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RESEARCH ARTICLE

Two different processes for sensorimotor synchronization in continuous and discontinuous rhythmic movements

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Abstract To account for sensorimotor synchronization, the information processing and the dynamical systems perspectives have developed different classes of models. While the former has focused on cycle-to-cycle correction of the timing errors, the latter deals with a continuous, state-dependent within-cycle coupling between the oscillating limb and the metronome. The purpose of the present study was to investigate the extent to which the two modeling frameworks partially capture the same behavior or, instead, account for different aspects of synchronization. A comparative two-level analysis (time intervals and movement trajectories) of synchronized tapping and synchronized oscillation data revealed distinct patterns of results with regard to (1) the relationship between the (a)symmetry of movement cycles and the achievement of timing goals, and (2) the sequential or within-cycle organization of synchronization processes. Our results support the idea that movement trajectories contribute to the achievement of synchronized movement timing in two different ways as a function of the (dis)continuous nature of movement. We suggest that the two modeling frameworks indeed account for different synchronization processes involved in the process of keeping time with the beat.

Keywords Timing · Synchronization · Sequential error correction · Continuous coupling · Rhythmic movement

A central issue in experimental psychology is understanding how sensory information is used in the control of motor timing. In skills as diverse as piano playing or swinging a racquet in tennis, the task of synchronization requires bringing a limb or limb-segment periodically to a certain location in the workspace, in relation to an event (metronome or another limb or person). The task of coordinating with respect to such a referential event (Pressing 1999) is commonly referred to as sensorimotor synchronization (see Repp 2005 for a review).

Diverse approaches to sensorimotor synchronization generally fall into one of the two dominant perspectives on timing and coordination issues: the information processing, or cognitive perspective which includes for example the linear error correction framework (Vorberg and Wing 1996), and the dynamical systems perspective which develops accounts in terms of limit-cycle dynamics of an oscillator coupled to an environmental stimulus (Schöner and Kelso 1988). The dynamical systems perspective has also been extended to rhythm perception with considerable success (see for example the dynamic attending theory: Jones and Boltz 1989; Large and Jones 1999). In the world of motor timing, the two perspectives have often been considered as two alternative and discordant approaches to the same issues. Although they could obviously take advantage of each other for the understanding of sensorimotor synchronization processes, the respective ways of doing experiments, analyzing data, and their conceptual repertoires may have contributed to a rather parallel development. Most notably, the information processing and dynamical systems perspectives have preferentially investigated "discrete" discontinuous, or "smooth" continuous movement tasks, respectively. They also have different preferential levels of analysis: while the information processing perspective mainly focuses on the sequential structure of movement timing and its errors (synchronization with respect to events, or time intervals), the dynamical systems perspective mainly focuses on the

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within-cycle dynamics of movement trajectory, addressing the stability properties of the system.

Linear error correction models

The modeling frameworks in the two approaches are also quite different. On the one hand, the linear phase correction framework in its different incarnations (e.g., Mates 1994; Pressing and Jolley-Rogers 1997; Schulze and Vorberg 2002; Semjen et al. 1998; Vorberg and Wing 1996; for a review see Repp 2005) is a direct extension of the Wing and Kristofferson model for self-paced tapping (Wing and Kristofferson 1973); it formalizes synchronization through a sequential, autoregressive correction of asynchronies with the basic general form:

$$\mathrm{ASYN}_{n+1} = (1-\alpha)\mathrm{ASYN}_n + (C_n + M_{n+1} - M_n) - \tau, \quad (1)$$

where α represents the autoregressive correction parameter, τ is the constant period of the metronome, and C_n and M_n represent the time intervals prescribed by the internal timekeeper and the random motor delays, respectively, as defined by the Wing and Kristofferson model. Note that in the tapping literature, synchronization is currently accounted for by a dual-process model that combines the above-mentioned phase correction process with a period correction process (Mates 1994; Repp 2001a, 2005; Repp and Keller 2004; Semjen et al. 1998). In contrast to phase correction (Eq. 1), period correction is assumed to adjust the timekeeper periods to the tempo of the metronome sequence and has been shown to be dependent on the awareness of timing perturbations. However, this higher-level cognitive process is assumed to be mainly involved in task conditions where participants have to adapt to detectable modulations of the metronome periods, rather than in the case of constant metronome periods (Repp 2001a, 2005; Repp and Keller 2004; Semjen et al. 1998).

Timing from continuous coupling

The driven oscillator framework with its many manifest versions (e.g., Assisi et al. 2005; Fink et al. 2000; Jirsa et al. 2000; Schöner and Kelso 1988; Torre et al. 2009) has formalized synchronization through a continuous within-cycle coupling function between the oscillating limb's dynamics and the metronome sequence, obeying the basic general form

$$\ddot{x} = \alpha\dot{x} - \beta\dot{x}x^2 - \gamma\dot{x}^3 - \omega^2 x + \epsilon_1 \cos\Omega t [+ \epsilon_2 x \cos\Omega t], \quad (2)$$

where α, β, γ, and ω are the parameters of a hybrid limit-cycle oscillator (Kay et al. 1987), Ω is the frequency imposed by the metronome, and ε_1 (and ε_2) are the strengths of the linear (and parametric) driving terms.

Thus, a core distinction between these two modeling approaches is the assumption of a sequential versus a within-cycle organization of the regulation of synchronization. Seeing that the theoretical divergence may be to some extent methodology-based, the two perspectives are often times not directly comparable. There are a few studies which have proposed to go beyond the apparent divergence, suggesting that the two theories might actually be complementary or even comparable (e.g., Krampe et al. 2002; Pressing 1998, 1999; Repp 2005; Schöner 2002). An essential step to take in drawing from both these approaches is to combine the hitherto separate levels of analysis in a comprehensive approach. Balasubramaniam et al. (2004) proposed to assess sensorimotor synchronization by connecting the properties of movement trajectories and the synchronization goal achievement. Balasubramaniam et al. notably showed that the degree of asymmetry in the limit-cycle dynamics of tapping correlated with the accuracy of synchronization with an auditory metronome. The authors interpreted these results within the phase correction framework (Vorberg and Wing 1996), arguing that the adjustment of trajectories supports the correction of synchronization errors. In view of such tight relationship between synchronization goals and movement trajectories, focusing either on the within-cycle trajectories or on the sequential correction processes for modeling synchronization may seem an arbitrary choice.

Although there might be no doubt that timing goals and movement trajectories are indeed related, the nature (tightness and directionality) of this relationship is not straightforward: taking the two extremes, one may either consider that the movement trajectories are entirely adapted as a function of the performance in achieving the required timing goals, or one may consider that consistency in movement and in the effector's dynamical properties determine temporal regularity. Thus, different specifications of this relationship would provide continuous coupling and discrete error correction models for synchronization with different theoretical and experimental predictions.

A careful look at the literature on self-paced movement timing, in particular on the current theoretical distinction between event-based (or explicit) and emergent (or implicit) forms of timing (Robertson et al. 1999; Zelaznik et al. 2000, 2002; Delignières et al. 2004, 2008; Spencer et al. 2003; Spencer and Ivry 2005; Ivry et al. 2002; Torre and Delignières 2008a) may shed useful light on this issue. Indeed, this distinction refers to different forms of interplay between the temporal ordering information and the motor implementation, as a function of whether one performs rhythmic discontinuous (e.g., tapping) or continuous (e.g., oscillatory) movements. Event-based timing, associated with discontinuous movement performance, is thought to involve an effector-independent representation of time intervals by an internal timekeeper which prescribes temporal goals to the effector system. In contrast, emergent timing, associated with continuous movement performance, is assumed to not involve such a hierarchical organization as temporal regularity emerges from the intrinsic dynamics of the effector system, with the modulation of some (not directly temporal) parameters such as the oscillator's stiffness. That is, the different relationships between the kinematic properties of movement and the timing goals in self-paced performance may provide an extendable frame for thinking about the respective relevancies of within-cycle coupling or sequential error correction models for synchronized performance.

The present study aimed to clarify whether movement trajectories might contribute to the achievement of synchronized movement timing in two different ways as a function of the (dis)continuous nature of movement. Said differently, are within-cycle dynamics and sequential error correction different aspects of the same phenomenon, or do they actually capture different synchronization processes? To this aim, we combined the two levels of analysis in a comparative study of a part of Balasubramaniam et al. (2004)'s results obtained for synchronized tapping and Torre and Delignières (2009)'s results obtained for synchronized oscillations.

We proceeded as following: First we verified that synchronized tapping and synchronized oscillations featured the distinctive correlation properties of event-based and emergent timing. Second, we examined the within-cycle dynamics, especially to assess the (a)symmetry in movement cycles. Finally, we examined the relationship between the (a)symmetric within-cycle dynamics and the achievement of synchronization to assess the respective contributions of within-cycle and/or sequential regulations. In particular, in the case that there is a sequential synchronization process involved, one can expect to observe a correlation pattern reflecting a cycle-to-cycle propagation effect between the variable implementing the correction, e.g., cycle asymmetry, and the corrected variable, i.e., the asynchrony with the metronome.

Methods

Synchronized tapping and oscillations: data collection

We conducted a comparative reassessment of synchronized tapping and synchronized oscillation data provided by two experiments previously published in Balasubramaniam et al. (2004) and Torre et al. (2009), respectively.

In both experiments, participants performed rhythmic unimanual movements in synchrony with an auditory metronomic signal delivered at a frequency of 2 Hz (movement periods of 500 ms). In the synchronized tapping experiment, participants ($n = 7$) performed finger tapping with the index finger of their dominant hand. The forearm was supported by an elevated surface and the finger taps were performed without any mechanical contact. Participants were instructed to synchronize the reversals of maximal finger flexion with the metronomic signal. A marker placed at the tip of the index finger allowed to record the tapping kinematics using a three-camera motion capture system (Qualisys ProReflex).

In the synchronized oscillation experiment, participants ($n = 12$) performed forearm (pronation/supination) oscillations with their dominant hand. The elbow was supported beside the body and oscillations were performed by holding a joystick with a single degree of freedom in the frontal plane. Participants were instructed to synchronize the reversals of maximal pronation with the metronomic signals. A potentiometer located at the axis of the joystick allowed recording of the oscillations kinematics. (More detailed descriptions of the methods are provided in Balasubramaniam et al. 2004; Torre et al. 2009.)

Data analysis

The synchronized tapping and oscillation data were assessed using the same analyses for direct comparison. After smoothing the row data series using a simple moving average technique, an appropriate algorithm allowed determination of the timings of movement reversals, i.e., maximal flexion and extension for tapping, and maximal pronation and supination for oscillations. We computed the series of periods, semi-cycle durations, and asynchronies with the metronome. The periods were computed as the time intervals between consecutive movement reversals on the beat (maximal flexion and maximal pronation for tapping and oscillations, respectively). We defined semi-cycles *To* the metronome as the semi-cycles moving from maximal extension to maximal flexion, or from maximal supination to maximal pronation; accordingly, semi-cycles *Away* from the metronome were defined as the semi-cycle moving back to maximal extension or maximal supination. Series of 50 consecutive movement cycles were submitted to further analysis.

The first step aimed at verifying that the rhythmic tapping and oscillation tasks involved event-based and emergent forms of timing, respectively. According to extensive literature on rhythmic movement timing and from our own previous work, one can consistently distinguish between event-based and emergent timing on the basis of the typical negative or non-negative lag 1 autocorrelation, respectively, of the series of produced periods[1] (Delignières et al. 2008; Lemoine and Delignières 2009; Torre and Delignières 2008a). Therefore, we computed the autocorrelation functions of the series of periods produced in the two conditions and tested for the difference to zero of the lag 1 autocorrelation.

The second step aimed at assessing the (a)symmetry of movement cycles. We summarized the within-cycle kinematics of synchronized taps and synchronized oscillations in average normalized limit-cycles computed over all participants in the same task. Each cycle was normalized using 80 points equidistant in time, and the 50 cycles were averaged point by point. Comparison of the average limit-cycles allowed graphical examination of the characteristic (a)symmetry of synchronized tapping and oscillation cycles. In addition, we quantified the temporal (a)symmetry between the semi-cycles *To* and *Away*. This (a)symmetry was determined cycle by cycle as the difference between the durations of the two semi-cycles expressed as a percentage of the current whole-cycle period: %Asymmetry = 100*(semi-cycle *Away* − semi-cycle *To*)/Period.

The third step aimed at characterizing the relationship between the cycle dynamics and the achievement of synchronized performance in tapping and oscillations. To this aim we tested for correlation between the degree of asymmetry in cycles and the within-trial variability of asynchronies. In order to refine the characterization of this relationship between cycle dynamics and timing goals, we subsequently examined the sequential organization of synchronization processes involved in tapping and oscillations: we computed the autocorrelation functions of asynchronies produced in the two conditions, and we used cross-correlation analysis to specify the patterns of correlations (1) between the asynchronies and the durations of the preceding two semi-cycles *Away* and *To*, and (2) between asynchronies and the durations of the following two semi-cycles *Away* and *To*.

[1] Event-based timing, associated with discontinuous rhythmic movement, has been conceived in accordance with the two-level architecture of the Wing and Kristofferson (1973) model: At the timekeeper level, discrete cognitive events delimit the successive time intervals to produce and trigger the execution of the taps at the motor level. The execution of each tap is assumed to be affected by a random (white noise) motor delay. Thus, each produced time interval is affected by differenced white noise which yields the negative lag 1 autocorrelation in the series of periods. Emergent timing, associated with continuous rhythmic movement, is assumed to involve a continuous regulation of the parameters (e.g., oscillator stiffness) that determine the period of an oscillating limb. Therefore, each produced period is affected by a single noise term which predicts no negative lag 1 autocorrelation in the series of periods.

Results

Event-based and emergent forms of timing

Figure 1 displays the autocorrelation functions computed on synchronized tapping and oscillation periods. The results showed that the mean lag 1 autocorrelation ($r = -0.34$) of series of periods produced in synchronized tapping was significantly negative ($t_6 = -5.80$, $p < 0.05$). In contrast, the mean lag 1 autocorrelation (r = -0.02) of synchronized oscillations periods did not significantly differ from zero (t_{11} = -0.47, $p > 0.05$). Both autocorrelation functions were not significantly different from zero beyond the first lag. This result strongly suggests the involvement of an event-based form of timing in synchronized tapping and an emergent form of timing in synchronized oscillations.

Symmetry of within-cycle trajectories

Figure 2 displays the average limit-cycles obtained for synchronized tapping and synchronized oscillations. For synchronized tapping, the average cycle exhibits a strong asymmetry with respect to the position axis, with a global upward shift that clearly distinguishes between a slow semi-cycle *Away* from the metronome and a fast semi-cycle *To* the metronome. In synchronized oscillations, in contrast, the average limit-cycle is nearly symmetric with respect to the position axis, showing a homogeneous distribution of velocities between the semi-cycles *To* and *Away*. Nevertheless, one can graphically notice a slight asymmetry with respect to the vertical (velocity) axis that is between the semi-cycles at the *Opposite* and *Around* the point where the metronome occurs in the movement cycles.

In the synchronized tapping condition, the durations of semi-cycles *To* and *Away* were significantly different ($t_6 = 6.80$, $p < 0.05$), with mean durations of 187 ms (±16) and 315 ms (±24), respectively. The mean percentage of temporal asymmetry was 25.5%. In the synchronized oscillations condition, the mean durations of semi-cycles *To* and *Away* were equal, 250 ms (±12) and 250 ms (±11), respectively. Obviously, the temporal asymmetry was 0%.

Relationship between synchronization goals and cycle dynamics

Results showed that the variability of asynchronies, assessed by the series' standard deviations, was higher ($t_{17} = -2.56$, $p < 0.05$) in synchronized oscillations (27 ms ± 8) than tapping (18 ms ± 3).

To examine the relationship between synchronization goals and cycle dynamics, we first computed linear correlations between the percentages of temporal asymmetry

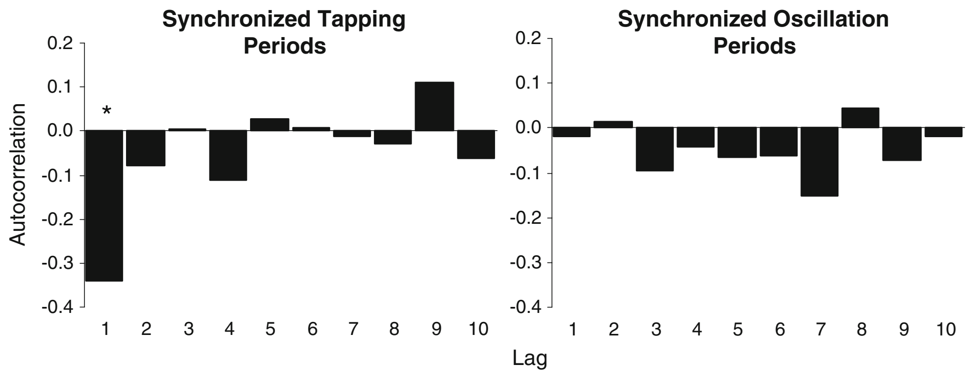

Fig. 1 Mean autocorrelation functions of periods produced in synchronized tapping and synchronized oscillation tasks. The lag 1 autocorrelation is significant ($p < 0.05$) for synchronized tapping but not for synchronized oscillations

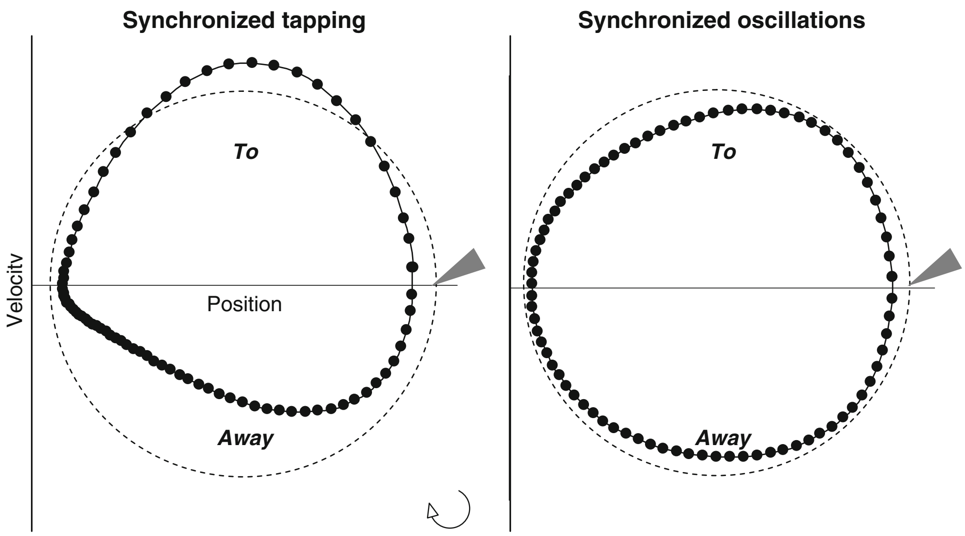

Fig. 2 Mean limit cycles computed over 50 cycles produced by participants in synchronized tapping and synchronized oscillations, after normalization of the number of data points per cycle (position and velocity units are set arbitrarily). The *gray pointer* represents the occurrence of the metronome signal in cycles. The *dashed circle* represents harmonic movement with equal distribution of velocity across the two semi-cycles. In the case of synchronized tapping performance, the semi-cycles *To* and *Away* from the metronome exhibit a strong asymmetry, with higher velocities being concentrated in the (fast) semi-cycle *To* the metronome. In contrast, semi-cycles *To* and *Away* are nearly symmetric (with respect to the position axis) in synchronized oscillations

and the variability of resulting asynchronies. The results showed a strong negative correlation ($r_5 = -0.76$, $p < 0.05$) between the degree of asymmetry between the semi-cycles *To* and *Away* and the variability of asynchronies produced by participants in synchronized tapping. In contrast, as oscillation cycles did not present any asymmetry between the semi-cycles *To* and *Away*, results also did not show any correlation between the degree of asymmetry and the variability of asynchronies in synchronized oscillations ($r_{10} = -0.06$, $p > 0.05$). Similarly, results did not show any correlation between the percentage of temporal asymmetry between the semi-cycles *Opposite* and *Around* and the variability of asynchronies in synchronized oscillations ($r_{10} = 0.04$, $p > 0.05$).

To go further into the assessment of the sequential course of synchronization processes in tapping and oscillations tasks, we examined the cross-correlation patterns between asynchronies and the two preceding and two following semi-cycles *Away* and *To* the metronome. The average results across participants are reported in Table 1. The obtained patterns were different for synchronized tapping and synchronized oscillations: In synchronized tapping, asynchronies were positively correlated with the durations of the directly preceding semi-cycles *Away* ($r_{48} = 0.38$, $p < 0.05$) and negatively correlated with the durations of the immediately following semi-cycle *Away* ($r_{48} = -0.48$, $p < 0.05$). In synchronized oscillations, the results showed a similar positive correlation between asynchronies and the directly preceding semi-cycles *Away* ($r_{48} = 0.34$, $p < 0.05$). However, asynchronies were negatively correlated with the following semi-cycles *To* ($r_{48} = -0.37$, $p < 0.05$) instead of the immediately following semi-cycles *Away*. Figure 3 illustrates the obtained cross-correlation patterns.

Finally, we considered the autocorrelation functions of the series of asynchronies. The strength of correlation between asynchronies separated by different lags is likely to provide information about the effectiveness of the corrective synchronization processes (Vorberg and Wing 1996). For instance, a positive correlation between asynchronies at lag 1 shows that a part of the asynchrony produced in the previous movement cycle persists in the immediately following cycle. The decay of the autocorrelation function over higher lags indicates how many cycles are needed on average to correct entirely for the synchronization error produced at any cycle in the series. The obtained autocorrelation functions exhibited different shapes: in synchronized tapping, the autocorrelation was significantly positive only at lag 1 ($t_6 = 4.93$, $p < 0.05$) while in synchronized oscillations it decayed more slowly, persisting significantly positive up to lag 4 ($t_{11} = 2.67$, $p < 0.05$).

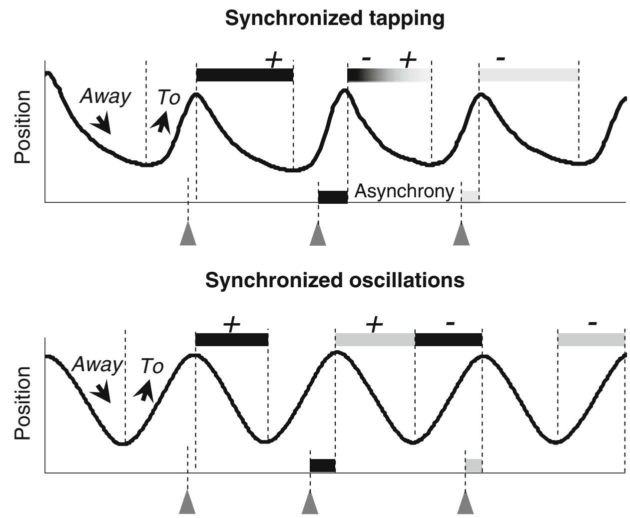

Fig. 3 Illustration of the cross-correlation patterns between the asynchronies and the two preceding and two following semi-cycles *To* and *Away* observed in synchronized tapping and oscillation tasks. The *plus* and *minus signs* represent the positive or negative correlations between the semi-cycles and the related asynchrony. The main point is that in the case of tapping the duration of a given semi-cycle (*Away*) is related with both the preceding and the following asynchronies, whereas in the case of oscillations two consecutive asynchronies do not happen to be correlated with the same semi-cycle

Discussion

Two current frameworks for modeling sensorimotor synchronization assume different forms of regulation: a continuous within-cycle coupling between the limb movement and the metronome *versus* a sequential error correction process based on asynchronies. We based on the article by Balasubramaniam et al. (2004) who argued that the temporal asymmetry in the cycle dynamics, in particular between the semi-cycles *To* and *Away* from the occurrence of the metronome, may serve the correction of consecutive asynchronies to achieve and maintain synchronization.

The present study was intended to clarify to what extent the two modeling frameworks partially capture the same behavior at different levels of the movement organization or, instead, account for actually different synchronization processes. Therefore, we focused on the relationship between the cycle dynamics and the achievement of synchronization goals in synchronized tapping and synchronized oscillations. We reanalyzed part of the synchronized tapping data by Balasubramaniam et al. (2004) and used this pattern of results as a reference pattern to which we compared the results obtained for synchronized oscillation (from Torre and Delignières 2009). The analyses yielded consistently contrasting patterns of results. Differences appeared both in the relationship between the (a)symmetry of movement cycles and the achievement of timing goals, and in the sequential versus within-cycle organization of synchronization processes.

Table 1 Average lag 1 cross-correlations ($p < 0.05$) between asynchronies and the two preceding and two following semi-cycles for synchronized tapping and synchronized oscillations, and for synchronized oscillations simulated by a model assuming a velocity-based within-cycle coupling (Torre et al. 2009)

Preceding semi-cycles			Following semi-cycles	
Away	To		Away	To
Tapping oscillations				
0.38	0.18	Asynchrony	−0.48	−0.09
0.34	0.12		−0.07	−0.37
Simulated oscillations				
0.82	0.01	Asynchrony	0.18	−0.72

Does temporal asymmetry in cycles serve synchronized timing goals?

The graphical examination and the quantification of the temporal asymmetry between semi-cycles showed a clear asymmetry between a fast semi-cycle *To* and a slow semi-cycle *Away* from the metronome in synchronized tapping. Moreover, the percentage of temporal asymmetry was strongly negatively correlated with the variability of the series of asynchronies: the more asymmetric were the produced movement cycles the more stable were the timing errors with respect to the metronome. In synchronized oscillations, in contrast, the semi-cycles *To* and *Away* were totally symmetric. Instead, there was a characteristic asymmetry between the orthogonal semi-cycles, i.e., the semi-cycles *Opposite* and *Around* the occurrence of the metronome; however, the degree of asymmetry was not correlated with the variability of the produced asynchronies in this case.

These contrasted results may seem counter-intuitive at first sight as they suggest that the asymmetry in movement trajectories indeed serves timing goals in the discontinuous movement framework, where models have largely disregarded the cycle dynamics so far, while it appears to be not related to the achievement of timing goals in a continuous movement framework, where focus has usually been on the within-cycle dynamics. However, a closer look at the organization of synchronization processes in tapping and oscillations might show that the nature of the relationship between movement trajectories and timing goals is merely different in nature in the two conditions.

Is there a sequential organization in the regulation of synchronization?

The core issue between current frameworks for modeling synchronized movement performance is the sequential *versus* within-cycle organization of the regulation of synchronization. Basically, one can consider that if there is a sequential regulation of synchronization (as assumed by the phase correction framework) it would imply that one can analyze a synchronized movement series in terms of a *before* and an *after* with respect to the occurrence times of the metronome: A given asynchrony with the metronome at occurrence n induces a corrective effect in the cycle following the metronome (i.e., in the semi-cycle *Away* from the metronome or in the semi-cycle *To* the next metronome occurrence), this corrective effect being supposed to regulate the asynchrony at occurrence $n + 1$, and so forth in the synchronized movement sequence.

Now, as cycle asymmetry appears to be serving the synchronization goals in tapping, what is the relationship between the assumed sequential organization of synchronization processes and this asymmetry? Also with regard to synchronized oscillations, the fact that the analysis did not show any asymmetry between the average durations of the semi-cycles *To* and *Away* does not preclude that the cycle-to-cycle variations of these durations may be related to the produced asynchronies in a sequential way. The cross-correlation analyses revealed distinct correlation patterns in synchronized tapping and oscillations (Table 1). As shown in Fig. 3, in the case of synchronized tapping, the cross-correlation pattern is consistent with a serial propagation effect between the correcting and the corrected variables: As previously shown by Balasubramaniam et al. (2004), current asynchronies are positively correlated with the preceding semi-cycle *Away* and negatively correlated with the immediately following semi-cycle *Away*. This correlation pattern supports the idea that synchronization is achieved through the sequential regulation of the durations of the semi-cycles *Away*. In contrast, the cross-correlation pattern obtained for synchronized oscillations is not consistent with a sequential organization of the regulation of synchronization, since consecutive asynchronies do not happen to be correlated with the same semi-cycle.

It is worth noticing that although the cross-correlation pattern in synchronized oscillations does not support models assuming sequential error correction, the finding of any significant cross-correlations between asynchronies and preceding and following semi-cycle durations may lead to one question the validity of within-cycle coupling models. Indeed, while it can naturally be understood that autoregressive correction of asynchronies as assumed by the phase correction framework may introduce such sequential dependencies into the series, it is intuitively much less evident that such dependencies could be a byproduct of a continuous within-cycle coupling function based on the oscillator's state variables (e.g., Jirsa et al. 2000; Torre et al. 2009). To test whether a within-cycle coupling allows accounting for the empirical cross-correlations, we simulated oscillation cycles using the model proposed by Torre et al. (2009) and adapted from Jirsa et al. (2000). In this model, a hybrid self-sustained oscillator is driven by a parametric coupling function based on the oscillator's instantaneous velocity (for details, see Torre et al. 2009):

$$\ddot{x} = \alpha\dot{x} - \beta\dot{x}x^2 - \gamma\dot{x}^3 - \omega_i^2 x + \epsilon_1 \cos\Omega t + \epsilon_2 \dot{x}\sin\Omega t + \sqrt{Q}\varepsilon_t \qquad (3)$$

In this equation, ω_i represents the linear stiffness parameter, α, β, γ represent the linear, Van der Pol, and Rayleigh damping parameters, respectively, and ε_1 and ε_2 are the strength of the linear and parametric driving terms. Q represents a white noise term. This model was shown to reproduce most of the empirical properties of synchronized oscillations, notably the global limit-cycle dynamics and the serial long-range correlation properties in the series of periods and asynchronies. For the present purpose we simulated 20 series of 100 cycles, using $\alpha = 0.5$, $\beta = 1.0$, $\gamma = 0.02$, $\Omega = 4\pi$, $\varepsilon_1 = 0.2$ and $\varepsilon_2 = 0.05$, and $Q = 0.5$. The cross-correlation pattern determined obtained for the simulated series is summarized in Table 1. Although the correlations were globally stronger for simulated series than for the experimental series, the model reproduced the empirical cross-correlation pattern. This means that the cross-correlations between asynchronies and the preceding and following semi-cycle durations in synchronized oscillations can indeed be considered as a product of a within-cycle coupling process while they are inconsistent with a sequential error correction process.

Different models for different ways to achieve sensorimotor synchronization

The examination of temporal asymmetry and cross-correlations evidenced consistently different patterns of results for synchronized tapping and synchronized oscillations and supported the idea that different synchronization processes were involved. These processes differ in two aspects: the role of movement trajectories in the achievement of synchronization and the sequential or within-cycle organization of the regulation of synchronization. In synchronized tapping, the present results are consistent with the current linear error correction framework, assuming that synchronization is achieved through a sequential correction process based on asynchronies. As initially argued by Balasubramaniam et al. (2004), one can consider that the asymmetry of the cycle dynamics, especially the regulation of the durations of the successive semi-cycles *Away* from the metronome implements the correction of synchronization errors.

In synchronized oscillations, in contrast, results show no relationship between the (a)symmetry of movement trajectories and the synchronization performance and are in accordance with the hypothesis of a continuous within-cycle coupling rather than a sequential correction process explicitly based on asynchronies. A parametric coupling function based on the instantaneous velocity of the oscillation limb (Torre et al. 2009) is consistent with the finding of a systematic asymmetry between the semi-cycles *Opposite* and *Around* the occurrence of the metronome in the case of synchronized oscillations, and it reproduced the pattern of cross-correlations between asynchronies and the preceding and following semi-cycle durations. Moreover, the assumption that asynchronies do not constitute a reference time interval on which synchronization processes are basing is consistent with the fact that synchronization seems less efficient in the case of oscillations than in the case of tapping: our results indeed showed that asynchronies were significantly more variable in oscillations than tapping. Moreover, the persistence (up to lag 4) of positive autocorrelations in the series of asynchronies in synchronized oscillations seems consistent with the idea of a progressive adjustment of oscillation periods, distributed over a number of successive movement cycles, rather than a cycle-to-cycle correction of asynchronies.

Accordingly, in view of this comparative study one may consider that movement trajectories play different roles in synchronization; they *serve* the timing goals by implementing error correction in the case of synchronized tapping, while they *implement* temporal regularity in the case of synchronized oscillations. This distinction is in line with the current theoretical distinction between event-based and emergent timing which has been grounded on self-paced timing tasks; it is moreover supported by the present results showing that the distinctive signatures of event-based and emergent timing (i.e., the negative versus non negative lag 1 autocorrelation in the series of produced periods) persisted in synchronized tapping and oscillations.

One might nevertheless be inclined to nuance this binary distinction between the ways to achieve synchronization in tapping and oscillations. In a study on tapping in synchrony with a subliminally perturbed metronome sequence, Repp (2001b) suggested that the observed imperfect adaptation to the timing perturbations may be due to a balance between two coexistent and competing processes in synchronized movement performance: (1)"sensorimotor coupling", responsible for adapting the movement to the timing sequence, and (2) "motor persistence" which tends to maintain the regularity of periodic movement. The author suggested that the balance between these two processes might be modified by some task factors which are likely to reinforce the influence of either sensorimotor coupling or motor persistence. Then, it seems worth posing the question of whether the two synchronization processes described in the present study, which are characterized by different relationships between movement trajectories and timing goals, are mutually exclusive indeed or, instead, represent dominant contributions to synchronized movement performance as a function of the task?

It has been argued that discrete or discontinuous movements involve different patterns of neural organization than rhythmic ones (Hogan and Sternad 2007; Schaal et al. 2004). However, there are several classes of movements such as those that are presented here that fall under the category of being rhythmic, but how they maintain their strict periodicity is under investigation. It would be interesting to investigate if there are indeed neural differences between the two kinds of synchronization tasks. Our results suggest that the strategies for error monitoring and correction used by the cerebellum and the basal ganglia to fine-tune a periodic motor command might be differently organized. In the case of the more discontinuous tapping movement, it has been previously argued that the velocity modulation in the two semi-cycles might be an active strategy used by the CNS to detect proprioceptive sensory information (Balasubramaniam 2006). A possible inference from the present results might be that when this asymmetry is not available to be exploited, a more continuous coupling function is used. Future neuroimaging studies could be designed to pick up on this difference to see if distinct neural regions are involved in these processes.

A recent study has also shown that during smooth continuous movements, there is an increased uncertainty in the CNS about the discrepancy between the planned and produced movements. This results in a diminished timekeeping ability (Elliott et al. 2009). On a related note, Balasubramaniam et al. (2004) also showed that mean squared jerk is a good predictor of timekeeping accuracy. While our study did not look at the values of this parameter in the two different synchronization tasks, one could speculate that the jerk values were lower for the synchronized oscillations. Comparing the optimization strategies and the role of jerk for the kinds of trajectory formation in synchronized tapping and oscillations is likely to be an important avenue for future research.

In sum, we support the idea that the two current classes of models for synchronized movement performance, the linear error correction framework (Mates 1994; Pressing and Jolley-Rogers 1997; Schulze and Vorberg 2002; Semjen et al. 1998; Torre and Delignières 2008b; Vorberg and Wing 1996) and the driven oscillator framework (Assisi et al. 2005; Fink et al. 2000; Jirsa et al. 2000; Schöner and Kelso 1988; Torre et al. 2009), cannot be considered as discordant and alternative accounts focusing on different aspects of the behavioral outcome of the same synchronization process. Rather, the two frameworks account for different synchronization processes involved as a function of movement, therefore having their own domains and limits of relevance. Further investigations should clarify to what extent these synchronization processes are mutually exclusive or complementary and accordingly judge the relevance of the two modeling frameworks for different task demands.

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