Implicit motor adaptation is driven by motor performance prediction error rather than sensory prediction error

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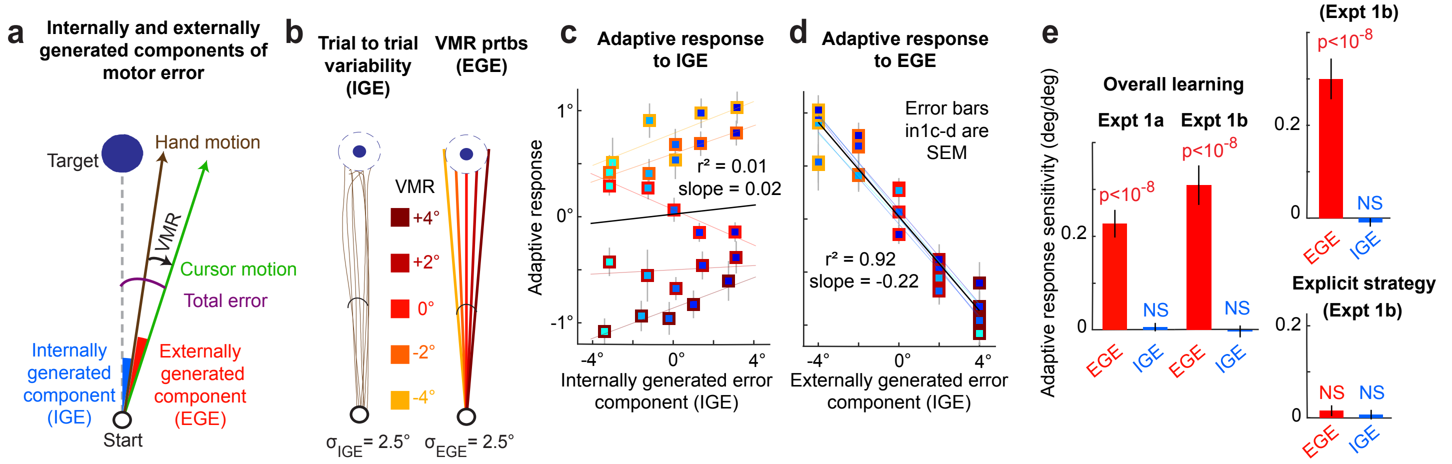
The motor system uses error signals arising during action to adapt future actions. A key question is how are useful error signals constructed from sensory information about action outcomes? Previous studies have suggested two forms of error that affect adaptation: sensory prediction error (SPE), the difference between the actual and predicted sensory information about an action, and motor performance error (MPE), the difference between actual performance and the task goal. These two errors differ in that MPE is dependent on the task goal, but SPE is not, whereas SPE is dependent on internal prediction, but MPE is not. It is widely believed that SPE drives implicit adaptation. Here, we find that, in line with the idea of SPE-driven implicit learning, prediction plays a key role in driving this adaptation, however SPE-driven learning itself fails to explain key features of the implicit adaptive response. Instead we find that motor performance prediction error (MPPE), the difference between predicted performance and the task goal consistently explains the implicit adaptive responses seen during a series of experimental manipulations that dissociate SPE, MPE, and MPPE by perturbing actions and goals both separately and in combination.

In a previous study, we dissected the observed motor error into externally-generated and internally-generated error components (EGE vs IGE) (Fig 1a). EGE is the component of motor error caused by external unpredictable perturbations, whereas IGE is the component caused by motor output noise. The findings showed that motor learning is driven specifically by EGE and not by IGE, indicating that the sensorimotor system is able to “clean up” the adaptive response by subtracting out the effects of internally-generated motor output noise from adaptive responses. In expt 1a, over the course of 1200 trials, we created small, randomly sequenced EGEs via visuomotor rotations (VMRs) of 0°, ±2° and ±4°. These small EGEs were of comparable size to the effects of motor output noise (Figure 1b), and the overall motor error on a trial was the sum of EGE and IGE components. We binned the population averaged data (N=20) into a 5x5 IGE/EGE grid based on the amount of IGE and EGE on each movement. The grid is plotted with squares colored to specify IGE (on the inside, with shades of blue) and EGE (on the outside, with shades of red). Remarkably, we found that single trial adaptive responses were insensitive to IGE (slope=0.02, r^2=0.01), but highly sensitive to EGE (slope=-0.22, r^2=0.92) (see Fig 1c-d). In a complementary unbinned analysis, we found similar results for the sensitivity of the adaptive response to EGE vs IGE (0.23 ± 0.03 vs -0.01 ± 0.01, t(19)=7.42, $p=10^{-6}$, Fig 1e). A second experiment (expt 1b) designed to measure strategy vs implicit adaptation while dissecting EGE and IGE, showed near zero strategy use (98% variance explained by implicit learning vs 2% by strategy), as expected since the perturbations were small, zero-mean, and random. Since EGE and IGE cannot be directly observed, the motor system must somehow dissect the observed error into EGE and IGE, if, as we found, the adaptive response differs between them. This could be accomplished by estimating IGE from motor output noise by using an efference copy of the motor command to predict action outcome and then subtracting that prediction from the planned motion. If these predictions are accurate, then EGE would be equivalent to the difference between actual performance and a prediction of the performance, which is the definition of MPPE.

VMR perturbations that induce EGE or MPPE also create SPE because these perturbations generate errors by perturbing actions. However, online target shift (TS) perturbations that induce EGE or MPPE would not create SPE because TS perturbations would perturb only the goal, not the motion (Leow et al 2018 *EJN*, Leow et al 2020 *J Neurosci*). Thus MPPE-driven (or equivalently EGE-driven) adaptation would predict that TS-perturbations would lead to implicit motor learning, whereas SPE-driven adaptation would not. In order to test these predictions directly, we designed an experiment where SPE-driven and MPPE-driven adaptation could be powerfully dissociated. Over the course of 2000 trials, we interspersed three types of perturbations: (1) VMR-only trials, which induced a combination of MPE and SPE (Fig 2a), (2) TS-only trials which induced MPE but no SPE (Fig 2d), and (3) VMR-TS trials with matched VMR and TS perturbations that canceled MPPE and but induced SPE, because of the VMR (Fig 2g). We binned the data into a 5x5 IGE/EGE grid like in expt 1, separately for the VMR-only, TS-only and matched VMR-TS trials. In the VMR-only perturbation condition, MPPE explained a far greater fraction of variance in the IGE/EGE grid data than IGE (R^2 values of 87% vs 1%, Fig 2b-c), replicating the findings of the previous study. Remarkably, we found that even when the perturbation was a target shift, EGE or MPPE explained a far higher fraction of variance in the IGE/EGE grid data than IGE (R^2 values of 70% vs 2%, Fig 2e-f), with adaptive responses that were clearly sensitive to EGE or MPPE but not IGE (sensitivity = -0.13±0.03 vs 0.02±0.03), in line with MPPE-driven but not SPE-driven learning. In the third condition, coupled VMR-TS trials that cancel EGE/MPPE but create SPEs in line with the VMR perturbation size, we found that the adaptive response sensitivity to this SPE was not significantly different from zero (-0.05±0.05, p=0.08), indicating that when SPE occurs in isolation from MPPE, little to no adaptative response is evoked. Here we found, however, a small but significant sensitivity to IGE (0.04±0.02, $p=10^{-4}$), suggesting that for this complex combination perturbation, motor output noise cancelation was not complete.

These results show that motor performance prediction error (MPPE)-driven learning robustly explains the pattern of adaptation to both goal and action perturbations (Figure 3a-b). Moreover, individual contributions from SPE or MPE-driven learning hypotheses are small compared to that of MPPE-driven learning in a combined model of learning (Fig 3c).

FIGURE 1 (Expt 1a: N=20; Expt 1b: N=20)



Error bars on all bar plots (in Fig 1 & 3) are 95% confidence intervals

FIGURE 2 (Expt 2: N=20)

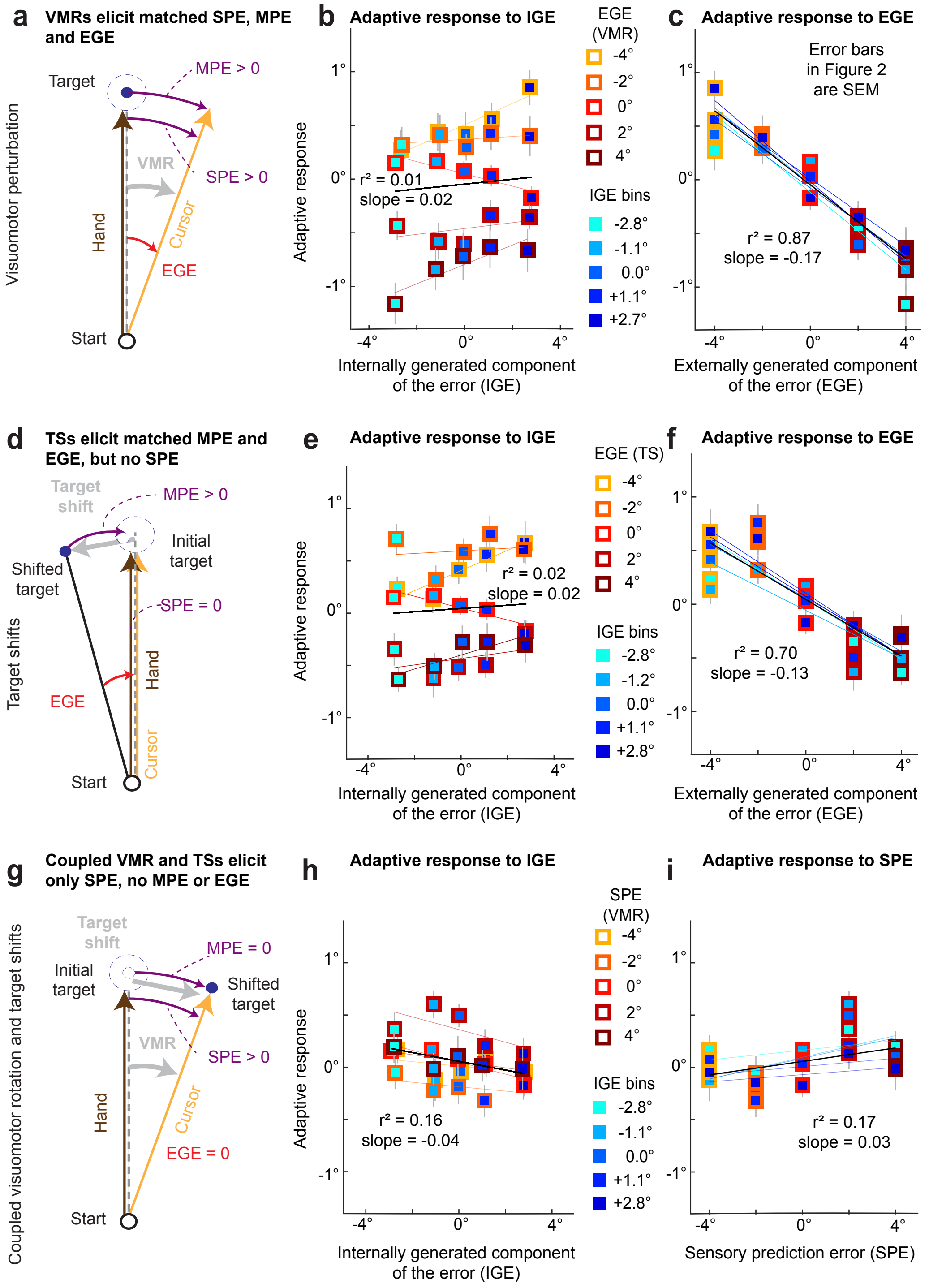


FIGURE 3