

Distinct processing of sensory-prediction error and target error during implicit motor adaptation

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Sensory-prediction error (SPE), the difference between predicted and actual sensory feedback, is recognized as the primary signal driving implicit motor adaptation. Recent reports have shown that target error (TE), the difference between the endpoint feedback and target location, may also impact implicit adaptation.¹⁻³ One method to demonstrate this involves a variant of a visuomotor rotation task, whereby the target is displaced after movement onset, such that the cursor lands within the target. Under such conditions, adaptation to the rotation is attenuated compared to when the target remains stationary. There are a number of potential explanations for this attenuating effect, including: 1) An intrinsic reward signal (due to the cursor successfully hitting the target) modulates the rate of adaptation from SPE; 2) the elimination of a TE signal from an implicit learning process that normally operates with TE and SPE-based processes working in parallel; 3) the displacement of the target has a distracting effect, which attenuates adaptation. To evaluate these hypotheses, we performed a series of experiments, systematically manipulating the size of the SPE and the size of the target displacement.

To induce adaptation, we used clamped visual feedback, in which the timing and extent of cursor motion is linked to hand motion, but the cursor trajectory is offset by a fixed angle relative to the target and thus independent of the hand trajectory (**Fig. 1a**). This manipulation, in combination with instructions to ignore the cursor feedback, induces implicit adaptation without contamination from explicit strategies.⁴ In the present experiments, we also jumped the target soon after movement initiation to manipulate TE (**Fig. 1b**). Participants were fully informed of this perturbation and instructed to ignore the jump, always aiming for the original target location. In this manner, the angular relationship of the hand with respect to the cursor feedback and displayed target location were not contingent on the participant's behavior, thereby allowing us to dissociate implicit responses to SPE and TE.

We first compared a standard clamp condition in which the feedback cursor deviated from the stationary target (and thus there is both SPE and TE) with a condition in which the target jumped and the feedback cursor moved directly to the original target location (TE only). In two experiments (Exp 1: $n = 12$; Exp 2: $n = 20$), robust sign-dependent changes in hand angle, the signature of adaptation, was observed in the former, but not in the latter (**Fig. 1**). These results indicate that TE alone is not sufficient to drive implicit adaptation.

However, the effect of TE may be conditional on the presence of SPE. To explore this possibility, we combined clamped cursor feedback with target jumps (**Fig. 2a-b** Exp 3: $n = 100$). The target jumps could either be towards the clamped cursor, including landing at the cursor location, or away from the cursor. When the target jumps towards the clamped cursor, the distance between the target and the cursor is diminished, which results in less TE; when the target jumps away from the clamped cursor, the distance between the target and the cursor increases, resulting in more TE. If learning is sensitive to TE magnitude, we would expect greater changes in hand angle when the target jumps away. Additionally, we asked whether the mere presence of a target "jump" might disrupt adaptation, independent of any putative effect of TE, perhaps by drawing attention away from the clamped cursor and thus weakening learning from the SPE. To assess this hypothesis, we flashed the target briefly in place (Jump in Place).

Both of these hypotheses were supported by the data (**Fig. 2c**). In support of the TE magnitude-dependent hypothesis, we observed an effect of jump direction: Relative to a No Jump baseline, adaptation was decreased when the target jumped towards the clamp and was maintained when the target jumped away from the clamp. In support of the distraction hypothesis, we observed a small attenuation of adaptation when the target jumped in place. The combination of these two effects may jointly account for the asymmetrical functions shown in **Fig. 2c**: An increase in TE when the target jumps away from the clamp may be offset by the distraction effect of the jump.

We developed a series of computational models to formally evaluate the hypotheses sketched above (**Fig. 3**). In one set of models, learning was limited to a single SPE-based process (**left column**); SPE could either be attenuated when the target jumped towards the cursor (**3c**) or attenuated as a function of the size of the target jump, independent of direction (**3e**). The latter model is an instantiation of the distraction idea. The other set of models (**right column**) included a TE-based process in which the error signal was a linear function of the distance between the clamp and the final position of the target. The results from Exp 2 qualitatively favor the Distracted SPE + TE model (**3f**) with the observed behavior (red) posited to be a composite of two learning processes, an SPE-dependent process sensitive to attentional distraction (grey gaussian) and a linear TE-dependent process (black). To evaluate this model in a more robust manner, we conducted a final experiment in which we used a larger range of target jumps ($n = 100$, **Fig 4**). The results again reveal a striking asymmetry related to the direction of the target jump and were best fit with the Distracted SPE + TE model. (Note: We also considered models in which the TE process saturated or was modulated by the distracting effects of targets jumps. These models provided worse fits than the Distracted SPE + TE model.)

Theoretically, the current results provide additional evidence that multiple implicit processes contribute to the behavioral changes observed in studies of sensorimotor adaptation, highlighting the contribution of a TE-sensitive process in addition to the traditional SPE-sensitive process. However, the results also point to a number of unappreciated constraints on the interaction of these two processes. First, the absence of any behavioral changes in the TE-only conditions of Exps 1 and 2 suggest a dependency whereby implicit recalibration of the sensorimotor system only occurs in the presence of SPE. Second, the results provide a more nuanced picture of the effect of displacing the target. Not only does this manipulation impact the sign and size of the TE, but it also appears to modulate the strength of the SPE signal.

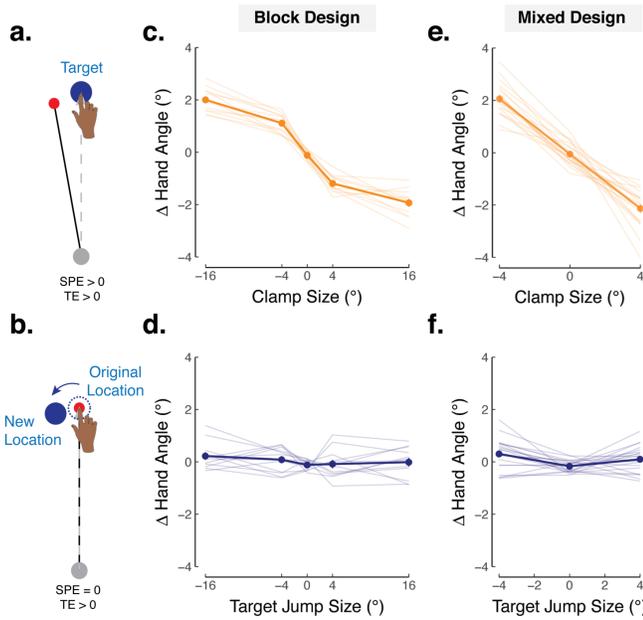


Figure 1: Target error alone is not sufficient for implicit adaptation. Using clamped visual feedback for testing implicit responses to: (a) SPE + TE, induced by offsetting the cursor trajectory at a fixed angle relative to the target, and (b) target error (TE), induced by jumping the target immediately after movement initiation, with the cursor clamped to 0° (the pre-jump target location). (c-d) Participants experienced 4 alternating blocks of target jumps and clamped feedback. The perturbations were delivered using a random schedule to prevent accumulated learning. We quantified adaptation by measuring how much the hand angle changed on trial $n + 1$ in response to the perturbation on trial n . (c) Using linear regression, we extracted a slope measure from each participant's data. We then performed a one-sample t-test against 0, revealing robust sign-dependent changes in hand angle during the clamp blocks (*Exp. 1*: $t_{11} = -17.1, p < 0.001$), (d) but not target jump blocks (*Exp. 1*: $t_{11} = -0.9, p = 0.40$). (e-f) Participants experienced a randomized zero-mean perturbation schedule with target jumps interleaved with clamped feedback. (c) Again, robust sign-dependent changes in hand angle were observed during the clamp blocks (*Exp. 2*: $t_{19} = -15.7, p < 0.001$), (d) but not target jump blocks (*Exp. 2*: $t_{19} = -1.0, p = 0.33$).

Figure 2 (right): Implicit adaptation is modulated by target error in the presence of sensory prediction errors. (a-b) Participants experienced a randomized zero-mean perturbation schedule where clamp size (between-participant: 3°, 7°) and target jump size (within-participant: No Jump, Jump in Place, Jump To/Jump Near, Jump Away) were both varied. (c) Robust changes in hand angle were observed when the target was stationary for both error sizes ($t > 6.0, p < 0.001$). Jumping away maintained adaptation (7°: $t_{129} = 0.6, p_{bonf} = 1, d_z = -0.1$; 3°: $t_{156} = 0.2, p_{bonf} = 1, d_z = 0$), whereas jumping to/near the clamp attenuated adaptation (7°: $t_{129} = -3.2, p_{bonf} = 0.01, d_z = -0.6$; 3°: $t_{156} = -3.7, p_{bonf} = 0.002, d_z = -0.7$). The comparison between Jump In Place and No Jump did not achieve significance for either error size ($p_{bonf} > 0.31$), but showed a small attenuating effect (7°: $d_z = -0.2$; 3°: $d_z = -0.4$).

Figure 4 (bottom): Implicit adaptation reflects the contribution of learning from target error and sensory prediction error, with the latter sensitive to distraction from target jumps. (a-b) Participants experienced a randomized zero-mean perturbation schedule (between-participant: 3°, 7°) × (within-participant: -30° through 30°). The Distracted SPE + TE model was the most strongly supported model based on average cross-validated R_{cv}^2 values.

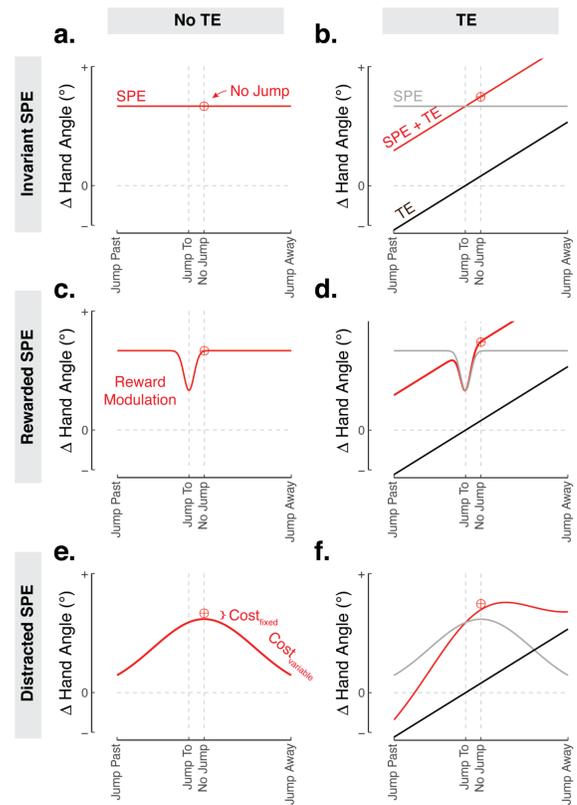
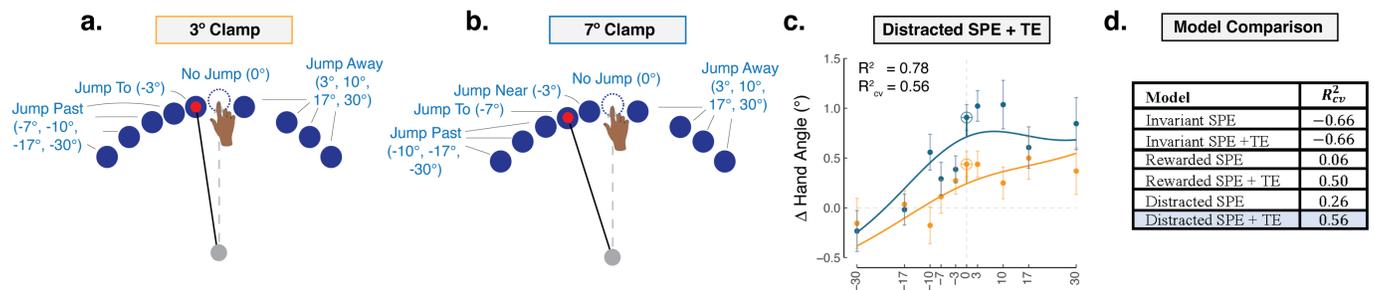


Figure 3: Modeling the influence of target jumps on adaptation to TE and SPE. SPE may be a) impervious to target jumps (b) attenuated when the cursor lands in the target (modulated by intrinsic reward), or (c) attenuated due to distraction from the motion of the jumping target, with the attenuation assumed to be a function of the jump size. Right column: Adaptation may also be driven by a TE-based learning process, assumed to be a linear function of the distance between the feedback and final position of the target. In d - f, red indicates expected behavior, the composite of the SPE process (grey) and TE-based process (black).