The magnitude of implicit sensorimotor adaptation is limited by continuous forgetting

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Sensorimotor adaptation is a learning process which is thought to keep motor skills well calibrated as the body or environment changes. Its operation during single-session experiments is generally well characterized by linear state-space learning models (Thoroughman & Shadmehr, 2000; Cheng & Sabes, 2006; Smith *et al.*, 2006). On each trial, these models update their state based on the error observed on each reach, and "forget" based on the accumulated learning. However, these models are driven by a single error signal that conflates two types of error, sensory prediction errors and task performance errors. Recent work suggests that these distinct error signals change behavior through different learning mechanisms (Miyamoto *et al.*, 2014; Taylor *et al.*, 2014; Bond & Taylor, 2015). The processes that respond to these different errors have distinct theoretical interpretations and likely different neural loci, making it important to characterize their operation in isolation, so that they can be better understood when operating together under normal conditions. Here we focus on implicit adaptation to a putative sensory prediction error, induced via task-irrelevant clamped visual feedback.

Implicit adaptation from a visual prediction error has been shown to be limited in magnitude, reaching a group-mean maximum of ~25°, even when large errors persist (Fig. 1b; Bond & Taylor, 2015; Morehead *et al.*, 2017; Kim *et al.*, 2017). We tested several plausible mechanisms that could account for this learning asymptote by first training participants to asymptote in response to clamped error feedback that was offset by -7.5°. This offset was then changed by ±15° so that it either increased in amplitude -22.5° or flipped direction to +7.5° (Fig. 2). Two candidate mechanisms, habituation to the error signal itself and cancellation of the error signal by forward model learning, predicted a symmetric response to this change in clamped feedback. This is because either change in direction of the clamp offset would once again make the stimulus novel, in the case of habituation, or once again unpredicted in the case of the forward model. In contrast, we observed a clear asymmetry in the response to these two changes of the clamp offset, with no change in behavior for the group exposed to the larger error (1.4° [95% CIs -2.9°, 5.7°]), relative to the large change we observed in the group whose error flipped sign (-44.1° [95% CIs -52.2°, 36.1°]).

These results suggest that the learning does not become asymptotic because the internal error signal has been negated, but rather that the error signal remains constant while something intrinsic to the learning process itself limits the magnitude of learning. One possibility is that there is a fundamental capacity limit for how much an internal model can be altered by implicit adaptation, another is that this asymptote reflects an equilibrium between a learning and forgetting processes, as described by traditional state-space motor learning models. To discriminate between these two hypotheses, we first introduced clamped feedback offset by -7.5°, allowing participants' learning to become asymptotic, then we removed visual feedback entirely, or only on 33% of trials (Fig. 3). Our results are consistent with the hypothesis that the asymptotic magnitude of implicit adaptation is a function of an equilibrium between learning and forgetting, as we observed robust forgetting when feedback was removed entirely and, when only removed on 33% of trials, the behavior of participants began to 'sawtooth', cycling with the presence or absence of feedback.

If the learning and forgetting equilibrium hypothesis was valid, it would necessarily predict the change in asymptote that we observed between the first and second halves of our experiments. In Figure 4, we plot the change in asymptote predicted by the equilibrium hypothesis for our experimental conditions, along with the actual measured change. Linear simple regression on these values displayed a slope of 0.98 [95% CIs .91, 1.1] and an R^2 of 92%, indicating that this hypothesis provides a good description of the learning dynamics in our tasks.

Our results show that implicit sensorimotor adaptation learns and forgets on each trial, as in traditional state-space models, and that adaptation asymptotes at ~25° in the presence of ongoing error, because this is the point in learning where these two factors come into equilibrium and balance each other out. Our work suggests that behavioral changes exceeding 25° in visuomotor adaption do not come about via sensory prediction error-driven implicit adaptation, and that there are fundamental limits on how much this process can learn.

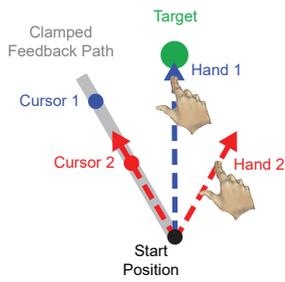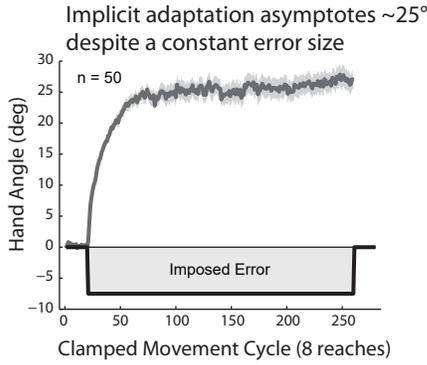## Fig. 1 - Implicit response to clamped feedback

Illustration of clamped feedback paradigm. The radial component of the cursor moves in sync with the hand, while the cursor direction is fixed, confining it to the path.

Implicit adaptation asymptotes ~25° despite a constant error size

n = 50

The introduction of task-irrelevent clamped feedback causes robust adaptation, but this learning asymptotes at about 25°.

Fig. 2 - Asymptotic magnitude does not come about via habituation or a forward model learning, but could arise from an equilibrium of learning & forgetting, or a capacity limit
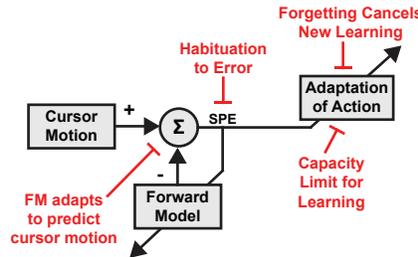
Plausible mechanisms, shown in red, modulate different steps in the learning process. Habituation and forward model cancellation affect generation of an error, while the other two candidate mechanisms modulate the learning step itself.
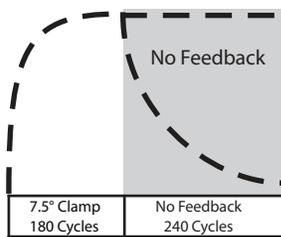
n = 10/group
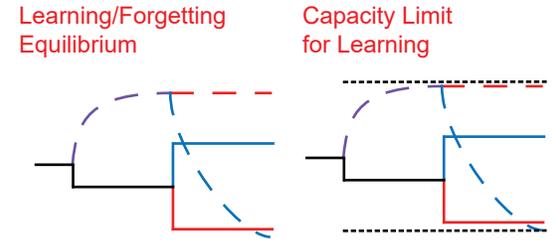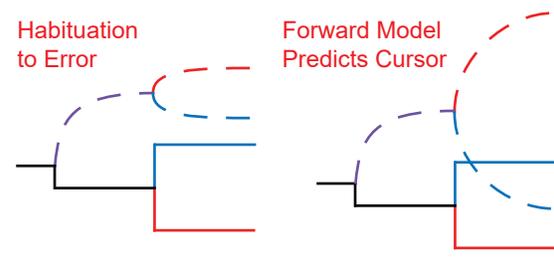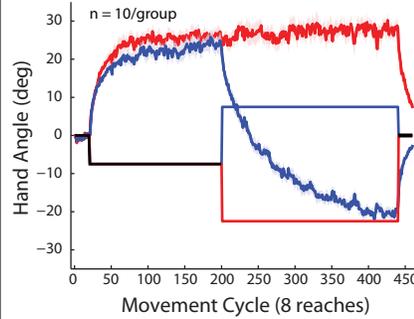
Above: Predicted adaptation for all four mechanisms evaluated when the clamp offset is changed by ±15° after asymptotic adaption is achieved. Notably, the top two mechanisms predict symmetric changes, whereas the bottom two predict asymmetric responses.

Left: Experimental data show asymmetric responses, in line with the bottom two mechanisms but not the top two.

Fig. 3 - Motor memories decay in the absense of the learning stimulus

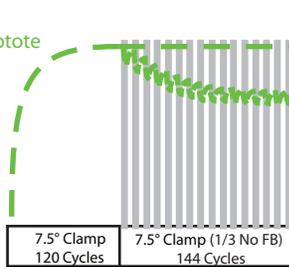**Task diagrams of the capacity limit and learning/forgetting equilibrium predictions**

100% Forgetting
0 x First Asymptote

Capacity Limit Prediction

No Feedback

Learning/Equilibrium Prediction

7.5° Clamp 180 Cycles | No Feedback 240 Cycles

33% Forgetting
.67 x First Asymptote

Capacity Limit Prediction
Learning/Equilibrium Prediction

7.5° Clamp 120 Cycles | 7.5° Clamp (1/3 No FB) 144 Cycles

Note that the learning/forgetting equilibrium hypothesis predicts that the adapted state will 'sawtooth' as the clamped feedback is cycled on and off, because there is no learning signal when feedback is removed.

Behavioral Results

100% Forgetting

n = 18

7.5° Clamp 180 Cycles | No Feedback 240 Cycles

33% Forgetting

n = 22

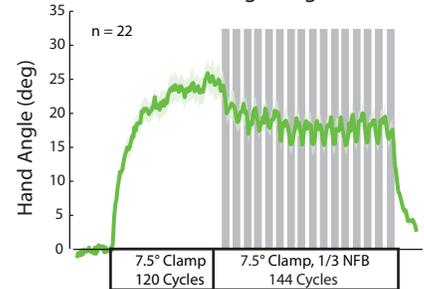7.5° Clamp 120 Cycles | 7.5° Clamp, 1/3 NFB 144 Cycles
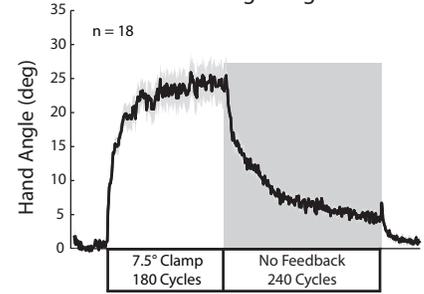
Fig 4 - The magnitude of asymptotic learning appears to be determined by an equilibrium between learning and forgetting

Summary of the change in asymptote observed over the four experiments above, plotted against the change expected from the learning/forgetting equilibrium hypothesis.
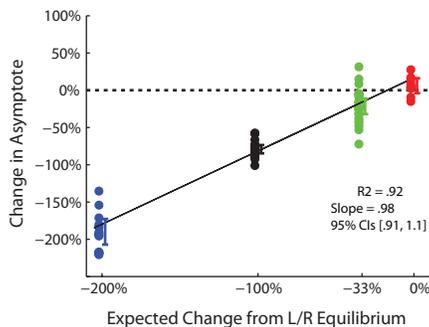

R^2 = .92
Slope = .98
95% CIs [.91, 1.1]

Illustration of the learning/forgetting equilibrium mechanism within and across trials. Clamped feedback induces an unchanging error on every trial, which drives learning, shown here in red. Forgetting, shown in blue, also occurs on every trial, but it is initially small because its forgets a percentage of the learning that has been accumulated. An asymptote is reached as adaptation progresses, because forgetting eventually cancels new learning.

Early   Middle   Asymptote

Learning   Forgetting

Imposed Error