Cancellation of internally-generated errors from the signal driving motor adaptation

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Motor learning is largely driven by errors in our actions. Such errors could be generated internally due to motor output noise present in the execution of a planned action, or externally due to perturbations imposed by the outside environment. For example, when a basketball player shoots free throws, she faces errors due to the inability to consistently execute her shooting motion and due to external perturbations from an imperfectly balanced ball. If adaptation were driven by overall motor error that combines the contributions of internally-generated motor output noise and environmental perturbations, the ability to adapt to the environmental perturbations would be muddied by noise in the adaptive state arising from the adaptation to internally-generated motor output noise. This effect would be especially deleterious in cases where errors due to internally-generated motor output noise were comparable to or larger in size than externally-generated errors due to environmental perturbations. Here we hypothesized that although the motor system cannot stop internally-generated motor noise from occurring, it can cancel the effect that this noise would have on error-dependent motor learning so that the adaptive responses to motor errors are not corrupted by internally-generated motor output noise.

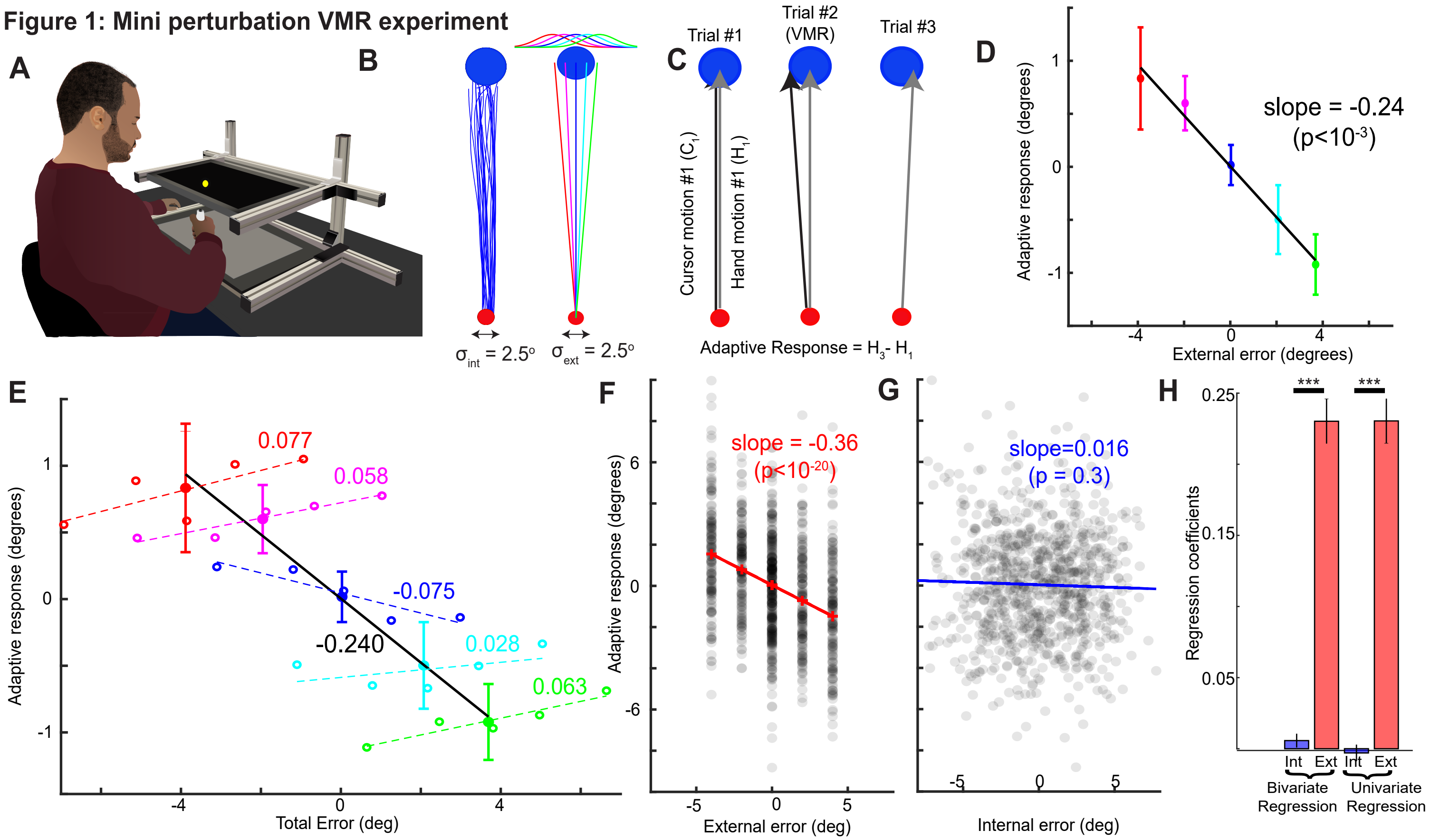
To determine whether internally- and externally-generated motor errors have different effects on motor adaptation, we designed an adaptation paradigm that (1) put these two components of motor error on equal footing by matching their amplitudes, and (2) allowed us to readily dissociate these two components by fully randomizing external perturbations over 1200 trials so that they would be statistically independent of internally-generated errors. Thus, in exp 1 (n=19), we pseudo-randomly delivered small visuomotor rotation (VMR) perturbations of 0^o, $\pm2^o$ and $\pm4^o$ such that root mean squared (RMS) perturbation was 2.5^o (Fig **1a-b**), a value chosen to match the $\sim2.5^o$ RMS error in movement direction observed in pilot data for the 9cm point-to-point reaching movements we used. Under these conditions, over 40% of trials would display motor output noise with an amplitude greater than 2^o, so that a $+2^o$ perturbation would result in a motor error $>4^o$ more than 20% of the time, but on the other hand, would result in a motor error $<0^o$ more than 20% of the time.

We began by examining the effect of externally generated errors by determining the average adaptation to each size perturbation (0^o, $\pm2^o$, $\pm4^o$), as shown in Fig **1d**. Unsurprisingly, we found a robust and approximately linear adaptive response, that was oppositely directed to the imposed perturbation with a gain of -0.240±0.05 (mean±SEM), meaning that $\pm4^o$ perturbations would elicit adaptive responses of about $\mp0.96^o$. What was surprising was what we found when examining the effect of internally-generated errors. We dissected the data from each perturbation size by binning it into quintiles for each participant based on the amount of internally-generated error, and then averaging across participants. Negative values of internally-generated error would lower the total error, whereas positive values would raise the total. As shown in Fig **1e**, the difference in the amount of total error between these quintiles was substantial, spanning 6.04^o on average between the lowest and highest quintile for each perturbation. However, the sensitivity that the adaptive response displayed to the difference in total error within each perturbation size, was far smaller in amplitude than the -0.240±0.051 sensitivity we found for externally-generated perturbation-driven errors. The largest amplitude sensitivity was 0.077±0.019 and the average across all 5 perturbation sizes was 0.012±0.028. As an example, when the lowest & highest quintiles for the +2deg perturbation are compared, the total error is different by 6.16^o yet the adaptive response is essentially unchanged with a difference of 0.173^o corresponding to a sensitivity of 0.028, indicating that different total errors have little effect on the adaptive response when externally-generated error is held constant. In a simpler and statistically more powerful analysis (Fig **1f-h**), we regressed the adaptive response observed for each trial $x(n+1) - x(n-1)$ onto the internally-generated and externally-generated components of the error on the preceding trial $e_{int}(n)$ and $e_{ext}(n)$. A bivariate version of this regression yielded error sensitivities of 0.230±0.016 and 0.006±0.005 to externally-generated and internally-generated errors ($p<10^{-8}$ for the difference in sensitivities), and a univariate version yielded error sensitivities of 0.231±0.016 and -0.003±0.006 to externally-generated and internally-generated errors ($p<10^{-8}$). In a follow-up expt (data not shown), we measured the amount of explicit strategy and, unsurprisingly, found little to no aiming in this randomized, small-perturbation paradigm, indicating that the observed adaptive response was primarily from implicit adaptation.

A potential confound in experiment 1 is that visuomotor rotation perturbations create a discrepancy between vision and proprioception. Hence, the larger adaptive response we found for the externally-generated errors could be due to greater adaptations for proprioceptive-visual sensory mismatches. To test this possibility, we designed an analog of Exp 1 that employed physical velocity-dependent force field (FF) perturbations so that hand and cursor motions would be perturbed in the same manner, eliminating any proprioceptive-visual mismatch. We used FF amplitudes of ±1.5 and ±3 Ns/m to approximately match the $\pm2^o$ and $\pm4^o$ displacements present in Expt 1. Using these physical perturbations, we obtained results which were strikingly similar to those from the VMR experiment, as shown in Fig **2**, with adaptive response sensitivities to externally- and internally-generated errors of -0.225±0.017 and -0.006±0.003, respectively ($p<10^{-8}$).

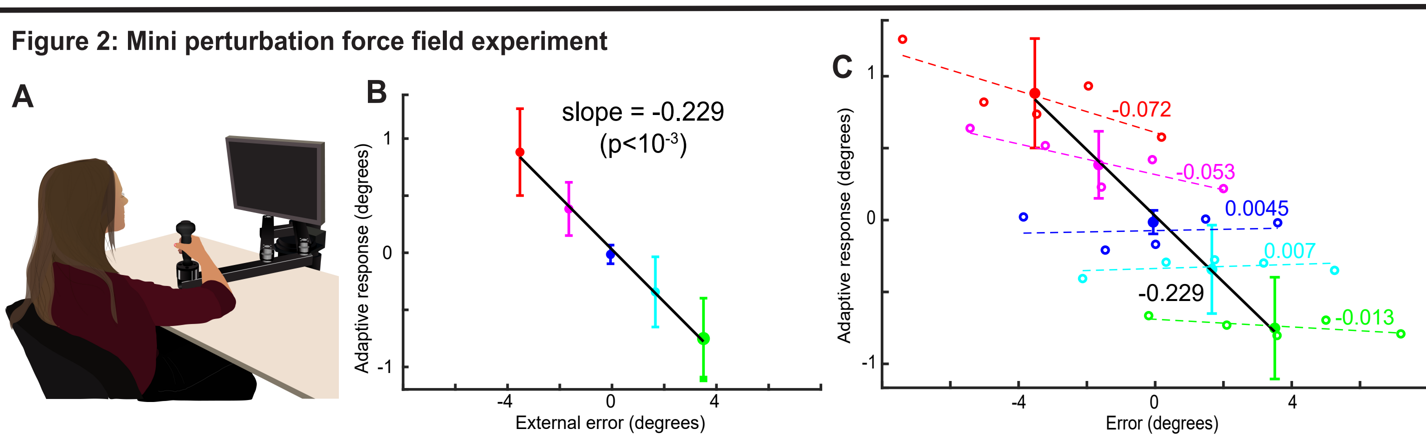
Together, our results indicate that the motor system deftly parses out the error signal for adaptation into internally- and externally-generated contributions, and specifically uses the externally-generated component to drive motor adaptation.

Figure 1: Mini perturbation VMR experiment



(A) Experimental setup for visuomotor rotation (VMR) experiment. Participants (n=19) made rapid 9 cm point-to-point reaching movements, where feedback of the cursor was either veridical or rotated from hand motion as determined by the perturbation sequence **(B)** To examine how the motor system responds to internal vs external errors, we introduced a controlled pattern of perturbations that reflect baseline movement variability (left panel). Specifically, we established a perturbation sequence by pseudorandomly sampling from a set of 5 different errors (-4° (red), -2° (magenta), 0° (blue), 2° (cyan), and 4° (green)), such that the resulting distribution had a standard deviation of 2.5°. **(C)** We defined the adaptive response (AR) to the error on a given trial (e.g., trial 2) as the change in hand angle (H) from the pre-error (trial 1) to the post-error trial (trial 3). We defined the total error as the angular deviation of the cursor direction (C) from the target direction on a trial. The internal error is the angular deviation of the hand direction (H) from the target direction. The external error is the VMR perturbation imposed on that trial. **(D)** Adaptive response to VMR perturbations which create externally-generated errors. Results suggest a linear sensitivity (with slope of -0.24) to errors, consistent with previous work. Note that the slope is negative, illustrating that the AR acts in the opposite direction of the imposed error. **(E)** Population-averaged AR are plotted for all instances of each perturbation size (filled circles) and for when these instances are divided into quintiles (5-equal sized bins for each participant) based on the amount of internally-generated error. The solid black line corresponds to the same regression as in panel (d), and the dashed colored lines correspond to regression across the quintiles within each perturbation size. Within each perturbation size, the sensitivity of the adaptive response to total error, as measured by the slope of each dashed line (indicated by the colored numbers), is several fold smaller, in all cases, than the slope of the black solid line which measures the sensitivity to externally-generated error, suggesting that adaptation is insensitive to total error when external error is fixed **(F-G)** Regression of adaptive response onto externally- and internally-generated errors for an example participant. Results mirror those in (e), indicating that differential learning rates are discernable for individual participants. **(H)** Regression coefficients from a bivariate and separate univariate regression of adaptive responses correspondng to the data in (f-g), but for all participants. Both regressions give similar results, suggesting little correlation between external and internal. *** $p<10^{-8}$. Error bars indicate 95% confidence.

Figure 2: Mini perturbation force field experiment



(A) To dissociate the external errors from any effect of visual-proprioceptive mismatch, we performed a second experiment (n=19) using a velocity-dependent force-field adaptation task to deliver physical perturbations that eliminated visual-proprioceptive mismatch. Here, participants made rapid 10 cm point-to-point reaching movements while holding onto a robotic arm handle that perturbs hand motion by applying lateral forces proportional to the hand velocity. **(B)** Adaptive response (AR) to external errors. The pattern of error sensitivity echoes that measured in experiment 1. **(C)** Population-averaged AR are plotted for all instances of each perturbation size (filled circles) and for when these instances are divided into quintiles based on the amount of internally-generated error. As in (b), results mirror those from experiment 1, suggesting that when visual-proprioceptive mismatch is eliminated, the differential response to internal and external errors is maintained. Error bars indicate 95% confidence.