Visuomotor Adaptation is a Disturbance Rejection Problem

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***Abstract*— This paper shows that visuomotor adaptation can be cast as a disturbance rejection problem. We begin by formalizing experimentally observed dynamic properties of adaptation in terms of the transient response of a stable linear system, and we discuss implications on the validity of classes of models. Next, we solve the visuomotor adaptation problem by invoking adaptive internal models. A theoretical result on stability is obtained using averaging theory. Simulations applied to a visuomotor rotation experiment with fast arm reaches show that the dynamic properties of adaptation are recovered using the model.**

I. Introduction

Sensorimotor adaptation is an error-driven process of movement modification characterized, firstly, by a specific repeated pattern of muscle activation with changes only in certain variables (e.g. endpoint position); second, the change occurs gradually over repetitive trials; and third, once adapted, subjects are unable to retrieve the prior behaviour except by re-adapting with the same gradual process [15]. Motor adaptation is termed *short-term* when it occurs over minutes or hours, contrasting with *long-term adaptation* that takes place over days or weeks [18]. *Visuomotor adaptation* is elicited by a *visual error* closely following the execution of a movement, e.g. saccades with an intersaccadic step of the target [11]; and the *visuomotor rotation experiment* with fast arm reaches [13], [20].

Error-driven LTI state models have proven to be resilient to capture many aspects of motor adaptation [21], [6], [14], [12]. Such models generally utilize abstract states with no physical meaning. Meanwhile, neuroscientists have posited that the physiological underpinning of adaptation is that the brain builds a *forward model* [10], typically an observer or Kalman filter, of either the plant [16], [24]; the error [22]; or the disturbance [12], [2]. Remarkably, the internal model principle [7] is not explicitly present in this discourse.

The goal of this paper is to show that visuomotor adaptation can be cast as a problem of disturbance rejection. In so doing, and unlike prior models, we take explicit account of the internal model principle. While our model is intended to be applicable in a variety of sensorimotor adaptation tasks, here we focus on short-term adaptation in the saccadic system and the visuomotor rotation experiment, both of which involve constant disturbances.

II. Dynamic Properties of Adaptation

We begin by formalizing the dynamic properties of adaptation. We make three simplifying assumptions. First, we focus on motor adaptation tasks involving a single output. That is, we restrict our attention to one degree of freedom of movement; for instance, horizontal movement of the eye, hand angle relative to a reference angle in a horizontal plane, forward (coronal) inclination of the body relative to a vertical reference, the horizontal angle of a dart thrown by a subject, and so forth. Second, we assume the model is linear time-invariant, as such models have promise to explain motor adaptation [21]. Third, we focus on constant disturbances, as currently there is a dearth of experiments with non-constant disturbances [5].

Motor adaptation experiments proceed in sequences of blocks of trials of specific types. A *baseline block* (B) of trials familiarizes the subject with the experimental aparatus under unperturbed (normal) conditions. A *learning block* (L) of trials occurs after a baseline block when a perturbation or disturbance is introduced. A *washout block* (W) follows a learning block when the perturbation is removed. An *unlearning block* (U) follows a learning block when the perturbation changes in sign but not magnitute relative to the learning block. A *relearning block* (R) is a second learning block with the same perturbation. A *downscaling block* (D) is a second learning block in which the perturbation is set to a fraction of its value in the first learning block.

Consider the discrete time system

$$\xi(k+1) = A\xi(k) + Ew(k) \tag{1a}$$

$$y(k) = C\xi(k) + Dw(k)\,, \tag{1b}$$

where $\xi(k) \in \mathbb{R}^n$ is the state, $w(k) \in \mathbb{R}^q$ is a disturbance, and $y(k) \in \mathbb{R}$ is the scalar measurement or output. Suppose that the unforced system (when $w(k) \equiv 0$) is asymptotically stable, i.e. $\sigma(A) \subset \mathbb{C}_1$, the open unit disk in the complex plane. In all definitions below, let $d_0 \in \mathbb{R}^q$ and $y_0 \in \mathbb{R}$ be constants and let $k_0 \geq 0$ be an integer. We assume that the disturbance is a constant vector $w(k) \equiv d_0$. Since the system is stable, we can define y_{ss} to be the steady-state value of y when $w(k) \equiv d_0$. Also $-y_{ss}$ is the steady state value of y when $w(k) \equiv -d_0$.

Savings is a behavior in which learning is sped up in the second learning block relative to the first one. Two experiments in which savings can be exhibited are BLUR or BLWR.

Definition 1 (Savings): Suppose we have discrete times $k_3 \geq k_2 > k_1 > k_0$ such that: $w(k) = d_0$ for $k \in [k_0, k_1) \cup [k_2, \infty)$, and $y(k_3) = y(k_0) = y_0$. Let T_{r0} and T_{r3} be the rise times starting at k_0 and k_3, respectively. We say (1a) - (1b) exhibits *savings* if $T_{r0} > T_{r3}$. Additionally, if $w(k) = -d_0$ for $k \in [k_1, k_2)$, then we say (1a) - (1b)

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exhibits *savings with counter perturbation (CP)*. If $w(k) = 0$ for $k \in [k_1, k_2)$, then we say (1a) - (1b) exhibits *savings with washout (WO)*. ◁

Remark 2: The rise time is the number of trials for $y(k)$ to reach 90% of its steady-state value. However, it need not be the case that $y(k)$ has already reached 90% of its steady-state value y_{ss} at discrete time k_1 when the first learning block ends. The rise time is computed by extending forward in time the solution curve of the relevant block of trials. ◁

Reduced savings is a behavior in which savings is reduced by inserting a washout block of trials after the unlearning block. After the washout block, relearning does not proceed as rapidly as in the savings experiment. Reduced savings may be exhibited in a BLUWR experiment.

Definition 3 (Reduced Savings): Suppose we have a duration $T_{wo} > 0$ and times $k_2 > k_{wo} + T_{wo} > k_{wo} > k_1 > k_0$ such that: $w(k) = d_0$ for $k \in [k_0, k_1) \cup [k_{wo} + T_{wo}, \infty)$, $w(k) = -d_0$ for $k \in [k_1, k_{wo})$, $w(k) = 0$ for $k \in [k_{wo}, k_{wo} + T_{wo})$, and $y(k_2) = y(k_0) = y_0$. Let T_{r0} and T_{r2} be the rise times starting at k_0 and k_2, respectively. We say (1a) - (1b) exhibits *reduced savings* if $T_{r0} \geq T_{r2}$ and $\lim_{T_{wo} \to \infty} T_{r2} = T_{r0}$. ◁

Anterograde interference is a behavior in which a previously learned task reduces the rate of subsequent learning of a different (and usually opposite) task. Anterograde interference may be exhibited in a BLU experiment.

Definition 4 (Anterograde Interference): Suppose there exist discrete times $k_2 > k_1 > k_0$ such that: $w(k) = d_0$ for $k \in [k_0, k_1)$, $w(k) = -d_0$ for $k \in [k_1, \infty)$, and $y(k_2) = -y(k_0)$. Let T_{r0} and T_{r2} be the rise times starting at k_0 and k_2, respectively. We say (1a) - (1b) exhibits *anterograde interference* if $T_{r0} < T_{r2}$. Moreover T_{r2} increases as the number of trials in the first learning block increases. ◁

Rapid unlearning is a behavior in which the rate of unlearning is faster than the rate of initial learning, if the number of trials in the learning block is small. Rapid unlearning may be exhibited in a BLW experiment.

Definition 5 (Rapid Unlearning): Suppose there exist discrete times $k_2 > k_1 > k_0$ such that: $w(k) = d_0$ for $k \in [k_0, k_2)$, $w(k) = 0$ for $k \in [k_2, \infty)$, and $y(k_1) = y_{ss} - y(k_2)$. Let T_{r1} and T_{r2} be the rise times starting at k_1 and k_2, respectively. We say (1a) - (1b) exhibits *rapid unlearning* if $T_{r1} > T_{r2}$. Moreover T_{r2} decreases as the number of trials in the first learning block decreases. ◁

Rapid downscaling is a behavior in which the rate of learning in a secondary learning block is faster when the disturbance is set to a fraction of its value in the initial learning block.

Definition 6 (Rapid Downscaling): Suppose there exist $\alpha \in (0, 1)$ and discrete times $k_2 > k_1 > k_0$ such that: $w(k) = d_0$ for $k \in [k_0, k_2)$, $w(k) = \alpha d_0$ for $k \in [k_2, \infty)$, and $y(k_1) = (1 + \alpha)y_{ss} - y(k_2)$. Also, we assume that the steady-state value of $y(k)$ for $k \geq k_2$ is αy_{ss}, and $|y(k_2)| > \alpha |y_{ss}|$. Let T_{r1} and T_{r2} be the rise times starting at k_1 and k_2, respectively. We say (1a) - (1b) exhibits *rapid downscaling* if $T_{r1} > T_{r2}$. Moreover T_{r2} decreases as the number of trials in the first learning block $k_2 - k_0$ decreases. ◁

Remark 7: The justification for the expression $y(k_1) = (1 + \alpha)y_{ss} - y(k_2)$ in the previous definition is as follows. To make a fair comparison between the rise times for the learning block and the downscaling block, the output $y(k)$ must vary over the same range of values. If the initial time for the measurement of rise time in the learning block is selected to be k_1, then the total variation of $y(k)$ from this time to steady-state is $y_{ss} - y(k_1)$. Similarly, for the downscaling block, the total variation of $y(k)$ is $y(k_2) - \alpha y_{ss}$. Equating these two expressions and solving for $y(k_1)$, we obtain the expression above. ◁

Spontaneous recovery is a behavior observed during the washout block of a BLUW experiment in which $y(k)$ partially "rebounds" to its value at the end of the learning block rather than converging monotonically to zero.

Definition 8 (Spontaneous Recovery): Suppose there exist discrete times $k_2 > k_1 > k_0$ such that $w(k) = d_0$ for $k \in [k_0, k_1)$, $w(k) = -d_0$ for $k \in [k_1, k_2)$, $w(k) = 0$ for $k \in [k_2, \infty)$, and $y(k_2) = y(k_0)$. We say (1a) - (1b) exhibits *spontaneous recovery* if the percent overshoot starting from $y(k_2) = y_0$ satisfies: $OS\% > 0$. ◁

III. Implications

We explore several implications of the dynamic properties of adaptation. First, an immediate fact also confirmed experimentally [11] is that they cannot arise from a first-order LTI model.

Lemma 9: Consider the stable system (1a)-(1b). If the system is first-order, then it does not exhibit savings, anterograde interference, rapid unlearning, rapid downscaling, or spontaneous recovery.

Now consider the open-loop model

$$x(k+1) = Ax(k) + Bu(k) \tag{2a}$$

$$y(k) = x(k) + d(k)\,, \tag{2b}$$

where w.l.o.g. $B > 0$. This linear system (2a) provides a high-level, abstract description of the change in quality of movement over successive trials of a single degree of freedom of the body. The integer k denotes the trial number, $x(k)$ is the state of that single degree of freedom at the end of the k-th trial, $d(k)$ is an additive disturbance at the k-th trial, and $y(k)$ is a measurement observed by the subject at the end of the k-th trial. The term $Ax(k)$ models a retention or memory mechanism of the state in the previous trial. Because $u(k)$ is a free variable, this scalar open-loop model places no restrictions whatsoever on the possible dynamics of the considered degree of freedom of the body. Finally, we define the observed *error* at the k-th trial to be

$$e(k) = r(k) - y(k) = r(k) - x(k) - d(k)\,, \tag{3}$$

where $r(k)$ is the desired (reference) position at the end of the k-th trial.

Suppose that $A = 1$, meaning the brain retains an exact memory of the last state (it may do so using proprioception

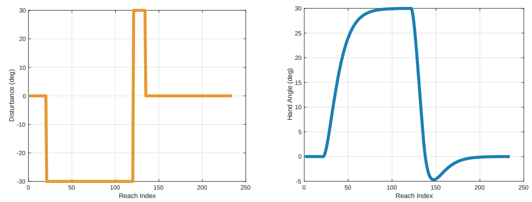

Fig. 1: The model (4) does not exhibit spontaneous recovery in a BLUW experiment. The hand angle does not rebound above zero during the washout block.

from the muscles). The simplest strategy to reject the disturbance in this case is to utilize error feedback, $u(k) = Ke(k)$, yielding an error model $e(k+1) = (1 - BK)e(k)$. If $|1 - BK| < 1$, then $e(k)$ tends to zero. Hence, the dynamics of adaptation would be first-order, contradicting Lemma 9. The proposal that the brain utilizes proprioception to be able to employ static error feedback seems unlikely, as confirmed experimentally for the saccadic system [11].

Next, consider an adaptive observer, as suggested in [25], to generate an estimate $\hat{x}(k)$ of $x(k)$. Let $\widetilde{x}(k) = \hat{x}(k) - x(k)$ be the estimation error, and suppose $\widetilde{x}(k+1) = (A - LC)\widetilde{x}(k)$ with L chosen such that $|A - LC| < 1$. Now we notice that if $r(k) = 0$, then $\hat{d}(k) := -\hat{x}(k) - e(k)$ is an accurate estimate of $d(k)$. Thus, to reject the disturbance $d(k)$ in the error dynamics, a linear feedback based on measurement of $e(k)$ and $\hat{x}(k)$ would suffice. For example, $u(k) = \frac{1}{B}\left[1 - A\right]\hat{x}(k) + Ke(k)$. The closed-loop system is

$$x(k+1) = (1 - BK)x(k) + (1 - A)\widetilde{x}(k) - BKd(k) \quad (4a)$$

$$\widetilde{x}(k+1) = (A - LC)\widetilde{x}(k)\,. \quad (4b)$$

The closed-loop eigenvalues are $1 - BK$ and $A - LC$ so we select K such that $0 < 1 - BK < 1$ (note that selecting $(1 - BK) < 0$ would result in oscillations not witnessed in adaptation experiments). One can prove this model is not capable to reproduce the dynamics of adaptation. Simulation results for a BLUW visuomotor rotation experiment are shown in Figure 1.

Finally, it has been proposed that the brain builds an internal model of the error dynamics [22]. Suppose $A = 1$ (see equation (3) of [22]) and consider

$$\hat{e}(k+1) = \hat{e}(k) - Bu(k) + G(e(k) - \hat{e}(k))\,. \quad (5)$$

The simplest controller to drive the error to zero using this observer is $u(k) = K\hat{e}(k)$. We select K and G such that $0 < 1 - BK < 1$ and $0 < 1 - G < 1$ for stability, as well as for consistency with experimental data (adaptation generally does not exhibit damped oscillations). In the next result we use the experimental observation that $x(k)$ is monotonic during learning and unlearning blocks.

Lemma 10: Consider (2) and (5) with $A = 1$ and $u(k) = K\hat{e}(k)$. Suppose $x(k)$ is monotonic over the unlearning block of a BLUW experiment. Then the closed-loop system does not exhibit spontaneous recovery.

Proof: Consider a BLUW experiment in which the baseline block occurs over a discrete interval $[0, k_1 - 1]$ with $d(k) = 0$; the learning block occurs over $[k_1, k_2 - 1]$ with $d(k) = d_0 < 0$; the unlearning block occurs over $[k_2, k_3 - 1]$ with $d(k) = -d_0 > 0$; and the washout block occurs over $[k_3, \infty)$ with $d(k) = 0$. We assume that $x(k_3) = -\epsilon$, where $0 < \epsilon < -d_0$ (such an index must exist since $x(k)$ asymptotically approaches $d_0 < 0$ in the unlearning block. That is, the washout block begins after $x(k)$ has crossed 0 during the unlearning block. See Figure 1. The solution over the washout block is

$$x(k) = (1 - BK)^{k - k_3}x(k_3) + \tilde{e}(k_3)\bar{A}z(k)$$

where $z(k) = [(1 - BK)^{k-k_3} - (1 - G)^{k-k_3}]$ and $\bar{A} := \frac{BK}{G - BK}$. To show that the system exhibits spontaneous recovery, we must show there exists a time $k_4 > k_3$ such that $x(k_4) > 0$. First, observe $-\epsilon(1 - BK)^{k-k_3} < 0$ for all $k \geq k_3$. Second, consider $z(k)$ and $\bar{A}$. If $0 < 1 - BK < 1 - G < 1$, then $\bar{A} < 0$ and $z(k) < 0$ for all $k \geq k_3$. Instead if $0 < 1 - G < 1 - BK < 1$, then $\bar{A} > 0$ and $z(k) > 0$ for all $k \geq k_3$. Thus, $\bar{A}z(k) > 0$ for $k \geq k_3$. Finally, we must consider the sign of $\tilde{e}(k_3)$. If we can show $\tilde{e}(k_3) < 0$, then $\tilde{e}(k_3)\bar{A}z(k) < 0$ for all $k \geq k_3$ and there is no spontaneous recovery. Observe that $\tilde{e}(k_3) = \hat{e}(k_3) - e(k_3)$. Then, $-e(k_3) = x(k_3) < 0$. Also, $x(k)$ is decreasing during the unlearning block and since $x(k+1) = x(k) + BK\hat{e}(k)$, then $\hat{e}(k_3) < 0$. Thus, we conclude that $\tilde{e}(k_3) < 0$ and hence, $x(k) < 0$ for $k \geq k_3$. ■

IV. Visuomotor Adaptation Model

In this section we develop a model of visuomotor adaptation by casting the problem as one of disturbance rejection of deterministic disturbances acting on a linear system. From (2)-(3) we obtain the *error model*

$$\begin{aligned} e(k+1) &= Ae(k) - Bu(k) + r(k+1) - d(k+1) \\ &\quad - Ar(k) + Ad(k) \\ &= Ae(k) - Bu(k) + \overline{d}(k)\,. \end{aligned} \quad (6)$$

We assume $\overline{d}(k)$ is an unknown deterministic signal generated by a linear exosystem

$$w(k+1) = Fw(k) + G\overline{d}(k)\,, \qquad \overline{d}(k) = \Psi w(k)\,, \quad (7)$$

where $w \in \mathbb{R}^q$ is the *exosystem state*, and $\Psi \in \mathbb{R}^{1\times q}$ are the unknown exosystem parameters. We assume, as usual, the eigenvalues of $S := F + G\Psi$ lie on the unit circle $\partial\mathbb{C}_1$, F is Schur stable, (F, G) is a controllable pair, and w.l.o.g. (Ψ, S) is an observable pair. The *disturbance rejection problem* is to find a controller such that $e(k) \longrightarrow 0$.

Consider the *adaptive internal model*

$$\hat{w}(k+1) = F\hat{w}(k) + Gu(k) \quad (8a)$$

$$\hat{\Psi}(k+1) = \hat{\Psi}(k) + \varepsilon\,\mathrm{sgn}(K)e(k)\hat{w}(k)^{\mathrm{T}} \quad (8b)$$

$$u(k) = Ke(k) + \hat{\Psi}(k)\hat{w}(k)\,, \quad (8c)$$

where $\hat{w}(k) \in \mathbb{R}^q$ is the state of the adaptive internal model, $\hat{\Psi}(k)$ is an estimate of Ψ, and $\varepsilon > 0$ is the *learning rate*. Substituting $u(k)$ into (8a) with $\hat{\Psi}(k) \equiv \Psi$, we obtain the familiar internal model $\hat{w}(k+1) = S\hat{w}(k) + GKe(k)$, thus satisfying the internal model principle [7]. In the sequel we focus on disturbance rejection of constant disturbances [11], [21].

Lemma 11: Consider (6)-(8) with $q = 1$, $S = 1$, $0 < F < 1$, $0 \leq A < 1$, and $\hat{\Psi}(k) \equiv \Psi$. There exists K such that $e(k) \to 0$ as $k \to \infty$.

Proof: Define the *estimation error*

$$\widetilde{w}(k) = \hat{w}(k) + \frac{1}{B} G e(k) - \frac{G}{B(1-F)} w(k) .$$

Let $\widetilde{\zeta}(k) := (e(k), \widetilde{w}(k))$. The closed-loop system is

$$\widetilde{\zeta}(k+1) = \tilde{A}_{cl} \widetilde{\zeta}(k) := \begin{bmatrix} A - BK + \Psi G & -B\Psi \\ \frac{1}{B}(GA - FG) & F \end{bmatrix} \widetilde{\zeta}(k) . \quad (9)$$

The characteristic polynomial of $\tilde{A}_{cl}$ is $\Delta_{cl}(z) = z^2 - (1 + A - BK) z + A - BKF$. An analysis based on a Jury table leads to stability conditions: $A - 1 < BKF < A + 1$; $0 < BK(1 - F)$; and $BK(1 + F) < 2(1 + A)$. Since $0 < F < 1$, the second condition is met by choosing $\mathrm{sgn}(K) = \mathrm{sgn}(B)$. Since $A - 1 < 0$, then $BKF > A - 1$. Finally, we choose K sufficiently small such that $BK < \min\{\frac{1+A}{F}, \frac{2(1+A)}{1+F}\}$, thus satisfying the first and third conditions. ■

Define $\zeta(k) := (e(k), \hat{w}(k))$, and consider the closed-loop system

$$\zeta(k+1) = \hat{A}_{cl} \zeta(k) + E_{cl} w(k) \quad (10)$$

where $\hat{A}_{cl} = \begin{bmatrix} A - BK & -B\hat{\Psi}(k) \\ GK & F + G\hat{\Psi}(k) \end{bmatrix}$ and $E_{cl} = \begin{bmatrix} \Psi \\ 0 \end{bmatrix}$. Define the parameter estimation error $\widetilde{\Psi}(k) := \hat{\Psi}(k) - \Psi$. Then $\widetilde{\Psi}$ has dynamics

$$\widetilde{\Psi}(k+1) = \widetilde{\Psi}(k) + \varepsilon \mathrm{sgn}(K) e(k) \hat{w}(k)^{\mathrm{T}} . \quad (11)$$

Theorem 12: Consider (6)-(8) with $q = 1$, $S = 1$, and F Schur stable. Let K be such that $\tilde{A}_{cl}$ is Schur stable. Then there exists $\varepsilon^* > 0$ such that for all $0 < \varepsilon < \varepsilon^*$, the equilibrium $(e, \widetilde{w}, \widetilde{\Psi}) = 0$ is locally exponentially stable.

Proof: To analyze stability we invoke averaging theory for discrete time systems [1]. The averaged system for (11) is

$$\widetilde{\Psi}_{av}(k+1) = \widetilde{\Psi}_{av}(k) + \varepsilon \mathrm{sgn}(K) f_{av}(\widetilde{\Psi}_{av}(k)) , \quad (12)$$

where

$$f_{av}(\widetilde{\Psi}) = \lim_{T \to \infty} \frac{1}{T} \sum_{j=\sigma+1}^{\sigma+T} e_{ss}(j) \hat{w}_{ss}(j) . \quad (13)$$

Here $e_{ss}(j)$ and $\hat{w}_{ss}(j)$ are the steady state responses of e and $\hat{w}$ to a constant input $\overline{d}(k) \equiv d_0$, under the assumption that $\hat{\Psi}(k) \equiv \hat{\Psi}$ is a constant, and the closed-loop system is stable. Also, we assume the limit in (13) exists uniformly in σ and for all $\widetilde{\Psi}$ in some neighborhood of the origin. The dependence of f_{av} on $\widetilde{\Psi}$ is implicit, as it will arise from the expressions for e_{ss} and $\hat{w}_{ss}$.

One can show that when $\hat{\Psi}(k) \equiv \Psi$, then $\tilde{A}_{cl}$ and $\hat{A}_{cl}$ have the same characteristic polynomial. Thus, if $\tilde{A}_{cl}$ is stable, then for $\hat{\Psi}(k)$ sufficiently close to Ψ, also $\hat{A}_{cl}$ is stable. Therefore, e_{ss} and $\hat{w}_{ss}$ are well-defined. Applying the $\mathbb{Z}$-transform to the closed-loop system (10) we obtain

$$e(z) = \frac{(z - F - G\hat{\Psi})}{\Delta(z)} \frac{d_0 z}{z - 1} \quad (14a)$$

$$\hat{w}(z) = \frac{GK}{\Delta(z)} \frac{d_0 z}{z - 1} , \quad (14b)$$

where $\Delta(z) := z^2 - \left(F + G\hat{\Psi} + A - BK\right) z + A(F + G\hat{\Psi}) - BKF$. This yields

$$e_{ss} = \frac{(1 - F - G\hat{\Psi})}{\Delta(1)} d_0 = -\frac{G\widetilde{\Psi}}{\Delta(1)} d_0 , \quad \hat{w}_{ss} = \frac{GK}{\Delta(1)} d_0 .$$

Returning to the averaged system (12), we have

$$\widetilde{\Psi}_{av}(k+1) = \widetilde{\Psi}_{av}(k) - \varepsilon \mathrm{sgn}(K) K \left(\frac{G d_0}{\Delta(1)}\right)^2 \widetilde{\Psi}_{av}(k) .$$

This system is exponentially stable if $0 < \varepsilon < \frac{2(\Delta(1))^2}{|K|(Gd_0)^2}$. Finally, it is straightforward to verify that the assumptions (B1-B6) in [1] are satisfied. Hence, we can invoke Theorem 2.2.4 in [1] to conclude the proof. ■

Remark 13: We have retained the parameter estimation equation (8b), even though it is not strictly necessary for disturbance rejection of constant disturbances, nor is it required to elicit the dynamic properties of adaptation. Parameter estimation not only allows for more complex disturbances, but also it provides adaptation of biological parameters $\{A, B, F, G\}$, which can experience a slow drift over days and weeks. ◁

In summary, our proposed model consists of (2a) describing the evolution over successive trials of the physical process; (2b) characterizing the measurement by the subject at the end of the kth trial; (8a)-(8b) describing brain processes, with (8a) evolving over minutes to model short-term adaptation, and (8b) evolving over days and weeks to contribute to (but not fully model) long-term adaptation. Finally, (8c) captures an important aspect (see Remark 14) that the motor command consists of a "primitive" error feedback combined with an estimate of the disturbance.

V. Simulation Results

Consider the *visuomotor rotation experiment* [13], [20], in which a human subject makes rapid reaches with a mouse or manipulandum from a start position to a target position on a computer screen. The hand is occluded from view, but its position at the end of each reach is momentarily presented by a cursor on the screen. In this scenario, $x(k)$ is the angle (in degrees) of the final hand position at the k-th reach relative to a reference line and measured at a predetermined radius from the start position; $d(k)$ is an experimentally imposed disturbance (in degrees) in the observed cursor angle on the k-th reach. The cursor angle at the k-th reach observed by the subject is $y(k) = x(k) + d(k)$. We assume w.l.o.g. that $r := 0$ is the constant reference angle of the target disk. If we assume only constant disturbances, no proprioception of the hand position ($A = 0$), and w.l.og. $B = 1$, the error model is: $e(k+1) = -u(k) - d_0$.

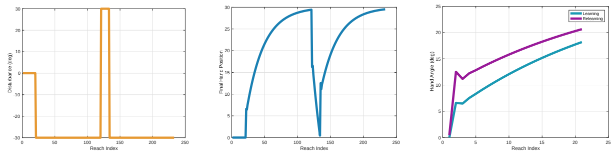

Fig. 2: Savings with CP in a BLUR experiment. In the right figure $x(k)$ during the learning block is plotted in blue superimposed with a horizontally shifted version of $x(k)$ during the relearning block in purple. The purple curve is larger than the blue curve corresponding to faster learning in the relearning block.

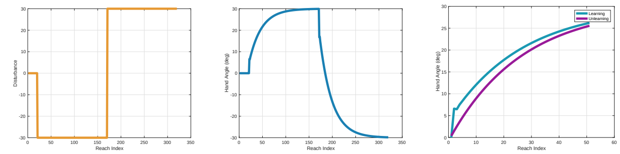

Fig. 4: Anterograde interference in a BLU experiment. In the right figure $x(k)$ over the interval of the learning block is shown in blue, and $-x(k+k_2)$ over the interval of the unlearning block is shown in purple. The blue curve is larger than the purple curve indicating that the learning rate is reduced in the unlearning block.

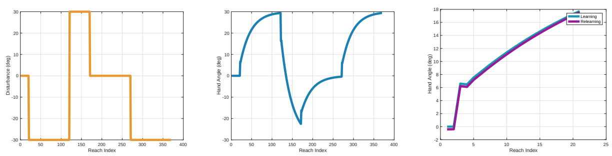

Fig. 3: Reduced savings in a BLUWR experiment.

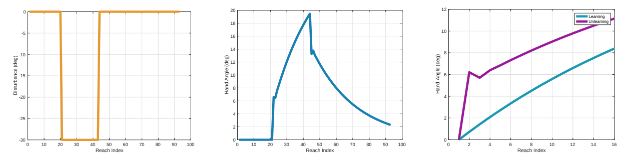

Fig. 5: Rapid unlearning in a BLW experiment.

Next consider saccade adaptation. It is known that proprioception plays no role in the saccadic system, so $A = 0$. Also w.l.o.g. let $B = 1$. The reference $r(k)$ represents the desired change in eye position (the desired saccade size) for the k-th primary saccade; $x(k)$ represents the change in eye position during the kth primary saccade; and $e(k)$ represents the error between the final eye position and the target position at the end of the k-th primary saccade. The disturbance $d(k)$ represents an experimentally imposed displacement of the target position introduced while the primary saccade is underway. The error is therefore given by $e(k) = r(k) + d(k) - x(k)$. If we further assume that within a block of trials the displacement is a constant d_0, then the error model is: $e(k+1) = -u(k) + r(k+1) + d_0$.

This error model seems not to be amenable to our analysis since the desired saccade size $r(k)$ varies from saccade to saccade. Therefore, we cannot regard $\overline{d}(k) = r(k+1)+d_0$ to be a constant disturbance. However, it is known that saccade adaptation occurs over *adaptation fields* [8] corresponding to primary saccades of roughly the same size and direction. This means that $r(k)$ can be regarded to be a constant r_0. The error model becomes $e(k+1) = -u(k) + r_0 + d_0$. In sum, we can study either the saccadic system or the visuomotor rotation experiment with the same parameters: $A = 0$, $B = 1$, and $S = 1$.

Figures 2-7 present simulation results for the visuomotor rotation experiment. As discussed above, we assume that $A = 0$ (no proprioception), $B = 1$, and $S = 1$ (all reference and disturbance signals are constant). Also, $K = 0.22$, $F = 0.8$, $G = 0.2$, $\varepsilon = 6e{-}7$, and $r(k) = 0$. In all figures, the left figure shows the disturbance $d(k)$ as a function of the index k and the middle figure shows $x(k)$. For example, the left figure in Figure 2 shows that $d(k) = 0$ during the baseline block, $d(k) = -30$ during the learning block, $d(k) = 30$ during the counter-perturbation block, and $d(k) = -30$ during the relearning block. The center figure shows that $x(k)$ approaches its steady-state value $x_{ss} = 30$ during the learning block, and the steady-state value $-x_{ss} = 30$ during the unlearning block.

The right figure in Figure 2 verifies that savings has occurred in the BLUR experiment. We plot $x(k)$ during the learning block superimposed with a horizontally shifted version of $x(k)$ during the relearning block. Precisely, $x(k)$ over the discrete time interval $k \in [k_0, k_0 + 20]$ is shown in blue, and $x(k + k_3)$ over the time interval $k \in [0, 20]$ is shown in purple. The time k_3 is the second time when $x(k_3)$ equals 0. We can see that the purple curve is larger than the blue curve, corresponding to faster learning in the relearning block. In Figure 3 a washout block with $d(k) = 0$ has been inserted between the learning and relearning blocks. In the right figure $x(k + k_1)$ over the time interval of the learning block is shown in blue, and $x(k+k_2)$ over the time interval of the relearning block is shown in purple. The discrete time k_1 near the beginning of the learning block and the discrete time k_2 near the beginning of the relearning block are selected such that $x(k_1) = x(k_2)$. We can see that the purple curve is almost identical to the blue curve, corresponding to reduced savings.

The striking similarity between our simulation results and the experimental results reported in Figure 3A of [11] is noteworthy. Particularly, the *inflections* noted in [11] and observed on the right of Figure 2 following the fast rise of $x(k)$ seem to be an intrinsic feature of the adaptation response of the saccadic system.

Remark 14: The appearance of savings can be understood in terms of the two components of the input (8c). When there is a sudden change in the disturbance, as is the case between learning/unlearning blocks, the $Ke(k)$ term responds proportionally to this error with K relatively small. Then the change in hand angle from one trial to the next is $(K-1)e(k)$, with $e(k)$ large, resulting in a fast change in the hand position at the start of each block. Instead, the change in $\hat{w}(k)$ is significantly slower. Also, ϵ is orders of magnitude smaller than G, so jumps in $e(k)$ have a negligible effect on

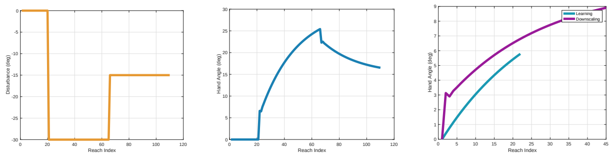

Fig. 6: Rapid downscaling in a BLD experiment.

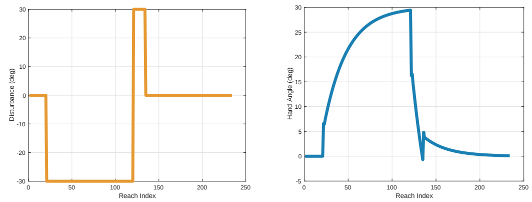

Fig. 7: Spontaneous recovery in an LUW experiment. The hand angle rebounds to a value greater than zero during the washout block, even though $x_{ss} = 0$.

$\hat{\Psi}(k)$ (the essence of averaging theory). ◁

Figures 4-6 demonstrate anterograde interference, rapid unlearning, and rapid downscaling, with the interpretations of plots analogous to the interpretations for Figure 2. Figure 7 demonstrates spontaneous recovery. The right figure shows $x(k)$, particularly that $x(k)$ rebounds to a value greater than 0 during the washout block corresponding to $k \in [140, 240]$, even though the steady state value for the washout block is $x_{ss} = 0$.

VI. Discussion

We have selected a form of the adaptive internal model resembling the continuous time model in [19], which we also utilized to model the oculomotor system in [3], [4] . One may choose other adaptive internal models such as those in [17], [9], [23]. Adaptive internal models are thought to reside in the cerebellum, and the cerebellum is known to have only two types of inputs. In our model, those two input types to the adaptive internal model (8a)-(8b) would be $u(k)$ (an *efference copy* of the motor command) and $e(k)$.

An influential model for sensorimotor adaptation is the *two-rate LTI model* of [21], obtained by curve fitting to real data for a force field experiment. The model includes slow and fast states which are both regarded as memory states in the brain (note the usage of terms "fast" and "slow" does not regard eigenvalues of the LTI system). By comparison, our model distinguishes a brain state $\hat{w}(k)$ from a physical state $e(k)$ that evolves in the world and must be sensed by the brain. Our fast state is $e(k)$, and it is fast because of the error feedback term $Ke(k)$ in the controller. Our slow state is the brain state $\hat{w}(k)$. Even slower, by many orders of magnitude, is the parameter estimate $\hat{\Psi}$.

A study of internal model architectures was made in [14], focusing on the coupling between fast and slow states. The authors concluded that a model with a single fast state with context switching (as a function of block type) between multiple slow states gave the best fit to experimental data. They ruled out two-state models in which the error does not appear directly in both equations. Our model is consistent with their findings: both $e(k)$ and $\hat{w}(k)$ utilize $e(k)$ in their updates. Also, the behavior of our slow state $\hat{w}(k)$ depends directly on the block type, exhibiting context switching as the block type changes.

References

[1] E.-W. Bai, L.-C. Fu, and S. Sastry. Averaging analysis for discrete time and sampled data adaptive systems. *IEEE Trans. Circuits and Systems*. Vol. 35, No. 2, February 1988.

[2] M. Berniker and K. Kording. Estimating the relevance of world disturbances to explain savings, interference, and long-term adaptation effects. *PLoS Computational Biology*. Vol. 7, issue 10, October 2011.

[3] M.E. Broucke. Adaptive internal model theory of the oculomotor system and the cerebellum. *IEEE Trans. AC*. Submitted, January 2019.

[4] M.E. Broucke. Model of the oculomotor system based on adaptive internal models. *IFAC World Congress*. July 2020.

[5] C. Cassanello, S. Ohl, and Martin Rolfs. Saccadic adaptation to a systematically varying disturbance. *J Neurophysiology*. Vol. 116, pp. 336-350, April 2016.

[6] S. Cheng and P. Sabes. Modeling sensorimotor learning with linear dynamical systems. *Neural Computation*. Vol. 18, pp. 760-793, 1996.

[7] B.A. Francis and W.M. Wonham. The internal model principle of control theory. *Automatica*. Vol. 12, pp. 457–465, 1976.

[8] M. Frens and A. van Opstal. Transfer of short-term adaptation in human saccadic eye movements. *Exp. Brain Res.* No. 100, pp. 293-306, 1994.

[9] J. Hoagg, M. Santillo, and D. Bernstein. Command following and disturbance rejection with unknown exogenous dynamics. *IEEE Transactions on Automatic Control*. Vol. 53, No. 4, pp. 912–928, May 2008.

[10] M. Jordan and D. Rumelhart. Forward models: supervised learning with a distal teacher. *Cognitive Science*. Vol. 16, pp. 307-354, 1992.

[11] Y. Kojima, Y. Iwamoto, and K. Yoshida. Memory of learning facilitates saccadic adaptation in the monkey. *J. Neuroscience*. Vol. 24, No. 34, pp. 7531–7539, August 2004.

[12] K. Kording, J. Tenenbaum, and R. Shadmehr. The dynamics of memory as a consequence of optimal adaptation to a changing body. *Nature Neuroscience*. Vol. 10, No. 6, June 2007.

[13] J. Krakauer, C. Ghez, and M. Ghilardi. Adaptation to visuomotor transformations: consolidation, interference, and forgetting. *J. Neuroscience*. Vol. 25, no. 2, pp. 473-478, January 2005.

[14] J. Lee, N. Schweighofer. Dual adaptation supports a parallel architecture of motor memory. *J Neuroscience*. Vol. 29, pp. pp. 1039610404, 2009.

[15] T. Martin, J. Keating, H. Goodkin, A. Bastian, W. Thach. Throwing while looking through prisms II. Specificity and Storage of Multiple Gaze-Throw Calibrations. *Brain*. No. 119, pp. 1199 - 1211, 1996.

[16] R.C. Miall and D. Wolpert. Forward models for physiological motor control. *Neural Networks*. Vol. 9, No. 8, pp. 1265–1279, 1996.

[17] V. O. Nikiforov. Adaptive controller rejecting uncertain deterministic disturbances in SISO systems. *European Control Conference*. pp. 1207-1212, 1997.

[18] F. Robinson, R. Soetedjo, and C. Noto. Distinct short-term and long-term adaptation to reduce saccade size in monkey. *J Neurophysiology*. No. 96, pp. 10301041. May 2006.

[19] A. Serrani and A. Isidori. Semiglobal nonlinear output regulation with adaptive internal model. *IEEE Conference on Decision and Control*. pp. 1649-1654, December, 2000.

[20] R. Shadmehr. *The Computational Neurobiology of Reaching and Pointing: A Foundation for Motor Learning*. MIT Press. 2005.

[21] M. Smith, A. Ghazizadeh, and R. Shadmehr. Interacting adaptive processes with different timescales underlie short-term motor learning. *PLoS Computational Biology*. Vol. 4, Issue 6, June 2006.

[22] K. Takiyama, M. Hirashima, and D. Nozaki. Prospective errors determine motor learning. *Nature Communications, 6*. No. 5925, January 2015.

[23] P. Tomei. Multi-sinusoidal disturbance rejection for discrete-time uncertain stable systems. *Automatica*. No. 79, pp. 144-151, 2017.

[24] K. Wei and K. Kording. Relevance of error: what drives motor adaptation? *J. Neurophysiology*. Vol. 101, pp. 655664, 2009.

[25] D. Wolpert, Z. Ghahramani, and M. Jordan. An internal model for sensorimotor integration. *Science*. Vol. 269, pp. 1880-1882, September 1995.