

RESEARCH ARTICLE | *Control of Movement*

Complementary spatial and timing control in rhythmic arm movements

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Nickl RW, Ankarali MM, Cowan NJ. Complementary spatial and timing control in rhythmic arm movements. *J Neurophysiol* 121: 1543–1560, 2019. First published February 27, 2019; doi:10.1152/jn.00194.2018.—Volitional rhythmic motor behaviors such as limb cycling and locomotion exhibit spatial and timing regularity. Such rhythmic movements are executed in the presence of exogenous visual and nonvisual cues, and previous studies have shown the pivotal role that vision plays in guiding spatial and temporal regulation. However, the influence of nonvisual information conveyed through auditory or touch sensory pathways, and its effect on control, remains poorly understood. To characterize the function of nonvisual feedback in rhythmic arm control, we designed a paddle juggling task in which volunteers bounced a ball off a rigid elastic surface to a target height in virtual reality by moving a physical handle with the right hand. Feedback was delivered at two key phases of movement: visual feedback at ball peaks only and simultaneous audio and haptic feedback at ball-paddle collisions. In contrast to previous work, we limited visual feedback to the minimum required for jugglers to assess spatial accuracy, and we independently perturbed the spatial dimensions and the timing of feedback. By separately perturbing this information, we evoked dissociable effects on spatial accuracy and timing, confirming that juggling, and potentially other rhythmic tasks, involves two complementary processes with distinct dynamics: spatial error correction and feedback timing synchronization. Moreover, we show evidence that audio and haptic feedback provide sufficient information for the brain to control the timing synchronization process by acting as a metronome-like cue that triggers hand movement.

NEW & NOTEWORTHY Vision contains rich information for control of rhythmic arm movements; less is known, however, about the role of nonvisual feedback (touch and sound). Using a virtual ball bouncing task allowing independent real-time manipulation of spatial location and timing of cues, we show their dissociable roles in regulating motor behavior. We confirm that visual feedback is used to correct spatial error and provide new evidence that nonvisual event cues act to reset the timing of arm movements.

motor control; multisensory integration; nonvisual feedback; rhythmic movement

INTRODUCTION

Rhythmic motor behaviors—walking, running, dancing, music, and sports to name a few—by their nature exhibit spatial and temporal regularity (Hogan and Sternad 2007). Consider the activity of juggling: a key goal is to toss the objects along explicit spatial trajectories, but skilled jugglers also intuitively

recognize that there are implicit constraints on motor timing, embodied in a juggling theorem credited to Claude Shannon (Beek and Lewbel 1995).¹ Studies of three-dimensional ball juggling indeed suggest that spatiotemporal regularity of ball trajectories emerges as a function of skill (Beek 1989; Huys et al. 2003) and may serve as a general reference to which the body coordinates its upper limb and postural sway movements (Huys and Beek 2002; van Santvoord and Beek 1996). Studies such as the above leave open the question of how humans process sensory feedback online, on a cycle-to-cycle basis, to establish these rhythmic behavioral patterns and regulate them around an approximately periodic pattern.

The goal of this study was to understand how sensory information is used to dynamically regulate rhythmic movement about average (or “nominal”) cyclical behaviors. Our task of choice is a simplified juggling paradigm known as vertical paddle juggling, which involves bouncing a ball up and down off a physical or virtual rigid elastic surface (Ankarali et al. 2014; de Rugy et al. 2003; Dijkstra et al. 2004; Schaal et al. 1996; Siegler et al. 2013; Sternad et al. 2001; Wei et al. 2007). Paddle juggling is a particularly well-suited task for addressing cycle-to-cycle regulation of rhythmic behavior because it is a simple task that nevertheless has similar (hybrid) dynamics to not only three-dimensional juggling but also whole body tasks like walking.

Initial behavioral studies of paddle juggling focused on the extent to which humans rely on sensory cues to achieve skilled juggling, a consequential question because of the existence of passively stable ball-bouncing strategies (Schaal et al. 1996). Although some studies provide evidence that humans are capable of exploiting such passive stability during skilled performance (Schaal et al. 1996; Sternad et al. 2001) and during initial task learning (Huber and Sternad 2015), more recent findings concur that humans rely on environmental cues to actively regulate their arm movement patterns (Siegler et al. 2010, 2013; Wei et al. 2007), justifying the use of closed-loop control models to characterize human behavior. This emerging consensus leads to the question of what feedback is important for regulating rhythmic behavior (a categorical question) and how this feedback is used to maintain spatiotemporal regularity endemic to rhythmic movements (a mechanistic one).

¹ Shannon, a pioneer in computing and information theory, was himself a juggler. His theorem describes a constraint for how the durations that a ball is airborne (“flight time”), that the ball occupies a hand (“dwell time”), and that a hand is empty (“vacancy”) must be allocated in periodic (stable) juggling patterns: (flight time + dwell time) × (no. of hands) = (vacancy + dwell time) × (no. of balls).

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Surprisingly, although the informational content of feedback in paddle juggling has been considered separately by the control theory (Ankarali et al. 2014; Avrin et al. 2017) and psychology (Fajen et al. 2009; Warren 2006) communities, few studies directly address the processing of feedback on a cycle-by-cycle basis in such juggling tasks, with a handful of notable exceptions. Wei and colleagues applied impulse perturbations to ball position and observed that jugglers corrected these perturbations more rapidly than predicted by the passive mechanics of the task, suggesting that humans actively control paddle swings on a cycle-by-cycle basis (Wei et al. 2007). Subsequent work by Siegler and colleagues separably manipulated height and timing of the ball's (continuously visible) flight path, thereby showing that visual information was sufficient to modulate changes in juggling accuracy and timing (Siegler et al. 2013).

Yet it is likely that nonvisual feedback plays a significant functional role (Siegler et al. 2010). Indeed, multiple lines of evidence suggest that haptic feedback is sufficient to maintain stable movements (Sternad et al. 2001) and that it may provide an additional cue leading to a categorical improvement over vision alone in how long a person can sustain a given level of accuracy (Ankarali et al. 2014). It is worth noting that elements of touch (de Rugy et al. 2003; Schaal et al. 1996; Sternad et al. 2001) or audio (Morice et al. 2007) feedback have almost universally featured in previous studies of paddle juggling, but control mechanisms underlying the use of nonvisual feedback in juggling, which may serve as timing cues because they signal collision events, have not been specifically investigated. The physical coupling between space and time makes it difficult to disambiguate the roles of vision from other sensory modalities; however, the effects on behavior of nonvisual feedback, and event-timing cues in general, can be parsed at a fine resolution by using closed-loop control models (Cowan et al. 2014; Roth et al. 2014) to infer state-space representations of cycle-to-cycle control.

To systematically study the role of such event-timing feedback in rhythmic movement, we asked human volunteers to perform a virtual reality paddle juggling task in which two types of sensory information were subtly perturbed: 1) the visual display of ball heights, focused at a small time window about ball peaks, and 2) nonvisual feedback in the forms of simultaneous audio and haptic cues at collisions. These perturbations manifested respectively as increases and decreases in displayed ball position or as advances and delays of when feedback of ball collision and apex event timings were presented.

Ball position and event timing are inherently coupled: the time between apex and collision provides a measurement of descent time, which in turn depends on previous ball height based on the laws of projectile motion. Thus if we delay or advance the timing of the collision cue relative to the actual ball-paddle collision, the brain might infer that the ball was higher or lower at the prior apex than previously believed; this would lead the juggler to adjust the subsequent paddle velocity so as to strike the ball lower or higher as necessary to correct for the perturbation. In this way, we hypothesized that perturbations to ball event timing would lead to changes in ball height vis-à-vis the juggler's change in control action. Alternatively, such timing cues could serve to selectively regulate the timing of movement (Siegler et al. 2010, 2013), with little direct impact on spatial control. The goal of this study was to distinguish these hypotheses by reducing visual feedback to-

ward the minimum thought to be necessary for skilled juggling (Austin 1976; Dessing et al. 2012; van Santvoord and Beek 1994) while independently perturbing spatial and event-timing feedback in order to identify their respective roles in the control of rhythmic arm movements.

Performance of paddle juggling, and other rhythmic tasks, can be conceptualized in terms of general information flow between the dynamics of a task ("plant") and the human brain and musculoskeletal system ("controller") (Fajen et al. 2009). We conducted one experiment with sinusoidal perturbations, to parse apart the input-output relationships between sensory cues and motor behavior. In a second experiment, we introduced step perturbations, both for additional insight into the cycle-to-cycle dynamics of control and as a validation of frequency-domain estimates.

MATERIALS AND METHODS

Apparatus

Figure 1 shows an overview of the paddle juggling task. Participants sat in front of a monitor (VG248QE; Asus, Taipei, Taiwan) displaying a ball of radius 1 cm and two bars separated by 35 cm (Fig. 1A). The upper bar served as a target, and the lower bar represented the position of the paddle in virtual reality. The participants controlled the virtual paddle by vertically moving the handle of a haptic paddle with the right hand (Okamura et al. 2002).

Participants sat at eye level to the target during experiments, with their elbows hanging loosely at approximately the height of the paddle axle. While manipulating the paddle, participants generally oriented their forearms and the handle of the paddle approximately parallel to the floor, such that movements of both their wrists and elbows were visibly apparent.

Handle motion was sampled by an encoder (CUI-103) connected to a hard-real-time data acquisition (DAQ) card (NI PCI-6229; National Instruments, Austin, TX). Encoder counts were smoothed online in real time with a causal ninth-order polynomial filter. Visual feedback was displayed on the monitor with screen rendering enforced at 17 ms/frame. Nonvisual feedback was presented in the form of simultaneous haptic and audio cues. Haptic feedback was delivered to the handle via an onboard motor (A-max 26 Series-110170; Maxon Precision Motors, Fall River, MA) connected to the DAQ board. Audio feedback was delivered by a buzzer (sound frequency 3,500 Hz) likewise connected to the board. The voltage pulses that were used to drive the haptic and audio feedback were kept constant; that is, the strength of haptic feedback and the volume of the audio feedback were not designed to scale with the force of the ball-paddle collisions.

To control the timing of event cues with high precision, the above-described task was implemented on a computer with a hard-real-time operating system (Linux Xenomai) (Brown and Martin 2010) within a software environment designed to exploit state-of-the-art low-latency capabilities of the system (Bruyininckx 2001; Quigley et al. 2009). As a result, all data collection and experimental events were controllable with 1-ms precision (1,000 Hz), with timing jitters to haptic and audio cues never exceeding 40 μ s (verified by direct measurements).

Task Overview

Experiments were carried out in accordance with protocols reviewed and approved by the Johns Hopkins Institutional Review Board. Each trial began with the suspension of a virtual ball onscreen at the target height, with a counter displayed slightly below. After a 3-s countdown, the counter disappeared and the ball was dropped. Ball physics were simulated with a one-degree-of-freedom ballistic

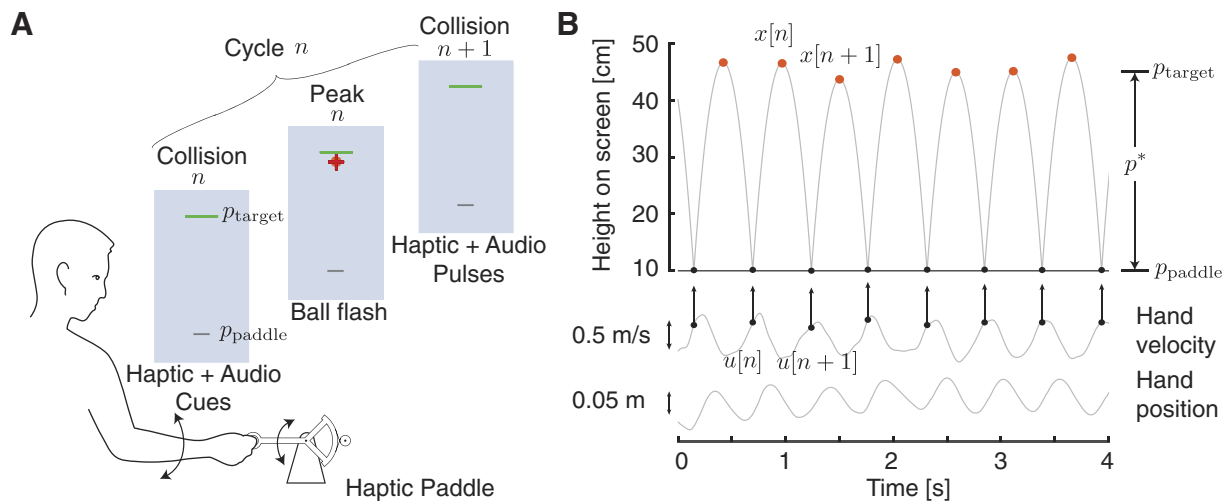


Fig. 1. Virtual reality paddle juggling task with restricted visual feedback. **A**: participants were shown 2 lines representing the position of the paddle (p_{paddle}) and a target (p_{target}) and tasked with bouncing the ball to the target by vertically moving the handle of a haptic paddle. Visual feedback cues were restricted to an ~ 221 -ms ball flash onscreen centered in time at ball peaks. Auditory and haptic feedback were given simultaneously at ball-paddle collisions. p_{paddle} was clamped in place (see *Apparatus*). **B**: example virtual reality positions of ball and paddle and veridical movements of the hand. Virtual ball position was constantly updated although only displayed near peaks ($x[n]$, orange dots), while p_{paddle} was kept constant. Hand velocity was continuously recorded from the haptic paddle, and its values at ball-paddle collisions ($u[n]$; upward-pointing arrows) were used to launch the ball. Hand position was computed off-line from recorded hand velocities.

flight model (see *Modeling*, Eq. 1) and an elastic collision equation (Eq. 3) (Schaal et al. 1996).

Participants were instructed to bounce the ball rhythmically in a vertical direction toward the goal as accurately and consistently as possible. They were told that exactly matching the goal height denoted perfect performance. Each time the ball reached its peak for a given bounce cycle, a red cross was temporarily drawn at that position (Fig. 1A, middle inset). Participants were also informed that allowing the ball to dribble on the paddle, such that rhythmicity was lost, would cause the ball to be redropped and the trial restarted. Specifics of the redrop criterion were not revealed; however, redrops were instigated as soon as peak ball position declined to $\sim 10\%$ of the target height (~ 3 cm above virtual paddle position).

Restriction of visual feedback. Visual feedback of the ball was confined to a ball flash interval, a 221-ms window symmetric about the peak ball position (13 frames total; schematized in Fig. 1A, middle inset, and Fig. 2, C and D). Prior studies indicate that this is approximately the minimum visual requirement for juggling and is representative of how much optical information of the ball skilled jugglers actually exploit (Austin 1976; Dessing et al. 2012; van Santvoord and Beek 1994).

In contrast to other paddle juggling studies (Siegler et al. 2013; Sternad et al. 2001), we also removed visual feedback of hand position by keeping virtual paddle position stationary while equating its velocity to the instantaneous velocity of the participant's hand (Fig. 1B). Such clamping of paddle position was implemented by simply not integrating the subject's hand velocity to update virtual paddle position. However, since all velocities were stored in computer memory, hand displacements could be easily reconstructed off-line. Participants moved their hands rhythmically in quasi-sinusoidal trajectories as expected from other paddle juggling apparatuses (Fig. 1B) and could learn to successfully perform the task after a single training session (see Fig. 3 and RESULTS).

Locking the virtual paddle position in this manner had the incidental effect of enforcing what is called "high-bounce" behavior, which is the assumption of several previous mathematical models that ball-paddle collisions occur at a constant height, similar to a ball bouncing on a table (Guckenheimer and Holmes 1983; Ronsse et al. 2010; Sternad et al. 2001). One consequence of the high-bounce assumption is that ball apex and collision times of an upcoming

bounce cycle can be predicted exactly by the preceding collision, enabling more accurate perturbations of event feedback.

Nonvisual feedback. Participants received nonvisual feedback via simultaneous audio and haptic cues for each ball-paddle collision. Because haptic feedback involved applying force impulses to the jugglers' hands, event timings were presented with a 33-ms delay bias to guarantee that no artifacts of these impulses would interfere with how jugglers struck the ball at collisions (Ankarali et al. 2014). No participants indicated that they perceived this delay.

Modeling

Because the points of interest in the juggling task are the ball peaks and the ball-paddle collisions, the kinematics of ball bouncing can be formulated as a discrete sequence of peaks and collisions, which are time indexed to juggling cycle number. Consequently, we state the physics of the task in discrete (as opposed to continuous) time, where the variable n refers to the n th juggling cycle, and we invoke analytical tools suitable for discrete-time analysis.

Figure 2A shows a model of sensory processing under the hypothesis that spatial and timing information are both used to control ball position ($x[n]$), which in turn improves ball accuracy and stability. In the following sections, we describe a perturbation scheme for evaluating our hypotheses and model structure and couch the dynamics of the task in terms of the model.

Time- and frequency-domain modeling. Perturbations to spatial and timing feedback (Fig. 2B) were applied to the restricted-vision paddle juggling task across multiple experiments to address two questions: 1) whether timing feedback serves to update ball state estimation in sequence with spatial feedback and 2) how spatial and timing feedback influences task control on a cycle-to-cycle basis. These perturbations assumed the form of artificial displacements to the rendered ball position at apex events and artificial delays of varying size to the timing of auditory and haptic feedback at collisions. The sizes and directions of these perturbations varied cycle to cycle in overall sinusoidal or step patterns.

Sinusoidal and step perturbations allow complementary assessments of human behavior in the frequency domain and the time domain, respectively. Sinusoidal perturbations (Fig. 2C, detailed in Eq. 10 below) are an effective way to estimate frequency responses because they

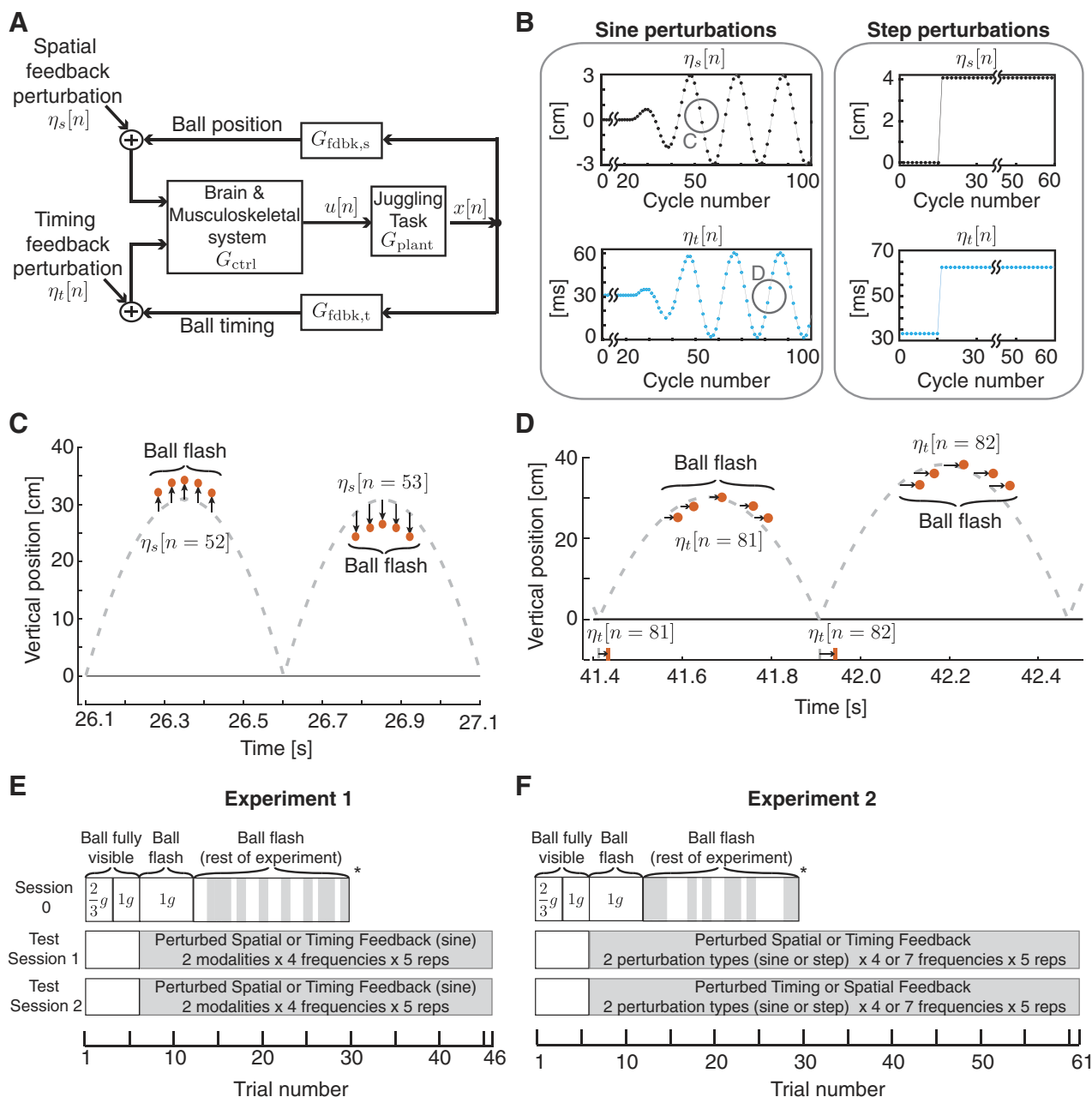


Fig. 2. Task model and perturbation experiments. **A**: block diagram model of information flow between human (G_{ctrl}) and juggling task (G_{plant}). The model assumes that ball spatial information at peaks ($x[n]$) gives rise to spatial ("ball position") and timing cues and predicts that spatial or timing perturbations ($\eta_s[n]$, $\eta_t[n]$) directly cause increases or decreases in paddle velocity at collisions ($u[n]$). G_{fdbk} is a putative gain that the juggler's nervous system applies to spatial or event-timing-related sensory feedback from the task ($G_{fdbk,s}$ and $G_{fdbk,t}$, respectively), based on whether the nervous system compensates out or follows this feedback (see Eq. 9). **B**: perturbation classes. Spatial perturbations (top) were offsets in displayed ball trajectory relative to actual ball position; timing perturbations (bottom) were variable delays in the timing of event cues (audio-haptic and ball flash onsets). Perturbations were applied cycle by cycle (dots) and varied sinusoidally ("sine perturbations") or stepwise ("step perturbations") over cycle number. Gray circles marked C and D cross-reference specific perturbation values illustrated in those respective panels. **C**: example of perturbed spatial feedback over consecutive cycles (here, cycles 52 and 53 in B). **D**: example of perturbed timing feedback (cycles 81 and 82 in B). **E** and **F**: schedules for experiments 1 and 2. Session 0 was a training session. Duration was the same for all participants, but because of individual differences in achieving skilled juggling, the exact number of trials varied (*). Test sessions 1 and 2 began with unperturbed (baseline) trials followed by random sequences of perturbed trials. Test sessions lasted 46 trials (6 baseline + 40 perturbation) in experiment 1 and 61 trials (6 baseline + 55 perturbation) in experiment 2. Shaded areas indicate actual (test sessions 1 and 2) or potential (session 0) time periods when perturbations were applied.

concentrate the energy of sensory inputs at selected frequencies across the sensorimotor bandwidth (Pintelon and Schoukens 2012). Such frequency spectra enable us to use spectral coherence methods to parse out how specific feedback (spatial and timing) influences participants' ball bouncing behavior (Bendat and Piersol 1980). This approach has proved useful and robust for inferring sensory input-motor output relationships in numerous biological systems (Cowan and Fortune 2007; Roth et al. 2011,

2012; Sponberg et al. 2015; Sutton et al. 2016). Step responses (Fig. 2D, detailed in Eq. 11 below), by contrast, provide an efficient, direct mechanism to interrogate system dynamics in the time domain (Pintelon and Schoukens 2012). Provided that humans juggle close enough to a target behavior on average, their control dynamics can be approximated with linear systems theory, such that frequency-domain responses predict time-domain responses, and vice versa.

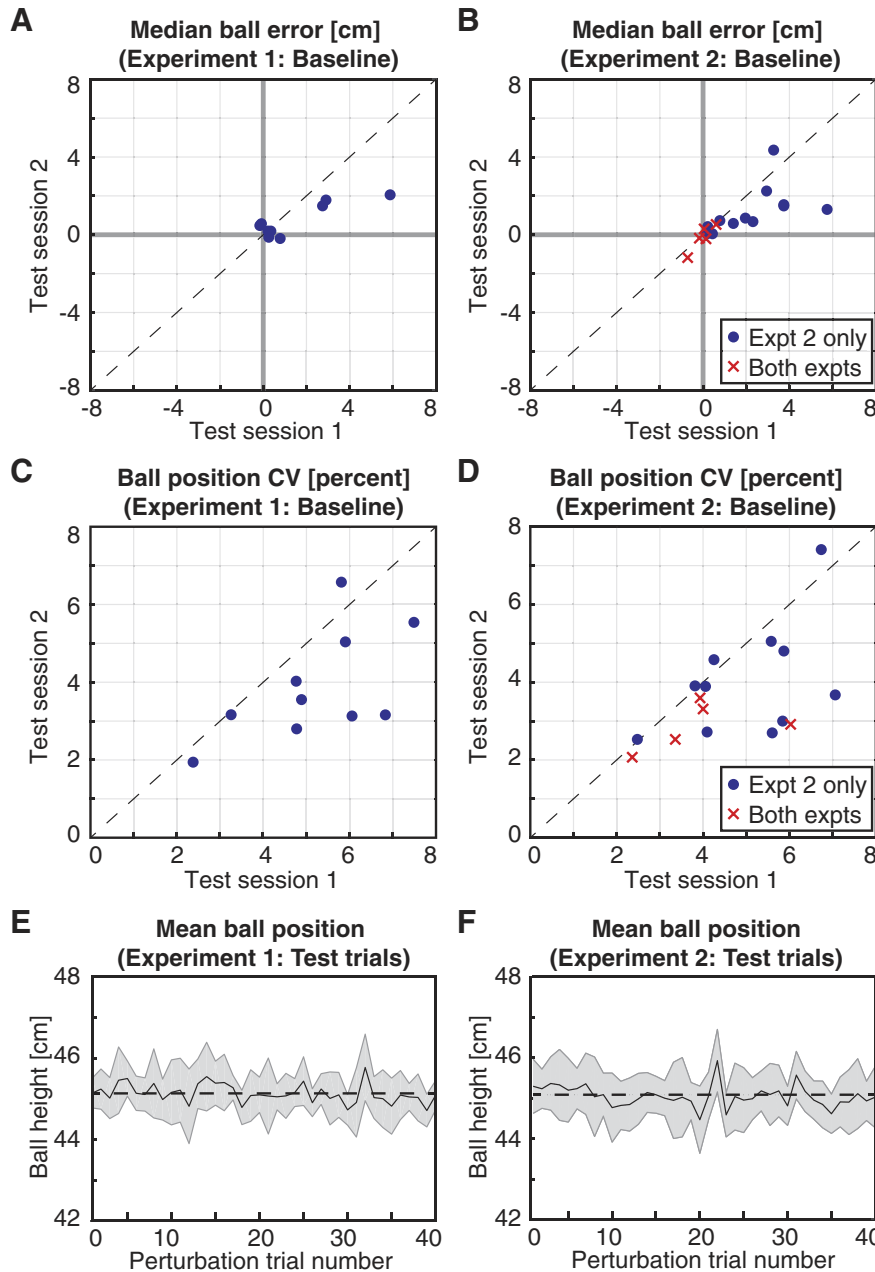


Fig. 3. Raw juggling performance during *test sessions 1* and *2*. *A*: baseline accuracy during *experiment 1* ($n = 10$ participants, 3 women, 7 men) calculated as the median ball target error over *trials 1–6* (see *Statistical analyses*). Participants (shown as dots) slightly reduced their target error between *test sessions 1* and *2* (median change of -3.4 mm; Wilcoxon signed-rank test, $P = 0.0926$). *B*: baseline accuracies for *experiment 2* ($n = 16$ participants, 8 women, 8 men). Participants reduced their target error between *test sessions 1* and *2* (median change of -4.2 mm; Wilcoxon signed-rank test, $P = 0.0072$). The accuracy of jugglers who did both experiments ($n = 5$) was only slightly different from the top 5 performers of *experiment 2* only (difference between median of repeat performers and top 5 *experiment 2* only performers was -3.8 mm; Mann-Whitney test, $P = 0.0556$), suggesting that the inclusion of jugglers with various experience did not cause undue bias. *C*: baseline coefficients of variation (CVs) of ball position for *experiment 1* computed for *trials 1–6* of *test sessions 1* and *2* (see *Statistical analyses*). Markers represent individual participants ($n = 10$, 3 women, 7 men). CV decreased slightly between test sessions, indicating improved precision (median CV change was -1.29% ; Wilcoxon signed-rank test, $P = 0.014$). *D*: baseline standard deviations of ball positions for *experiment 2* ($n = 16$, 8 women, 8 men). CV decreased between test sessions (median CV change was -0.61% ; Wilcoxon signed-rank test, $P = 0.0072$). No significant difference in precision was observed between repeat performers and those who did *experiment 2* only (Mann-Whitney test, $P = 0.691$). *E* and *F*: ball height distribution during perturbed cycles across trials for *experiment 1* (*E*) and for *experiment 2* (*F*). Each panel shows 1 representative juggler's median ball height for the session (dashed line) and 95% confidence interval for each trial. Participants successfully maintained ball position near the nominal despite feedback perturbations (maximum CV observed across perturbation trial over all experiments was 10.6%).

The analytical approach of MATERIALS AND METHODS and RESULTS is as follows. First, we present our task model in terms of (standard) time-domain dynamics. We then transform this model to the frequency domain and embed this model in the frequency-domain representation of a closed-loop system that includes the human controller (G_{Ctrl}). From there, we estimate the structure of G_{Ctrl} in the frequency domain, using a model selection and fitting methodology, and then finally transform this model to the time domain to make the cycle-by-cycle roles of feedback more transparent. We next address the components of the block diagram model in Fig. 2A separately, beginning with the task dynamics (G_{plant}).

Paddle juggling task. For the n th cycle of a rhythmic juggling pattern, let $\dot{b}^+[n]$ denote the vertical velocity of the ball immediately after collision with the paddle, $t_{\text{asc}}[n]$ and $t_{\text{desc}}[n]$ the duration of ball ascent and descent, and $b[n]$ the height of the ball at apex. By construction, the virtual paddle is clamped at a constant height p^* , and the participant's hand (paddle) velocity is $\dot{p}[n]$. The flight dynamics of the ball (ascent and descent) are

$$b[n] = p^* + \dot{b}^+[n]t_{\text{asc}}[n] + \frac{1}{2}gt_{\text{asc}}^2[n] \quad (1)$$

$$b[n] = -p^* - \frac{1}{2}gt_{\text{desc}}^2[n]$$

Gravitational acceleration is $g = -9.81$ m/s². Centering the coordinates about the constant paddle position p^* and simplifying Eq. 1 yields

$$b[n] = \frac{(\dot{b}^+[n])^2}{2g} \quad (2)$$

To compute the vertical velocity of the ball immediately after impact, we use a coefficient-of-restitution law, with $\alpha = 0.8$:

$$\dot{b}^+[n+1] = -\alpha\dot{b}^-[n] + (1+\alpha)\dot{p}[n+1] \quad (3)$$

Here $\dot{p}[n+1]$ is the hand velocity at the instant the ball reaches p^* . As a consequence of locking the paddle, ball ascent and descent times for a given cycle are symmetric and map one-to-one to ball launch velocity:

$$t_{\text{asc}}[n] = t_{\text{desc}}[n] = \frac{\dot{b}^+[n]}{g}$$

When presented with a target, jugglers tend to adopt rhythmic behaviors that stabilize ball peaks about a given height over time. We further assume for a given experiment that juggling behavior can be described by a unique set of (nominal) states, namely, ball position and velocity (b^* , $\dot{b}^*$), paddle velocity ($\dot{p}^*$), and cycle period (t_{flight}^*) (Ankarali et al. 2014). This is supported by previous studies that suggest that perturbations do not alter the preferred juggling height of subjects (Sternad et al. 2001; Wei et al. 2007):

$$\begin{aligned} \dot{p}^* &= (\dot{p}^-)^* = (\dot{p}^+)^* \\ \dot{b}^* &= \frac{(1+\alpha)}{(1-\alpha)} \dot{p}^* \\ \frac{1}{2} t_{\text{flight}}^* &= t_{\text{asc}}^* = t_{\text{desc}}^* = \sqrt{\frac{2}{g}(b^* - p^*)} = \sqrt{\frac{2}{g}(b^*)} \end{aligned} \quad (4)$$

Because our interest is in ball regulation, we focus on human and task behavior in the vicinity of the target $b^* = 0.35$ m, the associated nominal velocities of the ball and hand at collisions, namely, $\dot{b}^* = 2.62$ m/s and $\dot{p}^* = 0.29$ m/s, and the nominal ball cycle period, $t_{\text{flight}}^* = 0.53$ s. Ball-paddle dynamics in this neighborhood can be defined by the following linearization, where $x[n] = b[n] - b^*$ is target error and $u[n] = \dot{p}[n] - \dot{p}^*$ are excursions from the nominal behavioral states:

$$x[n+1] = \alpha x[n] + (1+\alpha) t_{\text{flight}}^* u[n+1] \quad (5)$$

This can be expressed in the frequency domain with the following equation, where $G_{\text{plant}}[z]$ is the frequency-domain transfer function (z transform) relating sensory feedback (in this case, spatial) to task output (relative changes in ball position):

$$G_{\text{plant}}[z] = \frac{b^*(1+\alpha)z}{g(z-\alpha)} \quad (6)$$

Linearizing Eq. 4 near nominal position shows how incremental changes in ball position map to proportional changes to ball descent or ascent times ($\Delta t[n]$):

$$\Delta t[n] = \sqrt{\frac{1}{2gb^*}} x[n] = C_s^t x[n] \quad (7)$$

where $C_s^t = \sqrt{1/(2gb^*)}$ s/m represents the approximate physical mapping from spatial information to timing information. Because this mapping is approximately constant, the relationship between timing feedback and ball position in the frequency domain is $C_s^t G_{\text{plant}}[z]$.

Sensory estimation and control. During stable ball juggling, if the human brain and musculoskeletal network behaved (approximately) as a linear system around the nominal ball height, there would be a direct relationship between frequency content of a given sensory input and of motor output via scaling factors encapsulated in the transfer function $H[z]$. In the context of ball juggling, this relationship can be expressed in the following frequency-domain equation (Nickl 2018):

$$X[z] = H_{\text{CL}}^s[z] N_s[z] + H_{\text{CL}}^t[z] N_t[z] \quad (8)$$

where $N_s[z]$ and $N_t[z]$ are the frequency spectra of the spatial and timing perturbations $\eta_s[z]$ and $\eta_t[z]$, respectively. If, consistent with our hypothesis, both spatial and timing cues directly inform the brain about ball positional state, perturbations to either spatial or timing cues would influence closed-loop control of ball position ($X[z]$) statistically equivalently through their respective transfer functions

$H_{\text{CL}}^s[z]$ and $H_{\text{CL}}^t[z]$. This hypothesis can be tested by sinusoidally perturbing spatial or timing feedback separately and comparing the strength of their coherences with ball position spectra ($X[z]$).

Within the transfer functions $H^s[z]$ and $H^t[z]$, the task dynamics and the dynamics of the human's control policy are lumped together (Nickl 2018). To separate out the dynamics of the human controller, and thereby distill out how either spatial or timing feedback influences movement, the block diagram (Fig. 2A) can be written as the following alternate form:

$$G_{\text{CL}} = \frac{G_{\text{plant}} G_{\text{ctrl}}}{1 + G_{\text{fdbk}} G_{\text{plant}} G_{\text{ctrl}}} \quad (9)$$

Here, $G_{\text{plant}}[z]$ is defined by the task physics, G_{fdbk} assumes the value of $[-1, +1]$ depending on whether the feedback is canceled or followed, and $G_{\text{ctrl}}[z]$ can be fit with model selection and fitting techniques (see *Data Analysis*). Behavior of this controller can be translated to the time domain via the inverse Fourier transform.

Experiments

To assess how jugglers processed spatial and timing feedback, we first trained them to perform the ball bouncing task under veridical feedback (congruent with the ball-paddle physics). After this baseline period, we specifically perturbed spatial (displayed ball height) and event-timing (collision and ball flash) feedback to assess their effects on task control. Perturbations varied in magnitude on each cycle. Over the course of a given perturbation trial, the overall sequence of perturbation magnitudes that were applied on each cycle described a sinusoid or step perturbation function. Thus the size and direction of a perturbation applied to a given feedback modality were equal to the perturbation function evaluated at that cycle number. Spatial feedback perturbations were implemented by adding a positive or negative height offset to the ball as it appeared onscreen near the apex ($\eta_s[n]$ in Fig. 2, B and C), so that it was rendered artificially higher or lower than the actual position. We perturbed timing feedback by adding a delay or advance to the collision timing on top of the 33-ms delay bias mentioned above ($\eta_t[n]$ in Fig. 2, B and D). The time that the ball was flashed onscreen for the subsequent apex was likewise perturbed for consistency.

A total of 23 unique participants completed one or both of two experiments, lasting three sessions each. For *experiment 1*, $n = 10$ naive participants were recruited (ages 18–27 yr, mean = 22.7 yr; 3 women and 7 men); for *experiment 2*, $n = 16$ individuals were recruited (ages 18–33 yr, mean = 24.4 yr; 8 women and 8 men, of whom 11 were naive and 5 had previously completed *experiment 1*). Before all experiment sessions, participants provided written informed consent per Institutional Review Board guidelines.

In both experiments, the purpose of *session 0* was to acclimate participants to the juggling apparatus and train them, through practice, to juggle continuously so that they could maintain ball accuracy and precision about the target for periods of up to 80–100 juggling cycles (Fig. 2, E and F). After an initial demonstration, participants practiced paddle juggling under increasingly difficult conditions for 12 trials: reduced gravity and full ball vision ($g = 6.54$ m/s², $\alpha = 0.8$) for *trials 1–3*; full gravity and full ball vision for *trials 4–6* ($g = 9.81$ m/s²); and full gravity and ball flash for *trials 7–12*. For the remainder of the session, they continued to juggle under full gravity and ball flash. On occasional trials, random perturbations to spatial or timing feedback were introduced, to give participants early exposure to these conditions. Crucially, the experimenter did not mention the existence of perturbations at any point of the study; however, participants were informed if gravity or the quality of visual feedback of the ball were changed (from full ball vision to 221-ms flash at apex). Beginning with *test session 1*, the displayed ball height and the timing of event cues were perturbed for the majority of trials (Fig. 2, E and F), as described below.

Experiment 1. Perturbations varied sinusoidally over juggling cycle number (Fig. 2B, left) after an initial epoch of 25 juggling cycles without perturbation and 25 juggling cycles of ramping to full amplitude. Full perturbation strength was sustained for >40 cycles. Perturbations varied by cycle number n and were applied to spatial ($\eta_s[n]$) or event-timing ($\eta_t[n]$) feedback as follows:

$$\begin{aligned}\eta_s^{\text{step}}[n] &= 0.03\sin(2\pi f_p n + \phi_p)[m] \\ \eta_t^{\text{step}}[n] &= 0.03\sin(2\pi f_p n + \phi_p) + 0.033[s]\end{aligned}\quad (10)$$

Each sinusoidal perturbation is defined by a characteristic frequency f_p and phase shift ϕ_p (the subscript “p” simply denoting that the signal is a perturbation). In *experiment 1*, perturbations of four different frequencies were applied: $f_p = [2/40, 7/40, 13/40, 17/40]$, in units of perturbation cycle per juggling cycle.² For example, the sinusoidal perturbation of frequency $f_p = 2/40$ repeats twice for each sequence of 40 ball bouncing cycles. Perturbations of each frequency were assigned one pseudorandom phase shift (ϕ_p) that was a multiple of $2\pi/40$, i.e., from the set $[0, 2\pi/40, 4\pi/40, \dots, 2\pi]$.

Experiment 2. In *test sessions 1* and *2*, perturbations were restricted to either spatial or timing feedback (with order counterbalanced across sessions). However, two types of perturbations were applied: sinusoidal, as defined in Eq. 10; and step, defined as follows in Eq. 11:

$$\begin{aligned}\eta_s^{\text{step}}[n] &= \begin{cases} 0 & n \leq N_d \\ \pm 0.04 & n > N_d \end{cases} [m] \\ \eta_t^{\text{step}}[n] &= \begin{cases} 0.033 & n \leq N_d \\ 0.033 \pm 0.03 & n > N_d \end{cases} [s]\end{aligned}\quad (11)$$

Here N_d is a delay that was uniformly distributed between 15 and 20 juggling cycles relative to the beginning of the trial.

The first 6 baseline trials in *test sessions 1* and *2* were followed by up to 55 perturbation trials, consisting of a randomized sequence of step and sinusoidal perturbations. Step perturbations were applied in 20 of these trials. The remaining trials consisted of sinusoidal perturbations, which assumed the four frequencies tested in *experiment 1* and, as time permitted, included the additional frequencies $f_p = [3/40, 7/40, 11/40]$ (perturbation cycles/juggling cycle) to estimate the frequency response in finer detail.

Data Analysis

Time-domain data extraction. For each participant, we analyzed the veridical ball position (displayed minus perturbation) and the trajectory of the hand, which was not displayed with the task. Hand kinematics were analyzed cycle to cycle by sectioning them into intervals based on the occurrence of events (collision or apex). Hand velocity was recorded by an encoder and filtered online during experiments, as it was used to compute launch velocity of the ball at collisions. Hand positions were computed off-line by integrating these velocity measurements. Additionally, we assessed the relative time shifting of the hand trajectory on each cycle by identifying the timing of the first crossing of the 95% maximum hand velocity point within a given cycle, coinciding approximately with the time of collisions (as illustrated in Fig. 4, C and D).

Because our focus is regulative behavior about a rhythmic average (defined by nominal states), all behavioral variables were analyzed with respect to their mean values. For sinusoidally perturbed trials this mean was computed within the 40-cycle window between *cycles 51* and *90*, when full perturbation strength was applied, and for step perturbed trials this mean was calculated within a 7-cycle window before a behavioral response to the perturbation was observed.

² For intuition on the timescale of the corresponding perturbation periods, assume that the juggling period is ~0.5 s, in which case the perturbations repeat every 10 s, 2.86 s, 1.54 s, and 1.18 s, respectively.

Estimating transfer (frequency-response) functions. For each sinusoidally perturbed trial, we first preprocessed the perturbation and behavioral signals (ball and hand kinematics) by rectangularly windowing off *cycles 51* and *90* to avoid spectral leakage (Pintelon and Schoukens 2012) and subtracting the mean over this interval. Thus all perturbations and motor responses were analyzed as deviations about the nominal behavior of the juggler for that trial.

We then calculated discrete Fourier transforms (DFTs) of these windowed signals in MATLAB (The MathWorks, Natick, MA). Transfer functions were estimated by standard methods: for each stimulus frequency, the DFT of the output behavior was divided by the DFT of the perturbation at that frequency, resulting in a N_p -point estimate of the transfer function corresponding to the number of unique stimuli. Mean transfer function values were computed by averaging raw (complex valued) DFT values and then computing magnitude and phase [translated to a $(-300, 60)^\circ$ domain]. Dispersions of magnitude and phase responses were determined by computing DFTs of individual measurements at each stimulus frequency and performing one of two operations: 1) computing a range from the minima and maxima of the magnitude and phase responses or 2) calculating standard error, based on bootstrap resampling among individual magnitude and phase responses. The type of dispersion measurement used is identified case by case in each figure.

Estimating spectral coherence. Defining $N[z]$ to be the DFTs of a perturbation (spatial or timing) and $X[z]$ to be the DFT of an output behavioral signal (ball or hand position or timing), coherence for a particular frequency of sensory perturbation (ω , in rad/s) is calculated as follows (Bendat and Piersol 1980):

$$C_{\eta,x}[\omega] = \frac{|R_{\eta,x}[\omega]|^2}{R_{\eta,\eta}[\omega]R_{x,x}[\omega]}\quad (12)$$

$|R_{\eta,x}|$ is magnitude of the cross-spectral density between the perturbation $\eta[n]$ and motor output $x[n]$, and $R_{\eta,\eta}$ and $R_{x,x}$ are, respectively, the power spectral densities of the perturbation and output. In the absence of noise, variables that are related by a (linear) transfer function have a coherence of 1. However, because of noise inherent in biological systems, it is common for input-output relationships to have coherences under 1 (sometimes substantially) and yet be well approximated by linear models (Kiemel et al. 2008; Roth et al. 2011; Sponberg et al. 2015).

Under the model in Eq. 8 we hypothesize that separately perturbing spatial ($N^s[z]$) or timing ($N^t[z]$) feedback will result in coherences with ball position $X[z]$ that are statistically equivalent. A systematic and significant differential effect on coherence based on input modality would evidence a different control structure where either spatial or timing feedback selectively affects ball spatial control, while the other influences some other aspect of movement.

Model fitting. To better understand the use of spatial and timing feedback on a cycle-by-cycle basis, we used step response data gathered from *experiment 2* to simulate step responses to the closed-loop system in Eq. 9. Candidate controller models were chosen from frequency-response functions of rational polynomial form (Oppenheim et al. 1999):

$$G_{\text{Ctrl}}^{M,N}[z] = \frac{U[z]}{Y[z]} = K \frac{\prod_{m=1}^M (z - a_m)}{\prod_{n=1}^N (z - b_n)}, \quad N \geq M \quad (13)$$

Here $z = \exp\{-j\omega\}$ is a complex-valued function of the stimulus frequency ω , and there are $N + M + 1$ real-valued scalar parameters, K , a_m , and b_n .

Terms M and N specify the algebraic “order” of the model. The variable M refers to the number of numerator terms (i.e., the number of “zeros”). The variable N refers to the number of denominator terms (“poles”). The causality constraint $N \geq M$ guarantees that outputs are never dependent on future inputs.

Model selection was based on a method (Madhav et al. 2013) that balances model accuracy and interperson reliability (“consistency” in

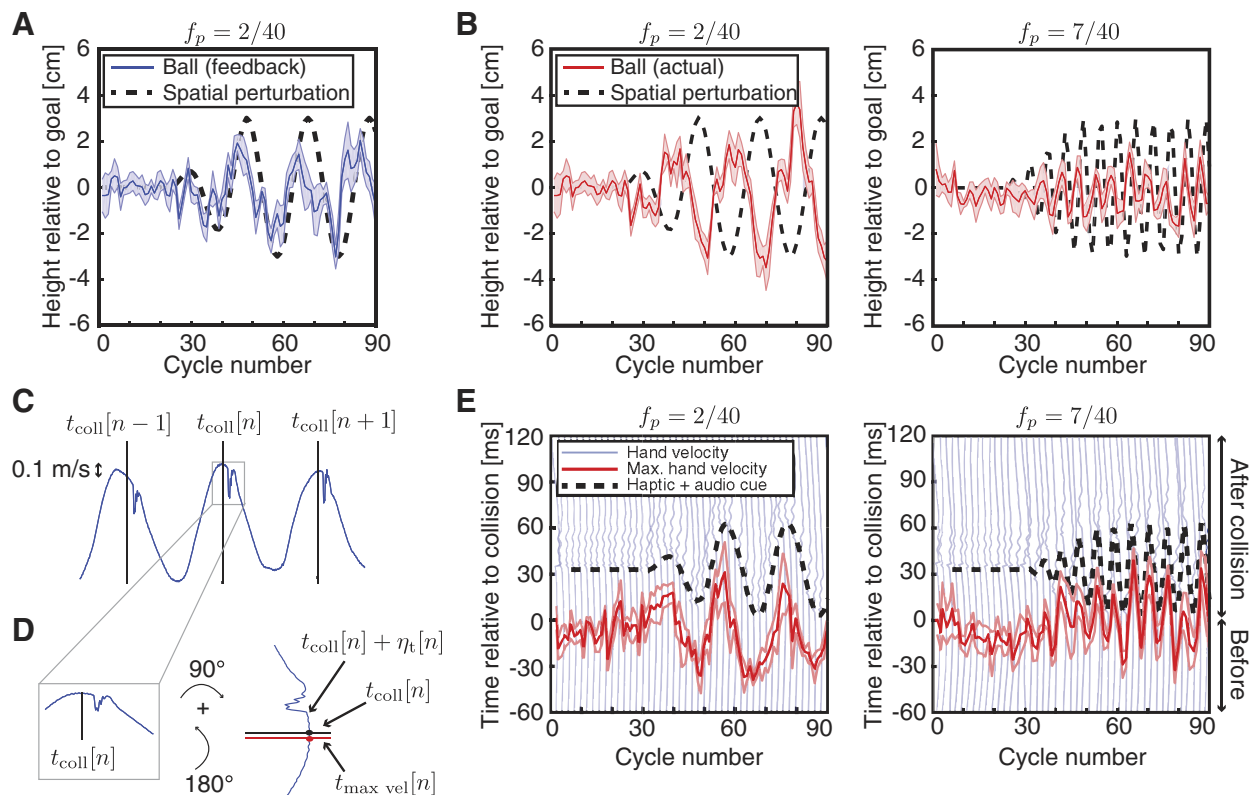


Fig. 4. Juggling behavior in time domain from a representative juggler in *experiment 1*. Perturbations (black dashed lines) are sinusoidal. Ball positions are plotted as the mean ± 1 SD over trials for given perturbations (5 trials). **A**: spatial perturbation at frequency $f_p = 2/40$ (2 stimulus cycles per 40 juggling cycles), and (perturbed) ball position feedback at apex as it appears onscreen. **B**: spatial perturbation and actual ball position (feedback minus perturbation). Responses to spatial perturbations of frequencies $f_p = 2/40$ (left) and $f_p = 7/40$ (right) are shown (mean ± 1 SD over 5 trials each). **C**: method of calculating hand timing. Hand velocity was partitioned into cycles. Haptic feedback, when delivered, pushes downward on the hand, leaving a divot in the hand velocity that can be used to verify when nonvisual feedback actually occurred. **D**: for visualization purposes in the behavioral plot of **E**, we rotate within-cycle hand velocity trajectories 90° clockwise and reflect them about the x -axis (equivalent to a 180° rotation), such that time increases toward the top of the plot. Time points of interest for hand timing analysis are marked: actual collision t_{coll} , time of audio + haptic feedback $t_{\text{coll}} + \eta_t$, and time that hand velocity crossed 95% of the maximum for the cycle ($t_{\text{max velocity}}$). **E**: timing (audio-haptic) perturbations and changes in timing of maximum hand velocity for a representative juggler under perturbations of frequencies $f_p = 2/40$ (left) and $f_p = 7/40$ (right). Maximum hand velocity at each cycle is shown as the mean ± 1 SD over 5 trials for each frequency. Continuous-time hand velocities between collisions (blue lines) are rotated (as in **D**) to give references for where maximum hand velocity and nonvisual cues occur. Note that the time of perturbed nonvisual feedback aligns with divots in the continuous-time hand velocities.

the colloquial sense). For each model (M, N) defined in Eq. 13 and each applied step perturbation (Eq. 11), a training data set was generated by averaging the step responses across all data, minus one participant (set aside as a test data point). Best-fit parameters of the model were determined by placing the particular form of G_{ctrl} in the closed-loop transfer function (Eq. 9); simulating the step response of this model; and iteratively fitting parameters (using `fmincon` in MATLAB) to minimize the squared error between the simulated and average participant data. With the resulting optimal (M, N) model, a leave-one-out cross-validation error was computed with the average of the excluded participant's data (test set). This process was repeated n times (once for each possible training set of $n - 1$ participants) to generate distributions of cross-validation errors and optimal parameter fits. For each candidate model, accuracy was determined as the average cross-validation error across participants, and reliability was determined as the maximum singular value of the residuals across the $n - 1$ best-fit parameter sets. The optimal (M, N) model was determined to be the one that maximized accuracy and reliability (or, equivalently, minimized both the cross-validation error and the singular value).

Statistical analyses. All statistical tests were performed in MATLAB and are indicated in figures and legends. Statistical tests are reported in text along with P values, test statistics, and degrees of freedom where appropriate. P values are reported to three decimal places and as $P < 0.001$ when they are minute.

Raw juggling performance was quantified in terms of accuracy and precision. Accuracy was measured in terms of the error between peak ball position and target height, and precision was measured by the coefficient of variation (CV) of ball height. Accuracy and precision for a trial are computed with 50-cycle epochs. To describe baseline performance as a measure of juggler skill achieved after familiarization with our task, we report the median accuracy and CV over trials 1–6 of test sessions 1 and 2, before any perturbations were encountered.

Changes in performance of jugglers between test sessions were analyzed with the Wilcoxon signed-rank test for matched samples; conversely, when samples were not matched (as in the case of distinct participants), the Mann-Whitney test was performed. To quantify group-level performance, we report maximum CV across participants for each session of each experiment, excluding outliers. For outliers, we adopted the standard definition of points less than $Q1 - 1.5(IQR)$ and greater than $Q3 + 1.5(IQR)$, where $Q1$ and $Q3$ are the first and third quartiles and interquartile range $IQR = Q3 - Q1$. Time-domain relationships between ball or paddle movements and cycle number are assessed with Spearman's correlation test, with rank-correlation coefficients (ρ) and significance levels included.

In *experiment 1*, the hypothesis that spatial and timing information are used similarly to inform the nervous system's estimates of ball position (i.e., a spatial response, see Eq. 8) was tested with a repeated-measures analysis of variance (ANOVA). In this analysis, indepen-

dent factors were the type of sensory information (spatial $\times$ timing), perturbation frequency (in perturbation cycles per juggling cycle), and task output class (ball position $\times$ paddle kinematics). As the dependent variable, we calculated cross-spectral coherence as a measure of the relative strength of coupling between sensory information and task output type. Post hoc comparisons were performed with Tukey's test of honestly significant difference.

In *experiment 2*, the cycle-by-cycle dynamics of sensory information processing for spatial and timing feedback were quantified with model selection procedures and evaluation metrics discussed in Madhav et al. (2013) as explained under *Model fitting*. Goodness of fit of these models in the time domain was measured with the coefficient of determination (r^2).

RESULTS

Participants Juggled Accurately Despite Intermittency of Visual Feedback

Our behavioral paradigm of providing intermittent visual feedback and locking the position of the paddle was new, to our knowledge. Although some participants commented that the difficulty of hitting the target varied throughout the experiments, none were able to articulate the reason for this difficulty. No volunteers were informed of the existence of perturbations.

The objective of *session 0* was to train participants to bounce the ball to the target with both accuracy and precision during baseline (unperturbed) conditions. In *experiment 1*, 10 participants learned to juggle consistently to the goal line under ball flash conditions by the start of *test session 1*. Three additional volunteers completed the protocol but were unable to juggle consistently to the goal line by the end of the third session and were thus excluded from further analysis. In *experiment 2*, all 16 participants (5 repeated from *experiment 1*) learned the same task within one session and were included in analyses.

We assessed baseline skill level of the successfully trained participants at the beginnings of *test sessions 1* and *2*, before introducing perturbations (Fig. 3). With continued exposure to the task, participants slightly improved in baseline accuracy (Fig. 3, *A* and *B*): across individuals, the baseline ball accuracy improved between test sessions for *experiment 1* (median change in error across subjects of -3.4 mm; Wilcoxon signed-rank test significance of $P = 0.0926$) and for *experiment 2* (median change in error across subjects of -4.2 mm; Wilcoxon signed-rank test significance of $P = 0.0072$). Likewise, baseline juggling precision improved (Fig. 3, *C* and *D*), as measured by the change in CV of ball peak position between test sessions of *experiment 1* (median CV change across participants of -1.29% , Wilcoxon signed-rank test significance of $P = 0.0137$) and *experiment 2* (median CV change across participants of -0.61% , Wilcoxon signed-rank test significance of $P = 0.0072$). In both experiments, jugglers tended to hit slightly above the displayed target, potentially as a strategy to avoid the redrop criterion, which was described to them only in general terms (see MATERIALS AND METHODS). Overall, restricting optical information to the apex did not seem to impede jugglers' ability to reach the target. By the beginning of *test session 1*, participants were able to hit the ball accurately (with median ball error <3 cm in 22 of 26 total experiments; median ball error <6 cm for all) and precisely (CV $<8\%$ for all experiments).

As noted in MATERIALS AND METHODS, $n = 5$ participants completed both *experiments 1* and *2* (Fig. 3, *B* and *D*).

However, their performance did not significantly differ from the top five performers of the naive subset of *experiment 2* participants in either accuracy (difference between median ball height error of repeat participants and that of *experiment 2*-only participants was -3.8 mm at the beginning of *test session 1*; Mann-Whitney test significance of $P = 0.0556$) or precision (difference in CV of ball position between repeat participants and *experiment 2*-only participants was -0.13% at the beginning of *test session 1*; Mann-Whitney test significance of $P = 0.691$), suggesting that prior task exposure did not unduly bias their raw performance.

Stability, in the context of paddle juggling, is characterized by a tendency of ball peak position to remain close to a participant's nominal, or average (which is ideally equal to the target position but, as we have shown, is slightly higher for our experiment). Our use of time- and frequency-domain modeling as complementary tools to understand cycle-by-cycle control of juggling is valid when ball errors over the course of the experiment stay within a relatively small error region about this average (see *Time- and frequency-domain modeling*). Juggling precision was maintained during perturbation trials, with a maximum CV over trials for each juggler not exceeding 11% (after correcting for outliers, as discussed in *Statistical analyses*). To give a sense of the centrality and spread of ball positions across trials, we show mean and 95% confidence intervals for two representative jugglers in Fig. 3, *E* and *F*.

Jugglers Corrected for Subliminal Perturbations, but Not as Expected

Under slow spatial perturbations (2 perturbation cycles per 40 juggling cycles; Fig. 4*A*), participants hit the displayed ball to the goal line on average. As expected, jugglers hit the ball higher or lower in an oscillating pattern at the frequency of, and approximately antiphase to, the perturbation (Fig. 4*B*, *left*). This perturbation cancellation reflects visual error correction. The magnitude of error correction decreases progressively with increasing perturbation frequencies (as can be seen by comparing Fig. 4*B*, *left* and *right*).

Unexpectedly, perturbations to timing of event feedback did not elicit strong or consistent responses in ball position. However, jugglers tended to shift the timing of their hand movements to track these timing perturbations (Fig. 4, *C–E*). Specifically, these time shifts appeared to be at the same frequency as perturbations but in phase with them. Similar but weaker magnitudes of timing behavior were observed as perturbation frequencies were increased (as can be seen by comparing Fig. 4*E*, *left* and *right*).

Broadly, this duality of behaviors suggests two distinct motor control responses that are based on feedback modality: 1) out-of-phase corrections to spatial perturbations, which may signify a compensatory behavior, and 2) in-phase following of timing perturbations, which may signify entrainment. Although Fig. 4 highlights data from one juggler, these patterns generalized across individuals.

Spatial and Timing Perturbations Reveal Dissociable Control Processes

Across all perturbation frequencies, the spectral power of ball position across subjects was almost exclusively concentrated at the same frequencies as spatial perturbations (Fig. 5*A*).

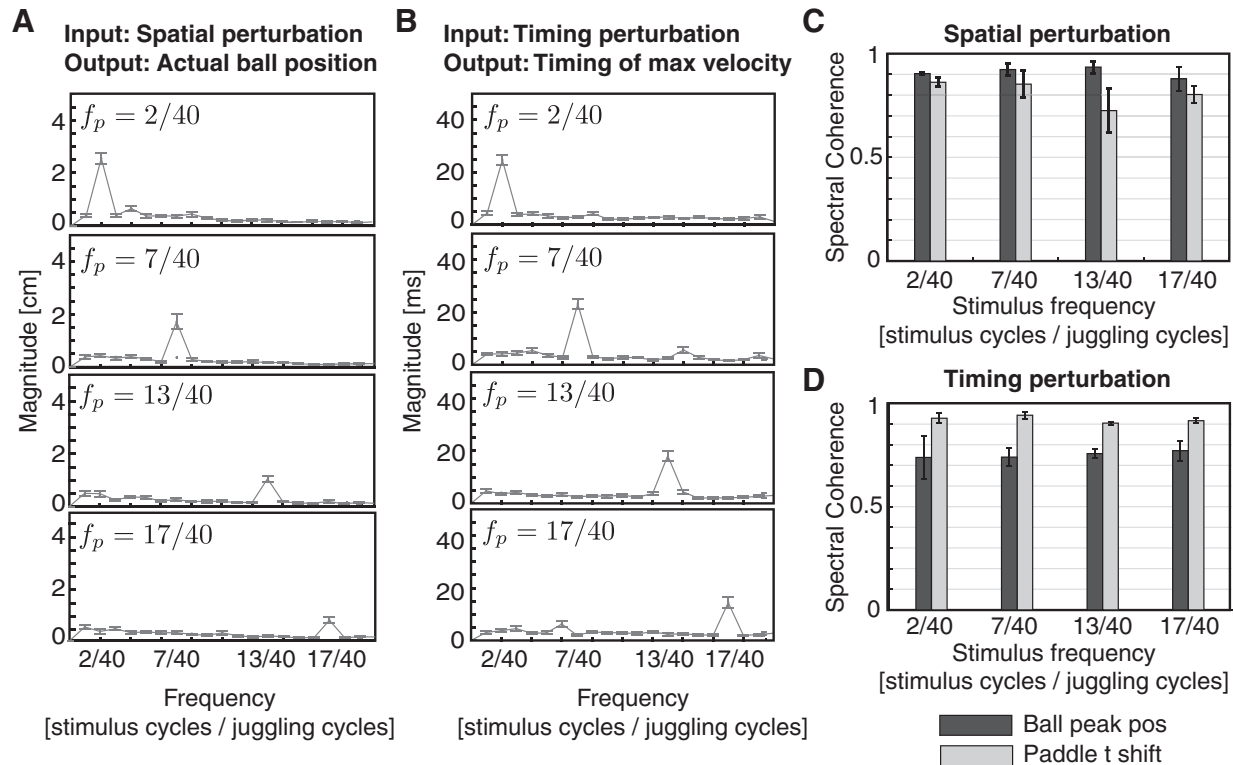


Fig. 5. Juggling behavior in the frequency domain across *experiment 1* participants ($n = 10$, 3 women, 7 men). *A*: frequency spectra of spatial perturbations (black stems) and ball height responses (mean ± 1 SE over participants). *B*: frequency spectra of timing perturbations and changes in 95% maximum velocity time point (mean ± 1 SE over participants). *C*: spectral coherence between spatial perturbations and the task outputs ball position (dark gray) and 95% maximum velocity time point (light gray). *D*: spectral coherence between event-timing perturbations and task outputs. Spectral coherence (*C* and *D*) is shown as the mean ± 1 SE across participants. A significant interaction between the factors of perturbation type (spatial or temporal) and task output (ball height or paddle timing shift) on spectral coherence was detected [2-way repeated-measures ANOVA, $F(3,159) = 81.0$, $P < 0.001$], suggesting that spatial and timing information have separable influences on ball height and hand timing.

Likewise, the spectral power of hand timing shifts across subjects was focused at timing perturbation frequencies (Fig. 5*B*). These correspondences hint at strong coherences between ball position and spatial feedback and also hand-timing and event-timing feedback.

Figure 5, *C* and *D*, show intersubject spectral coherence averages between each combination of perturbation modality and output behavior. The validity of the cross-modal integration model (Eq. 8) was tested by running a repeated-measures ANOVA on the influence of perturbation type (spatial or timing), perturbation frequency (2/40, 7/40, 13/40, 17/40), or task output class (ball position and timing of first 95%-peak hand velocity point within the given cycle) on the dependent variable of input-output spectral coherence. There is a significant interaction between perturbation type and behavioral response [2-way repeated measures ANOVA, $F(3,159) = 81.0$, $P < 0.001$], suggesting that the influences of spatial and event-timing feedback on control of rhythmic arm movements in paddle juggling are different. Within each perturbation modality, separate (1-way) ANOVAs revealed main effects of behavioral response [$F(1,79) = 25.3$, $P < 0.001$ for spatial perturbations, $F(1,79) = 57.3$, $P < 0.001$ for timing perturbations] but not of perturbation frequencies [$F(3,79) = 2.18$, $P = 0.10$ for spatial perturbations, $F(3,79) = 0.0752$, $P = 0.98$ for event timing perturbations], indicating that differences in correlation were primarily driven by stimulus type. Post hoc comparisons (Tukey's honestly significant difference test) showed that coherence of spatial perturbations was higher with

ball height than with hand timing shift at all frequencies, reaching statistical significance at 13/40 perturbation cycles per juggling cycle ($P < 0.001$). Conversely, the same analysis showed that coherence of event timing perturbations was significantly higher with hand time shift than with ball height for all frequencies: 2/40 ($P = 0.001$), 7/40 ($P < 0.001$), 13/40 ($P = 0.03$), and 17/40 ($P = 0.04$) perturbation cycles per juggling cycle.

Altogether, these analyses shed light on the nature of the differential effect of perturbation type on behavior: spatial perturbations preferentially induce coherent responses in a spatial behavior (namely ball bounce height), and perturbations to event timing preferentially induce coherent responses in a separate timing-related behavior (hand timing shifts).

Spatial Control Is Proportional-Integral and Explicitly Uses Error History

To quantify how the brain uses spatial and event-timing feedback to regulate movement on a cycle-by-cycle basis, we estimated parametric models of the spatial-motor and timing-motor control processes. As discussed in MATERIALS AND METHODS, model selection and fitting procedures were conducted on the step response data gathered in *experiment 2*. The outcome of these procedures for several control models $G_{\text{Ctrl}}^{M,N}$ is shown in Fig. 6. Model error (accuracy) was evaluated as the mean cross-validation error from the leave-one-out model to the remaining subject data, and reliability was measured by the

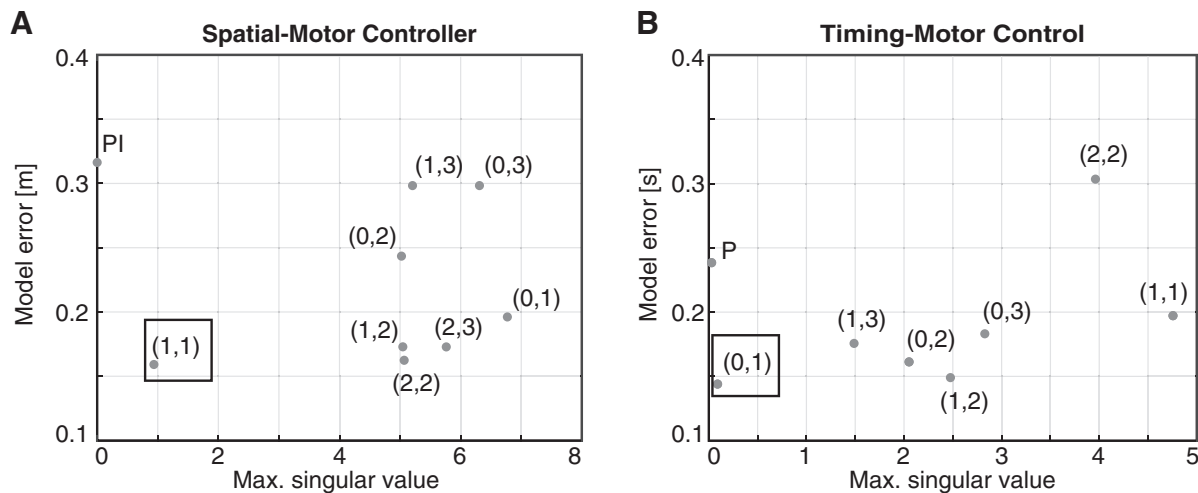


Fig. 6. Model selection plots for spatial-motor and timing-motor controllers from *experiment 2*, using method of Madhav et al. (2013). Models are labeled in terms of (M, N) , where M and N indicate the number of zeros and poles that influence control on the current cycle (see *Model fitting*). y-Axes show model error (average of leave-one-out cross validation error over $n = 16$ participants). x-Axes show model precision, measured by the maximum singular value of the parameter variance across leave-one-out fitting procedures. Best-fit models (minimizing x - and y -coordinates) are boxed. A: model selection plot for spatial-motor controller (input: spatial perturbation; output: ball position). Point marked PI is a pure proportional-integral controller (see *Spatial Control Is Proportional-Integral and Explicitly Uses Error History* for details). B: model selection plot for timing-motor controller (input: timing perturbation; output: timing shift of 95% maximum velocity point of paddle). Point marked P is a pure proportional controller (see *Timing Control Is Proportional and Explicitly Depends on Most Recent Observed Error* for details).

maximum singular value of the optimal parameters across all fits, larger values indicating less robustness of parameter values. Accordingly, the closer a model's average cross-validation error and maximum singular value are to the origin in Fig. 6, the more accurate and robust it is.

Figure 6 reflects the intuition that models with fewer parameters tend to have less accuracy but greater interjuggler reliability, as they tend to capture fewer nuances of data in favor of a parsimonious, yet more broadly valid, model. Nevertheless, both visual and nonvisual control are best fitted by simple models. For spatial control (Fig. 6A), the best model was of form $(M,N) = (1,1)$, which has the following time-domain representation:

$$u[n] = b_s u[n-1] + K(y_s[n] - a_s y_s[n-1]) \quad (14)$$

Here $u[n]$ is hand velocity, $y_s[n]$ is ball feedback error relative to the goal, and (b_s, a_s) are scalar coefficients representing the influence of the previous cycle's hand velocity and error. This corresponds to a proportional-integral (PI) model with a leaky error memory. The specific values estimated for the parameters (K, b_s, a_s) were $(-1.14, 0.92, 0.81)$, corresponding to a control law of $u[n] = 0.92u[n-1] - 1.14y_s[n] - 0.92y_s[n-1]$. We also fitted a pure PI model (Fig. 6A, with a_s clamped at 1) but found that it underfit the data.

Timing Control Is Proportional and Explicitly Depends on Most Recent Observed Error

Likewise, we fitted a parametric model of responses to event timing perturbations (Fig. 6B). The optimal controller was defined by $(M,N) = (0, 1)$, which is of the following time-domain form:

$$t_{\text{shift}}[n] = b_t t_{\text{shift}}[n-1] + K\eta_t[n-1] \quad (15)$$

Here $t_{\text{shift}}[n]$ is the shift in timing of the maximum hand velocity as shown in Fig. 4E. This law suggests that hand timing is chiefly influenced by the previous cycle's hand timing

and the most recently observed timing perturbation value; hence a proportional (P) law. Our estimates for the parameters (K, a_t) were $(0.77, 0.76)$, corresponding to a control law of $t_{\text{shift}}[n] = 0.77t_{\text{shift}}[n-1] + 0.76y_t[n-1]$. As for the spatial controller, we fitted a pure P model—in this case, a proportional, or P controller (Fig. 6B, with b_t clamped at 1)—but found that it similarly underfit the data.

Model Structure Generalizes Across Perturbation Types and Captures Individual Variability

Figure 7, A and B, compare the best-fit models derived from the above selection procedure to the step responses averaged across participants. Spatial perturbations corresponded to abrupt upward or downward jumps in displayed ball peak (Fig. 7A), whereas timing perturbations were abrupt advances or delays in the timing of event feedback (Fig. 7B). Consistent with responses to sinusoidal perturbations (Fig. 4), participants opposed spatial cue perturbations and followed timing cue perturbations.

We compared these model fits, estimated from step perturbations, to frequency-domain behavior measured from sinusoidal perturbations applied in *experiment 2* (Fig. 7, C and D; interjuggler mean and range shown). Under linearity of spatial and temporal control predicted by spectral coherence (Fig. 5), we expected the time-domain models inferred from step perturbations to coincide with the frequency-domain data gathered from sinusoidal perturbations. This is indeed the case, and this cross-validation further supports the validity of our fitted models.

The frequency-domain responses reflect functional differences in spatially and temporally guided control noted earlier. For conceptual clarity, these frequency-domain plots map from the current cycle's perturbation $\eta^{\text{sine}}[n]$ to the subsequent cycle's response $x[n+1]$ or $t_{\text{shift}}[n+1]$. The phase response of the spatial controller shows a 180° phase lag indicative of perturbation rejection (seen also in Fig. 4, A and B). Likewise,

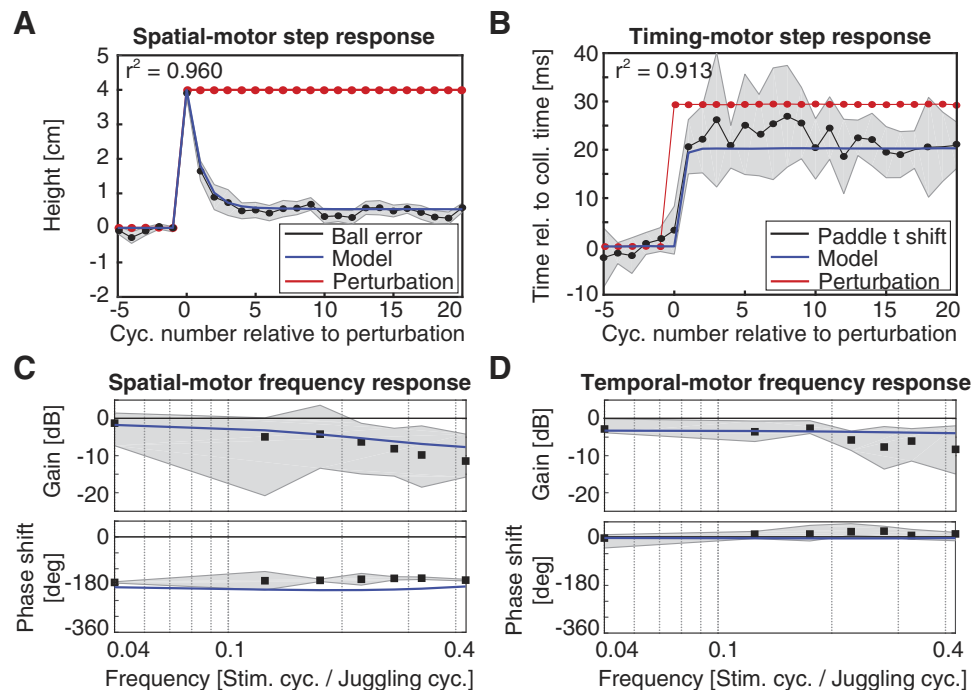


Fig. 7. Cross-validation of controller models using time- and frequency-domain human data in *experiment 2*. **A**: spatial step perturbations (red) and changes in ball position (black). Ball position is plotted as mean $\pm$ 1 SE of ball error over participants ($n = 16$: 8 women, 8 men). Perturbations were applied and ball position measured at the ball peak phase once per cycle (marked with dots). A best-fit model (blue) was fit to this averaged response by simulating the response of the model selected in Fig. 6A and optimizing its parameters to fit the human data in a least-squares sense. Goodness of fit of the model (in blue) to the behavioral data (in black) is assessed by the coefficient of determination r^2 . **B**: step perturbation, human behavioral response, and best-fit model for timing-motor controller. Response data were plotted and model fitting performed as in **A**. **C**: frequency response of spatial-motor controller, shown as Bode plot: magnitude response (top) and phase response (bottom). The best-fit model curve (blue) is the Fourier transform of the best-fit model to the time-domain step response in **A**. Human behavioral data (black squares) were generated from sinusoidal perturbations in separate trials from **A** (7 frequencies; see MATERIALS AND METHODS). Behavioral data shown are the average (black squares) and range of participant responses ($n = 16$: 8 women, 8 men). In calculating the Bode plot, ball position was advanced by 1 cycle to directly show the antiphase (180°) correction behavior of the controller. The best-fit model is consistent with the frequency responses across participants. **D**: frequency response of timing-motor controller. Plots and data are as in **C**. Hand timing shifts were advanced by 1 cycle during plot production, to directly show the in-phase (entrainment) nature of the controller.

hand time shifts are in phase with timing perturbations (0° phase lag), indicating following or entrainment (Fig. 4E).

Magnitude responses, however, show an additional subtlety about the strength of responses to perturbations with specific frequency content. In both cases, this strength (gain) becomes progressively weaker with increasing stimulus frequency, coinciding with a decrease in the amplitude of the response in the time domain as a function of increasing perturbation frequency (compare Fig. 4, *B* and *E*, left and right). In other words, spatial and timing responses are low pass.

Moreover, the rate of decrease (rolloff) of the spatial response is greater than for the timing response, suggesting that the bandwidth of the spatial closed-loop behavior is less than that of the timing closed-loop controller. Such a difference in sensorimotor bandwidth is reflected in the average step response data. The average response to spatial perturbations is in the form of a decreasing exponential (coefficient of determination $r^2 = 0.96$), a signature of a proportional-integral controller with memory of visual error. As expected, at late time steps there is a monotonic decrease in error with cycle number (Spearman's rank correlation test; $\rho = -0.43$; $P = 0.046$, computed in window starting 3 cycles after perturbation), suggesting a gradual continuation of error reduction symptomatic of relatively low-bandwidth correction. The step response to timing perturbations exhibits signatures of a step function ($r^2 = 0.91$) that quickly levels off so that

there is no significant correlation with cycle number (Spearman's rank correlation test: $\rho = -0.27$, $P = 0.22$, computed in window starting 3 cycles after perturbation). This rapid leveling off is consistent with relatively high-bandwidth sensorimotor behavior. The hand timing shift saturates at a value smaller than the perturbation magnitude, suggesting incomplete synchronization.

To examine the extent that these cross-subject trends applied to individual jugglers, we performed two additional lines of analysis. First, given the spatial- and timing-motor models chosen in our model selection procedure (Fig. 6), we plotted the optimal parameter fits for individual participants (Fig. 8) and compared with a bootstrapped sampling distribution of these parameters. Both the individual participants and the sampling distribution are roughly centered about the best-fit parameters determined for Eqs. 14 and 15. Unsurprisingly, individual participants tend to fall within the sampling distribution, with some outliers. Second, we directly compared best-fit models to data for individual subjects; Fig. 9 shows four representative subjects (Fig. 9, *A* and *B*: spatial perturbations; Fig. 9, *C* and *D*: timing perturbations), indicating that spatial-based and timing-based control are accurate models of subject behavior in the time domain at an individual level. As expected (Fig. 9, left), they also align with frequency-domain estimates, suggesting that the linearity of both control processes is not limited to a group effect.

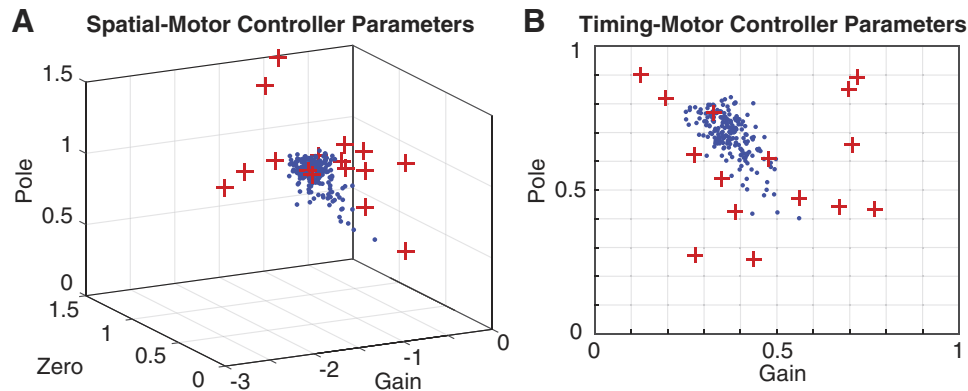


Fig. 8. Distributions of parameter fits for spatial and timing controllers of optimal type chosen in model selection procedure. The number of dimensions of each plot corresponds to the number of free parameters ($M + N + 1$; see MATERIALS AND METHODS). Red crosses correspond to optimal parameters for each individual participant ($n = 16$: 8 women, 8 men). Blue dots show sample distribution of best-fit parameters estimated from bootstrapping (200 points). A: sample distribution of spatial-motor controller parameters and best-fit parameters for individual jugglers. Gain, zero, and pole axes correspond to the parameters K , a_s , and b_s , respectively, in Eq. 14 in RESULTS. B: sample distribution of timing-motor controller parameters and best-fit parameters for individual jugglers. Gain and pole axes correspond to the parameters K and b_t , respectively, in Eq. 15 in RESULTS.

Nonvisual Event Cues Play a Role in Entrainment

Timing feedback appears to serve as a synchronization reference for upper-limb movements in our task. To better understand the implications of this synchronization on local hand kinematics and on ball stabilization, we investigated hand kinematics near the collision phase within ball bounce cycles (Fig. 10). Although visual feedback of the hand was persistently unavailable, this window in particular corresponded to when ball position was also not onscreen. Juggling cycles were first classified into bins defined by the size of nonvisual feedback timing perturbation for that cycle. Hand displacements were computed off-line from recorded hand velocities and then aligned to the timing of the actual collision instants predicted by the previous ball apex positions (not to the nonvisual cues). The small ripple in hand position that overlaps with the bin time (Fig. 10A) is reflective of the onset of haptic feedback, which imparts a brief impulse to the hand (as shown in Fig. 4, C–E). As expected, the hand is rising at the time of actual collisions (Fig. 10A). Between the instants of the actual ball-paddle collision and the perturbed haptic-audio cue, the distance the hand continues to rise before reversing direction is in proportion to magnitude of the timing perturbation (Fig. 10B; Spearman's rank correlation test: $\rho = 0.456$, $P < 0.001$).

Because the initiation of hand downswings occurs in a time window where there is no informative spatial feedback about the ball or paddle motion (i.e., ball flash is off), this hand reversal process may have been triggered by the audio-haptic collision cues themselves. Alternatively, because the timing of the ball flash window is also perturbed in order to avoid conflicting obviously with the nonvisual cue, it is theoretically possible that the hand reversals may be triggered by delayed processing of visual feedback of the ball. This would be the case especially if the timing of events in the current cycle and the previous cycle were both delayed or advanced by similar amounts (i.e., if consecutive perturbations were highly correlated).

To disambiguate between these two possibilities, we reran the above correlation analysis, but on the subset of trials where the timing perturbation of the current cycle was in the opposite direction of the previous cycle (i.e., consecutive perturbations were anticorrelated). When we thus considered only those cycles when the delay of audio-haptic feedback of the current cycle could not have been antici-

pated by the delay of visual feedback in the previous cycle, we found that the correlation between the distance the hand continued to rise before reversing and the amount of perturbation was unchanged (Spearman's rank correlation test: $\rho = 0.429$, $P < 0.001$). This suggests that hand reversals were triggered by nonvisual timing cues, namely, auditory and haptic.

DISCUSSION

Tasks such as walking, running, dancing, or playing a musical instrument require continuous interactions with environments and task constraints that vary dynamically. Paddle juggling is a simple yet powerful paradigm for understanding how the human brain controls spatial and timing variables to rhythmically act in dynamic environments that may feature intermittent feedback (Ankarali et al. 2014; Bazile et al. 2016; de Rugy et al. 2003; Dijkstra et al. 2004; Huber and Sternad 2015; Morice et al. 2007; Ronsse et al. 2010; Schaal et al. 1996; Siegler et al. 2010, 2013; Sternad et al. 2001; Wei et al. 2007).

Visual feedback has been shown to have a strong, perhaps dominant, role in regulating rhythmic movements in paddle juggling tasks (Avrin et al. 2017; Siegler et al. 2010, 2013). These findings, however, do not explain why nonvisual feedback (e.g., haptic and auditory) is sufficient to maintain spatial accuracy about an equilibrium pattern (Sternad et al. 2001) and capable of prolonging the duration for which such stability can be maintained (Ankarali et al. 2014). In a novel variant of paddle juggling where we restricted visual feedback to close to the minimum required for sustainable juggling (Austin 1976; Dessing et al. 2012; van Santvoord and Beek 1994) and separably perturbed spatial and event-timing cues, we shed light on the functional role of this nonvisual feedback, the dynamics with which it influences neural control, and how these non-visually based control processes interact with vision to subserve rhythmic movements.

A central feature of our analytical approach is the use of linear systems techniques. Although a full description of paddle juggling dynamics is nonlinear, the fact that accurate ball bouncing could be achieved with fairly modest paddle movements, position amplitudes commonly being < 10 cm as in Fig.

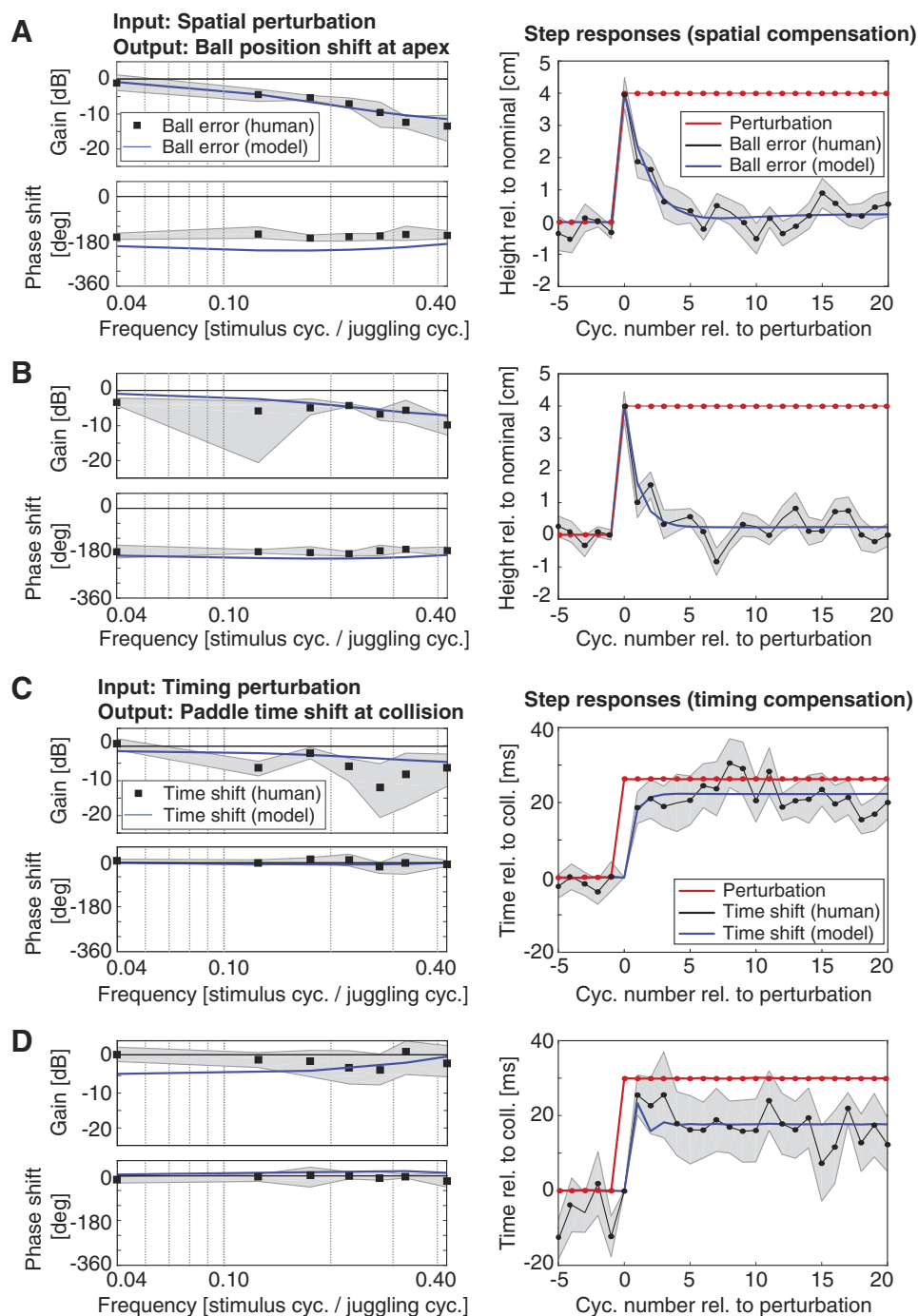


Fig. 9. Cross-validation of parametric models in frequency and time domains for representative participants in *experiment 2*. Each row (A–D) shows a representative juggler, and fitted models (blue) to step response data are compared with human data (black). Data and perturbations (red) were applied and recorded on a cycle-by-cycle basis (shown by dots). A: spatial-motor response for 1 representative participant. Bode plot (*left*) shows responses to 7 sinusoidal perturbation frequencies (see *Experiment 2*). Means and ranges across 5 trials are shown for each perturbation frequency. Cycle-by-cycle behavior (*right*) is plotted as mean $\pm$ 1 SE across 20 step perturbation trials. Model goodness of fit is indicated by coefficient of determination r^2 . B: frequency- and time-domain behavior for a different participant. Data are shown as in A. C and D: timing-motor response for 3rd and 4th representative participants. Data shown are plotted as in Fig. 7, B and D, and are computed across individual trials.

1B, suggests that ball position can be regulated by fairly small adjustments to paddle control and provides evidence in favor of our modeling assumptions.

Spatial and Temporal Feedback Have Separable Roles

Because nonvisual cues are prevalent at ball-paddle collisions and collision timing is coupled to ball peak height, we initially hypothesized that haptic and audio feedback provides timing information that the brain uses to refine its estimates of ball position. We developed a Bayesian model of cross-modal integration consistent with the intuition that artificially delaying these nonvisual cues could be interpreted by the sensori-

motor system as a sign that ball position was higher than previously expected, and vice versa. This model was contradicted by *experiment 1*, in which we applied sinusoidal perturbations selectively to spatial (visual) and event-timing feedback (visual and nonvisual) feedback and assessed the coherence between these sensory inputs and behavioral outputs related to spatial (ball position) and timing-related (hand-paddle shifts) aspects of movement. Contrary to our model predictions, correlations between spatial and timing feedback perturbations and ball position were significantly different. Whereas spatial perturbations were compensated as errors, perturbations to the timing of event feedback induced delays or

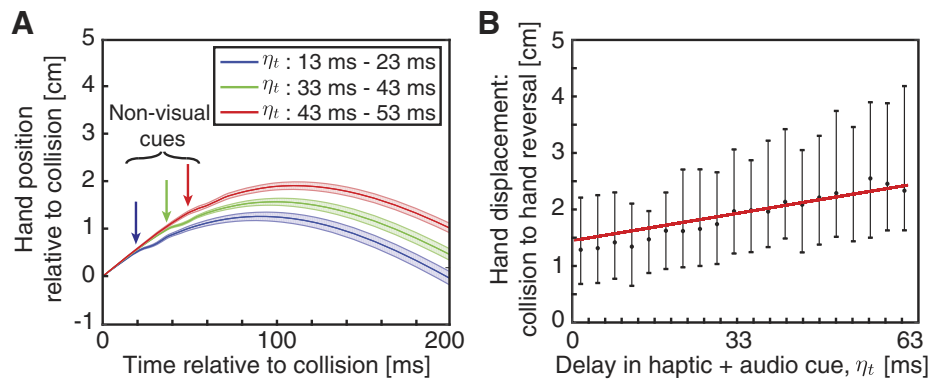


Fig. 10. Collision cues trigger reversals in arm movement direction. **A**: hand position trajectories (computed off-line), as functions of time relative to actual collisions, for 1 representative participant. Data are binned according to perturbation size (η_t). Each curve shows the mean $\pm$ 1 SE across trials ($n = 10$ cycles for η_t : 13–23 ms; $n = 9$ cycles for η_t : 33–43 ms; and $n = 13$ cycles for η_t : 43–53 ms). Downward arrows of each color show when haptic-audio timing feedback was applied. **B**: maximum hand displacement between actual collision and point of hand reversal after collision feedback compared with perturbation size η_t (x-axis). Data are pooled across all trials across participants. Median and 90% confidence bounds are shown for various binnings of η_t . Extent of hand movement following collision is positively and linearly correlated to perturbation amount (Spearman's rank correlation test; $\rho = 0.456$, $P < 0.001$).

advances in hand movement timing in the direction of perturbations. Spatial and temporal feedback, we conclude, are used by the human brain to solve complementary spatial and timing control problems. This result confirms that spatial and temporal regulation of rhythmic arm movements are complementary and at least partially separable processes, as found by Siegler and colleagues (Siegler et al. 2013), and provides new evidence that nonvisual feedback (sound and touch) specifically informs the latter control process. In light of our design choice not to scale auditory and haptic feedback to the strength of the impulse between the ball and paddle at collisions, however, we cannot rule out that the brain can infer spatial information from the intensity of collision cues when actually physically juggling or bouncing a ball, as in Sternad et al. (2001). Nevertheless, spatial and temporal regulation have now been observed in movements of various spatial scales—paddle movements in our task were roughly half the size of those reported in Siegler et al. (2010)—raising the possibility that these control processes generalize to at least some extent across scales of movement.

Event-Timing Feedback May Act as a Metronome to Synchronize Control

Through a combination of sinusoidal and step perturbations, we were able to develop parametric models characterizing the cycle-by-cycle influence of visual feedback on ball height regulation (paddle velocity) and of event-timing feedback on hand timing. These models generalized across perturbation type and held at group and individual levels. The control laws we estimated are in the form of first-order difference equations, reinforcing previous studies (Siegler et al. 2013) and models that suggest that error correction occurs on fast timescales in tasks as diverse as reaching (Scheidt et al. 2001) and rhythmic ball bouncing (Ankarali et al. 2014; de Rugy et al. 2003; Wei et al. 2007). Responses to nonvisual feedback in particular suggest that timing compensation occurs more quickly than visuo-spatial correction. This relative rapidity of correction is also visible in the changes of paddle half-period that have been observed under certain perturbations of ball visual trajectories (Siegler et al. 2013). It is potentially explained by the relatively

high bandwidth we found in the processing of timing cues (Fig. 7D and the magnitude responses in Fig. 9, left).

Interestingly, the entrainment of the maximum-velocity point of hand trajectories to the timing perturbation is consistent with behavior observed in the task of tapping to a metronome (Donnet et al. 2014). The proportional timing-control law is also consistent with models of timekeeping that have been used to account for metronome entrainment (Vorberg and Schulze 2002). Because internal timekeeping may be fragile in the absence of feedback, the findings of our study suggest that timing cues, for which nonvisual feedback is sufficient, may provide an important error signal whereby the brain's timekeeping mechanisms can be synchronized to a task-relevant clock.

According to the timing-control model for our data (Eq. 15), participants appear to process the perturbations as though they perceive them as timing errors. Operationally, a timing perturbation was defined as the difference between the timing of a collision or apex cue and when an event actually occurred. Mathematically, timing perturbations can be equivalently stated as an error between a measurement of time exuded by the environment via audio-haptic cuing and some internal estimate of time seated in the brain. Absent other evidence, the brain may interpret these false cues as a reflection of physical ground truth. In this case, this timing response can be viewed as the brain's attempt to reset its own noisy timekeeping to the rhythm of a task, and it may be that nonvisual cues act as a metronome that signals this rhythmicity. Our findings are consistent with observations in the temporal discrimination literature that suggest that, in the presence of temporally conflicting visual and auditory information, human perception of timing is biased in the direction of audition (Guttman et al. 2005).

Nonvisual Timing Cues Can Improve Robustness of Rhythmic Movement Control

Visual feedback of the full path of the ball during paddle juggling can serve as a potent phase-locking cue (Siegler et al. 2013), yet the use of audio and haptic cues as references about which to organize hand reversals (Fig. 10) may help explain

why vision is not necessary to sustain juggling, a fact demonstrated by humans (Sternad et al. 2001) and by robotic “blind jugglers” that sustain ball bouncing with a proportional control law similar to what we found for timing control (Reist and D’Andrea 2012). This entrainment may help explain why, even in the presence of visual feedback, nonvisual cues enhance spatial stability by enhancing the length of accuracy streaks (Ankarali et al. 2014).

That either visual or nonvisual feedback is sufficient for paddle timing suggests that rhythmic movements may entail a layer of control redundancy that can be masked by the potency of visuospatial information but nonetheless makes rhythmic motor control more robust (Roth et al. 2016). Such multimodal control may also help explain why audio and haptic feedback that is not explicitly spatial is sufficient to maintain spatial accuracy without vision (Sternad et al. 2001), can influence learning (Sigrist et al. 2013), or may prolong periods of stability in skillful performance (Ankarali et al. 2014). We also note that a categorical improvement in performance of state-of-the-art juggling robots coincided with the integration of microphones as contact detectors in paddles and the use of these measurements in estimation algorithms (Buehler et al. 1994; Rizzi and Koditschek 1996). Although many previous paddle juggling apparatuses featured nonvisual feedback (de Rugy et al. 2003; Morice et al. 2007; Schaal et al. 1996), it is possible that these additional nonvisual cues may make movements more robust. If bounce error variability is due primarily to motor noise [as argued in the modeling study of Avrin et al. (2017)], timing control may mitigate this variability by helping an actor time its movement extrema so that the most precise phases of movement occur at the most task-relevant events, such as ball-paddle collisions.

Neural Substrates for Timing Control and Visual Error Correction

Ball bouncing and other rhythmic behaviors, including tapping, circle drawing (Spencer et al. 2003), and locomotion, are characterized by an endemic regularity in both space and time (Hogan and Sternad 2007) that contrasts with discrete tasks such as reaching and manual exploration. Rhythmic task performance is often modeled as the coupling between an actor and a task, each represented by oscillators (Avrin et al. 2017; Fajen et al. 2009; Holmes et al. 2006). To successfully engage in this rhythmicity, the human must infer an appropriate spatial extent and frequency of movement (nominal states such as in *Eq. 4*); engage in a sequence of movements to reach these nominal states, whether by passive or active control or a mixture (Huber and Sternad 2015; Siegler et al. 2013; Wei et al. 2007); and actively regulate the extent and timing of their movements to maintain stability (Ankarali et al. 2014; Siegler et al. 2013).

Where are these complementary processes of spatial error correction and temporal entrainment seated in the nervous system? The cerebellum has a well-established role in visual error correction (Shadmehr et al. 2010; Smith et al. 2006), but it has also been broadly implicated in timing on millisecond scales (Ohmae et al. 2017). A study comparing the performance of ataxic and healthy individuals on a rhythmic circle drawing and tapping task showed that patients were selectively impaired only when explicit (nonvisual) temporal cues were

introduced during movement (Spencer et al. 2003), a finding that was interpreted as evidence of the cerebellum’s particular involvement in temporal regulation when timing goals are explicit.

On the other hand, an emerging body of evidence suggests that the premotor area and supplementary motor area play a crucial role in rhythmic movements. An functional MRI study of wrist movements suggests that these areas are selectively activated during rhythmic movements but relatively silent during discrete movements (Schaal et al. 2004). A more recent study of finger tapping in macaques suggests that individual neurons in supplementary motor area use rate coding to track an internal estimate of time relative to an external cue and that tapping errors have correlates in mistimings of these firing trajectories (Merchant and Averbeck 2017).

Perturbations during other phases of individual juggling cycles may further help to parse the relationships between stability and temporal entrainment. The consequences of imperfect timing on actions (biological or robotic) have implications that are only now beginning to be considered from a control theoretical standpoint (Carver et al. 2013; Lamperski and Cowan 2016). Analytical methods to more fully parse out the dynamics of skilled and unskilled rhythmic behavior are in their infancy (Logan et al. 2017) but may shed light on complementary roles of visual, haptic, and audio feedback at all phases of movement.

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DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the authors.

AUTHOR CONTRIBUTIONS

R.W.N., M.M.A., and N.J.C. conceived and designed research; R.W.N. performed experiments; R.W.N. analyzed data; R.W.N., M.M.A., and N.J.C. interpreted results of experiments; R.W.N. prepared figures; R.W.N. drafted manuscript; R.W.N., M.M.A., and N.J.C. edited and revised manuscript; R.W.N., M.M.A., and N.J.C. approved final version of manuscript.

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