

Immediate decay toward baseline performance during repeated variable error clamp movements

Andrew E. Brennan & Maurice A. Smith – Harvard School of Engineering and Applied Sciences

Adaptation paradigms, such as learning to adapt to a force field, are thought to be dominated by error-based learning, where corrections are made to counter previously observed errors. However, when errors are clamped to zero following adaptation, performance decays toward baseline levels despite the absence of an error signal to drive the decay.

A recent paper (Vaswani & Shadmehr, 2013) argued that this decay occurs because there is a change of context between the adaptation task, where variable errors are continually experienced even at asymptote, and the zero-error error clamp block where variability is minimal. The idea is that once the change in context is recognized, the previously-learned adaptation is deemed no longer relevant, resulting in a loss of adaptation. The authors examined two key predictions of this theory. First, individuals should not decay until they recognize (presumably unconsciously) the context change, resulting in delayed decay onset. Second, adding variability to the direction of error clamp trials so that the distribution of errors during the “decay” period matches that from the preceding adaptation period would obscure the change of context, eliminating decay or substantially prolonging its onset. Unfortunately, both sets of evidence in the Vaswani paper are potentially problematic as the delay analysis was inappropriately constrained for noisy data and the variable decay experiment was not balanced across force field orientations. Here we re-examine the context change hypothesis.

To examine whether decay displayed delayed onset, the paper fit the last 50 trials of force field exposure and all the force channel trials for each subject with a delayed exponential (Eq1) constrained with a delay $\lambda \geq 0$. The constraint on λ is problematic since fitting an unconstrained delayed exponential to noisy data could cause the best-fit delay, λ , to be corrupted in either direction – larger or smaller than the true value. However, if the true decay were to begin at zero, constraining λ to be positive would result in a biased estimate of decay onset, with the negative half of the unconstrained distribution pinned at zero and the positive values appearing relevant when in fact they are simply artefacts of fitting noisy data. In short, an analysis of whether λ is significantly positive should not constrain λ to be positive. To convincingly evidence a systematically positive delay before decay onset, λ would have to be fit without constraint.

$$\text{Eq1: } f(t) = \begin{cases} a, & t \leq \lambda \\ (a - b) \exp\left(-\frac{t - \lambda}{\tau}\right) + b, & t > \lambda \end{cases}$$

We thus tested the hypothesis that decay onset is delayed by analyzing error clamps following exposure to a force field in point-to-point movements using unconstrained fits (Experiment 1, Fig 2). However, we found that six of the ten subjects (about half) were best fit by negative values for λ . This supports the possibility that subjects decayed immediately but the fits were corrupted by noise, but challenges the hypothesis that decay onset is delayed with systematically positive λ values. Moreover, the asymmetric pattern of decay (Fig 2) suggests that the average amplitude of decay could be systematically underestimated if only a single force field direction were examined (Fig 5a&b).

To further investigate whether decay results from contextual change, we performed three additional experiments in which we could simultaneously examine (1) delay in decay onset and (2) whether the introduction of variability in the decay period could eliminate or reduce the amount of decay. In experiment 2 (N=10, Fig 3a), we examined the effect of a variably directed channel block (VDCB) in point-to-point movements. In experiment 3 (N=19, Fig 3b), we matched the VDCB experiment in the Vaswani paper, examining the effect of a VDCB in shooting movements without a baseline, but with balanced force field adaptation. In experiment 4 (N=10, Fig 3c), we examined the effect of a VDCB in shooting movements with a baseline. In all experiments, the variability in the decay period closely matched that experienced during training (26%, -4%, and 14% smaller during the decay periods for experiments 2, 3, & 4, respectively).

The distribution of individual subject delay values (λ) for these data showed that none of the groups displayed significantly more positive than negative delays ($p > 0.05$ in all cases), and the combined distribution shown in Figure 4 displayed a median that was, in fact, somewhat negative (-5.2 trials). This is at odds with the idea that decay onset is systematically delayed. Curiously, a small number of subjects appeared to display large positive delays, but further analysis revealed that these examples were poorly fit by the delayed decay function in Eq1, as shown in Fig 4c.

Moreover, decay of substantial amplitude, although sometimes highly asymmetric, was readily apparent in all experiments. Although all subgroups in our data displayed statistically significant decay ($p < 0.05$, Fig 5a), the amplitude of decay can be most appropriately visualized as the extent to which the separation of the two subgroups is reduced from late adaptation to late in the decay period – a measure immune to any overall asymmetry. When the subgroups were combined, all groups displayed highly significant decay ($p < 0.001$ in all 5 cases, Fig 5b), and none of the VDCB groups exhibited smaller decay than the fixed direction decay group from experiment 1 ($p > 0.1$ in all 4 cases, Fig 5b), at odds with the idea that the absence of performance variability causes the contextual change to be recognized, which induces decay. Together, our results challenge the hypothesis that decay primarily derives from the recognition of a contextual change and fall in line with previous theories that decay results from incremental forgetting and provides a mechanism for optimizing the tradeoff between effort and performance during adaptation (Emken et al, 2007 *JNP*; Smith et al, 2006 *PLoS Biology*).

Figure 1: Experiment illustration

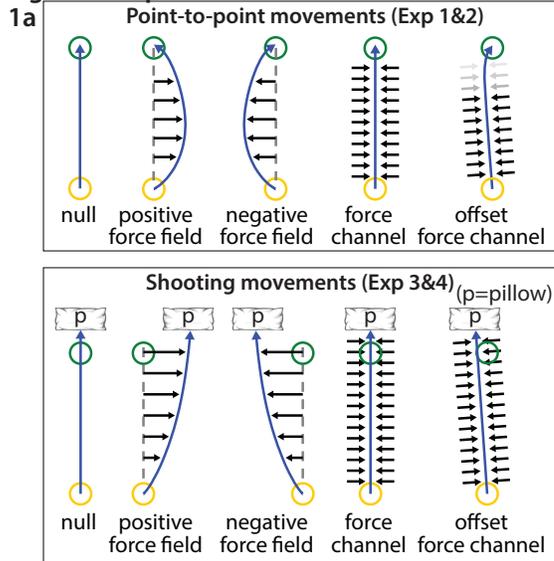


Figure 2: Learning & decay curves, fixed decay

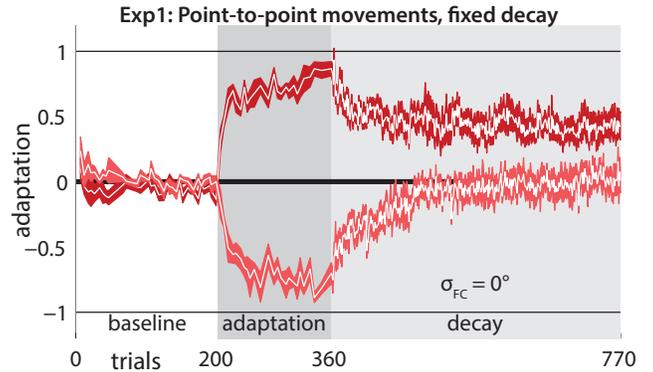


Figure 1. (a) Point-to-point movements were performed to the displayed target. During force field (FF) exposure, a force of the form $F_x = b \cdot V_x$; $F_y = -b \cdot V_y$ was applied to the hand, with $b=15\text{Ns/m}$ for positive FF trials and $b=-15\text{Ns/m}$ for negative FF trials. Force channel (FC) trials constrained lateral errors to near zero with an elasticity of 6N/mm . Offset FC trials guided the hand in a selected direction for the first 70% of the movement before the the channel dissipated over the following 100ms. Shooting movements were performed by moving through the target and hitting a virtual pillow (p). Force fields and force channels were applied in the same manner, except that offset force channels did not dissipate. (b) Velocity profiles demonstrate the differences between point-to-point and shooting movements.

Figure 3: Learning & decay curves - variable decay

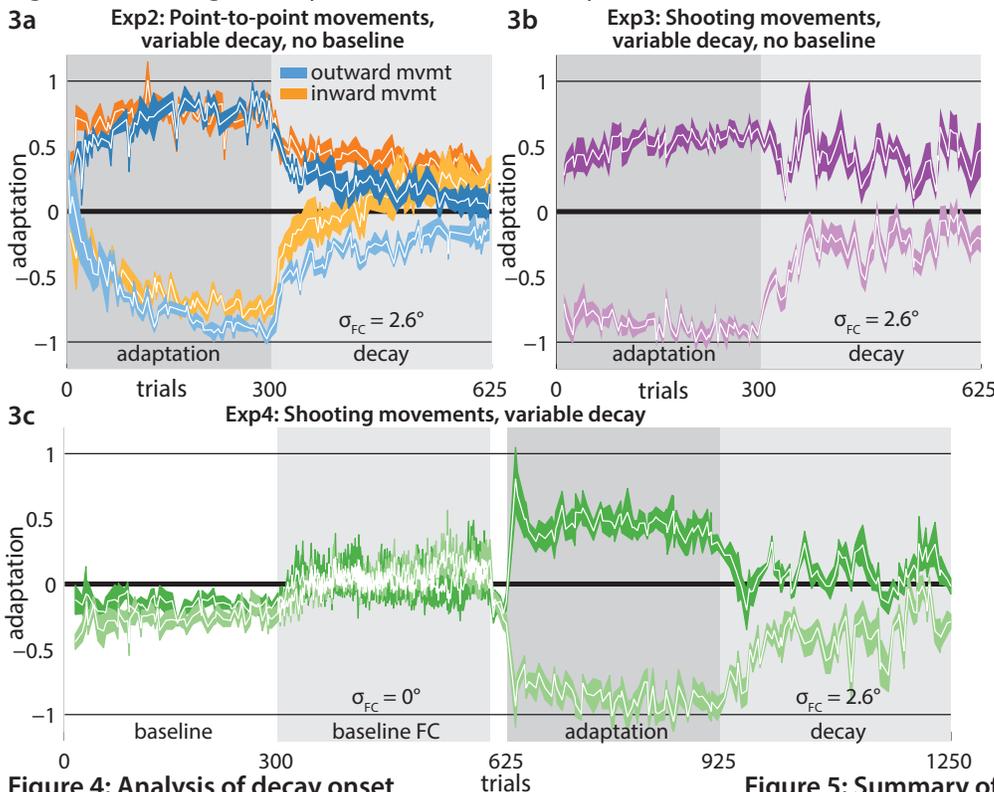


Figure 2. Exp1 consisted of point-to-point movements with baseline, FF, and FC blocks, where errors were clamped to zero in the last phase. Positive (negative) FF subgroup shown in dark (light) red. Strong but asymmetric decay was observed.

Figure 3. Exp2 (a) and Exp3 (b) consisted of FF exposure and variable FC blocks. In Exp2, subjects reached in both the outward and inward directions using point-to-point mvmts. (c) Exp4 was the same as Exp3, except for the inclusion of baseline and force channel trials before the FF was introduced. Positive (negative) FF shown in the darker (lighter) colour in all graphics.

Figure 4: Analysis of decay onset

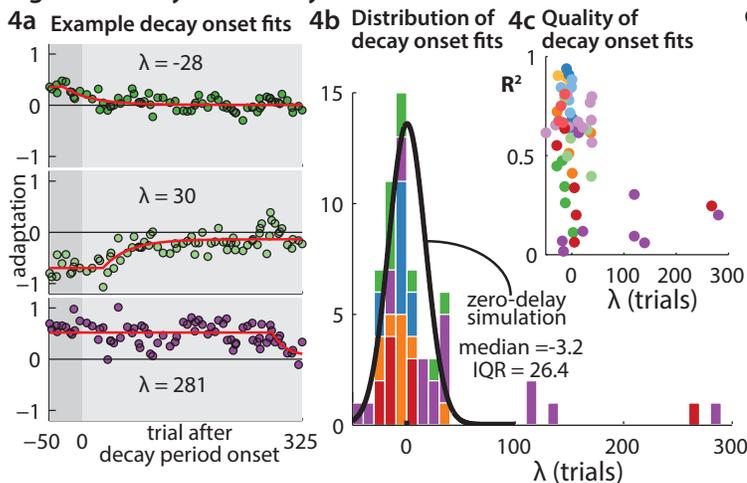


Figure 5: Summary of decay amplitudes

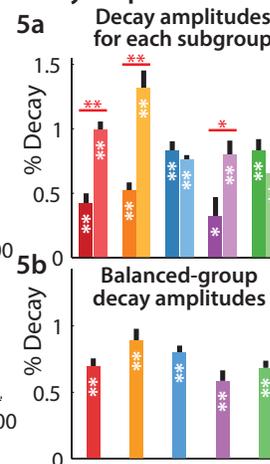


Figure 4: (a) Decay curves for three example subjects fit with delayed exponentials. (b) A histogram of the delay parameter λ for subjects in all experiments. Bars are coloured according to the experiment performed. Overlaid is a histogram derived from fits to simulated noisy decay curves with zero delay. (c) The goodness of fit, R^2 , plotted against the best-fit delay parameter, λ , shows that the subjects with large delays are not well fit by a delayed exponential (Eq1, main text).

Figure 5: (a) Decay calculated separately for the positive and negative subgroups is confounded with biomechanical factors and is highly variable. (b) Decay calculated using differences between the positive and negative subgroups is more consistent. Variable FC does not decrease decay in any exp. ($p>0.1$). (* indicates $p<0.05$; ** indicates $p<0.01$)