Savings is restricted to the temporally labile component of motor adaptation

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Savings, the faster relearning of a previously learned task, has been demonstrated in a variety of motor learning paradigms. Another key feature of motor learning is that part of it decays rapidly in time, but part is temporally-stable. In particular, we have recently shown that for force field and visuomotor rotation (VMR) learning a temporally-labile component, which rapidly decays with time constants of 15-20 sec, accounts for 20-25% of asymptotic adaptation. Here we investigate whether savings in VMR learning is specifically tied to a single component of this adaptation, i.e. is faster relearning a unique feature of the temporally-labile or the temporally stable component of adaptation?

We thus designed experiments in which 60-second delays ($60 \sec \approx 3\tau - 4\tau$), which would allow for the vast majority of temporally-labile adaptation to decay, were interspersed into the baseline and training periods for VMR learning, where participants made rapid (~290ms) 9cm point-to-point movements to a single 1cm target. This allowed us to effectively isolate the temporally-stable component of adaptation from the overall adaptation level during training so that adaptive changes in it could be measured in addition to the overall adaptation level as training progressed. Experiments consisted of three 80-trial training periods (T₁, T₂ and T₃) with 30° VMRs, and these 60-second delays were inserted before trials {-10, 10, 40 and 70} relative to the onset of each training period. In the first experiment (Exp1, N=14 participants), a short washout period (40 trials) was inserted between T₁ and T₂, whereas a prolonged (800 trial) washout period was inserted between T₂ and T₃, as shown in Figure 1b. 60s delays were also inserted every 40 trials during the 800-trial washout period in order to examine the washout of the temporally-stable component of adaptation.

Examination of the data from exp1 revealed that temporally-stable adaptation increased more slowly during training (compare the filled circles & solid lines in Fig 2a) and decreased more slowly during washout (τ >200 trials, Fig 2) than the overall adaptation (τ <15 trials, Fig 1a). As result, temporally-stable adaptation was significantly greater than zero late in the 40-trial washout period just prior to T_2 onset, but not late in 800-trial washout period prior to T_3 onset (cyan vs. green in Fig 3e), underscoring the importance of taking the baseline level into account when examining adaptation. In line with previous results demonstrating savings, we found that the adaptive change in performance relative to baseline (Eq. 1) appeared to be faster for overall learning in T_2 and T_3 compared to T_1 (cyan & green vs. blue in Fig 3c). When we quantified this savings as the increase in this adaptive change as a fraction of the ideal adaptation for T_2 and T_3 compared to T_1 (Eq. 2), we found significant savings during early training (trial 10) for T_2 (26.7±10.3% p=0.012, Fig 3d) but (as expected) little savings during late training (trials 40 & 70, Fig 3d). Surprisingly, we found no evidence of savings during any point in training for temporally-stable adaptation, including trial 11 which was adjacent to where savings was maximal in the overall adaptation (-8.4 \pm 8.3% p>0.8 for savings, Fig 3g). The data from T₃ allowed us to examine whether the lack of savings we observed in T₂ may have resulted from a ceiling-type effect from the non-zero baseline for temporally-stable adaptation prior to T₂ (cyan in Fig 3e). However, even with a prolonged washout period preceding it that resulted in full washout of both the overall and temporally-stable adaptation (green in Figure 2b,e), the data from T₃ were extremely similar to that from T₂, demonstrating substantial overall savings (29.3 \pm 9.2% p=0.004), but no temporally-stable savings (-13.6 \pm 6.9% p>0.8). These findings suggest that savings is restricted to the temporallylabile component of adaptation. Correspondingly, comparison of the overall vs. temporally stable savings early in training (trials 10 vs. 11) reveals highly significant differences (p<0.01) in both T₂ and T₃ (Fig 4).

The remarkable contrast we observed in Exp 1 between substantial savings in overall adaptation but no savings (with a trend toward negative savings) in temporally-stable adaptation was most compelling for T_3 learning, where the baseline levels of both the overall and temporally-stable adaptation were identical to that observed for initial learning (T_1). However, because two training periods ($T_1 \& T_2$) preceded T_3 , these results were not directly comparable to how savings is most commonly measured, following a single training period. We thus designed an experiment (Exp 2, N=14, Fig 1c & 2h-n) with a prolonged 800-trial washout block between T_1 and T_2 allowing a direct comparison of initial learning with relearning from fully washed out baselines after a single training period (Fig 2i,l). Here we found the same pattern of results as in T_2 and T_3 in Exp. 1: substantial savings for overall adaptation ($30.6\pm9.8\%$ p=0.004, Figure 2k) but no savings for temporally-stable adaptation ($-12.0\pm10.7\%$ p>0.8, Figure 2n). Taken together, our results demonstrate a stark contrast between temporally-stable and temporally-labile adaptation, with savings entirely restricted to the latter following both short and long washout periods after either one or two training periods. Thus although the capacity for savings can survive a prolonged washout and multiple time delays, its expression is limited to the temporally-labile component of adaptation.



Figure 1: Task description and learning curves. a: Diagram of the VMR task. Subjects made point-to-point movements with real-time visual feedback. This feedback was either veridical (baseline and washout blocks) or displaced by 30° about the starting position (training blocks). **b:** Learning curve for Exp. 1, showing the three training episodes (T_1 , T_2 , T_3) and the intervening washout periods. Note the faster readaptation (savings) from one training episode to the next and the spontaneous recovery of adaptation after a delay during washout (peaks at dotted lines). **c:** Same as (b) but for Exp. 2 showing similar savings.

Equations 1-2: Savings metric.

$$x_k(t) = \frac{\theta_k(t) - \theta_{0,k}}{V - \theta_{0,k}}$$

 $x_k(t)$: learning w.r.t. baseline (%) at trial t for T_k ; $x_k(t) = \frac{1}{V - \theta_{0,k}}$ $s_k(t)$: savings at trial t for T_k ; $\theta(t)$: movement direction at trial t; $\theta_{0,k}$: baseline for T_k ; V: ideal mvt. direction (30°) $s_k(t) = x_k(t) - x_1(t)$





Figure 2: The temporally stable component washes out very slowly. Shown is the decay of temporally-stable adaptation during the long 800-trial washout periods. Complete decay requires hundreds of washout trials. The time constants for decay are $\tau_1 = 256$ trials for exp. 1 (red) and $\tau_2 = 164$ trials for exp. 2 (blue), much longer than the duration of the short 40-trial washout period.







Figure 4 - Summary: Savings are restricted to the temporally labile component of adaptation.

a: Overall (OS), temporally-stable (TSS) and temporally-labile (TLS) savings for the 2nd (cyan) and 3rd (green) training episode for Exp. 1 & Exp. 2. OS & TLS are significantly greater than TSS (**) and only OS & TLS are greater than zero (**). **b:** Same as (a) but for Exp. 2. Results indicate no savings in the TS component of adaptation.