly correlated striatal and
582 hippocampal perfusion increases. *Neuroimage* **47**, 1797–1808 (2009).

583 24. Krakauer, J. W., Hadjiosif, A. M., Xu, J., Wong, A. L. & Haith, A. M. Motor Learning. **9**,
584 613–663 (2019).

585 25. Albouy, G. *et al.* Both the Hippocampus and Striatum Are Involved in Consolidation of
586 Motor Sequence Memory. *Neuron* **58**, 261–272 (2008).

587 26. Albouy, G., King, B. R., Maquet, P. & Doyon, J. Hippocampus and striatum: Dynamics
588 and interaction during acquisition and sleep-related motor sequence memory
589 consolidation. *Hippocampus* **23**, 985–1004 (2013).

590 27. Steel, A., Silson, E. H., Stagg, C. J. & Baker, C. I. The impact of reward and punishment
591 on skill learning depends on task demands. *Sci. Rep.* **6**, 1–9 (2016).

592 28. McDougle, S. D., Bond, K. M. & Taylor, J. A. Explicit and Implicit Processes Constitute
593 the Fast and Slow Processes of Sensorimotor Learning. *J. Neurosci.* **35**, 9568–9579
594 (2015).

595 29. Smith, M. A., Ghazizadeh, A. & Shadmehr, R. Interacting Adaptive Processes with
596 Different Timescales Underlie Short-Term Motor Learning. *PLoS Biol.* **4**, e179 (2006).

597 30. Trewartha, K. M., Garcia, A., Wolpert, D. M. & Flanagan, J. R. Fast but fleeting: Adaptive
598 motor learning processes associated with aging and cognitive decline. *J. Neurosci.* **34**,
599 13411–13421 (2014).

600 31. King, B. R., Fogel, S. M., Albouy, G. & Doyon, J. Neural correlates of the age-related
601 changes in motor sequence learning and motor adaptation in older adults. *Front. Hum.*
602 *Neurosci.* **7**, 1–13 (2013).

603 32. Siegert, R. J., Taylor, K. D., Weatherall, M. & Abernethy, D. A. Is implicit sequence
604 learning impaired in Parkinson's disease? A meta-analysis. *Neuropsychology* **20**, 490–495
605 (2006).

606 33. Hayes, H. A., Hunsaker, N. & Dibble, L. E. Implicit motor sequence learning in
607 individuals with Parkinson disease: A meta-analysis. *J. Parkinsons. Dis.* **5**, 549–560
608 (2015).

609 34. Döhring, J. *et al.* Motor skill learning and offline-changes in TGA patients with acute
610 hippocampal CA1 lesions. *Cortex.* **89**, 156–168 (2017).

611 35. Bernardi, N. F., Darainy, M. & Ostry, D. J. Somatosensory contribution to the initial stages
612 of human motor learning. *J. Neurosci.* **35**, 14316–14326 (2015).

613 36. Sidarta, A., Vahdat, S., Bernardi, N. F. & Ostry, D. J. Somatic and reinforcement-based

plasticity in the initial stages of human motor learning. *J. Neurosci.* **36**, 11682–11692 (2016).

37. Harris, J. A., Harris, I. M. & Diamond, M. E. The topography of tactile working memory. *J. Neurosci.* **21**, 8262–8269 (2001).

38. Sidarta, X. A., Vugt, X. F. T. Van & Ostry, D. J. Somatosensory working memory in human reinforcement-based motor learning. 3275–3286 (2018). doi:10.1152/jn.00442.2018

39. Shadmehr, R., De Xivry, J. J. O., Xu-Wilson, M. & Shih, T. Y. Temporal discounting of reward and the cost of time in motor control. *J. Neurosci.* **30**, 10507–10516 (2010).

40. Shadmehr, R., Reppert, T. R., Summerside, E. M., Yoon, T. & Ahmed, A. A. Movement Vigor as a Re fl ection of Subjective Economic Utility. *Trends Neurosci.* **xx**, 1–14 (2019).

41. Sterpenich, V. *et al.* Reward biases spontaneous neural reactivation during sleep. *Nat. Commun.* **12**, (2021).

42. Oldfield, R. C. The assessment and analysis of handedness: The Edinburgh inventory. *Neuropsychologia* **9**, 97–113 (1971).

43. Lardi, C., Billieux, J., D'Acremont, M. & Linden, M. Van der. A French adaptation of a short version of the Sensitivity to Punishment and Sensitivity to Reward Questionnaire (SPSRQ). *Pers. Individ. Dif.* **45**, 722–725 (2008).

44. Torrubia, R., Ávila, C., Moltó, J. & Caseras, X. The Sensitivity to Punishment and Sensitivity to Reward Questionnaire (SPSRQ) as a measure of Gray's anxiety and impulsivity dimensions. *Pers. Individ. Dif.* **31**, 837–862 (2001).

45. Hart, S. G. & Staveland, L. E. Development of NASA-TLX (Task Load Index): Results of

Empirical and Theoretical Research. in *Power Technology and Engineering* **43**, 139–183 (1988).

46. Brainard, D. H. The Psychophysics Toolbox. *Spat. Vis.* **10**, 433–436 (1997).

47. Pelli, D. G. The VideoToolbox software for visual psychophysics: transforming numbers into movies. *Spat. Vis.* **10**, 437–442 (1997).

48. Mawase, F., Uehara, S., Bastian, A. J. & Celnik, P. Motor Learning Enhances Use-Dependent Plasticity. *J. Neurosci.* **37**, 2673–2685 (2017).

49. Derosiere, G. & Perrey, S. Relationship between submaximal handgrip muscle force and NIRS-measured motor cortical activation. *Adv. Exp. Med. Biol.* **737**, 269–274 (2012).

50. Derosière, G. *et al.* Similar scaling of contralateral and ipsilateral cortical responses during graded unimanual force generation. *Neuroimage* **85**, 471–477 (2014).