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Explaining Savings for Visuomotor Adaptation: Linear Time-Invariant State-Space Models Are Not Sufficient

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Zarahn E, Weston GD, Liang J, Mazzoni P, Krakauer JW. Explaining savings for visuomotor adaptation: linear time-invariant state-space models are not sufficient. *J Neurophysiol* 100: 2537–2548, 2008. First published July 2, 2008; doi:10.1152/jn.90529.2008. Adaptation of the motor system to sensorimotor perturbations is a type of learning relevant for tool use and coping with an ever-changing body. Memory for motor adaptation can take the form of savings: an increase in the apparent rate constant of readaptation compared with that of initial adaptation. The assessment of savings is simplified if the sensory errors a subject experiences at the beginning of initial adaptation and the beginning of readaptation are the same. This can be accomplished by introducing either 1) a sufficiently small number of counterperturbation trials (counterperturbation paradigm [CP]) or 2) a sufficiently large number of zero-perturbation trials (washout paradigm [WO]) between initial adaptation and readaptation. A two-rate, linear time-invariant state-space model ($SSM_{LTI,2}$) was recently shown to theoretically produce savings for CP. However, we reasoned from superposition that this model would be unable to explain savings for WO. Using the same task (planar reaching) and type of perturbation (visuomotor rotation), we found comparable savings for both CP and WO paradigms. Although $SSM_{LTI,2}$ explained some degree of savings for CP it failed completely for WO. We conclude that for visuomotor rotation, savings in general is not simply a consequence of LTI dynamics. Instead savings for visuomotor rotation involves meta-learning, which we show can be modeled as changes in system parameters across the phases of an adaptation experiment.

INTRODUCTION

Perturbations to either environment or physical plant, as well as direct experimental manipulations of sensory feedback, can induce sensory error: a discrepancy between observed and predicted sensory feedback. Motor adaptation refers to when sensorimotor mappings change to reduce sensory error over successive movements. Adaptation can be modeled with state-space models (Cheng and Sabes 2006) that have sensory error (or perturbation) as input, sensorimotor mappings as hidden variables (states), and adaptation responses as output. Adaptation may reflect how the CNS establishes and maintains sensorimotor mappings throughout normal life (Kording et al. 2007). Memory for a newly learned mapping/state can take at least two forms: aftereffects [persistence of the adapted state into readaptation (Yamamoto et al. 2006)] and savings [a faster rate of readaptation compared with that of initial adaptation (Kojima et al. 2004; Krakauer et al. 2005)]. To assess savings independently of aftereffects, starting states for initial adaptation and readaptation should be equated. Thus far only two studies that meet this requirement have shown savings—one of

saccadic adaptation (Kojima et al. 2004) and our previous study of rotation adaptation for reaching movements (Krakauer et al. 2005). Aftereffects were eliminated in the saccade study by inserting counterperturbation trials between initial adaptation and readaptation (counterperturbation paradigm [CP]). Aftereffects were eliminated in the rotation study by inserting instead sufficient zero-perturbation trials to washout memory of the initial adaptation phase (washout paradigm [WO]).

Motivated by findings from the saccadic adaptation study (Kojima et al. 2004), Smith and colleagues (2006) demonstrated via simulation that a linear time-invariant (LTI) state-space model (Cheng and Sabes 2006; Donchin et al. 2003; Thoroughman and Shadmehr 2000) with two states (slow and fast) produces savings in CP. It is helpful to understand that this model (which we will refer to as $SSM_{LTI,2}$), as well as any LTI SSM used to model adaptation, can be mathematically represented in various ways. For example, Smith and colleagues (2006) chose to express output in terms of net sensorimotor mapping. However, output can be equivalently expressed in terms of sensory error. Likewise, input can be expressed either in terms of sensory error or perturbation. The point here is that, regardless of the specific form, an LTI system obeys superposition: the output to a sum of inputs equals the sum of the outputs to the individual inputs. Therefore no matter whether adaptation is expressed in terms of sensorimotor mapping or sensory error, savings produced by $SSM_{LTI,2}$ in CP results not from a change in system parameters between initial adaptation and readaptation, but rather from superposition of the adaptation responses to the perturbations corresponding separately to the 1) initial adaptation, 2) counterperturbation, and 3) readaptation phases of CP (Fig. 1).

Given that LTI systems obey superposition, we reasoned that the $SSM_{LTI,2}$ could not explain savings in a WO paradigm: Assuming a stable LTI SSM, application of some fixed, non-zero perturbation causes the state (i.e., the sensorimotor map) to change trial by trial such that sensory error is reduced. If from some trial onward, the perturbation is set to zero (i.e., washout trials are applied), the sensorimotor map must approach in the limit the same value it had prior to the initial adaptation. Thus with a sufficient number of washout trials the sensorimotor map will be arbitrarily close to this initial, naive value (corresponding to elimination of aftereffects). Therefore respecting superposition, the larger the number of washout trials, the closer the net adaptation response during the readaptation phase of a WO paradigm will be to the adaptation response (time-shifted, of course) to the initial adaptation. Thus

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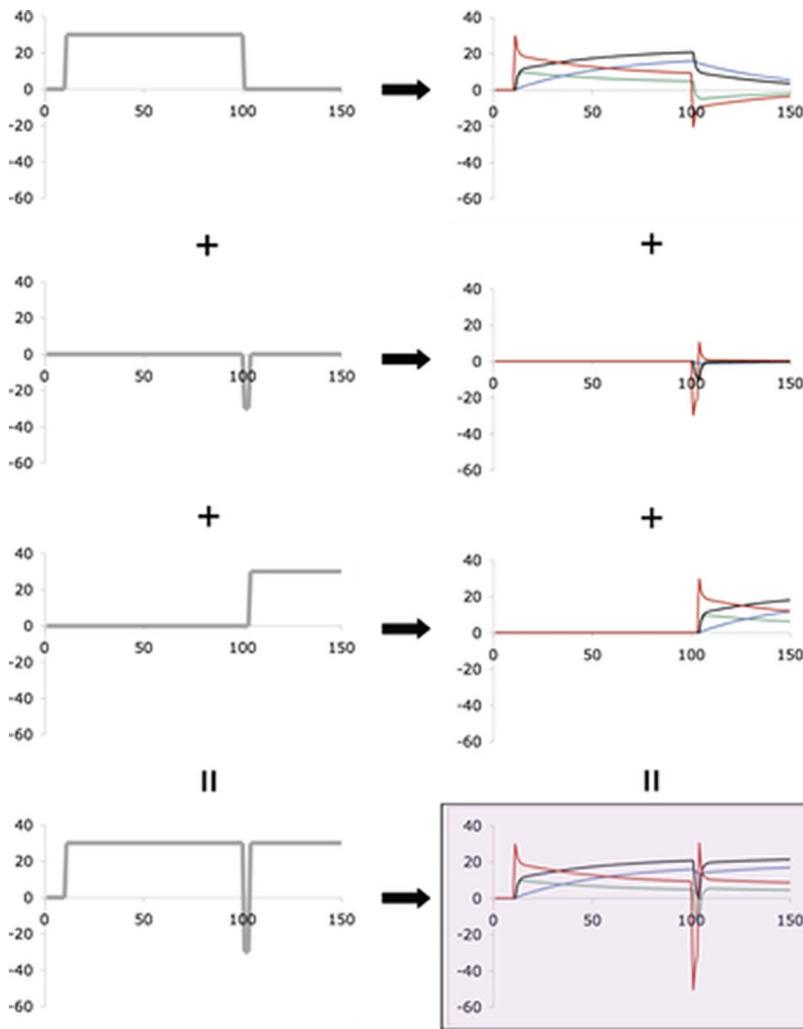


FIG. 1. Illustration of superposition for two-rate, linear time-invariant state-space model ($SSM_{LTI,2}$) [$a_{\text{slow}} = 0.992$, $b_{\text{slow}} = 0.02$, $a_{\text{fast}} = 0.59$, $b_{\text{fast}} = 0.21$, taken from the empirical estimates reported by Smith and colleagues (2006)] in the counterperturbation paradigm (*CP*). See Eq. 2 in the main text for the state-space model. The *left column* shows the input perturbation functions (abscissa is movement number n), whereas the *right column* shows both the outputs [equivalently in terms of directional error (red) and net sensorimotor map (black)] and the state variables [slow (blue) and fast (green)]. The *rows* correspond to a decomposition of the net input [(from *top*): initial adaptation stimulus, counterperturbation stimulus, readaptation stimulus, summed inputs]. As a consequence of superposition, the shaded plot in the *bottom right corner* is equal to both 1) the sum of the outputs to the separate inputs (sum down *right column*) and 2) the output to the summed inputs (transform from *left to right* in the *bottom row*). In the *CP* paradigm, superposition leads to obvious savings (i.e., a faster apparent rate of adaptation during the readaptation phase compared with the initial adaptation phase). Perturbation function for this *CP* paradigm: 0° for $1 \leq n \leq 10$, 30° for $11 \leq n \leq 100$, -30° for $101 \leq n \leq 103$, 30° for $104 \leq n \leq 150$.

in the limit there would be no savings. The same point was made by Smith and colleagues (2006) in that they showed via simulation for $SSM_{LTI,2}$ that as the number of washout trials inserted between the counterperturbation and readaptation phases in *CP* increased (i.e., as *CP* was converted into *WO*), the amount of savings tended to zero. Figure 2 illustrates the adaptation responses of the $SSM_{LTI,2}$ in a *WO* paradigm when the number of washout trials was sufficient to effectively “isolate” the adaptation response during the readaptation phase from that of the initial adaptation phase, leading to a lack of appreciable savings.

Here we measured savings as a change in rate constants rather than as a change in rates, to further avoid contamination by aftereffects. When modeling rate constant savings, there is an important distinction to be made (as implied earlier) between apparent rate constants (the empirical rate constant evident during a particular phase of an adaptation experiment) and system rate constants (model parameters that determine the input–output relationship of the system). Our goal for modeling rate constant savings, then, was to determine whether changes in apparent rate constants were best explained with a system whose parameters do (varying-parameter SSM: SSM_{VP}) or do not (SSM_{LTI}) change with experience. A system displaying savings as a result of a change in parameters would correspond to metalearning. We first demonstrated rate constant savings for

both *CP* and *WO* using the same task (planar reaching movements) and the same type of perturbation (visuomotor rotation). Then, in each paradigm, for the one- and two-rate SSM_{LTI} and SSM_{VP} , we 1) assessed the ability of each SSM to explain rate constant savings and 2) quantified model parsimony with the information-theoretic measure Akaike Information Criterion (AIC) (Akaike 1974; Bozdogan 1987; Burnham and Anderson 2002) to ensure that any potential superiority of SSM_{VP} over SSM_{LTI} with regard to explanation of savings was not offset by overparameterization.

METHODS

Subjects

A total of 14 right-handed subjects volunteered for the study. All were naive to the purpose of the study, signed an institutionally approved consent form, and were paid to participate. They were randomly assigned to either the *CP* [$n = 6$; mean age (SD) = 25.8 (6.6) yr; 3 M] or the *WO* [$n = 8$; mean age (SD) = 22.1 (0.6) yr; 6 M] experiments.

General experimental protocol

Subjects sat and moved a hand cursor by making planar reaching movements with the shoulder and elbow over a horizontal surface positioned at shoulder level. A center start position and a single target

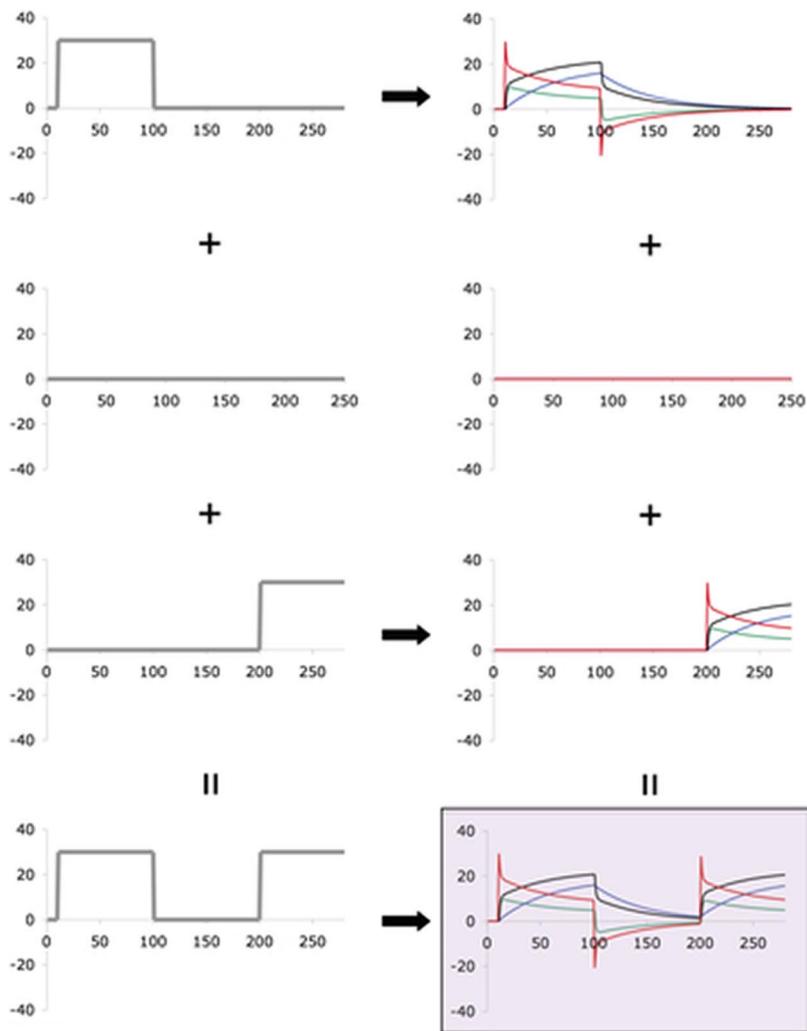


FIG. 2. Illustration of superposition for $SSM_{LTI,2}$ in the washout paradigm (*WO*). Formatting and system constants are the same as in Fig. 1. The rows correspond to a decomposition of the net input [(from top) initial adaptation stimulus, washout phase, readaptation stimulus, summed inputs]. Because a sufficient number of washout trials was inserted between the initial adaptation and readaptation stimuli to bring the state vector close to its naive value of (in this case) 0, the apparent rates of adaptation during the readaptation and initial adaptation phases are not nearly as distinguishable as in *CP* (Fig. 1). However, the directional error output (and thus savings) in response to the summed perturbations can be predicted simply from the superposition of the directional errors caused by the individual perturbations (this superposition being the red curve in the shaded plot), without additional concern for the values of the slow and fast components of the state vector (blue and green curves, respectively, in shaded plot). Perturbation function for this *WO* paradigm: 0° for $1 \leq n \leq 10$, 30° for $11 \leq n \leq 100$, 0° for $101 \leq n \leq 200$, 30° for $201 \leq n \leq 280$.

(45° clockwise from the 12 o'clock position, diameter 2 cm, 6 cm from start position) was projected onto a computer screen positioned above the arm. This same, single target position was used throughout the entire experiment in both *CP* and *WO* paradigms (i.e., target position was not varied across trials, subjects, or paradigms). A mirror, positioned halfway between the computer screen and the table surface, reflected the computer display, producing a virtual image of the screen cursor and the target in the horizontal plane of the finger tip. Hand positions calibrated to the position of the finger tip were monitored using a Flock of Birds (Ascension Technology, Burlington, VT) magnetic movement recording system at a frequency of 120 Hz. Anterior-posterior translation of the shoulder was prevented with a rigid frame around the trunk. The wrist, hand, and fingers were immobilized with a splint and the forearm was supported on an air-sled system. An opaque shield prevented subjects from seeing their arms and hands at all times.

Visuomotor rotation paradigms

There were two experimental paradigms, which involved the insertion of either counterperturbation (*CP*) or washout (*WO*) trials between initial adaptation and readaptation, respectively. A single target position was used in both paradigms (see *General experimental protocol*). The sign convention used for rotation was that counterclockwise rotation corresponded to positive angles. In both paradigms subjects were first familiarized with 40 baseline trials (0° rotation). In *CP* they then performed 80 trials of a $+30^\circ$ rotation (initial adapta-

tion) followed by 8 trials of a -30° rotation (counterrotation) followed by another 80 trials of the $+30^\circ$ rotation (readaptation). In *WO*, after the baseline trials subjects performed 80 initial adaptation trials with a $+45^\circ$ rotation followed by 40 trials of 0° rotation (washout) followed by 80 readaptation trials with $+45^\circ$. The reason we chose a rotation magnitude of 45° for the *WO* paradigm was to increase the signal-to-noise ratio of the adaptation data relative to our previous study, which used 30° (Hinder et al. 2007; Kojima et al. 2004; Krakauer et al. 2005). We would have chosen a 45° rotation magnitude for *CP* as well, but chose not to because a $+45^\circ$ rotation would have meant an initial error of -90° in the deadaptation phase; errors of this size may provoke cognitive strategies (Imamizu et al. 1995), which we sought to avoid. We empirically address this potential confound of different rotation magnitudes early in the RESULTS section.

Measurement of savings

In both *CP* and *WO* paradigms, apparent first-order rate constants were estimated (via nonlinear least squares) per subject separately for initial adaptation and readaptation from the first 30 values of directional error $e[n]$ according to

$$e[n] = ae^{cn} + b \quad (1)$$

where n is movement number, c is the rate constant (in units of movements $^{-1}$), and a and b are additional free parameters (both in units of degrees). S_{rc} was defined as $c_{\text{initial adaptation}}$ minus $c_{\text{readaptation}}$.

Rate constant savings would correspond to $S_{rc} > 0$. This method is reasonable to the extent that the early phase of adaptation can be well approximated by first-order behavior, even though the best model for the net data might be of higher order (Smith et al. 2006).

To assess the degree to which the various SSMs captured S_{rc} , Eq. 1 was also fit to the various SSM fits. That is, the SSM fits (see *State-space modeling*) were simply treated as $e[n]$ and fit by Eq. 1, again, per subject and separately for the initial adaptation and readaptation phases. The basic logic is that if a given SSM fits the data well, the fit of Eq. 1 to the fit of the SSM should capture S_{rc} well. We note that our variance estimator for S_{rc} comes from the variation in estimated S_{rc} across subjects (not the “residual” variation about each fit) and, in such a case, statistical inference will be valid even when “fitting to fits.”

State-space modeling

SSMs describe the entire $e[n]$ movement series for a given experiment, and (unlike Eq. 1) are not fit separately to the initial adaptation and readaptation phases. The parameters of each type of SSM of interest (described in the following text) were estimated separately in each subject. Linear, discrete-time SSMs for modeling motor learning data have been discussed by Cheng and Sabes (2006). The SSMs we use correspond to their Eq. 3.9 and we use their notation (except that we use lowercase boldface for vectors, uppercase boldface for matrices, and italics for scalars). Perturbation (visuomotor rotation angle in degrees) $r[n]$ and the output (reach direction at peak velocity relative to the target direction in degrees) $y[n]$ were scalars ($e[n] = r[n] - y[n]$). The state vector on movement n , $\mathbf{x}[n]$ ($= \{x_{slow}[n], x_{fast}[n]\}^T$) represents the components of the sensorimotor transformation, i.e., the angular discrepancy between the target direction and movement direction, on trial n . Therefore x_{slow} and x_{fast} are also in units of degrees. The state update equation is

$$\begin{aligned} \mathbf{x}[n+1] &= \mathbf{A}\mathbf{x}[n] + \mathbf{b}(r[n] - y[n] + b_x) + \boldsymbol{\eta}[n] \\ &= \mathbf{A}\mathbf{x}[n] + \mathbf{b}(e[n] + b_x) + \boldsymbol{\eta}[n] \end{aligned} \quad (2)$$

where

$$\mathbf{A} = \begin{bmatrix} a_{slow} & 0 \\ 0 & a_{fast} \end{bmatrix}$$

is the matrix of dimensionless retention rates, $\mathbf{b} = [b_{slow} \ b_{fast}]^T$ is the vector of dimensionless learning rates, b_x is sensorimotor bias (degrees), and the state noise vector $\boldsymbol{\eta} \sim \mathcal{N}(0, \sigma_{state}^2 \mathbf{I})$. The equation for the reach direction on trial $n+1$ is

$$y[n+1] = \mathbf{c}^T \mathbf{x}[n+1] + \gamma[n+1] \quad (3)$$

with the output noise $\gamma \sim \mathcal{N}(0, \sigma_{output}^2)$, and $\mathbf{c} = [1 \ 0]^T$ for one-rate models or $[1 \ 1]^T$ for two-rate models. For one-rate models a_{fast} and b_{fast} were constrained to be zero. Equation 2 can easily be reparameterized to have r be the input instead of e , and in figures we will use perturbation as the input (because it is under direct experimental control). Likewise, we will discuss the output in terms of both y and e .

The initial state was set equal to its steady-state value under zero perturbation from $-\infty$, which is

$$\mathbf{x}[1] = \begin{bmatrix} \frac{[-(a_{fast} - b_{fast} - 1)b_{slow}b_x - b_{fast}b_{slow}b_x]}{(a_{slow} - b_{slow} - 1)(a_{slow} - b_{slow} - 1) - b_{slow}b_{fast}} \\ \frac{[-(a_{slow} - b_{slow} - 1)b_{fast}b_x - b_{fast}b_{slow}b_x]}{(a_{slow} - b_{slow} - 1)(a_{fast} - b_{fast} - 1) - b_{slow}b_{fast}} \end{bmatrix}$$

The variance of $\mathbf{x}[1]$ was $\sigma_{initial}^2 \mathbf{I}$.

The SSM described by Eqs. 2 and 3 with fixed $[a_{slow} \ b_{slow} \ a_{fast} \ b_{fast}]$ is LTI (and so referred to as SSM_{LTI}). We also used a version of the above-cited SSM in which $[a_{slow} \ b_{slow} \ a_{fast} \ b_{fast}]$ were allowed to

take on different values for the experimental phases of initial adaptation, counterperturbation for CP (or washout for WO), and readaptation. We refer to these SSMs as “varying-parameter” SSMs (abbreviated as SSM_{VP}). SSM_{VP} are non-LTI (or, more precisely, not necessarily LTI) because they need not satisfy superposition. The idea behind using SSM_{VP} is that the experience of a perturbation during an early experimental phase (e.g., initial adaptation) might change the system parameters during a later phase (e.g., readaptation): Consider a particular system initially (i.e., in the absence of prior nonzero input) displaying LTI behavior. Let $r_1[n]$ be a perturbation function taking on a particular nonzero value for $0 \leq n \leq N$ and a value of zero everywhere else, and let the response of the system to $r_1[n]$ be $y_1[n]$. Let $r_2[n] = r_1[n - L]$ with $L > N$, and let the response of the system to $r_2[n]$ be $y_2[n]$. Let $r_3[n] = r_1[n] + r_2[n]$, and let the response of the system to $r_3[n]$ be $y_3[n]$. If the occurrence of the perturbation reflected in $r_1[n]$ changes the parameters of the system, then $y_3[n]$ will not equal $y_1[n] + y_2[n]$. This is because $y_2[n] = y_1[n - N]$, whereas the response to $r_2[n]$ having been preceded by $r_1[n]$ (i.e., to $r_2[n]$ as a component of $r_3[n]$) will not equal $y_1[n - N]$ as $[a_{slow} \ b_{slow} \ a_{fast} \ b_{fast}]$ will have been changed as a consequence of $r_1[n]$. Thus representing the system transform as $T(r)$, we would have $T(r_1[n] + r_2[n]) = T(r_3[n]) = y_3[n] \neq y_1[n] + y_2[n] = y_1[n] + y_2[n] = T(r_1[n]) + T(r_2[n])$, and thus $T(r)$ would be a non-LTI system.

The reason we use the abbreviation SSM_{VP} for these varying-parameter SSMs as opposed to simply $\text{SSM}_{non-LTI}$ is that SSM_{VP} is one very particular type of non-LTI SSM among many. We chose SSM_{VP} from among the immense class of non-LTI models because although it can manifest experience dependence, it is LTI within phase, which is congruent with our impressions of directional error data from previous visuomotor rotation paradigms (Kraauer et al. 2005).

We considered one- and two-rate versions of the SSM_{LTI} and the SSM_{VP} . Numbers of free parameters (k) per SSM were as follows: $k = 6$ for $\text{SSM}_{LTI,1}$; $k = 8$ for $\text{SSM}_{LTI,2}$; $k = 10$ for $\text{SSM}_{VP,1}$; and $k = 16$ for $\text{SSM}_{VP,2}$. For an explicit form for the likelihood $f(\mathbf{e} | \mathbf{p})$ of the directional error $\mathbf{e} = \mathbf{r} - \mathbf{y} = \{r[N_{initial}] - y[N_{initial}], r[N_{initial} + 1] - y[N_{initial} + 1], \dots, r[N_{max}] - y[N_{max}]\}^T$ for each of the four SSMs was derived from Eqs. 2 and 3. For SSM_{LTI} , $\mathbf{p} = [a_{slow} \ b_{slow} \ a_{fast} \ b_{fast} \ b_x \ \sigma_{initial}^2 \ \sigma_{state}^2 \ \sigma_{output}^2]^T$; \mathbf{p} was similar for SSM_{VP} except that the values of $[a_{slow} \ b_{slow} \ a_{fast} \ b_{fast}]$ were allowed to be different during the three phases of both CP and WO . $N_{initial} = 31$ and $N_{max} = 160$; for CP , $N_{initial} = 31$ and $N_{max} = 190$ for WO (see next paragraph for the reason that all 240 movements were not used). These values were chosen to allow fitting from the last 10 zero perturbation trials before the initial adaptation up until 30 trials into the readaptation. The form of $\log_e [f(\mathbf{y} | \mathbf{p})]$ corresponding to Eqs. 2 and 3 was derived such that, unlike expectation-maximization (Cheng and Sabes 2006; Shumway and Stoffer 1982), the states were not explicitly represented; thereby, maximum likelihood estimates (MLEs; Shao 2003) $\hat{\mathbf{p}}$ of \mathbf{p} were obtained from \mathbf{e} of each subject for each of the four SSMs by minimizing $-\log_e [f(\mathbf{y} | \mathbf{p})]$ with respect to \mathbf{p} using the MATLAB 7.4a (The MathWorks, Natick MA) routine `fmincon` via the method of Levenberg–Marquardt. Fits were also obtained to across-subject averages of \mathbf{e} , but these fits were used for display only, not for model selection (see *AIC*). The following linear constraints were used to reduce the occasion of nonconvergence: $0 \leq a_{slow}, a_{fast} \leq 1.1$; $0 \leq b_{slow}, b_{fast} \leq 0.8$; $-30 \leq b_x \leq 30$; $1 \leq \sigma_{initial}^2 \leq 200$; $0.1 \leq \sigma_{state}^2 \leq 200$; $1 \leq \sigma_{output}^2 \leq 200$; $a_{slow} - b_{slow} \geq 0.001$; $a_{fast} - b_{fast} \geq 0.001$. All fits were initialized with the values $\mathbf{p}_{initial} = [0.99 \ 0.05 \ 0.4 \ 0.2 \ 0 \ 10 \ 10 \ 10]^T$.

In expectation-maximization, one iteratively maximizes (with respect to \mathbf{p}) the expectation of $\log_e [f(\mathbf{x}, \mathbf{y} | \mathbf{p})]$ (with respect to \mathbf{x} conditioned on \mathbf{y} and \mathbf{p}); for SSM_{LTI} , this expectation has a computationally simple form (Cheng and Sabes 2006; Shumway and Stoffer 1982). However, we did not use the expectation-maximization method of obtaining the MLE of \mathbf{p} because we were not sure how to implement this method with SSM_{VP} . Instead, for both SSM_{LTI} and

SSM_{VP}, we maximized the more complicated $\log_e [f(\mathbf{y} | \mathbf{p})]$; the computational expense of determining $\log_e [f(\mathbf{y} | \mathbf{p})]$ was the only reason the entire 240 movement data sets were not used to obtain MLEs.

Obtaining MLEs of \mathbf{e} (both for plotting and for assessment of explanation of savings) involved substituting the expression for $\mathbf{y}[n]$ from Eq. 3 into Eq. 2, eliminating all random terms, and substituting $\hat{\mathbf{p}}$ for \mathbf{p}

$$\hat{\mathbf{x}}[n + 1] = \hat{\mathbf{A}}\hat{\mathbf{x}}[n] + \hat{\mathbf{b}}(r[n] - \mathbf{c}^T\hat{\mathbf{x}}[n] + \hat{b}_s) \quad (4)$$

$$\hat{e}[n + 1] = r[n + 1] - \mathbf{c}^T\hat{\mathbf{x}}[n + 1] \quad (5)$$

This fit \hat{e} is purely a function of $\hat{\mathbf{p}}$ and the deterministic \mathbf{r} , and so (by virtue of the \mathbf{r} we used in either paradigm) is not “bumpy”: \hat{e} represents our best estimate of the expected value of $e[n]$ given $\hat{\mathbf{p}}$ and \mathbf{r} . This can be contrasted with Kalman filtering (not used here), which yields the best estimate of the expected value of $e[n]$ given $\hat{\mathbf{p}}$, \mathbf{r} , and $e[n - 1]$ (Shumway and Stoffer 1982), which would tend to be “bumpy.” Although this latter type of fit better follows the data, it is not limited to the estimated deterministic response of the system, which is all that is of interest here.

AIC

Because the four different SSMs described earlier have different numbers of free parameters (k), model parsimony becomes an issue. This is because simply increasing k will improve apparent model fit (i.e., increase $\log_e [f(\mathbf{y} | \hat{\mathbf{p}})]$), even if the extra parameters are irrelevant to the true process generating the data. Thus the SSM with more parameters might conceivably appear to explain more savings than another, but in a manner not “worth” the extra parameters because adding extra parameters tends to reduce the stability of fits over repeated measurements (Stone 1977). The AIC provides a way to rank a set of candidate models in terms of how well they fit the data (Akaike 1974; Bozdogan 1987; Burnham and Anderson 2002) while accounting for the effect of varying k . The AIC for the i th candidate model is

$$\text{AIC}_i = -2\log_e [f_i(\mathbf{y} | \hat{\mathbf{p}}_i)] + 2k_i \quad (6)$$

and it is in units of information (Burnham and Anderson 2002). Let u_i equal the expectation (with respect to the data sample) of the Kullback–Leibler mean information for discrimination between candidate model i and the true data generating process; u_i is the risk function (i.e., the function to be minimized over i) for information-theoretic model selection and is related to total prediction error (Akaike 1974; Bozdogan 1987; Burnham and Anderson 2002). $\text{AIC}_i - \text{AIC}_j$ is an approximately unbiased estimator of $u_i - u_j$ (Akaike 1974; Bozdogan 1987; Burnham and Anderson 2002). That is, the AIC difference between two candidate models is an approximately unbiased estimator of their difference in information-theoretic model selection risk. However, the AIC is known to demonstrate a bias with respect to model selection risk toward selection of more overparameterized models (Hurvich and Tsai 1991), which will temper our inferences accordingly.

Since the difference in AIC between two models is only an estimator of their difference in risk, to control the false-positive rate when comparing the risk between models using the AIC would require a statistical test. Here, the null hypothesis of zero difference between pairs of SSMs in the population average risk was assessed via paired t -test using a two-tailed $\alpha = 0.05$. Because AIC differences do not have normal distributions, the use of t -test is not formally correct; however, parametric tests tend to be robust to violations of normality (Kirk 1982). Nevertheless, the Shapiro–Wilk W test (Shapiro and Wilk 1968) was used to assess the assumption of normality on the AIC differences for each of the six SSM pairings in both *CP* and *WO* paradigms; a threshold of $\alpha = 0.05$ for each W test was used as a criterion for deciding whether the violation of the normality assumption was acceptable.

We remark that although performing parametric statistical tests on independent and identically distributed samples of AICs is not a very common procedure, and was frowned on by Burnham and Anderson (2002), we cannot see any fundamental problem or contradiction in doing so. Indeed, we see it as a strength, given the likely variability between subjects in the relative risk between models, variability that is explicitly accounted for in statistical testing.

Using the AIC for model selection is different from statistical hypothesis testing of additional SSM parameters (one possible alternative to the AIC for model selection), which controls type I error rate (α) for a null hypothesis. Arguments against using hypothesis testing to perform model selection include the arbitrary selection of α , the multiple-comparison problem, the dependence of results on the order of entering variables in stepwise regression, and the philosophical issue of whether any null hypothesis can ever be true (Akaike 1974; Bozdogan 1987; Burnham and Anderson 2002).

RESULTS

Adaptation curves

The directional errors for both *CP* and *WO* manifested the essential qualitative behavior expected from previous studies of adaptation to visuomotor rotation (Krakauer et al. 1999, 2000; Wigmore et al. 2002). *CP* directional error data averaged across subjects ($n = 6$) is shown in Fig. 3A (data from a randomly selected single subject is shown in Supplemental Fig. S1A).¹ With respect to the *CP* data averaged across subjects, directional error on the first trial during the initial adaptation phase was on average $+33^\circ$, which is very close to the value of the perturbation value ($+30^\circ$) after taking into account a small sensorimotor bias, which led to a $+4^\circ$ offset during baseline trials. As expected, directional error decreased throughout the course of initial adaptation, approaching an asymptotic level of adaptation of approximately $+6^\circ$. The first trial of counterrotation (-30°) had a directional error of -54° , as expected from the asymptotic level of directional error during initial adaptation, which then increased to -23° on the eighth movement with counterrotated feedback. The first trial of readaptation had a directional error of $+36^\circ$ (i.e., within 3° of the first trial of initial adaptation, which indicates that aftereffects were to a good approximation eliminated). By visual inspection, the apparent rate constant of readaptation was substantially more negative (i.e., smaller decay time constant) than that of initial adaptation.

Figure 3B shows the directional error data averaged across subjects ($n = 8$) for *WO* (data from a randomly selected single subject are shown in Supplemental Fig. S1B). This paradigm yielded qualitatively very similar results to those of *CP*, accounting for the larger magnitude of the perturbation ($+45^\circ$ for *WO* vs. $+30^\circ$ for *CP*). Also, as expected, the directional error during the first trial of washout was approximately -36° , which is less than the magnitude of the 45° perturbation during initial adaptation (whereas in contrast, in *CP* the directional error during the first trial of counterrotation was -54° , which is substantially larger in magnitude than the corresponding value of the perturbation during initial adaptation). As in *CP*, aftereffects were successfully eliminated. Also as in *CP*, visual inspection suggests that the apparent rate constant of readaptation was substantially more negative than that of initial adaptation.

¹ The online version of this article contains supplemental data.

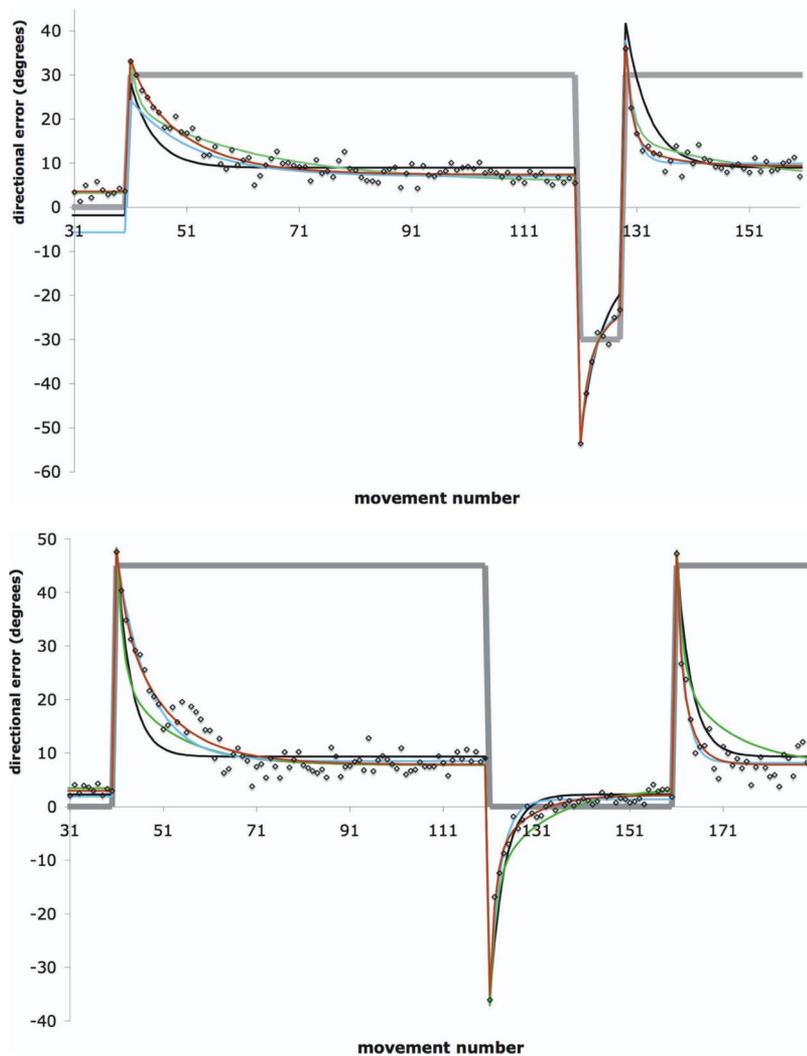


FIG. 3. The perturbation $r[n]$ (thick gray line), across-subject averaged directional error $e[n]$ (open diamonds) and SSM MLE fits (black line: $SSM_{LTI,1}$, green line: $SSM_{LTI,2}$, blue line: $SSM_{VP,1}$, red line: $SSM_{VP,2}$) for the (A) *CP* and (B) *WO* paradigms.

A potential confound in comparing and contrasting rate constant savings, S_{rc} , in the *CP* and *WO* paradigms was that they were associated with different rotation (perturbation) amplitudes during initial adaptation ($+30^\circ$ for *CP* and $+45^\circ$ for *WO*; see *Visuomotor rotation paradigms*, in METHODS), which could possibly be associated with different rate constants of adaptation. To assess this possibility, we compared the rate constants of initial adaptation between *CP* and *WO*. A single exponential (Eq. 1) was fit to the first 30 movements of the initial adaptation data from each subject in each paradigm to obtain an estimate of the apparent adaptation rate constant. The exponential rate constants (in units of movements $^{-1}$) during the initial adaptation phase were (mean \pm SD) -0.16 ± 0.14 for *CP* and -0.17 ± 0.16 for *WO*, which were not significantly different [$t(12) = -0.13$, two-tailed $P = 0.90$]. This shows that, on average, rate constants of initial adaptation were very similar between *CP* and *WO* (which is what would be expected under a LTI system), despite the different magnitudes of visuomotor rotation. For completeness, we note that this implies that their rates of initial adaptation (in units of degrees \cdot movements $^{-1}$) were different (greater for *WO*).

Besides the requirement for the LTI system to have a single rate constant regardless of perturbation amplitude, the output amplitude must also be strictly proportional to perturbation

amplitude. This was supported as the average ratio of estimated output amplitude (i.e., a in Eq. 1) to perturbation amplitude was very similar [$t(12) = 0.08$, two-tailed $P = 0.94$] for *CP* (0.922 ± 0.011) and *WO* (0.916 ± 0.029). This finding provides further support for an LTI system being a reasonable approximation to initial adaptation. It also implicitly provides evidence against adaptation having appreciable saturation or supralinear (two other types of nonlinear SSMs distinct from SSM_{VP}) characteristics in this perturbation range because this ratio would have been different between *CP* and *WO* if it did.

Initial adaptation: one-rate or two-rate?

In the immediately preceding text, we approximated the first 30 trials of initial adaptation as a single exponential to estimate apparent adaptation rate constants. However, this does not mean that the adaptation curves do not have multirate behavior. Therefore a preliminary question we sought to address is whether initial adaptation to a visuomotor rotation is a better fit by $SSM_{LTI,1}$ or $SSM_{LTI,2}$ (SSM_{VP} values were not relevant here because initial adaptation constitutes only one phase). Data reported for adaptation to a viscous-curl force field suggested a multirate (e.g., two-rate) system during initial adaptation (Smith et al. 2006). Determining whether there are

similarly two rates present during initial adaptation to a visuomotor rotation will be important for interpreting how the various SSM models fit CP and WO directional error data in their entirety.

Initial adaptation data were fit better by a $SSM_{LTI,1}$ than by a $SSM_{LTI,2}$, significantly in CP [for $AIC_{1-rate\ LTI}$ minus $AIC_{2-rate\ LTI}$: $t(5) = -37.9$, two-tailed $P < 0.001$] and only as a trend for WO [for $AIC_{1-rate\ LTI}$ minus $AIC_{2-rate\ LTI}$: $t(5) = -2.10$, two-tailed $P = 0.07$]. (The extremely high t -value for the former comparison was mainly due to very small variability across subjects in [$AIC_{1-rate\ LTI}$ minus $AIC_{2-rate\ LTI}$] for initial adaptation in CP; the average values of [$AIC_{1-rate\ LTI}$ minus $AIC_{2-rate\ LTI}$] for initial adaptation were -3.70 and -1.58 for CP and WO, respectively.) These results show that, ostensibly unlike adaptation to viscous-curl force fields (Smith et al. 2006), initial adaptation to either a $+30^\circ$ (in CP) or $+45^\circ$ (in WO) visuomotor rotation is better fit by a $SSM_{LTI,1}$ than a $SSM_{LTI,2}$. As a technical aside, we emphasize that these SSM fits were to the initial adaptation phase only, in contrast to the SSM_{VP} fits to all three phases we report later (see SSM fits) that, despite allowing for different learning and retention rates in each of the three paradigm phases, have a single sensorimotor bias parameter.

Savings

The presence of S_{rc} in both CP and WO paradigms was confirmed by comparing the apparent rate constants from the initial adaptation and readaptation phases. This method of measuring savings did not explicitly involve assuming any SSM but simply relied on the qualitative impression that at least the first few trials of motor adaptation to a constant perturbation is reasonably well modeled by Eq. 1 (Caithness et al. 2004; Krakauer et al. 2005; Mazzoni and Krakauer 2006),

although this would correspond to the response of $SSM_{LTI,1}$ to a constant perturbation. The rate constant c was significantly more negative (corresponding to faster learning, i.e., S_{rc}) for the readaptation than for the initial adaptation phase in both CP [$t(5) = 3.05$, one-tailed $P = 0.014$] and WO [$t(7) = 3.73$, one-tailed $P = 0.004$]. Furthermore, the magnitude of S_{rc} was not significantly different between CP and WO [$c_{initial\ adaptation}$ minus $c_{readaptation}$ (mean \pm SD) = 0.48 ± 0.39 for CP and 0.47 ± 0.36 for WO; $t(12) = -0.056$, two-tailed $P = 0.96$]. Also, we keep in mind the finding that apparent rate constants of initial adaptation were very similar between CP and WO (see Adaptation curves). Thus the two adaptation paradigms CP and WO did not appreciably differ from one another either in terms of S_{rc} (which was robust in both) or rate constants of initial adaptation (despite different perturbation magnitudes).

SSM fits

MLE fits of the four SSMs to $e[n]$ (simultaneously to all three phases of either the CP or WO paradigms; see State-space modeling in METHODS) were computed separately in each subject. The across-subject averages of the parameter estimates are provided in Table 1. To collectively illustrate the character of the fits, MLEs of the SSMs were also determined for the across-subject averaged time courses for both CP (Fig. 3A) and WO (Fig. 3B). Although quantitative comparisons between SSMs based on the fits obtained per subject are provided subsequently, a qualitative impression of the across-subject averaged fits is provided here: $SSM_{LTI,1}$ did a poor job of explaining savings in both paradigms, yielding initial adaptation that was too fast and readaptation that was too slow; this SSM also poorly fit the sensorimotor bias. $SSM_{LTI,2}$ did a reasonable job in CP but did a very poor job in the WO paradigm in which it manifested the same problem as

TABLE 1. Across-subject averages of the maximum likelihood estimates of SSM parameters

	CP				WO			
	$SSM_{LTI,1}$	$SSM_{LTI,2}$	$SSM_{VP,1}$	$SSM_{VP,2}$	$SSM_{LTI,1}$	$SSM_{LTI,2}$	$SSM_{VP,1}$	$SSM_{VP,2}$
Phase 1								
a_{slow}	0.924 (0.043)	0.991 (0.012)	0.971 (0.028)	0.986 (0.016)	0.960 (0.031)	0.983 (0.025)	0.979 (0.016)	0.986 (0.016)
b_{slow}	0.137 (0.057)	0.062 (0.016)	0.081 (0.039)	0.112 (0.057)	0.245 (0.099)	0.159 (0.046)	0.149 (0.078)	0.116 (0.048)
a_{fast}	N/A	0.629 (0.102)	N/A	0.369 (0.350)	N/A	0.519 (0.318)	N/A	0.492 (0.324)
b_{fast}	N/A	0.158 (0.051)	N/A	0.003 (0.005)	N/A	0.193 (0.104)	N/A	0.077 (0.076)
Phase 2								
a_{slow}	N/A	N/A	0.779 (0.150)	0.946 (0.140)	N/A	N/A	0.846 (0.102)	0.891 (0.099)
b_{slow}	N/A	N/A	0.093 (0.089)	0.064 (0.058)	N/A	N/A	0.242 (0.141)	0.144 (0.127)
a_{fast}	N/A	N/A	N/A	0.573 (0.263)	N/A	N/A	N/A	0.480 (0.284)
b_{fast}	N/A	N/A	N/A	0.120 (0.079)	N/A	N/A	N/A	0.230 (0.181)
Phase 3								
a_{slow}	N/A	N/A	0.834 (0.077)	0.792 (0.388)	N/A	N/A	0.955 (0.038)	0.975 (0.034)
b_{slow}	N/A	N/A	0.318 (0.187)	0.170 (0.123)	N/A	N/A	0.375 (0.137)	0.330 (0.170)
a_{fast}	N/A	N/A	N/A	0.400 (0.347)	N/A	N/A	N/A	0.548 (0.365)
b_{fast}	N/A	N/A	N/A	0.175 (0.256)	N/A	N/A	N/A	0.088 (0.114)
Sensorimotor bias								
b_x	2.707 (5.330)	-3.405 (2.233)	3.189 (43.382)	-4.101 (1.758)	-3.065 (10.986)	-4.071 (8.599)	2.562 (28.544)	-3.098 (13.398)
Hyperparameters								
$\sigma_{initial}^2$	36.107 (34.135)	1* (0.00)	48.071 (43.382)	1* (0.00)	1* (0.00)	1* (0.00)	12.209 (28.544)	5.737 (13.398)
σ_{output}^2	13.358 (4.537)	12.791 (3.604)	17.417 (4.702)	14.925 (5.970)	13.680 (10.986)	7.482 (8.599)	17.699 (12.473)	16.469 (12.408)
σ_{state}^2	6.378 (3.550)	2.530 (1.643)	1.255 (2.270)	1.167 (2.479)	9.911 (5.504)	8.195 (7.624)	3.539 (2.953)	2.123 (1.644)

Values are means, with SDs in parentheses. Due to our parameterization of the SSMs, the initial state and state noise variance estimates for two-rate models need to be multiplied by 2 to be comparable to the corresponding variance estimates for one-rate models. That the average and SD of phase 1 a_{slow} are the same in CP and WO to three decimal places for $SSM_{VP,2}$ is not a typographical error. An asterisk denotes that all subjects in that sample had estimates equal to a bound placed in that parameter. N/A, parameter not applicable for that SSM.

SSM_{LTI,1}: initial adaptation that was too fast and readaptation that was too slow. Although the SSM_{VP,1} did a reasonable job fitting *WO*, it did a much less reasonable one in *CP* in which it clearly misfit the baseline offset. We speculate this misfitting of the baseline offset was due to a competition between the sensorimotor bias term, on the one hand, and the learning and retention rates during initial adaptation, on the other, both of which determine the offset from zero directional error in baseline trials. Similar misfitting of the baseline offset by this SSM was also apparent in five of six of the individual subject fits (data not shown). SSM_{VP,2} fit the data well overall in both paradigms.

Table 2 shows the percentage of S_{rc} explained by the various SSMs in both paradigms. The SSM_{LTI,1} was unable to explain S_{rc} in either paradigm. The SSM_{LTI,2} was able to explain a nontrivial amount S_{rc} in *CP* but, as expected, negligibly explained S_{rc} in *WO*. Both of the SSM_{VP} explained substantial amounts of S_{rc} in both *CP* and *WO*, although the SSM_{VP,1} overestimated S_{rc} in *CP*.

It is important to consider the number of SSM parameters in addition to how well an SSM seems to fit the data overall. Model selection risk corresponds to net prediction error, which includes both systematic and random sources of misfitting (Akaike 1974). All other things being equal, increasing the number of parameters increases model selection risk. The AIC is an approximately unbiased estimator of model selection risk in that the AIC not only penalizes systematic misfitting by the model [through a dependence on \log_e (likelihood)] but also corrects in a theoretically reasoned way (Akaike 1974) for the number of model parameters. The across-subject average AICs (not the AICs corresponding to fits to the across-subject average data) of the various candidate SSMs to *CP* (trials 31–160) and *WO* (trials 31–190) are shown in Fig. 4, *A* and *B*, respectively. Plotted together with the AICs are the $-2 \log_e$ (likelihood) values (like AIC, the smaller the better). The $-2 \log_e$ (likelihood) values (which do not penalize the number of parameters) decrease necessarily as the number of nested SSM model parameters k increases (Burnham and Anderson 2002). In contrast, the AIC, which equals $-2 \log_e$ (likelihood) + $2k$, does not have to decrease as k increases (e.g., Fig. 4*B*).

For descriptive purposes, for each SSM pairing the proportion of subjects with AIC differences in a given direction are provided in Tables 3 and 4 for *CP* and *WO*, respectively. To compare the population average model selection risk between SSMs, paired t -tests on the AIC values from different SSM pairings were performed (two-tailed $\alpha = 0.05$). The Shapiro-Wilk W test was used to assess the t -test assumption of normality on the AIC differences for each of the six SSM pairings in both *CP* and *WO* paradigms; none of the W values for any of the pairings in either paradigm was significant at $\alpha = 0.05$ (12 W tests: median P value = 0.49, P value range = 0.09–0.93), indicating insufficient evidence to reject the null hypothesis of normality for any of the pairings. We therefore

proceeded with the use of t -test. The AIC of the SSM_{LTI,2} was significantly better than that of the SSM_{LTI,1} in both *CP* [$t(5) = 4.24$, two-tailed $P = 0.008$] and *WO* [$t(7) = 2.58$, two-tailed $P = 0.036$]. The AIC of the SSM_{VP,2} was better (although not significantly so at two-tailed $\alpha = 0.05$) than the SSM_{LTI,2} in both the *CP* [$t(5) = 1.76$, two-tailed $P = 0.138$] and *WO* [$t(7) = 1.44$, two-tailed $P = 0.192$]. That the AIC was better (albeit not significantly) for SSM_{VP,2} than for SSM_{LTI,2} in *CP*, is a pivotal finding. This is because if the SSM_{LTI,2} was a good approximation to the true data generating process in *CP*, its model selection risk in *CP* would be better than that of SSM_{VP,2} (because SSM_{VP,2} has more parameters than SSM_{LTI,2}). However, we keep in mind the bias of AIC toward overfitting with respect to model selection risk (Hurvich and Tsai 1991).

The AICs of SSM_{VP,1} and SSM_{VP,2} were not substantially different in *CP* [AIC_{1-rate varying-parameter} minus AIC_{2-rate varying-parameter}: $t(5) = 0.34$, two-tailed $P = 0.749$], although the former trended toward being favored over the latter in *WO* [AIC_{1-rate varying-parameter} minus AIC_{2-rate varying-parameter}: $t(7) = -2.29$, two-tailed $P = 0.056$]. Because these results did not indicate that SSM_{VP,2} was providing a consistently (i.e., in both *CP* and *WO*) better fit than SSM_{VP,1}, we were curious to see how multirate behavior was manifested, if at all, in any phase of either paradigm. To this end, we plotted the fast and slow state (Eq. 2) estimates from SSM_{VP,2} fit to the across-subject averaged $e[n]$, for both *CP* and *WO*. For *CP*, it appears that the fast state is substantial only during the counterperturbation phase (Fig. 5). Analogously, for *WO* the fast state is most apparent during the washout phase. This absence of a salient fast system during initial adaptation is expected based on our finding that the initial adaptation phase is best fit by a SSM_{LTI,1} (see *Initial adaptation: one-rate or two-rate?*). Figure 5 furthermore suggests essentially one-rate behavior for both *CP* and *WO* during readaptation, which indicates that S_{rc} relies almost entirely on a change in the parameters of the dominant, slow state. It may be that for adaptation to visuomotor rotation, fast states emerge substantially only when the net state is returning to 0° , as occurs during counterperturbation and washout.

DISCUSSION

To provide a more pure assessment of savings than that of most previous studies we eliminated aftereffects via either *CP* or *WO*, and we also used S_{rc} rather than rate savings. Comparable S_{rc} was observed for *CP* and *WO*. SSM_{LTI,2} was able to explain on average 65% of S_{rc} in *CP* but only 1.5% of S_{rc} in *WO*. In terms of SSM_{LTI,2}, this is because the fast and slow states, when subjected to enough washout trials, will both (aside from any sensorimotor bias) get arbitrarily close in expectation to zero (and this is true of any arbitrary order of LTI model, not just second-order). Since SSM_{LTI} parameters are fixed, the bringing of its state variables close to initial conditions will make its net output response during a second

TABLE 2. Percentage of savings explained by state-space model

	SSM _{LTI,1}	SSM _{LTI,2}	SSM _{VP,1}	SSM _{VP,2}
<i>CP</i>	$3.6 \times 10^{-5} \pm 2.9 \times 10^{-4}$ (8.5×10^{-5})	64.8 ± 57.0 (46.8)	156.6 ± 81.3 (152.2)	109.3 ± 81.3 (113.2)
<i>WO</i>	$-9.1 \times 10^{-5} \pm 3.2 \times 10^{-4}$ (0.0)	1.5 ± 2.1 (0.18)	87.5 ± 29.1 (87.8)	86.1 ± 22.8 (82.6)

Values are means \pm SD; median values are in parentheses.

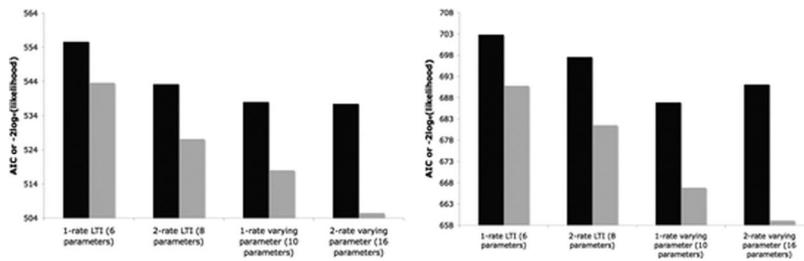


FIG. 4. The across-subject averaged Akaike Information Criterion (AIC, black) and $-2 \log_e$ (likelihood) (gray) values (to within an additive constant) of the candidate models for the (A) CP and (B) WO paradigms. Both measures assess model fit, but only the AIC penalizes for the number of parameters. For each measure, it is only the differences between models (within paradigm) that are meaningful. The units of both the AIC and $-2 \log_e$ (likelihood) are information, in the information-theoretic sense.

rotational perturbation look much like that during initial adaptation, and increasingly so with increasing numbers of washout trials. Given the empirical rate of initial adaptation, the 40 washout trials used in WO were sufficient to well approximate complete washout, making it impossible for a SSM_{LTI} to explain S_{rc} in WO. In contrast, both $SSM_{VP,1}$ and $SSM_{VP,2}$ (which can be non-LTI in the perturbation inputs) explained $>85\%$ of S_{rc} in both CP and WO. Furthermore, as measured by the AIC both $SSM_{VP,1}$ and $SSM_{VP,2}$ fit the overall adaptation movement series data better than either SSM_{LTI} in both CP and WO (although population-level inference was not significant). Together, these empirical findings lead to the following conclusions for adaptation to visuomotor rotation: 1) S_{rc} can occur even with complete elimination of aftereffects via washout between initial adaptation and readaptation, confirming a previous report (Krakauer et al. 2005); 2) this savings cannot be reasonably explained by a $SSM_{LTI,2}$ (and from theory, not by any SSM_{LTI}); and 3) S_{rc} seen with counterperturbation as well as S_{rc} seen with washout are both more parsimoniously explained as the consequence of experience-dependent changes in learning and retention parameters (as a result of initial adaptation) rather than as a property of a multirate LTI system.

S_{rc} observed here in WO for single target adaptation is consistent with the savings described in our previous work for multitarget rotation adaptation (Krakauer et al. 2005). Hinder and colleagues reported absence of savings in a WO paradigm (Hinder et al. 2007) but savings was determined from the fits of a power function to directional error ($e[n] = c_1 n^c_2$), which is a poor approximation because empirical adaptation curves tend not to asymptote at zero, whereas power functions must (a nonzero asymptote can be accommodated by, say, a $SSM_{LTI,1}$ by having a retention rate <1 and/or a sensorimotor bias). Perhaps this is why no savings was detected for WO even though visual inspection of their raw adaptation data (Fig. 2b from that report) suggests otherwise. Thus at the present time it would seem that savings can indeed occur even after washout eliminates aftereffects. This does not preclude the possibility that prolonged washout might eliminate savings, which is another potential explanation for the lack of savings reported by Hinder and colleagues (2007) and in the study by Kojima

and colleagues (2004), where savings was not seen after counterperturbation followed by washout trials.

Recently, in a perturbation/counterperturbation/error-clamp adaptation paradigm using viscous-curl force fields, it was demonstrated that $SSM_{LTI,2}$ could explain spontaneous recovery, a transient excursion of motor output during movements under error clamp in the same direction as that seen during adaptation to the initial perturbation (Smith et al. 2006). The early component of spontaneous recovery in $SSM_{LTI,2}$ is attributable to the rapid decay of the fast state, whereas the sluggish decay back to baseline is attributable to the slow decay (i.e., better retention) of the slow system. Spontaneous recovery has also been observed with saccades (Kojima et al. 2004). Smith and colleagues also showed via simulation that $SSM_{LTI,2}$ produces S_{rc} for CP. A heuristic explanation of savings for the $SSM_{LTI,2}$ in CP (with the convention that the initial perturbation is positive) is that the movements with counterrotated feedback eventually (when the net state reaches zero) bring the fast state to take on a substantial negative value (with the slow state having a value that is equal in magnitude but positive). That the fast system has a value substantially away from zero on the first readaptation trial (unlike the first initial adaptation trial) in conjunction with the fact that the fast system retention parameter is smaller than that of the slow system, allow the fast system to respond with a more rapid correction to the perturbation during readaptation than to the perturbation during initial adaptation (Smith et al. 2006). However, perhaps a more clear way to understand the S_{rc} produced by $SSM_{LTI,2}$ in CP is that it is simply the result of the superposition of the separate adaptation responses to the initial adaptation, counterperturbation, and readaptation perturbations (critically with the latter necessarily being identical to that for initial adaptation). Thinking in terms of superposition, we can also understand why $SSM_{LTI,2}$ cannot produce savings in WO without worrying explicitly about the slow and fast systems: the net output seen during readaptation will be a superposition of the separate adaptation responses to the initial adaptation, washout, and readaptation perturbations; the system response to the initial adaptation, however, has

TABLE 3. Number of subjects showing AIC differences in a particular direction in CP

	$SSM_{LTI,1}$	$SSM_{LTI,2}$	$SSM_{VP,1}$	$SSM_{VP,2}$
$SSM_{LTI,1}$	N/A	6/6	6/6	5/6
$SSM_{LTI,2}$	—	N/A	4/6	5/6
$SSM_{VP,1}$	—	—	N/A	3/6
$SSM_{VP,2}$	—	—	—	N/A

The value of each cell is the proportion of subjects whose AIC is lower (i.e., better) for the SSM of the column relative to the SSM of that row.

TABLE 4. Number of subjects showing AIC differences in a particular direction in WO

	$SSM_{LTI,1}$	$SSM_{LTI,2}$	$SSM_{VP,1}$	$SSM_{VP,2}$
$SSM_{LTI,1}$	N/A	7/8	6/8	6/8
$SSM_{LTI,2}$	—	N/A	6/8	6/8
$SSM_{VP,1}$	—	—	N/A	2/8
$SSM_{VP,2}$	—	—	—	N/A

The value of each cell is the proportion of subjects whose AIC is lower (i.e., better) for the SSM of the column relative to the SSM of that row.

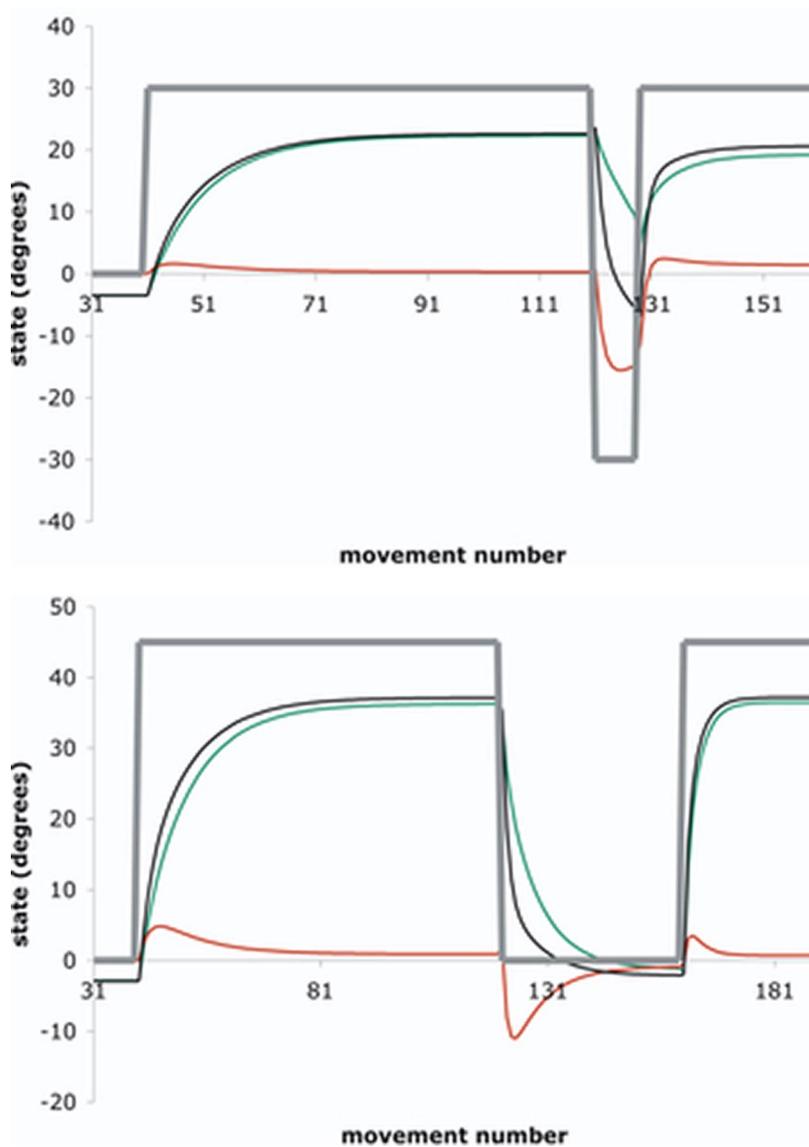


FIG. 5. The fast (red line), slow (green line), and net = fast + slow (black line) state variables estimated from the fit of $SSM_{VP,2}$ to the across-subject averaged directional error $e[n]$ are plotted for the (A) *CP* and (B) *WO* paradigms. The perturbation $r[n]$ (thick gray line), i.e., the deterministic input to the system, is also plotted.

decayed essentially to nil during the washout phase (and will continue to decay), the response to the washout trials themselves is nil, and the response attributable to the readaptation stimulus must simply be a shifted version of the response to the initial adaptation stimulus.

Given that $SSM_{LTI,2}$ is able to explain spontaneous recovery in a viscous-curl force field (Smith et al. 2006), we need to ask why $SSM_{LTI,2}$ did not do a better job of explaining savings in *CP* compared with $SSM_{VP,2}$. A sufficient answer lies in our finding that for the initial adaptation phase, the fit of $SSM_{LTI,1}$ was superior to that of a $SSM_{LTI,2}$ in both *CP* and *WO*, which means that there was no appreciable two-rate behavior during initial adaptation in our data. Thus $SSM_{LTI,2}$ could not satisfactorily explain savings even in *CP* because (under $SSM_{LTI,2}$) two-rate behavior is not something that can suddenly emerge at readaptation. Rather, it must be evident even at initial adaptation. In contrast to the lack of two-rate behavior during initial adaptation in our visuomotor rotation data, the viscous-curl force-field data reported by Smith and colleagues (Fig. 3*d* from that report) manifest clear two-rate behavior during initial adaptation (Smith et al. 2006). A possible explanation for this

discrepancy is the difference in the nature of perturbations used in the two experiments. Viscous-curl force-field perturbations have a proprioceptive component, whereas visuomotor rotations do not. Malfait and Ostry (2004) showed that salient viscous-curl force-field perturbations led to interlimb transfer of adaptation in extrinsic coordinates, whereas more gradual perturbations led only to intralimb transfer in joint-centered coordinates. They suggested that the salient perturbation engaged a cognitive/explicit mechanism distinct from the implicit mechanisms thought to underlie adaptation in joint-centered coordinates. Similarly, it has recently been shown that there is a form of response to sudden force-field perturbations that appears to be categorical rather than scaled to the size of the error (Fine and Thoroughman 2006). In contrast, we have shown that explicit strategies do not contribute to rotation learning (Mazzoni and Krakauer 2006). Perhaps then the two-rate behavior evident in force-field adaptation is due to an explicit component absent in rotation learning. Therefore at the current time we must restrict our finding that $SSM_{LTI,2}$ is worse at explaining savings in *CP* than $SSM_{VP,2}$ to visuomotor rotation.

The AIC was used here to assess parsimony of the candidate SSMs in the contexts of the *CP* and *WO* paradigms. The AIC does not measure the ability of the models to explain savings per se (which is why we also directly assessed savings). Rather, the AIC estimates the overall closeness, in terms of Kullback–Leibler mean information for discrimination, of the estimated, candidate model to the true but unknown data-generating process (Akaike 1974; Burnham and Anderson 2002); this closeness does not solely depend on the ability to explain savings. All other things being equal, however, a model that explains more savings than another should be closer in terms of Kullback–Leibler information to the truth and therefore have a lower AIC. As it turned out, direct measurements of the amount of savings explained by the various SSMs were grossly consonant with the AICs, with the SSM_{VP} explaining more savings as well as having better AICs (albeit, not significantly) than those of the SSM_{LTI} . The use of the AIC complemented the direct measurement of savings because the former takes into account increasing instability in the estimated fit associated with increasing parameter number, whereas the latter does not. Thus that the SSM_{VP} did not have significantly worse model selection risk (and even trended toward being better) than the SSM_{LTI} suggests that the SSM_{VP} made up for their larger number of parameters by the extent to which they reduced model bias (i.e., fit systematic aspects of the data). In contrast, if we had included a highly overparameterized candidate model, it might have explained savings the best of all, but its AIC would likely have been the worst of all. However, a caveat of model selection with AIC is that it is known to be biased toward selecting overparameterized models when the ratio of the number of observations to the number of parameters is low (Hurvich and Tsai 1991); we do not know the size of this bias for the problem we investigated here.

The appeal of $SSM_{LTI,2}$ in the context of motor adaptation is that with a small number of static parameters it is nonetheless capable of producing a fairly rich array of behavioral phenomena (Smith et al. 2006). That savings in *WO* cannot be explained by such a model is in a sense unfortunate. However, a more subtle yet perhaps more interesting aspect of the current findings is that they underscore the fact that the ability of a model to theoretically produce a certain phenomenon (in this case, S_{rc} in *CP*) does not imply that the model can actually explain the empirical phenomenon. The paradox is resolved by realizing that it is not just the choice of model type, but also the values of the model parameters that determine the input–output behavior of a system. So, although $SSM_{LTI,2}$ can produce S_{rc} in *CP*, it does so appreciably only when its parameter values are such that two-rate behavior is sufficiently salient. It so happened that, empirically, two-rate behavior during initial adaptation was weak, which made the $SSM_{LTI,2}$ fit to the S_{rc} effects in *CP* mediocre. The situation in *WO* was different because there it can be understood from superposition that it is impossible for $SSM_{LTI,2}$ to substantially explain S_{rc} .

Kording and colleagues (2007) described an elegant model of sensorimotor adaptation based on Bayesian estimation (“Bayesian learner”). In this model, the brain implements Kalman filtering to obtain a posteriori estimates of sensorimotor perturbation states (“disturbance states” in Kording et al.) associated with different timescales, which it then uses to correct sensorimotor maps (i.e., adapt). This Bayesian learner model can be roughly understood as a generalization of the

$SSM_{LTI,2}$ of Smith and colleagues (2006) that represents perturbations over a wide range of timescales instead of only two. As the Kalman gain approaches steady state, Kalman filtering approaches an SSM_{LTI} . Thus a Bayesian learner that assumes fixed, known state and measurement error covariance matrices will be LTI , and thus obey superposition, at steady state. Therefore like $SSM_{LTI,2}$, such a Bayesian learner would fail to explain the savings we observed in *WO*.

In contrast to SSM_{LTI} (Kording et al. 2007; Smith et al. 2006), the SSM_{VP} values investigated here were allowed to change their parameters in an experience-dependent manner and in this way were able to generate the non- LTI behavior required to explain S_{rc} in *WO*. Said in another way, this experience dependence of SSM_{VP} parameters enabled meta-learning (i.e., learning to learn; Abraham and Bear 1996). Similarly, the Bayesian learner could also manifest meta-learning by allowing its assumed state and/or measurement error covariance matrices to vary (Kording et al. 2007); such a Bayesian learner would also be SSM_{VP} . It would be interesting to determine whether such a varying-parameter Bayesian learner—which estimates rather than assumes state and measurement noise parameters—can explain the savings we observed in *WO* more parsimoniously than the SSM_{VP} investigated here.

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