Learning from error: history of past errors dictates sensitivity to error

David J. Herzfeld[1], Pavan A. Vaswani[2], Mollie K. Marko[1], Reza Shadmehr[1]
[1]Dept of Biomedical Engineering, Johns Hopkins Univ. School of Medicine, [2]Dept of Neuroscience, Johns Hopkins Univ.

When we make a movement error, we modify our motor output in the next trial to compensate for the error[1]. During adaptation there are two important variables that determine how we learn: error and error-sensitivity. This error-sensitivity or “learning rate” determines how much we learn from a single error. Previous models of motor adaptation have assumed that error-sensitivity is relatively constant. However, recent results indicate that both humans and monkeys learn more from small errors as compared to large errors[2,3]. In addition, subjects can change the amount they adapt to error when the structure of the errors is predictable as opposed to when perturbations are induced randomly[4]. These results indicate that the brain may have a method for adjusting error-sensitivity based on the history of past errors and size of the errors. How might this be done?

Suppose that, in principle, the brain could modulate the amount it learns from error. Our hypothesis is that the brain can up-regulate or down-regulate error-sensitivity as a function of the history of prior errors. Given error $e^{(n)}$, the subject adapts its behavior in the next trial: $u^{(n+1)} = u^{(n)} + \Psi(e^{(n)})e^{(n)}$ via error-sensitivity $\Psi^{(n)}$. In the next trial, the subject generates motor command $u^{(n+1)}$, predicts $\hat{y}^{(n+1)}$ and receives feedback $y^{(n+1)}$. By comparing the two successive prediction errors $e^{(n-1)}$ and $e^{(n)}$, the learner has a local measure that can guide its error-sensitivity. For instance, if the sequence of errors are getting smaller, i.e. $e^{(n)} < e^{(n-1)}$, then the brain might increase error-sensitivity for that error size (i.e. up-regulate $\Psi(e^{(n)})$). In the opposite case, i.e. $e^{(n)} > e^{(n-1)}$, $\Psi(e^{(n)})$ is too large and should be down-regulated. Mathematically, this produces the following rule for changing error-sensitivity: $\Psi^{(n+1)}(e^{(n)}) = \sum w_i g_i(e^{(n)})$ where $w_i^{(n+1)} = w_i^{(n)} + \eta \operatorname{sign}(e^{(n-1)}e^{(n)}) g_i(e^{(n-1)})$ and $g_i(e)$ is a Gaussian basis function. The basic idea is that error-sensitivity is modified based on the sequence of errors. This model predicts that in an experiment in which perturbations are correlated, subjects will increase their error-sensitivity. However, when perturbations are uncorrelated, they will decrease error-sensitivity (Fig. 1). It makes the additional prediction that error-sensitivity changes are local to the actual error magnitudes experienced, and do not generalize to all errors. We performed an experiment to test these predictions.

According to our model, subjects should be able to modulate error-sensitivity for two different errors simultaneously, i.e., increase error-sensitivity for one error, while decreasing it for another. Subjects (n=16) held the handle of a stationary force transducer and made ballistic isometric force pulses. A cursor displayed the maximum amount of force that the subject produced in relation to a prescribed goal force (Fig. 2). We perturbed the location of the cursor by applying two different force offsets. In one case, we used a large force offset, resulting in a large error relative to the goal force (±8N). In the second case, we used a small force offset, producing small errors (±4N). We measured the initial error-sensitivity to magnitudes of +8N and-4N in the beginning of the experiment by observing the percentage of the error that was compensated in the next trial. Subjects then experienced anti-correlated errors in the large (+8N) error condition. In contrast, we presented correlated errors in the case of the small error magnitude (+4N). At the end of the experiment, we performed a second probe of the error-sensitivities to +8N and -4N errors. Our model predicted that subjects will decrease their error-sensitivity for the large magnitude error while simultaneously increasing the sensitivity for the small errors. The data supports these predictions (Fig. 3). The correlated (small) error showed a significant increase in adaptation compared to the baseline, whereas the anti-correlated (large) error showed a decrease in the mean adaptation.

The increase in error-sensitivity to the -4N probe cannot be explained by the traditional view of “savings” (when adaptation followed by extinction results in faster relearning to a second presentation) since subjects had not experienced earlier -4N learning blocks. In addition, decreases in error-sensitivity to the +8N probe cannot be explained by a decrease in error-sensitivity across all error magnitude since the -4N probe shows increased error-sensitivity. Together, these results suggest that the brain maintains a history of errors, and modulates error-sensitivity based on this local history.

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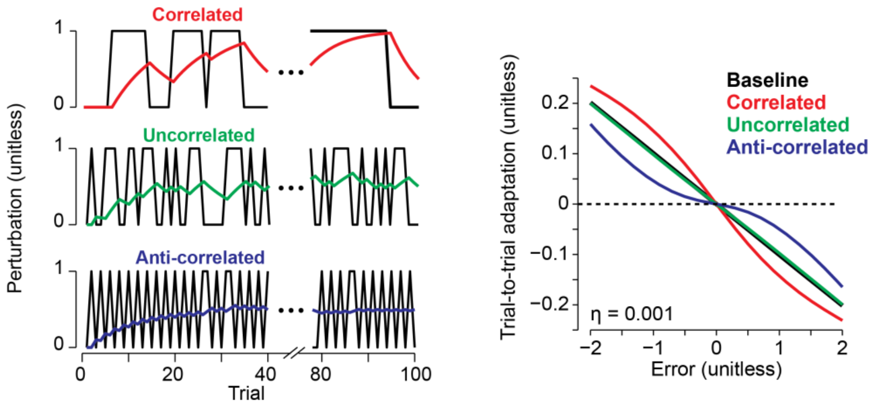
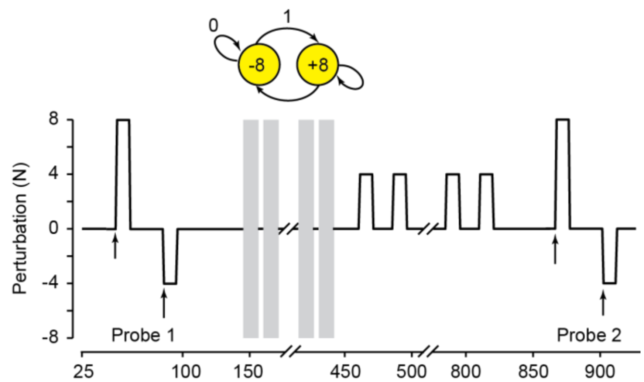


Fig. 1. Model of error-sensitivity. When two consecutive errors are correlated, the learner should increase its error-sensitivity at that error magnitude, producing an increase in trial-to-trial adaptation. However, if the error is transient, then error-sensitivity should be down-regulated. Note that increased error-sensitivity is indicated by greater trial-to-trial adaptation in the opposite direction of the error.The model predicts different amounts of trial-to-trial adaptation for various perturbation schedules. In an environment in which perturbations are likely to repeat (correlated), error-sensitivity increases; when perturbations are like to change (anti-correlated), error-sensitivity decreases. In the left sub-plot, the black line is perturbation magnitude and the color lines are the predicted motor output of the model. Notice that even though the perturbations are only of magnitudes "0" and "1," the model predicts changes in error-sensitivity for a "-1" error.

Fig. 2. Experimental paradigm. Subjects were asked to produce 16N ballistic isometric force pulses. On some pulses, we perturbed the visual feedback of the cursor by an additive offset (y-axis of right figure). We determined subjects' error-sensitivity to +8N and -4N errors in the beginning (Probe 1) and end (Probe 2) of the experiment by measuring the amount they adapted to the first perturbation. Subjects were initially exposed to an environment in which the errors were anti-correlated, by perturbing the cursor with alternating +8N and -8N perturbations (grey vertical bars). Subjects then experienced a series of ten +4N perturbations, after which they were allowed to decay back to baseline force output over 15 null perturbation trials.



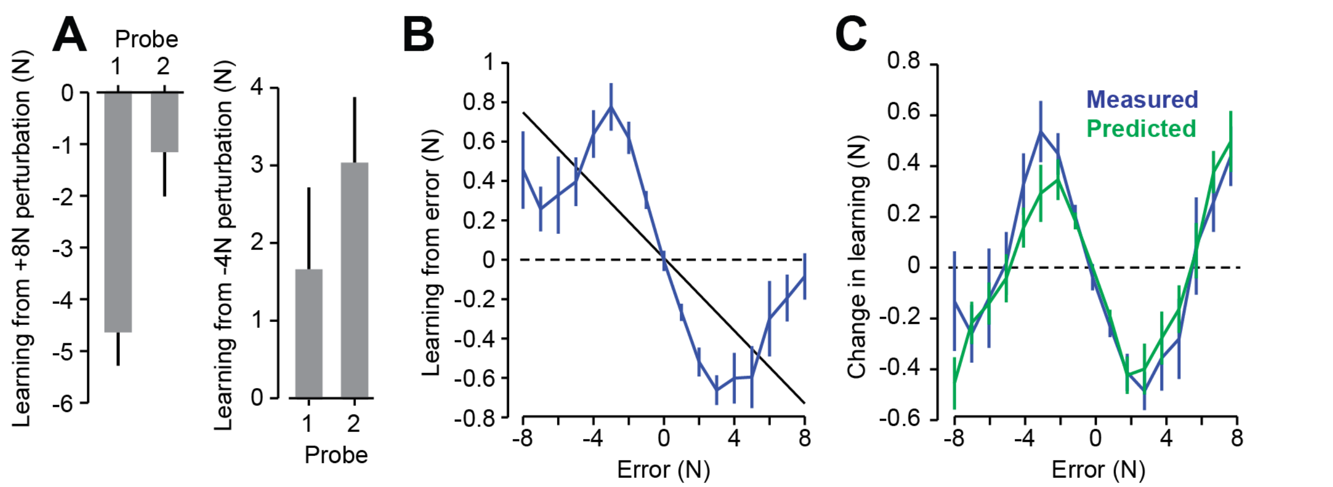


Fig. 3. Experimental results. Error-sensitivity is local to the experienced error. **A.** After initially experiencing a +8N error, subjects adapted to more than 50% of the error on the next trial. After experiencing an anti-correlated 8N environment, subjects decreased their error-sensitivity to an 8N error, adapting to less than 15% of the error at the end of the experiment. However, when subjects experienced a series of consistent 4N errors over the same time period, they increased their error-sensitivity to -4N errors over the course of the experiment. **B.** Trial-to-trial adaptation over the course of the experiment binned across error sizes. The best-fit line (shown in black) represents the learning from error if error-sensitivity were constant across all error sizes. Adaptation to ±4N errors shows increases adaptation relative to this constant sensitivity whereas ±8N errors shows a smaller amount of adaptation. **C.** Change in learning relative to the best-fit constant error-sensitivity for subjects (blue). We used the model to predict the change in learning across error magnitudes by evaluating our learning rule for each subject. The predicted change in learning (green) matches well with the measured values ($R^2 > 0.8$). Error bars denote SEM across subjects.