Balancing out dwelling and moving: optimal sensorimotor synchronization

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Cos I, Girard B, Guigon E. Balancing out dwelling and moving: optimal sensorimotor synchronization. J Neurophysiol 114: 146-158, 2015. First published April 15, 2015; doi:10.1152/jn.00175.2015.-Sensorimotor synchronization is a fundamental skill involved in the performance of many artistic activities (e.g., music, dance). After a century of research, the manner in which the nervous system produces synchronized movements remains poorly understood. Typical rhythmic movements involve a motion and a motionless phase (dwell). The dwell phase represents a sizable fraction of the rhythm period, and scales with it. The rationale for this organization remains unexplained and is the object of this study. Twelve participants, four drummers (D) and eight nondrummers (ND), performed tapping movements paced at 0.5–2.5 Hz by a metronome. The participants organized their tapping behavior into dwell and movement phases according to two strategies: 1) Eight participants (1 D, 7 ND) maintained an almost constant ratio of movement time (MT) and dwell time (DT) irrespective of the metronome period. 2) Four participants increased the proportion of DT as the period increased. The temporal variabilities of both the dwell and movement phases were consistent with Weber's law, i.e., their variability increased with their durations, and the longest phase always exhibited the smallest variability. We developed an optimal statistical model that formalized the distribution of time into dwell and movement intervals as a function of their temporal variability. The model accurately predicted the participants' dwell and movement durations irrespective of their strategy and musical skill, strongly suggesting that the distribution of DT and MT results from an optimization process, dependent on each participant's skill to predict time during rest and movement.

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MANY BEHAVIORS such as singing or playing music require internal estimates of elapsed time from a past event or of remaining time to a future event (e.g., the beats of a metronome) to timely generate our actions (e.g., to tap on beat). This ability to produce movements synchronously with temporal events, called sensorimotor synchronization (Repp and Su 2013), either can occur spontaneously as during a synchronous applause at a concert hall or may result from long practice as in musical ensemble performance.

Sensorimotor synchronization faces two constraints. First, processes involved in time production and perception tasks are governed by a form of Weber's law (Ivry and Hazeltine 1995; Merchant et al. 2008; Wing and Kristofferson 1973), i.e., variability increases with the duration of temporal intervals. Second, movements take time to be prepared and executed and are variable in space and time (Hancock and Newell 1985). How the brain actually predicts time between external events

and produces synchronized motor behaviors remains poorly understood.

Current theories of sensorimotor synchronization focus either on the production of abstract timing signals (event timing theory) or on the emergence of time from abstract dynamics (emergent timing theory), irrespective of the necessary production of an anticipated motor output to mark time (Schöner 2002; Wing and Beek 2002). However, there is strong evidence that the structure of movement significantly contributes to timing. For example, typical rhythmic movements involve a "beat stroke" aimed at a synchronization point and a preparatory "backstroke" with the possibility of a motionless phase (dwell) in between (Hove and Keller 2010; Repp and Su 2013; Stetson 1905). The beat stroke is in general faster than the backstroke (Balasubramaniam et al. 2004; Doumas and Wing 2007), and it is faster in subjects having better synchronization (e.g., drummers; Krause et al. 2010). The dwell phase is robustly defined in kinematic recordings by position and velocity thresholds (Hove and Keller 2010), represents a sizable fraction of a cycle (e.g., 15-40% in van der Wel et al. 2009; \sim 50% in Hove and Keller 2010; 9–36% in Hove et al. 2014), and scales with the cycle duration (in humans: Bienkiewicz et al. 2012; Billon and Semjen 1995; Hove et al. 2014; van der Wel et al. 2009; Vaughan et al. 1996; in monkeys: Donnet et al. 2014). Obviously, as actual cycle duration is the sum of dwell and movement durations, accurate synchronization should result from proper coordination between the dwelling and moving phases. The goal of this study was to understand the nature of this coordination. As musicians are especially skilled in sensorimotor synchronization (Franěk et al. 1991; Krause et al. 2010; Repp and Doggett 2007), characteristics of dwell/movement coordination in this population should be particularly revealing.

We combined experimental and computational methods to study a discrete paced tapping task in two groups of participants (drummers and nondrummers) to address two specific questions regarding the organization of sensorimotor synchronization into dwell and movement phases: 1) Is this organization of behavior related to the inherent temporal variability of dwell and movement phases? Is the duration of each phase optimal according to some specific principle? 2) Does this organization depend on timing (musical) expertise? We discuss our results in the framework of the statistically optimal nature of human sensorimotor behavior.

MATERIALS AND METHODS

Ethics Statement

The experiment was approved by the Ethical Assessment Committee at the Université Pierre and Marie Curie (protocol IRB-

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20141400001072). Subjects signed a consent form prior to participating in the experiment and in accordance with the ethical guidelines of the Université Pierre and Marie Curie and with the Declaration of Helsinki.

Participants

Twelve right-handed subjects (8 men and 4 women) participated in a behavioral experiment (single session)—12 of 12 rated >85% in the Edinburgh protocol of handedness (Oldfield 1971). They had no known neurological disorders and normal or corrected to normal vision, and they were uninformed as to the purpose of these experiments. Four subjects had specific musical training as drummers (S9–S12, D group; average training of 5 yr). The remaining eight subjects were assigned to the [nondrummer (ND) group (S1–S8)].

Apparatus and Task Design

The task apparatus consisted of a table with a thick rubber band (2 \times 4×30 cm) placed on the side closest to the subject (Fig. 1A). The task consisted of making vertical movements with the right hand index finger aimed to tap on the rubber band, which we recorded by tracking an active infrared marker taped on top of the fingertip side. The position of the marker was tracked by a real-time CODA motion capture system (Charnwood Dynamics, Rothley, UK), sampling at 200 Hz, controlled by a personal computer running Windows XP (Microsoft). The same computer stored the kinematic data recordings. A second personal computer running Ubuntu 12.04 was used to control the task flow of events, to synchronize and trigger the recordings on the CODA computer, and to produce rhythmic acoustic cues (frequency 700 Hz, 30 ms, 40 dB) through loudspeakers placed 2 m in front of the subject. The kinematic and flow data were stored in a MySQL database (Oracle, Redwood Shores, CA) and analyzed with custom-written MATLAB scripts (MathWorks, Natick, MA).

Experimental Procedure: Synchronization Task

In the synchronization sessions (Fig. 1), subjects were given the general instruction of tapping periodically with their right index finger



on the hard rubber band by waving their arm (mainly by rotation about the elbow), maintaining their wrist static and a comfortable but fixed bodily posture. Two tapping conditions were used: 1) the preferred frequency (PF) condition involved unpaced tapping movements (Fig. 1B, top), and the subjects were instructed to tap at the frequency they felt most comfortable with; 2) the fixed frequency (FF) condition involved paced tapping movements (Fig. 1B, bottom). Each subject performed four blocks of trials per session: one PF and three FF blocks (Fig. 1B). First, the PF block consisted of three sets of five trials each: five movement preferred amplitude (PA), five smaller than free amplitude (SA), and five larger than free amplitude (LA). Each trial lasted 50 s. Each FF block intended to characterize the subjects' behavior at five frequencies (see below) and at the three aforementioned instructed amplitudes: PA, SA, and LA. Within each FF amplitude block, we ran five trials per metronome frequency (total of 25 trials). Each FF trial consisted of approximately 25 consecutive acoustic cues, signaled at one of the following intervals (in s): 2 (0.5 Hz), 1 (1 Hz), 0.67 (1.5 Hz), 0.5 (2 Hz), and 0.4 (2.5 Hz) (the subjects of the ND group were not tested at LA/2.5 Hz because of the difficulty of this condition). The rationale for this choice of frequencies is addressed in DISCUSSION. Consequently, the respective trial duration at each frequency was 50 s (0.5 Hz), 25 s (1 Hz), 17 s (1.5 Hz), 12.5 s (2 Hz), and 10 s (2.5 Hz). In this case, subjects were instructed to synchronize the finger contacts on the rubber band with the acoustic cues. No cues were provided prior to trial onset to facilitate initial synchronization, and no further instruction was given regarding spatial accuracy. The order of the four main blocks was randomized across subjects.

At the beginning of each FF trial, the subject placed the right-hand finger on the rubber band and waited for the acoustic sequence to start (Fig. 1*B*). In the case of PF trials, only two acoustic signals were given per trial, one to signal the beginning and one the end of the trial (50 s apart). An intertrial interval (ITI) of 10 s was imposed between trials.

Experimental Procedure: Reaction Time Task

In the reaction time (RT) control session, the task was similar to the FF task (Fig. 1B), except that subjects were told to react to the

Fig. 1. A: task apparatus, showing a subject seated at the table tapping on a hard rubber band. B: time course of a typical preferred frequency (PF, top), and fixed frequency (FF, bottom) trial. T, metronome period; ITI, intertrial interval. C: definitions of kinematic landmarks: contact (open circle), movement onset (filled circle), peak amplitude (gray circle), and position of peak upswing (up triangle) and downswing (down triangle) velocity. Definition of time intervals: cycle time (CT) is the time between 2 successive contacts: dwell time (DT) is the time between preceding contact and onset; movement time (MT) is the time between onset and contact: asynchrony (AS) is the time between acoustic cue (vertical dashed line) and contact (measured negative when contact occurs before the cue). D: 2 sample trajectories at a small (SA) and a preferred (PA) amplitude for 2 typical subjects. Note that the subjects follow different motor strategies to synchronize, by dwelling in contact with the rubber band (zero elevation) (subject S9) or by making overall slower movements (subject S5).

acoustic cue with a tapping movement rather than to synchronize the contact on the rubber band. To prevent synchronization, a jitter (20% of the period) was added to the temporal sequence of cues. Again, each subject performed three blocks of trials per metronome frequency (0.5, 1 Hz), each at a specific amplitude: PA, SA, or LA. Each trial lasted 25 s.

Data Processing

We recorded three-dimensional kinematic data. The recorded movements were essentially vertical, so we considered the vertical component as relevant to the synchronization task. The position signal was low-pass filtered at 400 Hz (5th-order Butterworth) and differentiated to obtain velocity. The filtered position and velocity signals were parsed with an ad hoc algorithm, designed to locate the following events (Fig. 1C): contact (amplitude < 1% of the standard deviation of the trajectory amplitude), movement onset (amplitude > 5% of the standard deviation of the trajectory amplitude), peak amplitude, and time and value of peak upswing and peak downswing velocity. From these landmarks, we calculated the following: 1) asynchrony is the synchronization error measured as the difference between the time of metronome acoustic cue and contact time (for FF task only); 2) movement time (MT) is the time interval between movement onset and contact; 3) dwell time (DT) is the time interval between preceding contact and movement onset; 4) cycle time (CT) is DT + MT (time interval between successive contacts). As an order of magnitude, there was a mean of 96 points per subject and condition (i.e., amplitude and frequency) and 1,147 points for the group to compute statistics.

Data Analysis

Our analysis was organized in three parts. *I*) We assessed whether the subjects complied with task instructions. For each subject, we calculated mean asynchrony and mean amplitude for each metronome frequency and amplitude instruction. Data of all subjects, D group or ND group, were pooled to obtain group means. 2) We quantified characteristics of movement (time interval between onset and contact) in terms of peak velocity, time to peak velocity, and trajectory to reveal relationships between kinematics and synchronization. *3*) We studied how DT and MT contributed to CT (since CT = DT + MT) and how variability of these quantities influenced their contribution (% of DT and MT in CT). Variability of a quantity was defined as the standard deviation of this quantity and plotted against the mean value of the quantity to reveal scalar timing properties.

Relevant points. The results were plotted as a function of metronome period rather than frequency. Because of the large amount of data, we systematically focused on the results of the PA condition only, as the two other FF conditions (SA, LA) led to similar results (unless specified otherwise in the text). Data from PF conditions were dealt with selectively to assess whether they were consistent with corresponding FF conditions. In general, we report single-subject data and mean data across subjects (or groups), yet in some cases mean data were redundant and are not reported. We did not address control of movement amplitude at a given frequency.

RESULTS

The results are organized into three sections corresponding to the three main aspects of data analysis (see MATERIALS AND METHODS): 1) general kinematic analyses, 2) contribution of movement kinematic to synchronization, and 3) influence of temporal variability on the structure of the movement cycle. Each subject is described by a number (nondrummers: S1-S8; drummers: S9-S12). As a preliminary, Fig. 1D shows a few trajectory cycles of two subjects, performing the task at a SA and their PA for a metronome frequency of 1 Hz. The traces show that both subjects accurately synchronized the contact on the rubber band, by the end of the downswing phase, with the metronome acoustic cues. The strategy of *subject S9* for PA and FA cycles consisted of a dwell phase maintaining the finger on the rubber band, followed by a fast upswing and downswing phases to return back to zero elevation at the next beat (see Fig. 1D, *left*). Ten of twelve subjects (83.3%) opted for this strategy. By contrast, *subject S5* preferred to make long but slow movements and short dwell intervals. Only 2 of 12 subjects (16.7%) opted for this strategy. This first observation shows that all subjects distributed their cycles into a dwell and a movement phase. We analyzed the behavioral structure on an individual subject basis.

General Kinematics of Synchronized Tapping Movements

Asynchrony. Since the goal of the task was to produce tapping movements synchronizing the contact at zero elevation with the metronome beat, we first assessed the asynchrony (error of synchrony) as a measure of task performance. Figure 2 shows the average asynchrony for each frequency and amplitude for two typical subjects (Fig. 2A) and the average across subjects (Fig. 2B). In agreement with previous studies (Aschersleben and Prinz 1995), we typically observed a negative asynchrony, i.e., the contact preceded the acoustic cue [Kolmogorov-Smirnov (KS) test, $P < 10^{-18}$ for all amplitude and frequency conditions] by <100 ms for all subjects. The main tendency of negative asynchrony was to increase with the duration of the interval (Fig. 2B), although it varied largely for some subjects when the period was longer than 1 s (see *subjects S11* and S9 in Fig. 2A). KS tests on the distributions of asynchrony error across consecutive frequencies yielded significant differences in all cases (P < 0.05), with the exception of PA trials (1 vs. 2 Hz, P = 0.29). Remarkably, a comparison of the asynchrony as a function of musical training (D vs. ND groups) showed that musical training dramatically diminished the asynchrony error (KS test, $P < 10^{-17}$), reaching average values ~5 ms for frequencies larger than 1.5 Hz (see Fig. 2C, period smaller than 0.67 s). Asynchrony error for drummers is consistent with previous results (Hove et al. 2014; Krause et al. 2014). Asynchrony error for nondrummers is larger than previously reported because of two subjects (S6 and S8) with unusually large negative asynchrony errors.

Movement amplitude. Figure 3 shows the peak movement amplitude recorded during the movement phase for a typical subject (Fig. 3A) and the distributions across subjects for each amplitude condition (Fig. 3B) as a function of the metronome period. The peak amplitudes were smaller in the SA condition (5-15 cm), average for the PA condition (20-40 cm), and the largest for the LA condition (60-80 cm), demonstrating that each subject complied with the instructed amplitude guideline. Furthermore, the movement amplitude in the PF condition varied consistently with movement amplitude in the FF condition for the SA, PA, and LA conditions (Fig. 3B). Individual KS tests across amplitude distributions at each frequency indicate statistically significant differences in all cases (P < 10^{-5}). Furthermore, the peak amplitude grows along with the metronome period, consistently with previous results (Dahl 2011), although its growing rate weakens as the period expands. To assess the dependence on the metronome period, we performed a two-way ANOVA on the amplitudes with factors



Fig. 2. A: asynchrony (temporal synchronization error) as a function of interval duration [in s: 0.4 (purple), 0.5 (blue), 0.67 (green), 1 (yellow), 2 (red)] for 2 subjects. Dashed line, diamond, SA; solid line, circle, PA, dashed line, square, larger than free amplitude (LA). Note the very small SE bars plotted at each dot. B: same as A, averaged across subjects. C: comparative analysis of the asynchrony for drummers (open symbols) and nondrummers (filled symbols) as a function of the metronome period for SA (*left*), PA (*center*), and LA (*right*) trials. Kolmogorov-Smirnov (KS) test: ** $P < 10^{-10}$.

amplitude and period duration, obtaining significant effects $(P < 10^{-5})$ for both main factors (amplitude: $P < 1.0 \times 10^{-15}$, F = 241.53; frequency: $P < 2.01 \times 10^{-152}$, F = 180.38) and for the interaction between them (amplitude × frequency: $P < 2.38 \times 10^{-105}$, F = 64.65). Post hoc KS tests across amplitude distributions at consecutive periods yield significant differences for all three amplitude and frequency conditions (SA $P < 2.6 \times 10^{-3}$, PA $P < 10^{-5}$, LA $P < 10^{-5}$).

Contribution of Movement Kinematic Structure to Synchronization

Peak velocities. Figure 4A shows the distributions of peak velocities during the upswing (Fig. 4A, *left*) and downswing (Fig. 4A, *right*) phases for all three amplitude conditions as a function of metronome period, averaged across subjects. As a general trend, the average peak velocity of SA and PA trials remains invariant as the period increases and exhibits a dramatic decrease in the LA case. This observation holds for both the upswing and downswing phases. Furthermore, a comparison of peak velocities during upswing and downswing phases (see Fig. 4B) shows that upswing movements are slower than downswing movements. KS tests between upswing and down-

swing peak velocity distributions for SA, PA, and LA conditions yielded *P* values smaller than 5×10^{-5} (SA), 6×10^{-5} (PA), and 4×10^{-5} (LA) in all cases. In a complementary fashion, we compared the average peak velocity of drummers vs. nondrummers for the SA, PA, and LA conditions, which were consistent with these very same trends (see Fig. 4*C*). However, the drummers exhibited a significantly larger peak velocity than the nondrummers, during both upswing (KS test, P < 0.01) and downswing (KS test, $P < 10^{-10}$) phases for all amplitudes. This suggests a different strategy for each group, as quicker movements may be instrumental in the better synchronization ability of the drummers. We note that peak velocity in the PF condition was consistent with peak velocity in the FF conditions.

Velocity profiles. Upswing and downswing phases exhibit remarkably different kinematic properties, strongly dependent on the metronome period (see Fig. 5). Specifically, the time to peak velocity was the closest to the half of the phase (near to symmetric) when the period was the shortest (0.4 s, 2.5 Hz) and progressively shifted backward (upswing) and forward (downswing) as the period increased (see data from 3 typical subjects in Fig. 5). These observations correspond to velocity



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Fig. 3. A: peak movement amplitude as a function of interval duration for a single subject. Colors and symbols as in Fig. 2. Solid line, PA; dashed lines, SA and LA. Filled black symbols correspond to PF conditions. B: average amplitude across subjects. Distributions across trials and subjects are shown as Gaussian curves (using mean and SD of pooled data). Open symbols correspond to PF data (amplitude vs. actual period).



Fig. 4. A: upswing (*left*) and downswing (*right*) peak velocities as a function of interval duration averaged across subjects. Same format as Fig. 3B. B: comparison between upswing and downswing peak velocity. Black symbols correspond to the PF data. C: comparative analysis of peak upswing (*top*) and downswing (*bottom*) velocity for drummers vs. nondrummers for each amplitude condition. KS test: *P < 0.01, $**P < 10^{-10}$. Note that the period in the PF condition (black symbols) is not in general the same for drummers.

profiles near symmetric at shorter periods, which became progressively asymmetric as the period increased (Fig. 5B).

Rationale for Cycle Organization: Temporal Variability

Behavioral cycle organization. We focus next on the organization of the behavioral cycle into dwell (DT) and movement (MT) intervals. A priori, the subjects could freely organize their behavior within the interval between acoustic cues. However, their behavior was regular, as the MT and DT grew linearly with the metronome period at all conditions (see PA MT and DT for 3 typical subjects in Fig. 6A). This result holds for all amplitude conditions (SA and LA not shown). However, we could identify two different strategies to assign MT and DT for different subjects by expressing their values as a percentage of CT (Fig. 6B): the first strategy consisted of maintaining an almost constant ratio of MT and DT per cycle irrespective of metronome period, e.g., subjects S3 and S8 (Fig. 6B, left and center). By contrast, the second strategy consisted of trading off the proportion of MT by DT as the metronome period increased,

e.g., *S9* (Fig. 6*B*, *right*). The individual strategy of each subject may be visually identified in Fig. 6*C*, which shows the MT and DT expressed as a percentage of CT for each subject. From a total of 12 subjects, 6 nondrummers and 1 drummer behaved consistently with the first strategy and 2 nondrummer and 3 drummers were consistent with the second strategy. These results are consistent with the observations of Hove et al. (2014) on staccato and legato tapping styles on a more restricted range of periods (400–700 ms; see their Fig. 2).

Temporal variability to determine MT and DT. The aforementioned two strategies characterize the choice of DT and MT during tapping behavior in a macroscopic fashion but do not explain the rationale underlying that specific cycle organization. We observed that DT durations were typically shorter than MT durations (see range of values on y-axis of Fig. 7B) and that their variability grew faster (see Fig. 7A). Furthermore, we observed that the variability of MT and DT for our subjects was consistent with Weber's law, i.e., standard duration of estimated and produced intervals increased linearly with Downloaded from http://jn.physiology.org/ by 10.220.33.1 on July 11, 2017



Fig. 5. A: time to upswing and downswing peak velocities as % of upswing and downswing duration, respectively, as a function of metronome period, for 3 subjects. Color codes are as in Fig. 2. Black symbols correspond to PF data. B: average velocity profiles during MT for each metronome period, normalized to fit the same time interval.

duration (Ivry and Hazeltine 1995; Peters 1989). Since the overall goal of the task was to synchronize the contact at zero elevation with the acoustic signals, we hypothesized that the selection of MT and DT interval duration was such that the synchronization error over the entire cycle was minimal. In other words, subjects were optimizing variability over the entire cycle to determine their preferred MT and DT.

To test this operational hypothesis on a single-subject basis, we first fitted the variability (standard deviation) of MT and DT interval duration with the following formula:

$$\sigma_X = \alpha_X X + \beta_X \tag{1}$$

where X stands for DT or MT (Hudson et al. 2008; Ivry and Hazeltine 1995), obtaining the fitting coefficients (α , β) by linear regression. The fit was consistent with Weber's law for all subjects and amplitude conditions [$R^2 = 0.71 \pm 0.34$ (SA), 0.84 \pm 0.19 (PA), 0.87 \pm 0.10 (LA)]—see three typical subjects in Fig. 7A.

Second, we assessed whether the distribution of CT into DT and MT resulted from a trade-off between the relative variability of these processes, aimed at optimizing the variability over the entire cycle. Ultimately, the goal was to synchronize the contact on the surface with the metronome beat, and it would be logical that subjects had exploited the specifics of their personal skill (in terms of variability) to attain that goal. Furthermore, previous evidence exists for the case of spatial variability only (Battaglia and Schrater 2007; Faisal and Wolpert 2009) and of temporal variability for single intervals during reaching movements (Hudson et al. 2008). To test this hypothesis, we first assumed independence of DT and MT and we calculated their optimal duration for each subject and amplitude condition by minimizing the overall cycle variability as described by *Eq. 2*:

$$\sigma_{\rm CT}^2 = \sigma_{\rm DT}^2 + \sigma_{\rm MT}^2 \tag{2}$$

In other words, the optimal DT and MT resulted from combining their intrinsic variability such that the overall cycle variability was minimal. Using *Eq. 1* and *Eq. 2* and CT = DT + MT, we obtain

$$\sigma_{\rm CT}^2 = (\alpha_{\rm DT} {\rm DT} + \beta_{\rm DT})^2 + [\alpha_{\rm MT} ({\rm CT} - {\rm DT}) + \beta_{\rm MT}]^2$$

After derivation, the optimal DT (and similarly MT) may be expressed as

$$DT = \left(\alpha_{MT}^2 CT + \alpha_{MT} \beta_{MT} - \alpha_{DT} \beta_{DT}\right) / \left(\alpha_{DT}^2 + \alpha_{MT}^2\right) \quad (3)$$

Overall, the DT and MT predicted by this principle were consistent with the observed DT and MT for the three subjects shown in Fig. 7*B*. We used two complementary methods to validate the model in a systematic manner. First, in a qualitative manner, we visually inspected the model fitting of the subjects' behavior (Fig. 7*B*). To that end, we classified the 34 available cases (12 subjects \times 3 amplitudes – 2 cases excluded because of lack of data) into two categories, as a function of the difference of magnitude between MT and DT. The first category (20/34) corresponds to MT >> DT, e.g., Fig. 8*A*. The model MT and DT predictions matched the experimental data in 19/20 cases of this category. The second category (14/34) corresponds to

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 $MT \approx DT$, e.g., Fig. 8*B*. The model MT and DT predictions accurately matched 9/14 cases of this category. The two cases poorly explained by the model are shown in Fig. 8*C*. When we inspected these two cases in further detail, we observed that the subjects combined different motor strategies within or between frequencies (e.g., they first tapped with long DTs and eventually modified their strategy to short DTs), which precludes a proper measurement of their variability associated with a single strategy.

Second, we quantified the model's predictions with an efficiency metric for each MT or DT interval:

$$E_X = 100 \left(\frac{R_{X \text{mod}}^2}{R_{X \text{data}}^2} \right) \tag{4}$$

where X stands for MT or DT. The denominator corresponds to the R^2 obtained from a linear regression over the data (as in Fig. 6A) and the numerator to the R^2 measure of the goodness of fit of the model (Draper and Smith 1998; http://en.wikipedia. org/wiki/Coefficient_of_determination)—see Fig. 7B. By construction, the efficiency is smaller than 100, but it may also assume negative values if the numerator is negative. The E_X values obtained are shown in Fig. 8D for each individual subject and amplitude, for both DT and MT. We observed that

Fig. 7. A: MT and DT standard deviation (std) for 3 subjects as a function of MT and DT, respectively, with regression lines. Numbers at *top* are R^2 coefficients. Color codes are as in Fig. 2. B: same as Fig. 6A and model predictions (black for MT, gray for DT).



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Fig. 8. *A*: accurate model fit for 2 subjects with MT >> DT. Same format as Fig. 7*A*. *B*: accurate model fit for 2 subjects with MT \approx DT. *C*: loose model fit for 2 subjects. *D*: efficiency metric (black, MT; gray, DT) for each subject and amplitude (from *top* to *bot*-*tom*). Dashed line indicates the 90% efficiency threshold. Results from the qualitative analysis are indicated by the category (1, MT >> DT; 2, MT \approx DT; +, accurate; -, nonaccurate; *, missing data). Negative efficiencies are omitted.

first-category cases (MT >> DT) yielded a high MT and low (in general negative) DT efficiency. This effect is due to a strong sensitivity of the goodness of fit to the slope of the data. If we restrict our analysis of the first category to MT, mean efficiency is 97.00 \pm 2.54. If we establish an arbitrary threshold of 90%, the quantitative analysis is consistent with the qualitative analysis in 19/20 cases (i.e., provides the same classification previously established by visual inspection). For the second category (MT \approx DT), the efficiency of DT was significantly larger than for MT. If we focus our analysis of the second category on DT, the mean efficiency is 96.02 ± 3.11 . The quantitative analysis is consistent with the qualitative analysis in 14/14 cases according to the 90% threshold. In conclusion, the two proposed methods of validation are consistent with each other and support the close-to-optimality of the subjects' behavior. Remarkably, the same principle of optimization holds for the two previously described strategies (Fig. 6*B*).

Finally, we considered it necessary to control for the hypothesis of independence between DT and MT, i.e., to control for the covariance factor between DT and MT. If the durations of DT and MT were not independent, the expression of the CT variability should include the covariance term, as shown by Eq. 5:

$$\sigma_{\rm CT}^2 = \sigma_{\rm DT}^2 + \sigma_{\rm MT}^2 + 2\text{cov}(\rm DT, MT)$$
 (5)

where cov(DT,MT) stands for the covariance between DT and MT. However, our results show that the covariance was negative in 93% of the cases (subject × amplitude × frequency), in a range between -0.0433 and 0.0004, with mean -0.0015 ± 0.0062 (or in terms of correlation -0.45 ± 0.31). Overall, this means that for 93% of the cases *Eq.* 2 as initially presented

establishes a hard upper boundary for the added variability of DT and MT, as described by *Eq.* 6:

$$\sigma_{\rm CT}^2 \le \sigma_{\rm DT}^2 + \sigma_{\rm MT}^2 \tag{6}$$

Therefore, the minimization of the right-hand side of Eq. 6, as proposed in the model, obliges the minimization of the left-hand side term, as initially hypothesized.

Although we have fitted our model with the FF data only, we have also included the PF data in Figs. 3-8 for completeness. The PF data were in general consistent with the FF data, i.e., a metric obtained in the PF condition approximates well the metric that would presumably be obtained in the FF condition for the same frequency. This result suggests that the measures of temporal variability that were used in our model (Fig. 7A, *Eq. 1)* may not be specific of the FF condition only but reflect a general principle encompassing the characteristics of temporal prediction during dwell and movement intervals irrespective of instructed frequency. This is consistent with the results of Sternad et al. (2000) in the case of force production.

Reaction Time Task

So far we have described the results obtained in the synchronization task. However, we wondered whether our observations about behavioral organization and kinematics were specific of the requirement of synchronization of the task. To disambiguate this, we performed an additional control experiment in which two subjects were instructed to tap on the rubber band in response to the metronome acoustic cues [reaction time (RT) task, see MATERIALS AND METHODS], the results of which are summarized in Fig. 9.

MTs and peak amplitudes are shown for each instructed amplitude, frequency, and subject in Fig. 9A. As a general





Fig. 9. Summary of reaction time (RT) control task results. *A*: peak movement amplitude as a function of interval duration for both subjects and related MTs as a function of interval duration (black, 1 s; gray, 2 s). Note that SE bars at each dot are very small. Diamond, SA; circle, PA; square, LA. *B*: MT (filled symbols) and DT (open symbols) expressed as % of CT for PA amplitude as a function of metronome period for both subjects. *C*: average velocity profiles during MT for both metronome periods (amplitude PA), normalized to fit the same time interval. *D*: time to upswing (open symbols) and downswing (filled symbols) peak velocities for PA amplitude as a function of metronome period for both subjects.

trend, the MTs were remarkably shorter $(0.49 \pm 0.096 \text{ s}$ for 2-s period, $0.32 \pm 0.072 \text{ s}$ for 1-s period) than those obtained in the synchronization task $(1.45 \pm 0.45 \text{ s}$ for 2-s period, $0.73 \pm 0.19 \text{ s}$ for 1-s period; see Fig. 6A), although they increased with the duration of the period in a similar fashion and the amplitudes remained relatively constant. The percentage of MT per cycle decreased mildly with cycle duration, and the DT increased (Fig. 9B, only PA amplitude), in a fashion similar to some of the subjects trading off MT and DT in the synchronization task (see Fig. 6B, S9).

Despite these similarities, the structure of velocity profiles across tasks was markedly different from that of the synchronization experiment (compare Fig. 9C and Fig. 5B, red and yellow). For instance, the velocity profile of synchronized tapping at 0.5 Hz (Fig. 5B, red) had early and late peaks for upswing and downswing movements, respectively. No such phenomenon was observed in the RT task (Fig. 9C). This is confirmed by the analysis of time to peak velocity (Fig. 9D and Fig. 5A). In the RT task, time to peak velocity during upswing and downswing was 40-45% of upswing and downswing duration (Fig. 9D). By contrast, the time to peak velocities in the synchronization task were 20% and 80% of those intervals, respectively (see Fig. 5A). In other words, the velocity profiles of the RT task were relatively symmetric, while those of the synchronization task were highly skewed toward the beginning and end of the cycle, suggesting that the specific temporal distribution of the cycle is strongly task dependent.

DISCUSSION

In the present study we describe the rationale underlying the concomitant choice of the duration of dwell and movement phases for the production of tapping movements synchronized with a rhythm: the duration of dwell and movement phases was selected so as to minimize the overall cycle variability (see *Eqs. 2* and *3*). Our experimental results consistently matched the predictions of a model implementing this principle, therefore supporting a flexible coordination of timing processes based on each subject's intrinsic variability (see Figs. 7 and 8). Remarkably, the principle of overall variability minimization

for the selection of DT and MT duration extends to all subjects irrespective of their skill (drummers and nondrummers).

Our experiment used a set of tapping frequencies ranging from 0.5 to 2.5 Hz. Importantly, this range was chosen so as to obtain a broad range of DT and MT while allowing the task to be performed correctly and consistently with Weber's law. Studies involving long tapping periods showed that the proportion of reactive responses (i.e., when the participant taps in reaction to the acoustic cue) remains low for periods below 2 s (frequencies above 0.5 Hz; Baath and Madison 2012; Mätes et al. 1994; Miyake et al. 2004; Repp and Doggett 2007). Furthermore, the variability of cycle duration increased quite linearly with period for periods below 2-2.5 s (frequencies > 0.4-0.5 Hz; Krampe et al. 2005; Mätes et al. 1994; Repp 2010). It has been proposed that performance in subsecond and suprasecond timing tasks is mediated by two different systems (Lewis and Miall 2003). For instance, in synchronizationcontinuation tapping tasks, performance is affected by dualtask processing at slow (1,100-ms period) but not fast (700 ms) tempo (Maes et al. 2015). However, there is evidence that metronome-guided synchronization (our task) behaves differently. In particular, concurrent attention-demanding tasks have been reported to be influential on synchronization when the period exceeds 1,800 ms only—frequencies < 0.55 Hz (Miyake et al. 2004).

Sensorimotor synchronization has received significant attention for over a century (Repp 2005), yet relatively modest successes have been attained in the theoretical formalization of how movements are organized and generated to synchronize with external rhythms (Repp and Su 2013). Time has been traditionally considered "a mental abstraction, applicable to, but represented independently of any particular effector system" (Wing and Beek 2002). Although this may be appropriate to describe some aspects of intertapping intervals, such as asynchrony, variability, or correlations, this view of time fails to accommodate the fundamental fact that these properties result from an anticipated, timely process of preparation and production of highly stereotypical synchronous movements (Shaffer 1982; Torre and Balasubramaniam 2009). These

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movements may be typically characterized by a sizable dwell (motionless) phase (Billon and Semjen 1995; Brontë-Stewart et al. 2000; Du 2011; Hove and Keller 2010; Inui et al. 1998; Onla-or and Winstein 2001; Spencer et al. 2003; Todor and Smiley-Oyen 1987; van der Wel et al. 2009; Vaughan et al. 1966, 1998), which precedes a preparatory backstroke phase, and a faster beat stroke phase aimed at a synchronization point (Balasubramaniam et al. 2004; Doumas and Wing 2007; Hove and Keller 2010; Krause et al. 2010; Torre and Balasubramaniam 2009). Consistently with these observations, our results provide some additional insight about the entire cycle preparatory process. Importantly, the systematic scaling of dwell duration with the metronome period strongly suggests that dwelling is an active, deliberate process rather than a purely mechanical reaction to accommodate the next stroke. Furthermore, our results show that uncertainty and variability are at the heart of this process.

Uncertainty is a strong determinant of our sensorimotor behavior (Trommershäuser et al. 2008; Wolpert and Landy 2012). We commonly face noisy, underspecified situations in which decision and action must be undertaken. In many of these situations, we actually take uncertainty into account to guide our choices. A recurrent claim is that we behave as ideal observers or actors, i.e., that we possess internal knowledge of the structure of uncertainty and that we exploit it optimally for estimation and control (Battaglia and Schrater 2007; Faisal and Wolpert 2009; Trommershäuser et al. 2008). However, supporting evidence comes from specific situations in which participants receive explicit feedback about their performance as part of the task (e.g., gain/loss, success/failure), which allows the optimization of their performance as a function of a specific cost function (Trommershäuser et al. 2005). However, it remains to be seen whether a similar conclusion may be reached in the absence of an explicit, reported measure of performance at each trial, i.e., under more natural conditions. Partially addressing this issue, our results suggest that this may be the case when participants need to synchronize their displacements with an external rhythm. In our experiments, we found that most participants made an optimal use of their own temporal uncertainty during dwelling and moving to produce synchronized movements. Certainly, previous studies suggested a similar principle underlying the management of spatial uncertainty (Battaglia and Schrater 2007; Faisal and Wolpert 2009), and another single study showed that human subjects can compensate for the inherent temporal variability of their movements to maximize gains in a reaching and pointing task (Hudson et al. 2008). However, to the best of our knowledge, this is the first study in which optimality and temporal variability are reconciled in a parsimonious fashion so as to explain how DT and MT duration may fall out from a preparatory process, aware of one's own skill at predicting time during different behavioral phases.

A large variety of models of sensorimotor synchronization have been proposed, but most of them focus exclusively on temporal processing (e.g., error correction to maintain synchronization accuracy and precision), disregarding the motor aspect of synchronization (Jacoby and Repp 2012; van der Steen et al. 2015). Some models have been based on continuous dynamical systems and generate emergent rhythmic trajectories as limit cycle attractors of these systems (Kay et al. 1991; Schöner 2002; Vaughan et al. 1996). However, whether these trajectories could represent the discrete course of a tapping task remains highly debated (Delignières and Torre 2011; Schöner 2002). Furthermore, these latter models disregard the goal of the tapping task, i.e., precise synchronization. By contrast, our model stands as a new approach to sensorimotor synchronization based on the interplay between timing and motor processes.

Our experiment involved two groups of participants with different musical skills (drummers and nondrummers). The tapping behavior of the drummers was consistent with previous observations in musicians compared with nonmusicians, i.e., reduced asynchrony, lower variability, faster displacements (Franěk et al. 1991; Krause et al. 2010; Repp and Doggett 2007; review in Repp and Su 2013). Despite these differences, our model of coordination between dwell and movement explains the tapping behavior of the participants irrespective of their musical skills. Thus, in the framework of our experiment, musical expertise does not correspond to a specific, optimal skill that would be present in musicians and absent or less optimal in nonmusicians. On the contrary, all the participants seem to use the same optimal skill but with different inputs, i.e., their idiosyncratic variability in dwelling and moving. More specifically, drummers have a low temporal variability in dwelling, which, according to the model, explains why they use longer DT than nondrummers (see below for further discussion).

There are at least two limitations to this study. First, the proposed model is based on an arbitrary division of the period cycle between dwell and movement intervals. Alternatively, we could have divided each cycle into a beat stroke (downswing) and an extended backstroke (upswing) phase that includes the DT or into a backstroke and an extended beat stroke phase that includes the DT. Other divisions involving any stable kinematic landmark (e.g., peak velocity) would also be possible. Therefore, we cannot specifically claim that the nervous system specifically trades off DT and MT to control synchronization. In fact, we resolved to define dwelling in kinematic terms through the use of a velocity threshold, although we ignore whether specific motor processes are involved in this phase. However, although tapping on a force plate (Vaughan et al. 1998) or measuring EMG could help characterize the functional nature of the dwell phase, this would not fundamentally change our conclusions.

Despite this limitation, we may argue that dwelling corresponds to a motionless phase that could be profitably exploited to save energy. Interestingly, the drummers favored long dwell phases, $\sim 20-80\%$ of a cycle, compared with $\sim 20\%$ for the other subjects, consistent with an energy saving strategy. Furthermore, we confirmed a positive correlation between accuracy and beat stroke velocity (Krause et al. 2010), questioning the boundaries of more classical views suggesting the invariant nature of the beat stroke phase, e.g., that its duration is relatively independent of movement amplitude and tempo (Doumas and Wing 2007; Hove and Keller 2010; Stetson 1905).

The second limitation is related to the inescapable relationship between temporal and spatial variability. We interpreted movement variability as a result of temporal uncertainty (Newell et al. 1979). In computational terms, this means that we should draw a duration according to a given statistics and generate a spatially precise movement of this duration. Alternatively, we could have chosen a precise duration and generated a spatially variable movement as a consequence of uncertainty in control and estimation processes, e.g., signal-dependent noise (Harris and Wolpert 1998; Todorov and Jordan 2002). In this case, temporal variability could result from online corrections to match a desired final position, although the proper computational context remains to be elucidated (Guigon 2010; Rigoux and Guigon 2012). In fact, these observations divert us to the profound issue of how time is dealt with in motor control, and to the failure of current models to properly accommodate it. For example, a striking observation is about the shape of the velocity profile. The peak velocity occurred early in the trajectory during the upswing phase, as observed for movements toward spatial goals (Boyle et al. 2012; MacKenzie et al. 1987). Conversely, we observed peak velocities late in the trajectory during the downswing phase, as previously shown for movements aimed toward temporal goals (Craig et al. 2005; Rieger 2007; Walter and Rieger 2012). Although computational models could possibly explain the emergence of the former velocity profile, e.g., Huh (2012), to the best of our knowledge none of them can generate velocity profiles with late peak velocities as those observed experimentally. Related to this, an interesting and promising future research avenue may be the formalization of the relationship between synchronization and temporal interception (Craig et al. 2005; Lee 1998; Repp and Su 2013). In this context, a movement toward a temporal goal may be guided by an internal representation of the growing time to the goal. Interception of accelerating targets leads to asymmetric velocity profiles (Port et al. 1997) similar to those obtained during synchronizing downswing beat strokes.

Sensorimotor synchronization is a simple and sensitive tool that has been widely used to investigate functions and dysfunctions of key neural structures such as the basal ganglia (Nagasaki et al. 1988; Nakamura et al. 1978; Wing et al. 1984) and the cerebellum (Ivry et al. 1988; Ivry and Keele 1989; Spencer et al. 2003). Based on brain imaging and neuropathological deficits, most studies have suggested the implication of these neural structures for timing (Buhusi and Meck 2005; Coull and Nobre 2008; Ivry and Keele 1989; Ivry and Spencer 2004). Yet, after 30 years of research, no clear consensus has emerged about the specific nature of their implication (Claassen et al. 2013; Coslett et al. 2010; Jones et al. 2011). Our results offer a promising new avenue to contribute to this goal. First, they suggest that general analyses of synchronization should not be restricted to measures of accuracy and variability only but should additionally be based on kinematic and dynamic (if available) data, e.g., Jobbágy et al. (2005). Surprisingly, relatively few studies have quantified amplitude and velocity of rhythmic movements in patients with Parkinson's disease as a means to characterize bradykinesia and hypometria (Konczak et al. 1997; Ling et al. 2012). Second, our results point to the central role of dwelling in the context of temporal synchronization. Interestingly, several clinical studies have reported an increased DT in sequential and repeated movements in Parkinson's disease patients compared with control subjects (Agostino et al. 2003; Brontë-Stewart et al. 2000; Jones et al. 1992; Onla-or and Winstein 2001). Franco and Turner (2012) have shown that the selective blockage of dopamine transmission in monkey sensorimotor striatum leads to increased waiting times in the transition between cued reaching movements and selfinitiated, return movements. No similar result has been reported for cerebellar disorders, suggesting that the proposed analysis of finger tapping can lead to clean-cut functional dissociation between both areas putatively contributing to time prediction and control.

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DISCLOSURES

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

AUTHOR CONTRIBUTIONS

Author contributions: I.C., B.G., and E.G. conception and design of research; I.C. and E.G. performed experiments; I.C. and E.G. analyzed data; I.C., B.G., and E.G. interpreted results of experiments; I.C., B.G., and E.G. prepared figures; I.C., B.G., and E.G. drafted manuscript; I.C., B.G., and E.G. edited and revised manuscript; I.C., B.G., and E.G. approved final version of manuscript.

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