Robust Use-Dependent Learning in Arm Movements
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Previous work has suggested that repetition of a learned movement induces bias towards that movement when executing similar movements (Classen et al 1998, Diedrichsen et al 2010, Verstynen and Sabes 2011, Hammerbeck et al 2014). Such use-dependent learning is thought to be a slow process rooted in long-term potentiation (LTP) in the motor cortex (Han et al. 2008, Galea and Celnik 2009, Verstynen and Sabes 2011), which reflects an unsupervised learning mechanism that does not require error or reward feedback. Little is known, however, about use-dependent learning and forgetting dynamics. Additionally, it is unclear whether previously reported data on arm reaching movements reflect “pure” use-dependent effects, or are influenced by performance feedback (Hammerbeck et al 2014, Verstynen and Sabes 2011). Here, we test the hypotheses that use-dependent learning: 1. has a slow time course and requires extensive training; 2. is relatively resistant to time-based forgetting and to washout; and 3. does not require feedback from the environment.

Subjects took part in a two-day Time Course experiment (Fig. 1) in either a no feedback (No FB, N = 10) or full feedback condition (Full FB, N = 10). Subjects held a pen on a tablet to reach to targets displayed on a horizontal screen without vision of the hand or online feedback. Endpoint error and score feedback were presented after each trial in Group 1 (Full FB). No feedback was presented on 80% of the trials in Group 2 (No FB; error feedback on the remaining 20% of trials was needed to prevent drift in reach direction unrelated to use-dependence). Subjects repeated 476 reaches in a single direction on Day 1 and 238 on Day 2. In a novel aspect to our study, probe targets located ±90° from the repeated direction were inserted pseudorandomly every 4-6 trials to measure the dynamics of the bias towards the repeated direction. Over the first 100-200 trials during Day 1, both groups slowly developed biases that reached 4.3° ± 1.4° (mean ± SEM) in Group 1 and 2.6° ± 1.1° in Group 2 (one-tailed t-tests for comparison to 0°, Group 1 p = 0.006, Group 2 p = 0.018; no significant difference between groups, two-tailed t-test, p = 0.34; – see Fig 1a). Notably, this bias showed little decay by the beginning of Day 2 in Group 2, only decreasing to 2.0° ± 0.8° (not significantly less than the end of Day 1 based on one-tailed t-test, p = 0.12). Group 1 bias did significantly decay to 1.4° ± 0.6° by the beginning of Day 2 (one-tailed t-test, p = 0.017), but remained significantly greater than 0° (one-tailed t-test, p = 0.028). The bias rose again to 4.5° ± 1.0° for Group 1 and 4.2° ±1.4° for Group 2 during Day 2 training. It did not fully washout in Group 1 when subjects executed 203 reaches in random directions with error and score feedback available, reaching 2.2° ± 1.1° (Fig. 1b; significantly greater than 0° based on one-tailed t-test, p = 0.043). In Group 2, bias did washout to 1.8° ± 1.1° (not significantly greater than 0° based on one-tailed t-test, p = 0.065), but still showed a trend towards being greater than 0°.

These results show that use-dependent learning: 1. has a slow time course; 2. can be induced without error or reward (score) feedback, and 3. can last over 24 hours and is relatively robust to washout. Our results regarding the hypothesis that use-dependent learning can be induced without feedback support previous work demonstrating that error-based and use-dependent learning can be dissociated (Diedrichsen et al 2010). However, the apparent slow time course and relatively small bias evident in our data conflicted with previous work in which large use-dependent biases of 15° occurred within only 90 trials of repetitve reach training (Verstynen and Sabes 2011). To resolve this discrepancy, we replicated that study (N = 8, VS Replication experiment with error and score feedback; see Fig. 2) and confirmed that a large mean bias could be induced within 90 repeated trials to the same target (e.g. mean bias measured across 90 trial block: 14.3° ± 6.4° – see Fig. 2b). To verify whether both our Time Course and VS Replication data sets could be reconciled, we utilized an adaptive Bayesian model from Verstynen and Sabes (2011) (Fig. 3a). This model predicts reach direction on a given trial by a weighted combination of the sensory estimate of the target direction and the prior expected target direction (Fig. 3a, Eq. 1). The prior mean and variance are updated on each trial to reflect the distribution of experienced targets (Fig. 3a, Eq. 2 & 3).

Critically, we found the model fit to the Time Course experiment data predicted well the biases shown in the VS Replication experiment (Fig. 3). The model revealed that different frequencies of probe trials, and not necessarily a slow use-dependent learning time course, led to the discrepancy in use-dependent bias between the two experiments. In the Time Course experiment, more frequent probe trials (distant from the repeated training direction) slowed the reduction of the prior variance (Fig. 3a, Eq 3), thus decreasing the weight of the prior (Fig. 3a, Eq. 1) and slowing bias development compared to the VS Replication experiment, in which probe trials were less frequent and sometimes closer to the repeated direction (Fig. 2).

In summary, our results establish the consistency of use-dependent learning across multiple paradigms and its independence from feedback effects. They also underline the potential importance of use-dependent learning as an independent mechanism in motor learning. In addition, the robustness of use-dependent learning to time-based and movement-based forgetting is potentially important for rehabilitation strategies after stroke. In particular, use-
dependent learning may lead to the entrenchment of compensatory movements: after such compensatory movements are “used” numerous times, it may be difficult to re-train “normal movements”, even with full feedback, as suggested by our washout paradigm.

**EXPERIMENTAL RESULTS**

Figure 1. a) Schematic of Training (blocks 1-6 on Day 1 and 1-3 on Day 2; 103 trials each) and Washout (end of Day 2; 203 trials) during the Time Course experiment. During Training, the 135° target is repeated. Probes (shown in red) are given every 4-6 trials at ±90° from the repeated direction to measure use-dependent bias towards the repeated direction. During Washout, non-probe targets occur in random directions. b) For both Group 1 (Full FB; reward and error feedback given on non-probe trials) and Group 2 (No FB; no feedback given on 80% of non-probe trials), use-dependent bias develops similarly on both days.

Figure 2. a) Schematic of blocks (90 trials each) given in the VS Replication experiment (block order randomized for subjects). Each block provides training targets (with error and score feedback) drawn from one of the four distributions shown. b) For each probe distance, use-dependent bias towards mean reach direction shown for each block. Note large biases generated compared to Time Course experiment despite shorter training.

**SIMULATION RESULTS**

Figure 3. a) Adaptive Bayesian model of use-dependence used to predict reach direction on each trial (Verstynen and Sabes 2011). The prediction of reach direction (Eq 1) is a weighted sum between sensory estimate of target direction \( \hat{\theta} \) and prior mean direction \( \bar{\theta} \), based on relative certainty in prior (\( \sigma_p \)) vs. sensory target estimate (\( \sigma_i \)). After each trial, both \( \hat{\theta} \) and \( \sigma_p \) are updated based on previous target direction and learning rate \( \beta \) (Eq 2 & 3). \( \beta, \sigma_i \) are free parameters fit to data. Experiencing a narrow range of target directions causes become small, increasing certainty in the prior and hence bias towards \( \bar{\theta} \). b) Model prediction of VS Replication data using parameters fit to time course data. Importantly, the model can well-predict the larger biases that occur in the VS Replication experiment.

**References**