

Haptic feedback enhances rhythmic motor control by reducing variability, not improving convergence rate

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Ankarali MM, Şen HT, De A, Okamura AM, Cowan NJ. Haptic feedback enhances rhythmic motor control by reducing variability, not improving convergence rate. *J Neurophysiol* 111: 1286–1299, 2014. First published December 26, 2013; doi:10.1152/jn.00140.2013—Stability and performance during rhythmic motor behaviors such as locomotion are critical for survival across taxa: falling down would bode well for neither cheetah nor gazelle. Little is known about how haptic feedback, particularly during discrete events such as the heel-strike event during walking, enhances rhythmic behavior. To determine the effect of haptic cues on rhythmic motor performance, we investigated a virtual paddle juggling behavior, analogous to bouncing a table tennis ball on a paddle. Here, we show that a force impulse to the hand at the moment of ball-paddle collision categorically improves performance over visual feedback alone, not by regulating the rate of convergence to steady state (e.g., via higher gain feedback or modifying the steady-state hand motion), but rather by reducing cycle-to-cycle variability. This suggests that the timing and state cues afforded by haptic feedback decrease the nervous system's uncertainty of the state of the ball to enable more accurate control but that the feedback gain itself is unaltered. This decrease in variability leads to a substantial increase in the mean first passage time, a measure of the long-term metastability of a stochastic dynamical system. Rhythmic tasks such as locomotion and juggling involve intermittent contact with the environment (i.e., hybrid transitions), and the timing of such transitions is generally easy to sense via haptic feedback. This timing information may improve metastability, equating to less frequent falls or other failures depending on the task.

haptics; juggling; metastability; limit cycle; multisensory integration

TERRESTRIAL LOCOMOTION (Holmes et al. 2006) and other rhythmic motor control tasks, such as juggling (Schaal et al. 1996) and finger tapping (Yamanishi et al. 1979), often involve *hybrid transitions*, namely discrete changes in the contact configuration of the animal with its surrounding environment. There is important information conveyed in the timing of these transitions: a measurement of an early or late hybrid transition carries information about the state of the body and/or environment.

We hypothesize that providing sensory feedback to the nervous system regarding the timing and state of these transitions can enhance motor control performance. Specifically, we investigate the role of haptic cues during virtual paddle “juggling.” A similar juggling paradigm has been extensively explored by Sternad and colleagues (Ronsse et al. 2010;

Ronsse and Sternad 2010; Schaal et al. 1996; Sternad et al. 2001; Wei et al. 2007), laying the theoretical and experimental foundation upon which the current study is built. In a theoretical model of paddle juggling, Schaal et al. (1996) showed that if the nominal motor pattern, measured in terms of the “average” periodic trajectory of the paddle during steady-state juggling, exhibits negative accelerations at the time of ball-paddle collision, then the system would be open-loop stable; in other words, if the nominal paddle motion were replayed in open-loop (in a Gedanken experiment), then small perturbations to the ball would diminish over time, and the ball would return, asymptotically, to its nominal bouncing height. This is often referred to as “open-loop stability” in the literature, but this term is misleading because human hand motions are clearly not executed in an open-loop fashion. Indeed, the human paddle juggling behavior is a closed-loop system that relies on active sensory feedback (vision and haptic feedback). Both our own data and prior studies (Wei et al. 2007, 2008; Ronsse and Sternad 2010; Siegler et al. 2010, 2013) support the fact that active sensory feedback plays a significant role in paddle juggling. Thus, when referring to the stability of the nominal pattern, this article adopts the term “nominal stability.”

Sternad et al. (2001) drew the intriguing conclusion that nominal stability seemed to improve in the presence of haptic feedback. To the best of our knowledge, this observation, that a change in the availability of enriched sensory information causes subjects to adopt a different nominal pattern, has not been repeated in another behavior or in the same behavior by a different research group.

In the present study, we reexamine the role of haptic feedback in juggling. Our juggling task is virtual: users “juggle” by using this virtual paddle controlled via a haptic interface to repeatedly hit a virtual ball on a computer screen. The haptic timing cue is provided in the form of a brief mechanical impulse imparted to the subject's hand via the haptic paddle.

We indeed confirmed that the haptic timing information improves juggling performance as previously reported, but we were unable to corroborate previous findings (Sternad et al. 2001) that nominal stability depends on the availability of haptic information. More surprisingly, we also found no difference in the closed-loop convergence rate in the two haptic conditions. Therefore, haptic feedback did not change the closed-loop “gain” nor the nominal pattern, contradicting previous findings. As described in the DISCUSSION and APPENDIX, there are several possible reasons for this discrepancy, including the differences in the experimental setup between our work

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and that of Sternad et al. (2001), although it appears likely that the difference arises from complexities in estimating paddle acceleration at impact (see APPENDIX). Irrespective of these differences, our results show that rhythmic motor performance can be enhanced due to a haptic timing cue, despite no apparent change to the nominal (open-loop) or closed-loop convergence rates.

How does haptic feedback improve performance without affecting either closed-loop or nominal convergence rate? In an effort to understand the closed-loop mechanism underlying the significant performance improvement haptic feedback affords over vision alone, we adopted a stability metric, the mean-first-passage-time (MFPT) that incorporates not only the deterministic dynamics but also the stochastic nature of the system (Talkner et al. 1987). This metric has been used to describe the long-term metastability of rhythmic locomotion of robotic systems (Byl and Tedrake 2009). There are two primary ways to improve metastability (that is, to increase the MFPT). One way is to decrease the noise, and the other is to increase the convergence rate. We illustrate later in this article that decreasing the noise (e.g., sensory or motor) can have a much more dramatic effect on improving the MFPT than quickening convergence.

If long-term metastability were enhanced by a haptic timing cue, despite no change in convergence rate, it would suggest that the haptic cue enhanced the estimate of the ball and paddle state, thus reducing the nervous system's uncertainty. By contrast, increasing the feedback gain itself would increase the convergence rate.

Juggling as a Model System in Neuroscience and Robotics

How animals control rhythmic behavior, such as locomotion and juggling, is one of the grand challenges in neuroscience. It has been examined at all levels of biological organization from individual ionic currents (Dale and Kuenzi 1997), to central pattern generating networks (Ijspeert 2008; Mulloney and Smarandache 2010), to whole organism dynamics (Holmes et al. 2006), and it has been analyzed using behavior (Mulloney and Smarandache 2010), physiology (Harris-Warrick and Cohen 1985), and modeling (Holmes et al. 2006; Cohen et al. 1982).

Yet, detailed computational models of rhythmic motor behavior remain limited. Indeed, while the tools for this type of analysis are emerging (Revzen and Guckenheimer 2008, 2011), they are still in their infancy. Perhaps more importantly, rhythmic motor behaviors may recruit different computational circuits than those used during discrete motor tasks (Schaal et al. 2004). Thus it is essential to rigorously quantify rhythmic motor behavior and create models of such behaviors without assuming that lessons learned for discrete motions will apply.

Our main goal in this work is to understand the rules of rhythmic motor coordination. Terrestrial locomotion generally involves extremely complicated biomechanics, and even the simplest and most impoverished models are challenging to analyze (Holmes et al. 2006; Schwind and Koditschek 2000) and control (Carver et al. 2009a; Ankarali and Saranlı 2010). Yet, several studies on neuromechanical systems (Cowan and Fortune 2007; Chiel et al. 2009; Tytell et al. 2011; Hedrick and Robinson 2010) highlight the role of biomechanics in decoding the neural circuits that control locomotion. To overcome these

challenges and to isolate neural systems from biomechanics, this article considers a virtual one-dimensional paddle juggling task, which has extremely simple mechanical dynamics compared with other tasks such as walking, running, or flying.

Juggling has been addressed from several perspectives, including nonlinear dynamics (Guckenheimer and Holmes 1983; Holmes 1982; Tufillaro and Albano 1986; Chatterjee et al. 2002), robotics and control (Buhler et al. 1990, 1994; Zavala-Rio and Brogliato 2001), and human movement analysis (de Rugy et al. 2003; Morice et al. 2007; Wei et al. 2007; Ronsse et al. 2010; Siegler et al. 2010, 2013). From the human movement analysis point of view, several researchers (Schaal et al. 1996; Ronsse and Sternad 2010; Ronsse et al. 2010; Wei et al. 2007, 2008) have investigated the same simplified juggling task we consider here in which a ball is stabilized in the air by hitting it upwards with a paddle. Despite its apparent simplicity, rhythmically bouncing a ball raises fundamental questions common to the study of general rhythmic movements (including walking). To rhythmically juggle a ball requires fine tuning of the movements of the hand to hit the ball with the appropriate velocity, at the right place, and at the right time. The result of successful juggling is a hybrid dynamical system that displays limit-cycle-like behavior, just as with walking. The wide interest in this behavior likely arises from its simplicity, experimental tractability, and relevance to neural control. Of course, this simplicity is relative as juggling can exhibit surprisingly complex behavior (thanks to its hybrid dynamic nature): Guckenheimer and Holmes (1983) showed that a ball bouncing on a periodically driven planar surface exhibits a wide variety of motions, including steady states, period bifurcations, strange attractors, and chaotic motion.

MATERIALS AND METHODS

To analyze human motor control of a rhythmic behavior, we used a one-degree-of-freedom (1-DOF) haptic device and a virtual environment (Fig. 1A). In our experiments, subjects manipulated a haptic paddle with their hand, causing a virtual paddle to move up and down on the computer screen and "juggled" by using this virtual paddle to repeatedly hit a virtual ball, much like bouncing a table tennis ball. The paddle and ball physics were simulated and conveyed to the participant haptically via force impulses at impact rendered with the 1-DOF haptic interface and visually via rendered ball and paddle movement on a computer screen (Fig. 1A). The goal was to cause the ball to reach its apex between two horizontal lines. Example data acquired from this system are depicted in Fig. 1B. In the APPENDIX, we describe the rationale for using a virtual juggling setup over a physical juggling setup.

Experiments

Eighteen college- and graduate-school-aged participants (2 female, 16 male) attempted to perform the given juggling task. The experiments were approved by the Johns Hopkins University Institutional Review Board (IRB). Each experiment consists of a demonstration session, four training sessions, and two final data collection sessions. The duration of each session was 2.5 min. Between each session, participants were given 30-s rest to prevent fatigue.

During the demonstration session the experimenter explained how to use the haptic device to the participant and then performed a brief demonstration of the juggling task. For training and data collection sessions, we asked participants to bounce the ball so as to repeatedly cause the ball to reach its apex within the goal region. In training

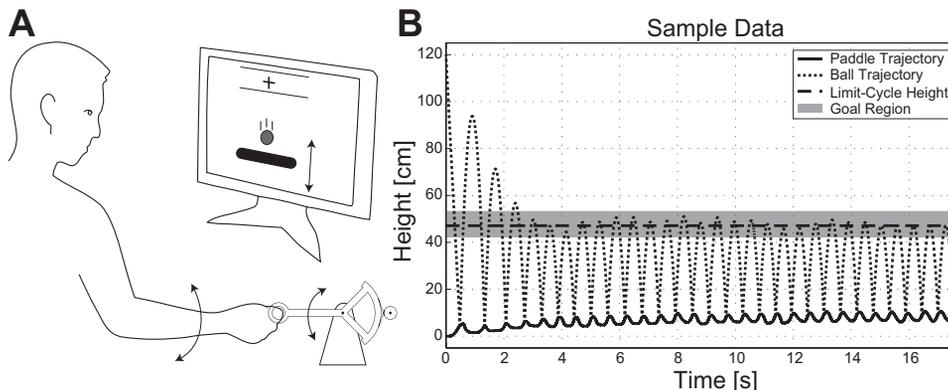


Fig. 1. Virtual paddle juggling setup and sample data. *A*: paddle juggling using a haptic interface. The one degree-of-freedom (1-DOF) haptic device measures the vertical displacement of a subject’s hand and uses this to control the position of a virtual paddle. A ball is rendered to the computer screen. When the ball strikes the paddle, a brief force impulse can be provided depending on the experimental condition. The goal is to bounce the ball (gray circle) under the influence of gravity so that it reaches apex (bold plus sign) within a goal region (between the parallel horizontal lines) using a virtual paddle (horizontal rectangle). *B*: sample data obtained with our experimental setup. Paddle and ball trajectories are depicted as solid and dotted curves, respectively. Users were instructed to maintain the ball within the goal region (gray). The initial apex of the ball is outside the goal region for this illustrative example (in experiments, the first apex was set to the middle of the goal region). However, the user achieves successful rhythmic juggling within $t \approx 3$ s and maintains this throughout the trial.

sessions, the subjects performed the task with and without haptic feedback based on a fixed order: 1) without haptic feedback, 2) with haptic feedback, 3) without haptic feedback, and 4) with haptic feedback.

The purpose of the training sessions was to enable subjects acclimate to the environment and behavior. In the data collection sessions, one session was performed without haptic feedback and the other session was performed with haptic feedback. Half of the subjects started the data collection sessions without haptic feedback, and the other half started with haptic feedback.

Experimental Setup and Virtual Reality Implementation

Experimental apparatus. The haptic device measured the displacement of a user’s hand, which was mapped to the position of the virtual racket on the screen. Depending on the experimental condition, the haptic paddle could simulate the virtual ball-paddle collision by providing a force impulse to the hand. The juggling paddle was coupled to a DC motor (A-max 26 Series-110170; Maxon Precision Motors, Fall River, MA) with a back-drivable capstan mechanism. Haptic force feedback was simulated via generating an impulsive torque to the motor shaft. The DC motor was also equipped with a HEDS 5540 quadrature laser encoder (Avago Technologies, San Jose, CA) that was used for measuring the rotation in the motor shaft. The virtual reality part of the system was developed in the C# programming language environment (Microsoft, Redmond, WA), and the loop rate of the whole system was 1 kHz.

Mechanical system model and virtual reality implementation. Paddle juggling, like many other rhythmic dynamic tasks, is a hybrid dynamical system. Roughly speaking, a hybrid dynamic system is one for which smooth dynamics are punctuated with discrete “jumps” triggered by threshold functions (Guckenheimer and Johnson 1995). In this context, we divide the ball dynamics into two parts: a continuous flight phase describing the dynamics of flight, and a discrete transition phase describing the state transitions due to collision between the paddle and the ball. Table 1 provides the notation we use throughout the article. Neglecting aerodynamic drag, flight dynamics of the ball take the form

$$\ddot{b} = -g, \tag{1}$$

subject to appropriate position and velocity initial conditions, where b , \dot{b} , and \ddot{b} denote the height, velocity and acceleration of the ball,

respectively. To implement the physics digitally on a computer, we discretized the continuous dynamics in (1). Let t_k denote the time of the k th time step, and let

$$z_k = \begin{bmatrix} b(t_k) \\ \dot{b}(t_k) \end{bmatrix}$$

denote a discrete-time state variable. Then,

Table 1. Notation

Parameter	Units	Description
System parameters		
g	m/s^2	Gravitational acceleration
α		Ball-paddle coefficient of restitution
b_{max}	m	Upper limit of goal region
b_{min}	m	Lower limit of goal region
Continuous-time variables		
t	s	Time
b	m	Height of ball
\dot{b}	m/s	Velocity of ball
\dot{b}^-	m/s	Velocity of ball just before the collision
\dot{b}^+	m/s	Velocity of ball just after the collision
p	m	Position of paddle
\dot{p}	m/s	Velocity of paddle
\ddot{p}	m/s^2	Acceleration of paddle
Discrete-time variables at specific events		
k		Index of apex events
t_k	s	Time of k th ball apex event
$b_{apex}[k]$	m	Apex height at k th cycle
b_{ss}	m	Steady-state value of ball apex height
$x[k]$	m	Deviation of ball apex height around steady-state
\ddot{p}_{impact}	m/s^2	Acceleration of paddle at collision

$$\mathbf{z}_{k+1} = \begin{bmatrix} 1 & \Delta t_k \\ 0 & 1 \end{bmatrix} \mathbf{z}_k + \begin{bmatrix} -\frac{1}{2} g \Delta t_k^2 \\ -g \Delta t_k \end{bmatrix}$$

where $\Delta t_k = t_{k+1} - t_k$ is the time between two sampling instants. In real ball-paddle dynamics, a collision event is triggered when the ball hits the paddle, which occurs when the following conditions are satisfied:

$$\begin{aligned} b &= p, \\ \dot{b} &< \dot{p}. \end{aligned}$$

(where p , \dot{p} , and \ddot{p} are the height, velocity and acceleration of the paddle, respectively), which were approximated in discrete-time (to implement in virtual reality) as the first discrete time, t_k , for which

$$\begin{aligned} b(t_k) &< p(t_k), \\ \dot{b}(t_k) &< \dot{p}(t_k). \end{aligned}$$

The ball position and velocity were simulated and were therefore known to the numerical precision of the computer, but the paddle position and velocity were estimated in real time from optical encoder measurements. To estimate paddle velocity, encoder position data were low-pass-filtered and passed through a backward difference filter.

To model the discrete transition due to collision between the paddle and the ball, we assumed that the collisions were purely elastic and the mass of the paddle was infinite such that the paddle velocity was not affected by the collision. Based on these assumptions, using the coefficient of restitution rule, the discrete transition at the collision instant was defined as

$$\begin{aligned} b^+ &= b^-, \\ \dot{b}^+ &= -\alpha \dot{b}^- + (1 - \alpha) \dot{p} \end{aligned} \quad (2)$$

where α is the coefficient of restitution. In the experiments with haptic feedback, we applied an impulsive force (short duration 10 ms, constant magnitude) proportional to the impact velocity to the haptic paddle, $v_{\text{imp}} = v_p - v_b$, (with a gain of 0.1 Ns/m) immediately after collision. We manually tuned the amplitude and duration of the haptic feedback in our preliminary analysis based on the authors' perception of the haptic experience, such that the haptic feedback was noticeable, natural, and within the capabilities of our haptic device hardware.

Task Performance

We asked the participants ($n = 18$) of our experiment to keep the apex height of the ball within a goal region, and they performed the task both with and without haptic feedback. To ease the task for the participants, we displayed a plus sign showing the last apex height of the ball (Fig. 1A). We also asked the participants their opinions about the difficulty level of completing the task with and without haptic feedback.

First, we analyzed the importance of haptic feedback based on two performance measures: percentage of outliers (PO) and coefficient of variation (CV). Percentage of outliers corresponds to the percentage of apex heights that are not inside the goal region. Lower PO values indicate good performance. CV is the coefficient of variation of apex height values, which is found by dividing the standard deviation of the data set to the mean value and multiplying by 100. CV captures the variability of the behavior.

Since our goal was to study successful rhythmic juggling behavior, we excluded the unsuccessful experimental data. Two of the subjects were unable to produce successful rhythmic juggling regardless of haptic condition, and their performance was unacceptably poor in both cases for both metrics (PO values $>80\%$ and CV values $>60\%$). A third subject achieved stable juggling with haptic feedback (PO = 19.8% and CV = 6.2%), but this subject failed to produce successful

rhythmic juggling without haptic feedback (PO = 70.2% and CV = 85.3%). Since this subject produced no useful data without haptic feedback, we excluded all of the subject's data from our statistical analysis (although this subject supports our general finding that haptic feedback enhances performance). As a result, we analyzed the data of 15 subjects.

Nominal Behavior and Nominal (Open-Loop) Stability

Nominal stability, also called open-loop or passive dynamic stability, is an important concept in rhythmic dynamic behaviors (Dickinson et al. 2000; Chatterjee et al. 2002), and it has been analyzed extensively, especially for legged locomotion (Full et al. 2002; Garcia et al. 1998; Geyer et al. 2005; McGeer 1990).

In previous studies on paddle juggling behavior, researchers extensively investigated nominal (open-loop) stability (Schaal et al. 1996; Sternad et al. 2001; Wei et al. 2007, 2008): nominal stability in paddle juggling would imply that if the average motor pattern were recorded, and played repeatedly, then small errors in ball motion would diminish over time, even without sensory feedback. The open-loop juggling model initially introduced by Schaal et al. (1996) requires that the paddle motion has to be strictly time periodic and the paddle has to hit the ball with an upward velocity. Under these conditions, ball bouncing becomes a nonlinear dynamical system, operating near a limit cycle (Holmes et al. 2006). A limit cycle is an isolated periodic trajectory that is a solution to the equations governing the dynamical system. If all trajectories in a sufficiently small neighborhood of the limit cycle converge to the limit cycle, the limit cycle is said to be stable. One way to test for stability is to analyze the eigenvalues of the Poincaré return map (Guckenheimer and Holmes 1983; Ghigliazza et al. 2003; Ankarali and Saranlı 2010); if the eigenvalues all have magnitudes less than unity, then the system is (locally) stable.

Schaal et al. (1996) showed that under the conditions described above, open-loop stability of the juggling pattern is guaranteed if and only if the acceleration of the paddle at the impact (\ddot{p}_{impact}) satisfies

$$-2g \frac{1 + \alpha^2}{(1 + \alpha)^2} < \ddot{p}_{\text{impact}} < 0. \quad (3)$$

In human subject trials with a physical (not virtual) paddle juggling system, Schaal et al. (1996) and Sternad et al. (2001) found that in fact subjects adopt impact accelerations that satisfy the constraint in (3), suggesting that paddle juggling is nominally stable. One major issue associated with negative impact acceleration is that it unavoidably creates a deviation from optimal nominal input effort [which is achieved at zero acceleration (Sternad et al. 2001)]. In other words, there is a trade-off between open-loop stability and nominal energetic cost. Previous results (Schaal et al. 1996; Sternad et al. 2001; Wei et al. 2007) suggest that humans sacrifice energetic optimality to achieve nominal stability.

In this study, we analyzed impact accelerations with and without haptic feedback (see Fig. 4A). Previously, Sternad et al. (2001) analyzed nominal stability during ball bouncing and also compared impact accelerations with and without haptic feedback ($n = 3$ participants).

Let T denote the period of the nominal paddle trajectory. To analyze nominal stability, we only require characterization of the paddle trajectory in the vicinity of ball-paddle collision. For each impact time, t_k , we measured the paddle position over a 0.1-s time interval, $[t_k - 1 \text{ s}, t_k]$. We applied a causal smoothing filter, *rlowess*, in Matlab (Mathworks, Natick, MA) to the paddle position data and estimated velocities using a central difference approximation. These velocity estimates were further smoothed (*rlowess* in Matlab).

After filtering, we fit a third-order polynomial to the smoothed velocity data:

$$v[\Delta t] = a_0 + a_1 \Delta t + a_2 \Delta t^2 + a_3 \Delta t^3 \quad (4)$$

$$\Delta t = t - t_k \quad (5)$$

where a_0, a_1, a_2, a_3 were the paddle trajectory polynomial coefficients, averaged across impacts within a single trial. In addition to limit-cycle analysis, we used these polynomials to derive the impact accelerations as described above.

As an alternative to this filtering and estimation method, one might have used simple noncausal linear filters (which have the benefit of introducing zero phase lag) to the paddle data for the experiments with haptic feedback (Schaal et al. 1996; Sternad et al. 2001; Wei et al. 2007, 2008). However, our analysis in the APPENDIX shows that the rapid negative force applied to the paddle at impact generated a small but significant negative acceleration, and noncausal filters therefore produced consistent biases to the velocity and acceleration estimates at the impact instant.

Computation of the limit cycle also required the period T . One possible estimation of the period would be the average of the elapsed times between successive impacts. However, this method produces estimates for the limit cycle period that do not, in general, satisfy the constraint that the ball must have the same speed before and after impact, i.e., $\dot{b}^+ = \dot{b}^-$. Enforcing this constraint, we computed the period of the limit cycle as

$$T = \frac{2(1 + \alpha)}{g(1 + \alpha)} \ddot{P}_{\text{impact}} \quad (6)$$

Open-loop stability based on the acceleration constraints from Eq. 3 provides a categorical result, stable or unstable, not a graded measure of stability. Thus we estimated the nominal (linearized) return-map eigenvalues that measure convergence (or divergence) rate of the limit cycle. To find eigenvalues, we first found the states of the system, paddle position, ball position, and ball velocity at the instant of impact. We numerically estimated the linearized return map (Jacobian matrix) by using a finite-difference approximation. The eigenvalues of this Jacobian matrix characterize nominal stability.

Closed-Loop System Identification

We use Poincaré nonlinear oscillator theory and assume that the closed-loop behavior is a rhythmic dynamical system operating near a limit cycle (periodic orbit). Poincaré return maps reduce the continuous rhythmic dynamical system to a lower dimensional discrete-time system that describes the behavior in terms of its step-to-step transitions, i.e., a discrete-time nonlinear dynamical system. The stability of this new system is equivalent to the stability of the complete system (Holmes 1990), and most of the essential properties of the behavior are preserved by this discrete-time dynamical system.

We fit a linear dynamical system model of the apex-to-apex dynamics as an estimate of the closed-loop Poincaré return map. Our method relies on the fact that local flow of a (hyperbolic) dynamical system is governed by its linearized version. We assume that, in our experiments, subjects remain within a local region where the linear dynamics dominate. Based on our assumptions and motivations we fit a linear stochastic dynamical system, an auto regressive (AR) Gaussian model, to the apex height data for each subject and for each haptic condition. A first order AR model takes the form

$$x[k] = ax[k - 1] + e[k], \quad e[k] \sim \mathcal{N}(0, \sigma^2), \quad (7)$$

where $x[k] = b_{\text{apex}}[k] - b_{\text{ss}}$ is the relative displacement of the ball apex height at time k , measured with respect to b_{ss} , the steady-state apex height. We estimated the parameters using least-squares that minimizes the following loss function

$$E = \sum_{k=1}^N e[k]^2. \quad (8)$$

In addition to the first-order AR model in Eq. 7, we also tested zeroth- and second-order AR models and computed the loss functions in Eq.

8. Note that zeroth-order AR model simply treats the evolution of apex heights as a pure noise process centered around the nominal height. We compared the quadratic losses provided by both zeroth-, first-, and second-order models, (i.e., E_0, E_1 , and E_2), by evaluating the relative improvement at each order increase, $100 |E_{n+1} - E_n| / E_{n+1}$, which must be traded off with the addition of extra parameters. The mean improvement of the first-order model with respect to zeroth-order model was substantial (20%), whereas the mean improvement of the second-order model with respect to the first-order model was negligible (2%). Thus we selected the first-order AR model for our data analysis. The order of the fitted model can also be considered as the dimension of the slow, template dynamics (Full and Koditschek 1999; Revzen and Guckenheimer 2011) that emerge in the closed-loop behavior. The parameter a in Eq. 7 is the eigenvalue of the dynamics that measures convergence rate, namely the slowest time constant associated with recovery to equilibrium, one of the most common metrics for quantifying stability of dynamical systems.

Our fitted AR model is a “black-box” model that makes fewer assumptions than the open-loop juggling model by Schaal et al. (1996). However, since it is a linear model there could be nonlinear effects that cannot be captured by our model. There could be nonlinear control strategies such as the “mirror law” (Buehler et al. 1994) or robust hybrid stabilization (Guckenheimer 1995). However, we approximate the system in a local region around the goal, where the linear dynamics likely dominate.

Mean First Passage Time

MFPT is a stability metric that incorporates time and stochasticity and has been recently applied to legged locomotion (Byl and Tedrake 2009). Recently Milton et al. (2009a,b) used MFPT to measure performance in a human balance control task and Venkadesan et al. (2007) used MFPT in the context of a hand manipulation task; however, these tasks are not rhythmic hybrid dynamical systems, thus our methods and approach regarding MFPT generally build more directly upon the derivations by Byl and Tedrake (2009).

The MFPT is also referred to as the mean time between failures. For juggling, the passage time refers to the number of cycles until the apex of the ball fails to land in goal region; in the example depicted in Fig. 2A, the passage time is four cycles because the ball apex first lands outside the goal region on the fourth successive cycle. Note that passage time in our task is a discrete random variable, unlike the interpretation in some previous studies (Milton et al. 2009a,b; Venkadesan et al. 2007), where passage time is measured in seconds and is a continuous random variable.

The MFPT metric is the probabilistic expectation of the passage time. Of course, this must be estimated from data. We propose two different estimation methods for the MFPT: estimation directly from failure events and estimation based on a stochastic dynamical model.

The first method is a direct statistical approach, which does not require a stochastic dynamical model for the system. For a given trial, we record all the observed passage times (times between failures). Let $\{k_{p,1}, k_{p,2}, k_{p,N}\}$ be the set of observed passage times. Our goal is to estimate the MFPT, $\hat{\mu}_{\text{mfpt}}$, from data. The sample mean of the data gives such an estimate:

$$\hat{\mu}_{\text{mfpt}} = \frac{1}{N} \sum_{i=1}^N k_{p,i}. \quad (9)$$

Assuming that passage times are independent and identically distributed geometric random variables, Eq. 9 corresponds to the maximum likelihood estimate, namely $\hat{\mu}_{\text{mfpt}} = E[\mu_{\text{mfpt}}]$. Direct estimation via the sample mean in Eq. 9 is simple but may require many failures to obtain a low-variance estimate. Unfortunately, failure is often a rare event so this method may be impractical. Estimating mean time between falls in human locomotion, for example, would require waiting until subjects actually fall, which is challenging due to safety

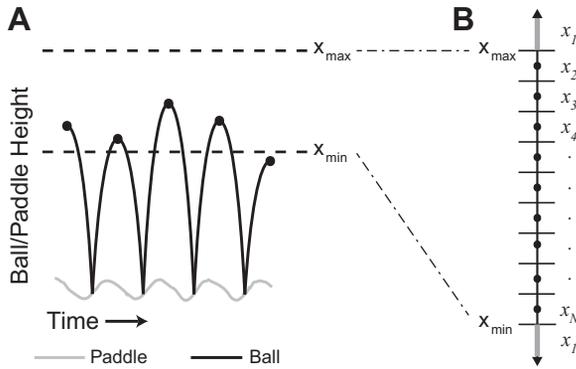


Fig. 2. Passage time and computational modeling for mean-first-passage-time (MFPT). *A*: data from a single example trial (not used for analysis) showing the ball height (dark gray) paddle height (light gray). Four cycles (5 consecutive apex heights) are shown (filled circles at peaks of ball height). Here, the user failed to keep the apex height of the ball within the goal region at the fourth cycle. Accordingly, passage time (# of cycles) for this trial was 4. *B*: discretization process for model-based MFPT computation. We discretized the state space (apex height of the ball) into a finite set of representative states (bins). By convention the first state was assigned to the whole failure region (shown in light gray). Thus for our juggling paradigm, the first state corresponds to apex heights that lie above or below the goal region. All other states are equally spaced within the goal region. Fifty bins were used to compute the MFPT; increasing the number of bins to 100 produced negligible differences in numerical values (<0.01%).

and other reasons. For our juggling experiments, the goal (hitting the ball to reach apex within a desired region) was designed so that subjects typically fail at least two to three times in a single experiment (often more). However, there are many trials for which we have few enough failures that large uncertainty in MFPT estimate is inescapable via the direct sample mean estimate.

To overcome this issue, we developed a second, model-based, method built on the derivations by Byl and Tedrake (2009). They estimated MFPT for a simulated robotic system, and thus the equations of motion (including noise terms) and the feedback control laws were completely specified. However, in the present work, our goal is to estimate MFPT from experimental data; no model is known a priori. Therefore, to apply the technique, we first must fit a stochastic dynamic model to behavioral data. We use the first-order AR model fitted to the data (see Eq. 7 above). This model must be augmented to include a definition of failure (passage). For our experimental setup, failure is defined as the first apex event that exceeds the limits of the goal region (see Fig. 2). In other words, the state $x[k]$ is a failure if $x > x_{max}$ or $x < x_{min}$ (where $x_{max} = b_{max} - b_{ss}$ and $x_{min} = b_{min} - b_{ss}$).

To compute MFPT from this model requires the assumption that there exists a metastable distribution (Talkner et al. 1987), which we now assume. The state (apex height) evolution in Eq. 7 represents a discrete time, continuous-state Markov process. For computational purposes, we discretize the state space into a finite set of states as illustrated in Fig. 2B. After that we compute the stochastic state transition matrix, \mathbf{T} :

$$T_{ij} = \Pr(X[n] = x_j | X[n-1] = x_i). \quad (10)$$

T_{ij} is the probability of going to j th state from i th state. Since x_1 corresponds to the failure region, we consider it as the absorbing state, such that

$$T_{11} = 1, T_{1j} = 0 \forall j \neq 1. \quad (11)$$

For all other elements we use the AR model in Eq. 7 to complete the stochastic state distribution matrix. The n -step dynamics are revealed by the Chapman-Kolmogorov equation,

$$p[n] = p[n-1]\mathbf{T}, \quad (12)$$

where $p[n]$ is the state distribution vector defined as

$$p_i[n] = \Pr(X[n] = x_i), \quad (13)$$

Assuming that the second-largest eigenvalue of \mathbf{T} is less than one, this absorbing Markov chain will have a unique stationary distribution, with the entire probability mass in the absorbing state. Since there is only one absorbing state and it is possible to jump to the absorbing state from any state (due to properties of Gaussian noise), our system inherently satisfies this assumption. The stochastic state transition matrix \mathbf{T} in our problem takes the following specific form

$$\mathbf{T} = \begin{bmatrix} 1 & \mathbf{0} \\ \mathbf{r} & \bar{\mathbf{T}} \end{bmatrix}, \quad (14)$$

with $\mathbf{T} \in \mathbb{R}^{N \times N}$, $\bar{\mathbf{T}} \in \mathbb{R}^{(N-1) \times (N-1)}$, $\mathbf{0} \in \mathbb{R}^{1 \times N}$, $\mathbf{r} \in \mathbb{R}^{(N-1) \times 1}$. The dynamics of escape to the absorbing state can be investigated using eigenmode analysis (Byl and Tedrake 2009). Let us order the eigenvalues of \mathbf{T} , λ_i , in order of decreasing magnitude. The transition matrix from an absorbing Markov chain will have $\lambda_i = 1$, with (left) eigenvector $v_1 = [1 \ 0 \dots 0]$ representing the stationary distribution on the absorbing state. The magnitude of the remaining eigenvalues ($0 \leq \lambda_i < 1, \forall i > 1$) describe the transient dynamics and escape rate to the stationary distribution.

We assume that the second-largest eigenvalue, λ_2 , (which is also the largest eigenvalue of $\bar{\mathbf{T}}$, i.e., $\lambda_2 = \bar{\lambda}_1$) is close to (but still less than) 1, $\lambda_2 \ll -1$ and also $\lambda_2 \gg \lambda_3$, which means that initial conditions (in eigenmodes 3 and higher) decay quickly, and eigenvector of $\bar{\mathbf{T}}(v_1)$ associated with $\lambda_2 = \bar{\lambda}_1$ describes the long-living (metastable) distribution of the state. The metastable distribution is given by v_1 , the eigenvector associated with largest eigenvalue of $\bar{\mathbf{T}}$ with proper normalization. Under these circumstances MFPT is approximated by

$$\hat{\mu}_{mfpt} \approx \frac{1}{1 - \lambda_2}, \quad (15)$$

Note that the submatrix $\bar{\mathbf{T}}$ is a positive matrix (not to be confused with positive-definite matrix), such that based on Perron-Frobenius theorem the largest eigenvalue of $\bar{\mathbf{T}}(v_1)$ is always positive, and the magnitudes of all other eigenvalues are strictly lower than $\bar{\lambda}_1$, i.e., $\bar{\lambda}_1 \in \mathbb{R}^+$ and $\bar{\lambda}_1 > |\bar{\lambda}_j| \forall j > 1$.

Making use of Eq. 15 is practically equivalent to assuming that metastable distribution is a good summary of the initial conditions. In fact, if the initial condition is a random variable that is drawn from the metastable distribution, Eq. 15 is the exact MFPT of the system. By assuming that $\lambda_3 \ll \lambda_2 \ll -1$, the distribution will tend to quickly converge to the metastable distribution, making Eq. 15 a good approximation.

To test the reliability of the metastable distribution, we computed the MFPT starting from different initial conditions and generated confidence bounds on the MFPT estimate given by Eq. 15. The vector of MFPTs ($\hat{\mu}_{mfpt}$) for all nonabsorbing states can be computed as

$$\vec{\mu}_{mfpt} = \begin{bmatrix} \hat{\mu}_{mfpt,2} \\ \vdots \\ \hat{\mu}_{mfpt,N} \end{bmatrix} = (\mathbf{I} - \bar{\mathbf{T}})^{-1} \mathbf{1}, \quad (16)$$

where $\mathbf{1} = [1 \dots 1]^T$ and $\hat{\mu}_{mfpt,i}$ denotes the MFPT starting from initial condition x_i . Specifically, we computed the 5th and 95th percentiles of $\vec{\mu}_{mfpt}$ to form a confidence bound on Eq. 15.

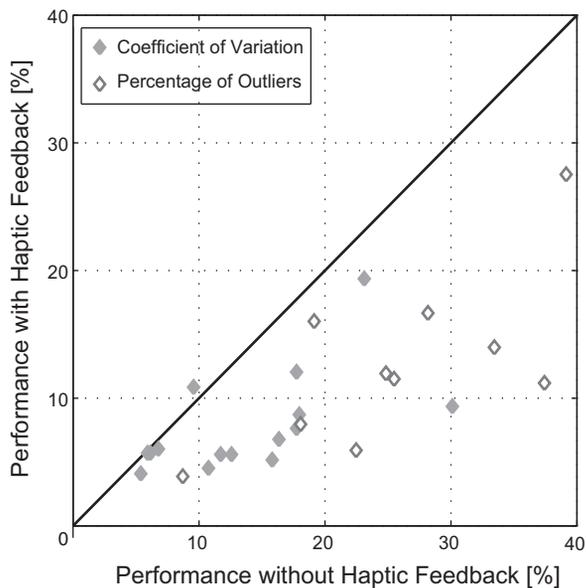


Fig. 3. Haptic feedback enhances performance. Performance in 2 metrics percentage of outlier apex heights (PO; hollow markers) and coefficient of variation (CV; solid markers), was significantly improved with haptic feedback; larger values of these metrics indicate inferior performance. Each marker compares the performances (based on one of the metrics) of a single individual for the 2 haptic conditions. Performance was enhanced by haptic feedback for points lying below the 45° line.

RESULTS

Subjects Believe Haptic Feedback Improves Their Performance

After completing the experimental session, all participants completed a brief questionnaire on their perception of task difficulty with and without haptic feedback. Among the 15 participants whose data were not excluded, 13 participants reported that the task seemed easier with haptic feedback. Two (out of 15) subjects reported no apparent difference in both cases. Among the three participants whose data were excluded, one subject reported that the task seemed easier without haptic feedback. This subject was also one of the subjects who failed to perform the task in both haptic conditions. The other subject who failed to perform the task in both haptic conditions was among the group that reported no apparent difference in both haptic conditions. Finally, the subject who did well with haptic

feedback, but failed to achieve rhythmic juggling without haptic feedback, reported that the task was easier with haptic feedback.

Objective Measures Confirm that Haptic Feedback Improves Performance

Each subject (excluding the 3 whose data was not included) performed better with haptic feedback in at least one performance metric (see Fig. 3). Based on the PO metric, each subject performed better with haptic feedback and the difference in performance was statistically significant ($P < 10^{-5}$, paired t -test). For the CV metric, all but one subject also performed better with haptic feedback and this performance improvement was also statistically significant ($P < 10^{-3}$, paired t -test).

Nominal Stability is Fragile and Unchanged by Haptic Feedback

Impact accelerations illustrated in Fig. 4A show that majority (13 out of 15) of the participants did not adopt predominantly negative mean impact accelerations in either haptic condition, contradicting previous results (Sternad et al. 2001). According to Sternad et al. (2001), the impact acceleration is predominantly negative if it satisfies $\dot{p}_{\text{impact}} \in [-6, -2] \text{ m/s}^2$. For the experiments with haptic feedback, they reported a median impact acceleration across all individuals of $\dot{p}_{\text{impact}} -4.16 \text{ m/s}^2$, whereas for the no haptic feedback experiments the median impact acceleration is $\dot{p}_{\text{impact}} -0.31 \text{ m/s}^2$. Even in a recent juggling study (Wei et al. 2007) from same group, reported mean impact acceleration with haptic feedback is not predominantly negative ($\dot{p}_{\text{impact}} -1.75 \text{ m/s}^2$, mean across 7 individuals and 4 different coefficient of restitution values), but this study did not compare impact accelerations with and without haptic feedback.

In our experiments, all subjects exhibited many positive impact accelerations, even for those whose average impact accelerations were negative. Therefore, while the mean impact accelerations across individuals for both haptic conditions were slightly (but statistically significantly, $P < 0.05$, one-sided t -test) negative (see Table 3), nominal stability does not appear to be a robust strategy: for 21 out of 30 trials (15 subjects \times 2 haptic conditions), 25% or more of the impact accelerations were positive. Indeed, statistics

Fig. 4. Haptic feedback does not enhance nominal stability. A: impact acceleration statistics of each individual. Markers and error bars indicate the means \pm SD. B: combined statistics of impact accelerations based on grouping the mean impact acceleration of each individual with respect to haptic condition. Shaded light gray region in both figures illustrates the open-loop stable trajectories according to Eq. 3 for $\alpha = 0.8$. Haptic and no haptic feedback conditions are depicted by solid gray and hollow black markers, respectively.

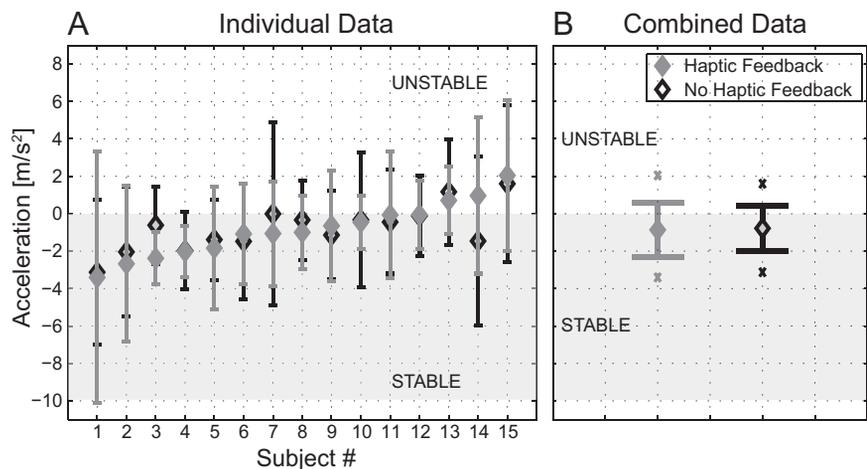


Table 2. Eigenvalues of the nominal behavior

	$ \lambda _{\max}$														
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
HF	0.8	0.8	0.8	0.8	2.00	1.54	0.8	0.8	0.94	1.43	0.8	0.8	0.8	0.8	0.94
No HF	0.8	0.8	0.8	0.8	1.82	0.8	0.8	0.8	0.84	1.65	0.8	0.8	1.00	0.8	0.8

Italic numbers indicate subject numbers. HF, haptic feedback.

of the data from Wei et al. (2007) suggest similarly nonrobust nominal stability; even though the mean impact acceleration of each individual was negative in that study, for five out of seven participants at least 15% of the impact accelerations were positive.

We examined whether haptic feedback changes nominal stability by comparing the mean impact accelerations for each individual between the two haptic conditions, as shown in Fig. 4B. We found no statistically significant difference ($P > 0.4$, paired t -test). Thus haptic feedback cannot be shown to have had an effect on nominal stability, which contradicts previous conclusions (Sternad et al. 2001).

Table 2 lists the magnitude of the largest eigenvalues for each subject and condition, computed based on limit cycle estimates (see MATERIALS AND METHODS). Many subjects achieved a nominal eigenvalue of 0.8 (based on the average impact acceleration) in both haptic conditions, corresponding to the best (smallest) nominal eigenvalue possible, given the coefficient of restitution used in our experiments ($\alpha = 0.8$) (Schaal et al. 1996). As for our nominal stability analysis based on paddle accelerations (see Fig. 4), we observed no significant improvement in the open-loop eigenvalues with the addition of haptic feedback ($P > 0.65$, paired sign test). Note that the eigenvalue distribution was nonnormal because a significant fraction of the eigenvalues were concentrated at the coefficient of restitution of 0.8, and thus we used the more conservative signed test rather than a t -test, which is not based on normality.

Also, although we did not observe predominately negative accelerations in paddle trajectories (Fig. 4), the “typical” subject seems to achieve the best possible nominal eigenvalue in both haptic conditions. However, this observed nominal stability is fragile since many accelerations for each subject lies in the open-loop unstable region (nominal eigenvalue > 1).

Closed-Loop Eigenvalues Are Stable but Unchanged by Haptic Feedback

Nominal stability, which was not dependent on the haptic condition, could not explain the performance enhancement afforded by haptic feedback during rhythmic juggling. Thus we examined the closed-loop dynamics. Specifically, we fitted a first-order AR model to the apex height time-series data (see MATERIALS AND METHODS) and analyzed the closed-

Table 3. Mean impact accelerations in different studies

	Our Study	Sternad et al. (2001)	Wei et al. (2007)
HF	-0.863	-4.16	-1.75
No HF	-0.778	-0.31	—

Mean impact accelerations (\ddot{p}_{impact}) are in m/s^2 .

loop eigenvalues to quantify the stability of the behavior. The closed-loop eigenvalues of each subject are illustrated in Fig. 5.

Comparing the closed-loop eigenvalues with the nominal eigenvalues listed in Table 2 reveals that the least stable closed-loop eigenvalue in both haptic conditions, $\lambda_{\max} = 0.58$, is significantly more stable than the best eigenvalue, $\lambda_{\text{best}} = 0.8$, that could be achieved in open loop. Clearly, active sensory feedback control played a critical role in this juggling task. Similarly, Wei et al. (2007, 2008) and Ronsse and Sternad (2010) observed that a purely passive model failed to explain measurements of closed-loop behavior in terms of “relaxation times” (convergence rate), thus indicating the existence of active error corrections.

Even though active feedback control clearly plays a role for the behavior, we observed no statistically significant trend in closed-loop eigenvalues between the two haptic conditions ($P > 0.3$, paired t -test). In fact, about half (7 of 15) of the subjects had more stable eigenvalues without haptic feedback. The results based on both the closed-loop and open-loop eigenvalues suggests that haptic feedback was not used by the nervous system to regulate the convergence rate in this juggling

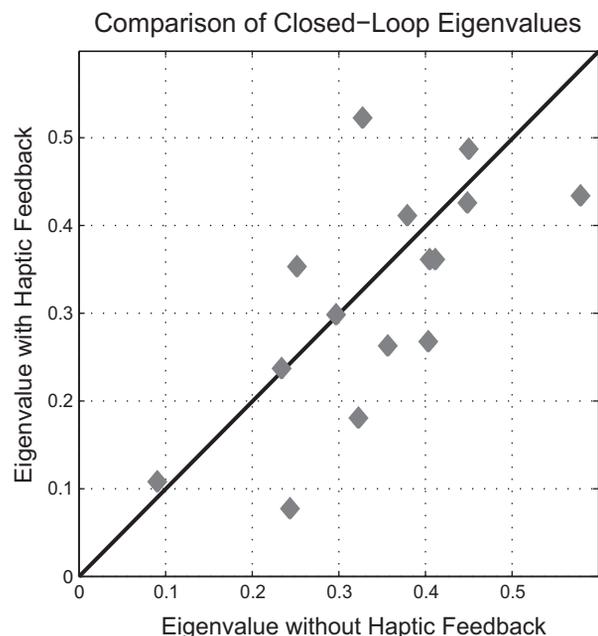


Fig. 5. Haptic feedback does not enhance (decrease) closed-loop eigenvalues. The closed-loop eigenvalues identified from experiments with and without haptic feedback are not significantly different. Each marker in the figure corresponds to an individual's closed-loop eigenvalues without (abscissa) and with (ordinate) haptic feedback. The 45° line indicates ideal agreement in eigenvalues of conditions with and without haptic feedback.

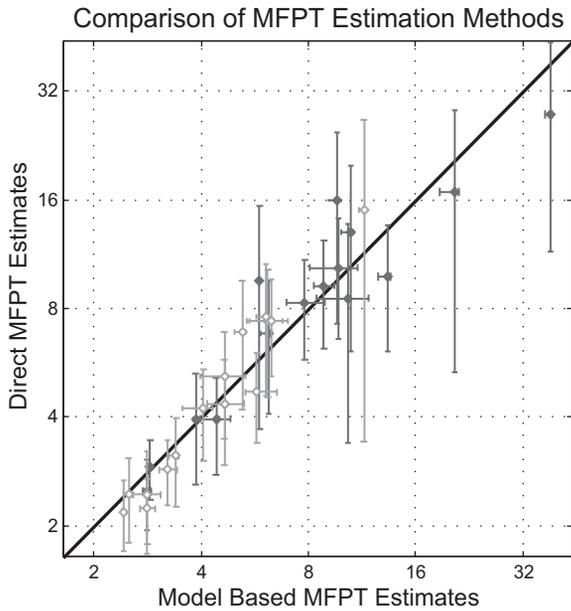


Fig. 6. Direct and model-based MFPT estimates agree. Markers indicate the MFPT estimates (the horizontal axis is model-based, and the vertical axis is direct estimation; see MATERIALS AND METHODS) for all users and both haptic conditions (with and without haptic timing cue). The 45° solid black line would indicate ideal agreement between direct and model-based MFPT estimation. Vertical and horizontal error bars indicate the 95% confidence bounds for the direct and model-based MFPT estimates, respectively.

task, and the performance improvement must be explained by other means.

Haptic Feedback Significantly Improves Mean First Passage Time

MFPT provides a measure of stochastic stability for the closed-loop behavior. We verified the consistency of the two independent MFPT estimation methods (see MATERIALS AND METHODS) by directly comparing them. Since each estimation method used the same data in categorically different ways, there were differences in the estimates; however, there was a strong correlation between estimates obtained via the two distinct methods (see Fig. 6). The 95% confidence bounds (direct estimates) overlapped with the model-based estimate in all cases. Thus the two methods were independent, but mutually consistent, ways to assess the stochastic stability of the behavior.

We also observed the statistics of the λ_2 and λ_3 (second and third largest eigenvalues of \mathbf{T} in Eq. 14, respectively) distributions obtained from our experimental data. The mean and standard deviations of the λ_2 and λ_3 data were $(\mu_2, \sigma_2) = (0.8, 0.1)$ and $(\mu_3, \sigma_3) = (0.15, 0.09)$ respectively; given that these eigenvalues are bounded between 0 and 1, λ_3 was much lower than λ_2 , as expected. To test further the reliability of Eq. 15 (i.e., model-based MFPT estimates), we scrutinized our assumptions by computing 95% confidence bounds on Eq. 15. The confidence bounds (Fig. 6) indicated that the uncertainty of the model based method was much lower than the uncertainty of the direct estimation method.

As shown in Fig. 7, each subject's MFPT was higher (i.e., more stable) with haptic feedback and the differences were significant ($P < 10^{-4}$, direct method and $P < 0.005$, model-based method; paired t -test).

DISCUSSION

What is the mechanism by which the haptic cue at the instant of ball-paddle collision improves juggling performance? We suspected that the haptic cue would quicken convergence. Surprisingly, however, haptic feedback had no significant effect on the convergence rate as measured by either the nominal or closed-loop eigenvalues of the dynamics in our study. Instead, we found that long-term metastability, namely, the "persistence" of the system, was enhanced. The haptic timing cue is a measurement that decreases the nervous system's uncertainty of the ball's state. Decreasing noise may improve stability as measured by persistence, while potentially having very little effect on convergence rate. Indeed, it may not be the speed of convergence but rather the infrequency of failures that matters most for a great many behaviors.

Stability: Convergence or Persistence?

It has long been hypothesized that human motor control commands are derived from an economic policy made by the nervous system, such as optimizing energetic cost, reward rate, and stability (Kuo et al. 2005; O'Connor and Donelan 2012; Harris and Wolpert 1998; Shadmehr et al. 2010; Kiemel et al. 2011). However, little is known about how stability might affect the neural controller or how stability might be evaluated in such a cost function.

The most common measure of system stability is the tendency of a system to return to steady state after a perturbation. This tendency can be measured in terms of a system's eigenvalues. Thus it is natural to hypothesize that one of the goals of the nervous system is to effectively regulate the eigenvalues of the closed-loop behavior. If this measure of stability were important, then one might predict faster convergence rates in

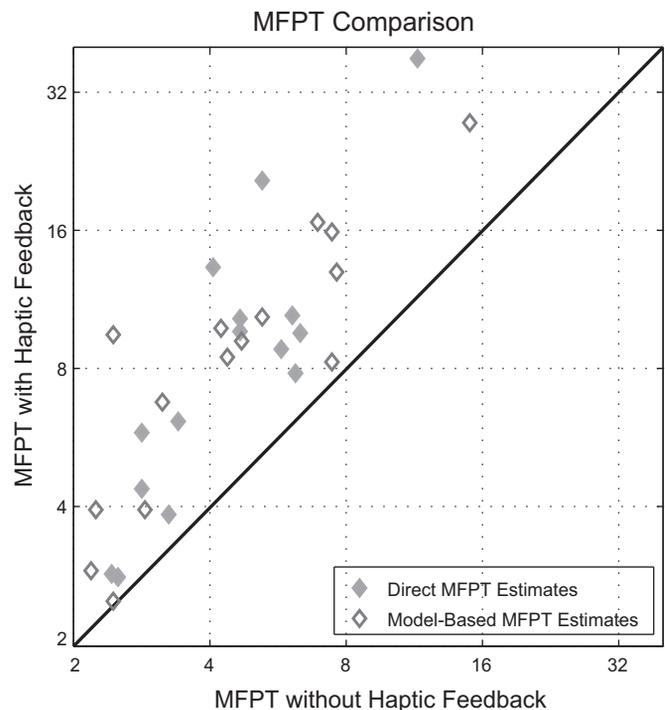


Fig. 7. Haptic feedback enhances metastability as measured by MFPT. Markers indicate the MFPT values without (horizontal axis) and with (vertical axis) haptic feedback. Direct and model-based MFPT estimates are depicted by solid light gray and hollow dark gray markers respectively.

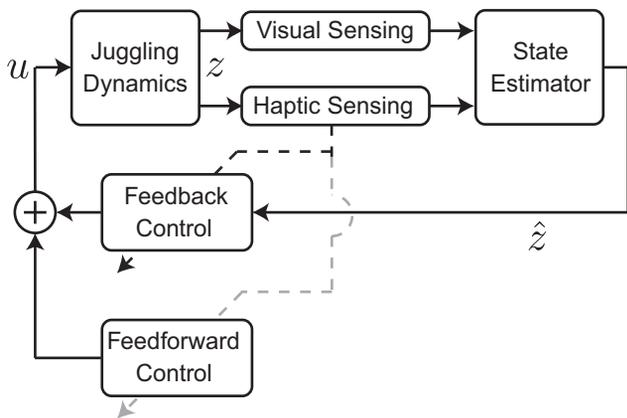


Fig. 8. Simplified schematic representation of juggling behavior with different hypotheses on the role of haptic feedback. Dashed lines represent (slow) parametric or “structural” tuning of the dynamics. Solid lines represent (fast) dynamical signals. z and \hat{z} represent the actual and estimated (continuous and discrete) states of the dynamics, respectively. The u is the control input to the juggling dynamics which is regulated by the feedforward and feedback controllers. In principle, haptic sensing information could be used for tuning or regulation of feedforward (nominal) motor patterns (dashed light gray line), regulation of feedback controllers (dashed dark gray line) and/or state estimation (solid line). We found that neither the feedforward pattern nor the feedback gains were altered by the presence of haptic feedback. This suggests that haptic feedback serves mostly a state-estimation-like role that reduces uncertainty, thus improving performance in paddle juggling.

the presence of haptic feedback. In paddle juggling, we investigated the two main possible ways of regulating the convergence rate. One way is shaping the nominal paddle trajectories without adjusting the feedback controller, and the other way is regulating the feedback controller itself. The human nervous system might choose either (or both) ways to tune the stability of the behavior. Different hypotheses on the role of haptic feedback for human paddle juggling behavior are illustrated in Fig. 8.

In contrast to previous results (Sternad et al. 2001), we observed no statistically significant change in nominal patterns, suggesting that haptic feedback did not enhance nominal stability (Fig. 4). Perhaps this is not so surprising: it seems counterintuitive that adding haptic sensory information would decrease optimality. Recall that increasing nominal stability of the nominal pattern requires higher (absolute) negative accelerations at impact; thus immediately before impact the paddle (and arm) must reach a peak velocity that is actually substantially higher than the impact velocity. Producing faster arm motions than nominally necessary likely wastes energy. However, since it is possible to regulate convergence rate in rhythmic ball motion using active closed-loop neural feedback without changing the nominal trajectories, there may be no need to sacrifice energetic optimality for nominal stability. Therefore, we investigated the stability of the closed-loop system (Fig. 8) by analyzing its eigenvalues.

The closed-loop eigenvalues illustrated in Fig. 5 verify our hypothesis that the closed-loop dynamics are dramatically more stable than the nominal eigenvalues. Indeed, the slowest closed-loop eigenvalue extracted from all trials was significantly more stable than the best possible nominal eigenvalue of 0.8. However, the addition of haptic feedback did not change the closed-loop stability (Fig. 5). Taken together, these results strongly suggest that haptic feedback provided at the moment of ball-paddle collision had no significant effect in conver-

gence rate (in either nominal or closed-loop). Thus the regulation of convergence rate cannot explain the difference in performance in between two haptic conditions.

Rate of convergence to an equilibrium point, while commonly used and easy to quantify, is hardly the only measure of stability that is relevant to rhythmic behaviors (Pratt and Tedrake 2006; Chatterjee et al. 2002). Moreover, different stability measures may yield qualitatively different results. For example, Chatterjee et al. (2002) showed that open-loop linear stability does not correlate well with the size of the domain of attraction for an open-loop juggling model. More recently, Byl and Tedrake (2009) applied the MFPT as a stability metric to quantify long-term metastability. The MFPT can be thought of as the tendency of a system to persist for long periods of time, rather than the tendency of a system to converge.

Eigenvalues again play a role, but here the eigenvalue of interest, λ_2 (see Eq. 15), is the one associated with the (statistical) “escape rate” of the system—the associated MFPT is given by $\hat{\mu}_{\text{mfpt}} = 1/(1 - \lambda_2)$. We suspect that the eigenvalues of the dynamics fail to explain the performance improvement with added haptic feedback due to their deterministic nature; they cannot capture stochastic characteristics of the real system. Therefore, we adopted the MFPT as stability metric because it embraces the inherent stochasticity of the system. All biological systems suffer from some uncertainty or stochasticity, thus MFPT, i.e., persistence, may be a useful alternative to traditional eigenvalues, i.e., convergence, as a measure of stability. Indeed, our analysis with MFPT shows that haptic feedback enhanced the long-term closed-loop metastability as measured via the MFPT (Fig. 7).

We suspect that the primary effect of haptic feedback in this task was to mitigate noise or uncertainty (a natural consequence of adding additional sensory information), thereby enhancing persistence of the dynamics and ultimately improving subject performance in the task.

To illustrate the profound effect of decreasing uncertainty on metastability and persistence, compared with aggressively regulating the convergence rate, in Fig. 9 we illustrate the dependence of MFPT on two parameters, the eigenvalue and the uncertainty, of a scalar stochastic dynamical system with additive white Gaussian noise. Uncertainty in Fig. 9 is measured in the form of a normalized standard deviation (standard deviation divided by the vertical size of the goal region). As shown, a decrease in normalized standard deviation is dramatically more effective than a decrease in the eigenvalue in terms of improving MFPT-based stability. In other words, minimizing the deterministic eigenvalues (which may be highly sub-optimal) is ineffective compared with mitigating noise, and thus the first goal of additional sensory measurements may be to reduce uncertainty, not regulate convergence rate.

Sensing of Hybrid Transitions for State Estimation

Rhythmic motor control tasks, such as legged locomotion, often involve “hybrid transitions,” namely discrete changes in the contact configuration of an animal with its surrounding environment. When a rhythmic system operates near a limit cycle (see MATERIALS AND METHODS), these hybrid transitions punctuate the system dynamics at particular instants in phase (Revzen and Guckenheimer 2008), a measure of the time elapsed since the beginning of a cycle, relative to the overall

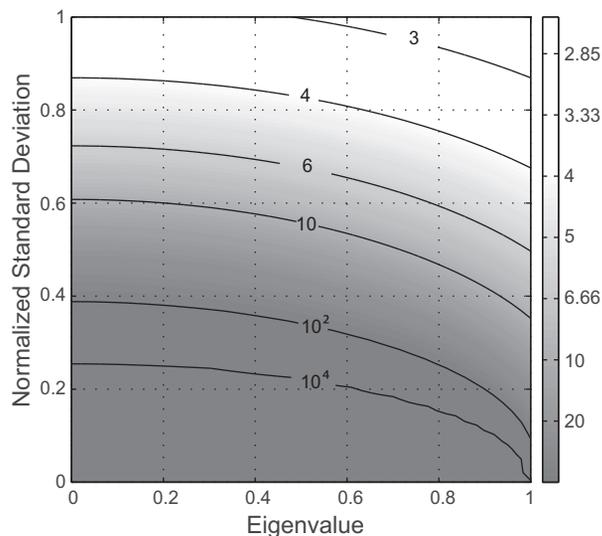


Fig. 9. Reducing noise is more effective for increasing MFPT than regulating eigenvalues. The MFPT is shown as a function of the eigenvalue and uncertainty of a scalar stochastic dynamical system with additive white Gaussian noise (see Eq. 7). Upper and lower failure limits are symmetric with respect to the origin. Uncertainty is measured in the form of a normalized standard deviation, which is computed by dividing the standard deviation by the size of the goal region ($b_{\max} - b_{\min}$). Darker means more stable (i.e., higher MFPT) in the contour plots.

cycle time. Sensing the timing and state of hybrid transitions may enhance rhythmic motor control performance.

Haptic sensing plays a critical role in motor control, as has been shown for rhythmic finger movements (Elliott et al. 2010; Wing et al. 2010; Studenka et al. 2012) and continuous haptic feedback during dynamic manipulation tasks (Huang et al. 2007; Forsyth and Maclean 2006). However, surprisingly few neuroscience studies address how haptic feedback, especially provided by hybrid transitions, enhances neural control during dynamic rhythmic behaviors such as juggling (Sternad et al. 2001).

To furnish a mechanistic explanation for how haptic sensing may enhance performance in this rhythmic dynamical task, it is natural to interpret our results in terms of state estimation and feedback control (Kuo 2002; Schaal et al. 2007). In this context, one possibility is that the nervous system may process haptic cues at hybrid transitions to improve state estimation, thereby reducing uncertainty, as has been demonstrated in legged robotic systems (Gur and Saranli 2012; Lin et al. 2005). The estimated states could be used by a separate controller whose goal may be regulating energy, cost of transport, stability, etc. This interpretation resembles the “separation principle” in the linear-quadratic-Gaussian (LQG) control problem (Athans 1971). LQG is an optimization problem where the goal is to minimize a cost function for linear systems that suffer from uncertainty in the form of additive Gaussian noise, and the solution involves a combination of a Kalman filter and linear-quadratic regulator (LQR). The Kalman filter optimally estimates the states and the LQR optimally applies state feedback-based only on state estimates to control the plant. A loose analogy can be drawn between the LQG problem and our paddle-juggling control problem: adding haptic feedback in the juggling problem amounts to adding an additional sensor measurement. Assuming linear dynamics around the nominal trajectory, and applying the separation principle,

then only the estimator, i.e., the Kalman filter, would be affected by the number of measurements, and the state feedback gains would remain the same. Our data suggest that this mechanism could be at play for the human motor control of paddle juggling. Indeed, it has been shown that the human nervous system integrates haptic cues with other sensory modalities in a statistically optimal fashion for estimating the size of an object (Ernst and Banks 2002) and for synchronizing finger motions (Elliott et al. 2010; Wing et al. 2010). Thus it is possible that humans may integrate haptic and visual feedback under a Kalman-filter-like strategy to estimate the states of the ball (and hand) in paddle juggling behavior while keeping the controllers fixed. Our findings suggest that haptic cues during hybrid transitions improve state estimation and a separate controller uses these state estimates for control, in a manner not dissimilar from a separate Kalman filter plus a LQR controller for a linear control system. However, the separation principle does not necessarily apply to nonlinear systems such as juggling. For example, since the removal of sensory information can decrease the reliability of sensor-based state estimates, the nervous system may rely on shaping nominal paddle motions to improve nominal stability and less on sensory feedback. Sternad et al. (2001) reported the reverse of this in paddle juggling, where the addition of haptic feedback caused steady-state hand trajectories to become more nominally stable but also energetically more costly. We were unable to reproduce this result.

“Perfect-Time” Control

Almost all control system formulations implicitly depend on the assumption that time can be perfectly observed. What happens if this assumption is violated, i.e., if the chronometer is imperfect? Perhaps due to the remarkable precision of engineered clocks, this question has been largely ignored. Neural control systems in nature, by contrast, exhibit significant temporal variability (Bieńkiewicz et al. 2012). Thus, while neglecting uncertainty in time leads to accurate control systems for many engineering applications, perfect timekeeping may be a poor assumption for the modeling and analysis of biological control systems. Yet, all computational models of human motor control implicitly assume that time is known to the neural controller (Harris and Wolpert 1998; Todorov 2005; Kuo 2005; Shadmehr and Krakauer 2008; Shadmehr et al. 2010), including our own prior work (Carver et al. 2009b).

Both open- and closed-loop controllers may be time varying, thus both categories of control policies may suffer from the imperfections in chronometry. For example, Lamperski and Cowan (2013) extended the finite-horizon LQR problem to account for temporal uncertainty and showed that in this context the classical solution produces suboptimal results. Open-loop control policies, such as for juggling (Schaal et al. 1996), even more sharply illustrate the potential problems in assuming perfect timekeeping. An open-loop control policy is typically formulated as a function that maps the time t into control input $u(t)$. However, time must be measured and/or estimated; is it appropriate to call this open-loop control or rather perfect-time feedback control (LaValle and Egerstedt 2007)? Indeed, it is even possible for a system that has been stabilized using open-loop (perfect-time feedback control) to

be destabilized by small imperfections in timing (LaValle and Egerstedt 2007).

Open-loop control is appealing because it potentially obviates the need for complex computations and active feedback (McGeer 1990; Schaal et al. 1996; Garcia et al. 1998; Full et al. 2002; Geyer et al. 2005). Since the animal nervous system does not have access to a precise master clock, the nervous system must estimate and process time (Buonomano and Karmarkar 2002; Barclay et al. 2012; Eagleman 2008), likely integrating feedback from sensory stimuli. Carver et al. (2013) showed that even for a simplified model of motor control, time estimation requires complex computations. Thus open-loop control does not, after all, eliminate the need for feedback or complex computations, since time itself must be estimated. Perhaps sensory feedback provided during hybrid transitions not only enhances state estimates but also enhances time estimates, therefore decreasing uncertainty in both feedback and feedforward control, ultimately enhancing long-term metastability. Recently, Studenka et al. (2012) showed that adding event based tactile feedback in a rhythmic circle drawing task can enhance the structure of timing variability, supporting our theory regarding the connection between haptic feedback and human timing.

APPENDIX

Virtual vs. Physical Paddle Juggling

Our preference toward virtual juggling (de Rugy et al. 2003; Wei et al. 2007, 2008; Ronsse and Sternad 2010; Ronsse et al. 2010) over physical juggling (Schaal et al. 1996; Sternad et al. 2001) stems from our ability to control the physical dynamics that the human interacts with during control. Indeed, these dynamics play a critical role in decoding and understanding neural circuits that control motion (Cowan and Fortune 2007; Chiel et al. 2009; Tytell et al. 2011; Hedrick and Robinson 2010).

One of the main limitations of the physical juggling used in (Schaal et al. 1996; Sternad et al. 2001) was that it required two experimental systems, one that displays haptic feedback, and a distinct system that did not. Specifically, with haptic feedback, the subject controlled the motion of a physical paddle whose surface remained horizontal via a mechanical linkage, and the paddle hit a table tennis ball that was fixed to a hinged boom. Because the linkage was mechanical, impact forces were transmitted nearly instantaneously to the user's hand. To create the no-haptic feedback condition, by contrast, a telerobotic system mechanically decoupled the user's hand from the paddle. The user's hand motions provided a reference trajectory that was tracked by a robotically controlled paddle. In this case, haptic feedback regarding the ball-paddle collision was not transmitted back to the user's hand. This setup introduced a confound: the setup without haptic feedback included an entire telerobotic system with its own dynamics (including potential filtering and phase lags), which likely affected results. Indeed we show below (in the specific context of offline filtering), that subtle differences to filtering dynamics can dramatically alter estimates of impact acceleration. Therefore, in this article we reexamine the role of haptic feedback in a context where the two experimental conditions (with vs. without haptic feedback) are directly related.

Estimating the time of the ball-paddle collision, and the acceleration of the paddle at that instant, is coupled in the physical apparatus. When the ball bounces, it imparts significant (negative) momentum to paddle. The time at which the ball reaches a local minimum is used to estimate impact time (Schaal et al. 1996; Sternad et al. 2001). Because the ball's rapid positive acceleration and reversal is concomitant with the negative momentum changes to the paddle, the point in time

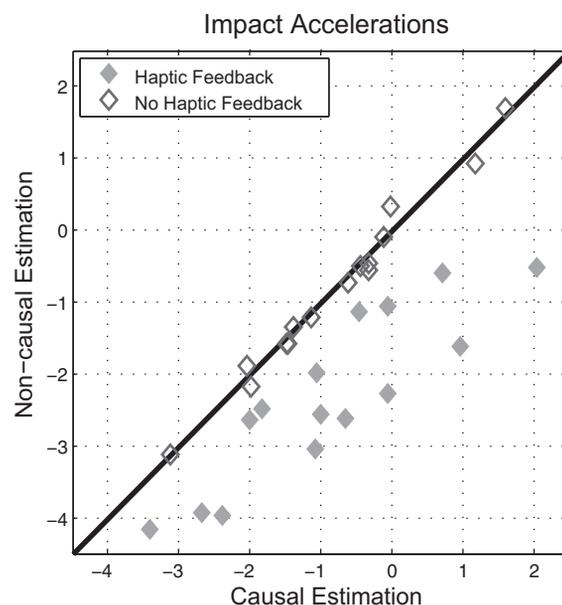


Fig. A1. Noncausal filtering biases the estimate of impact acceleration with haptic feedback. Markers indicate estimated impact accelerations (abscissa and ordinate belong to causal and noncausal estimates, respectively). Hollow dark markers and solid light markers correspond to scenarios without and with haptic feedback, respectively. The 45° solid black line would indicate ideal agreement between causal and noncausal estimates.

corresponding to a local minimum in the ball height also corresponds to a moment when the paddle has already necessarily accelerated downward. The detection of impact time and the estimation of acceleration at impact are fundamentally coupled in this physical juggling system in a way that leads to a negative bias in the estimated impact accelerations for the haptic condition, a bias consistent with previous findings (Sternad et al. 2001).

The coupling of detecting the moment of ball-paddle impact and estimating acceleration at impact can be eliminated in virtual juggling since the computer can detect the (virtual) impact, and only then impart the force to the haptic paddle. This allows us to (causally) determine impact acceleration without being potentially biased by our method for detecting impact time based on physical accelerations of the paddle and/or ball.

Causal vs. Noncausal Impact Acceleration Estimation

As described in MATERIALS AND METHODS, to estimate the acceleration of the paddle at the time of impact we follow a causal method and only the kinematic information before the time of impact is used. As an alternative to our filtering method, one might have used simple noncausal filters (Wei et al. 2008, 2007; Schaal et al. 1996; Sternad et al. 2001; Ronsse et al. 2010), which have the benefit of introducing zero phase lag and thus are quite commonly used in data analysis. However, the force that we applied to the paddle during the impact instant generated a small but significant negative acceleration at the hand, and noncausal filters therefore produced consistent biases to acceleration estimates at the impact instant. For smoothly changing data, noncausal filters typically provide accurate estimates so we developed a causal filter that, for the no-haptic feedback case (without force impulse generation), our scheme provided similar results to a well-tuned causal filter. Figure A1 illustrates our comparison of causal and noncausal mean impact acceleration estimates of each individual and for both haptic conditions. For the data without haptic feedback both estimation methods agree showing no statistically significant difference ($P > 0.3$, paired t -test). However, in the haptic case the noncausal estimation method resulted in significant negative bias

compared with causal estimation method ($P < 10^{-6}$, paired one-sided t -test). These results show that noncausal impact acceleration estimation methods can generate misleading negative acceleration.

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DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the author(s).

AUTHOR CONTRIBUTIONS

M.M.A., H.T.S., A.D., A.M.O., and N.J.C. conception and design of research; M.M.A. and H.T.S. performed experiments; M.M.A. and N.J.C. analyzed data; M.M.A. and N.J.C. interpreted results of experiments; M.M.A. and N.J.C. prepared figures; M.M.A. and N.J.C. drafted manuscript; M.M.A., A.M.O., and N.J.C. edited and revised manuscript; M.M.A., H.T.S., A.D., A.M.O., and N.J.C. approved final version of manuscript.

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