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# Quantifying phase correction in sensorimotor synchronization: Empirical comparison of three paradigms

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# 1. Introduction

# 1.1. Background

Establishment and maintenance of synchrony between a rhythmic movement and an external rhythm, such as a metronome in the simplest case, require some form of error correction. Otherwise the variability inherent to the movement would accumulate from cycle to cycle and inevitably lead to phase drift, even if the mean periods are identical (Vorberg & Wing, 1996). Two error correction processes have been distinguished: phase correction and period correction (Mates, 1994a, 1994b). Phase correction is a local within-cycle adjustment of the movement timing, whereas period correction is a longer lasting change of the underlying tempo of the movement and thus affects future cycles as well. Whereas phase correction is largely automatic and does not require conscious perception of synchronization errors, evidence suggests that period correction is under greater cognitive control and dependent on conscious perception of a tempo change in the external rhythm (Repp, 2001b; Repp & Keller, 2004). In the present study the focus is

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#### ABSTRACT

Tapping in synchrony with a metronome requires phase error correction, a process often described by a single-parameter autoregressive model. The parameter ( $\alpha$ ) is a measure of sensorimotor coupling strength. This study compares  $\alpha$  estimates obtained from three experimental paradigms: synchronization with (1) a perfectly regular metronome (RM), (2) a perturbed metronome containing phase shifts (PS), and (3) an "adaptively timed" metronome (AT). Musically trained participants performed in each paradigm at four tempi, with baseline interval durations ranging from 400 to 1300 ms. Two estimation methods were applied to each data set. Results showed that all  $\alpha$  estimates increased with interval duration. However, the PS paradigm yielded much larger  $\alpha$  values than did the AT paradigm, with those from the RM paradigm falling in between. Positional analysis of the PS data revealed that  $\alpha$  increased immediately following a phase shift and then decreased sharply. Unexpectedly, all PS  $\alpha$  estimates were uncorrelated with the RM and AT estimates, which were strongly correlated. These results suggest that abruptly perturbed sequences engage a different mechanism of phase correction than do regular or continuously modulated sequences.

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on phase correction, as tempo was not varied systematically within rhythmic sequences.

If the rhythmic movement is continuous (i.e., oscillatory), phase correction will likewise be continuous and can then be described in terms of a differential equation for unidirectional coupling (entrainment) between nonlinear oscillators (e.g., Large, 2008; Pressing, 1999: Torre & Balasubramaniam, 2009). If the movement is discontinuous and thereby generates discrete events, such as finger contact with a solid surface in tapping, phase correction, although potentially deriving from a continuous internal oscillatory process, will be observed only intermittently (especially if only the time of the tap is recorded, as is commonly done) and then can be described in terms of an autoregressive model. A simple linear model, according to which the timing of each tap is adjusted by a proportion  $\alpha$  of the most recent asynchrony (Mates, 1994a; Pressing, 1998; Vorberg & Schulze, 2002; Vorberg & Wing, 1996), is generally considered to give an adequate characterization of phase correction in synchronization with a metronome if the tempo is not very fast.<sup>1</sup> Asynchrony is defined as the difference between the time of a tap and the time of





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<sup>&</sup>lt;sup>1</sup> At fast tempi or with difficult rhythms, adjustments to tap timing may be based on the previous two asynchronies (see Pressing, 1998; Semjen, Schulze, & Vorberg, 2000; Vorberg & Schulze, 2002). In the Discussion section, we point out another potential complication, due to fractal noise in the data.

a metronome tone; it is negative if the tap leads the tone. Stated formally (Vorberg & Schulze, 2002),

$$I_n = T_n - \alpha A_n + M_{n+1} - M_n, \qquad (1)$$

where  $I_n$  is the interval between two taps,  $T_n$  is the variable interval generated by an internal timekeeper,  $\alpha$  is the phase correction parameter,  $A_n$  is the asynchrony associated with the tap initiating  $I_n$ , and  $M_{n+1}$  and  $M_n$  are variable motor delays associated with the two taps. Because it can easily be shown (see Vorberg & Schulze, 2002) that

$$I_n = C_n + A_{n+1} - A_n, \qquad (2)$$

where  $\mathsf{C}_{\mathsf{n}}$  is the current interval between two metronome tones, it follows that

$$A_{n+1} = (1-\alpha)A_n + T_n + M_{n+1} - M_n - C_n.$$
(3)

Eq. (3) describes a recursive relation between successive asynchronies governed by the parameter  $\alpha$ . Alpha is analogous to the coupling parameter in an oscillator model and captures the efficiency or gain of phase correction, reflecting the strength of sensorimotor coupling. In theory (Vorberg & Schulze, 2002), stable synchronization requires  $\alpha$  to be between 0 and 2, but values larger than 1 (i.e., overcorrection, resulting in successive adjustments resembling a damped oscillation) have rarely been reported (though see Repp, 2011b). The mean asynchrony in tapping with a metronome is typically not zero but negative (i.e., taps tend to anticipate metronome sounds). It may correspond to the subjective point of synchrony, so that phase correction is based not on raw asynchronies but on perceived asynchronies (i.e., deviations from the subjective point of synchrony). However, substituting perceived for raw asynchronies does not change the basic linear model.

The linear model of phase correction does not require that the external rhythm be completely regular. The model is assumed to apply to synchronization with any kind of rhythmic sequence (Pressing, 1998), as long as asynchronies do not get very large. For example, when intermittent timing perturbations such as phase shifts (changes in the duration of a single interval) are introduced into a metronome to create unexpected changes in asynchrony, the model predicts that the corrective phase shift of the tap immediately following a perturbation - the phase correction response (PCR) - should, on average, be proportional to the perturbation (more precisely, to the change in asynchrony it causes, which on average is equal to the perturbation but has the opposite sign), with  $\alpha$  being the proportionality constant. Repp (2002a, 2002b, 2011b) has shown that this is indeed so for small perturbations up to about 15% of the baseline inter-onset interval (IOI) of the metronome, though there is sometimes an asymmetry, with positive PCRs (tap delays) being larger than negative PCRs (tap advances). When perturbations get large, the PCR gets proportionally smaller, which indicates a nonlinear (sigmoid-shaped) dependence of  $\alpha$  on perturbation magnitude across the range from -50% to 50% of the IOI (see also Engbert et al., 1997; Engbert, Krampe, Kurths, & Kliegl, 2002). Thus the linear phase correction model with a fixed  $\alpha$  is valid only for relatively small perturbations and asynchronies, where the sigmoid function is linear.

The strong linearity of the PCR function as it passes through zero indicates that even subliminal perturbations are corrected (Repp, 2000, 2001a, 2001b; Thaut, Tian, & Azimi-Sadjadi, 1998). There is no discontinuity, reflecting a perceptual threshold, in the function. The linearity suggests a mechanism that is either based on subconscious registration of all perturbations or asynchronies, regardless of magnitude, or on time points (event onsets) instead. Hary and Moore (1985, 1987) proposed that participants reset their tapping phase either in response to the preceding metronome sound, which on average results in perfect phase correction ( $\alpha = 1$ ), or in response to the preceding tap,

which implies absence of phase correction ( $\alpha = 0$ ). Random alternation (as suggested by Hary & Moore) or dynamic competition (Repp, 2001a, 2001b) between these two processes can explain  $\alpha$  values between 0 and 1, as commonly observed. The idea of such mixed phase resetting is similar to the notion of unidirectional coupling between oscillators, which obviously does not involve mediation by perception; rather, there is competition and equilibrium between the dynamics of the driving and driven oscillators. It is worth noting, however, that the mixed phase resetting model is formally identical to the asynchrony-based linear phase correction model (Eq. (3)); the difference is merely conceptual (see Repp, 2005; Schulze & Vorberg, 2002) and need not concern us here.

Jacoby and Repp (submitted for publication) have recently presented a general linear framework for error correction in synchronization that subsumes all kinds of linear models. For an even more general theory of referential behavior that encompasses linear and nonlinear models, see Pressing (1999).

# 1.2. Estimating alpha

As a measure of sensorimotor coupling strength, the magnitude of the phase correction parameter  $\alpha$  is of interest as a dependent variable in studies of individual differences in normal or clinical populations and in comparisons of experimental conditions designed to affect coupling strength. Existing empirical studies have often relied on the perturbation method to estimate  $\alpha$ , for example to compare musicians and non-musicians (Repp, 2010) or to show that  $\alpha$  increases with the baseline IOI of the metronome (Repp, 2008, 2011b). It is not known, however, to what extent these findings are specific to the perturbation method and its associated method of estimating  $\alpha$  (described below). There are other ways of estimating  $\alpha$ that do not require intermittent perturbations, and the purpose of the present study was to compare estimates from three different synchronization paradigms for the same individuals. In this section, we describe briefly the different paradigms and their associated estimation methods for obtaining  $\alpha$ .

# 1.2.1. Regular metronome (RM paradigm)

Although the linear phase correction model has been developed formally in considerable detail (Mates, 1994b; Pressing, 1998; Schulze & Vorberg, 2002; Vorberg & Schulze, 2002; Vorberg & Wing, 1996; Williams, 2006), estimating  $\alpha$  from tapping in synchrony with a perfectly regular metronome is not entirely straightforward. There is a simple analytic solution (Pressing, 1998; Vorberg & Schulze, 2002) according to which

$$\alpha = 1 - AC2/AC1, \tag{4}$$

where AC1 and AC2 are the lag-1 and lag-2 autocorrelations (or autocovariances, ACVs) of the time series of asynchronies, respectively. However, because AC1 approaches zero when phase correction is optimal in terms of yielding minimal variability of asynchronies (which, interestingly, occurs at an  $\alpha$  value of less than 1; Vorberg & Schulze, 2002), estimates of  $\alpha$  using this formula can be unstable. Also, values of AC2 can be quite unreliable if they are based on short time series (Repp & Keller, 2008). Vorberg and Schulze (2002) furthermore point out an estimation bias in ACVs. To avoid this bias, they recommend a computer optimization approach to find the  $\alpha$ value that yields the best approximation to the empirical ACV function (i.e., ACV as a function of lag). For further details, see the Methods section.<sup>2</sup>

<sup>&</sup>lt;sup>2</sup> Pressing (1998) introduced another method, the method of bins. It seems not to have been applied since the original publication (though see Williams, 2006), and we will not consider it further here.

# 1.2.2. Metronome with phase shifts (PS paradigm)

An alternative and seemingly more straightforward method of estimating  $\alpha$  requires introducing occasional abrupt timing perturbations (typically phase shifts, which are changes in single IOIs) into a metronome and examining the PCRs of the immediately following taps (e.g., Repp, 2001a, 2008). The PCR is usually calculated as the difference between the PCR asynchrony and the preceding asynchrony. As long as the perturbations stay within about  $\pm$  15% of the IOI, the PCR of the next tap will generally vary as a linear function of perturbation magnitude (Repp, 2002b, 2011b), and the slope of this regression line (which expresses the PCR as a proportion of phase shift magnitude) is the estimate of  $\alpha$ .

# 1.2.3. Adaptively timed sequences (AT paradigm)

This method was first used in unpublished work by Vorberg (2005) and then was extended by Repp and Keller (2008). Repp and Keller employed computer-controlled metronomes that had a fixed underlying period (IOI = 500 ms) but varied in their timing because the computer was endowed with various degrees of phase correction capability, following the linear model of Vorberg and Schulze (2002). Thus, the timing of the metronome varied from one tone to the next, depending on the asynchronies generated by the participant. The phase correction parameter assigned to the computer,  $\alpha_c$ , was varied between 0 and 1. The computer adjusted each metronome IOI by adding  $\alpha_c A_n$  to the baseline IOI duration ( $C_n$  in Eq. (3) above), thereby assisting the human participant in reducing asynchronies. The setting of  $\alpha_c = 0$  resulted in a perfectly regular metronome. The lag-1 autocorrelation (AC1) of the asynchronies was found to decrease linearly from positive to negative values as  $\alpha_c$  increased. As mentioned above, the AC1 is zero when phase correction is optimal (i.e., when the variance of asynchronies is minimal). In the AT paradigm, phase correction is optimal ( $\alpha_{opt}$ ) when the sum of human and computer phase correction  $(\alpha_h + \alpha_c)$  is optimal (Vorberg, 2005). It follows that

$$\alpha_{\rm h} = \alpha_{\rm opt} - \alpha_{\rm c} * \tag{5}$$

where  $\alpha_c^*$  is the value of  $\alpha_c$  for which AC1 = 0 (i.e., the x-axis intercept of the regression line relating AC1 and  $\alpha_c$ ). Repp and Keller obtained an independent estimate of  $\alpha_{opt}$  by computer simulation of their data. Importantly, their simulations showed the data to be consistent with the assumption that  $\alpha_h$  remained constant as  $\alpha_c$  increased.

#### 1.3. Aims of the present study

The purpose of this study was to compare  $\alpha$  estimates obtained from the PS paradigm, which has been used extensively by the first author in the past (e.g., Repp, 2001a, 2001b, 2002b, 2008, 2011b), with estimates obtained from the RM and AT paradigms. In particular, we asked whether (1) all three paradigms yield  $\alpha$  estimates of the same magnitude, (2) all estimates increase with baseline IOI duration, as estimates obtained from the PS paradigm have been shown to do (Repp, 2008, 2011b), and (3) all estimates are highly correlated (i.e., reflect the same individual differences in phase correction efficiency).

Our study was fueled by a growing suspicion that the PS paradigm yields higher  $\alpha$  estimates than other paradigms. For example, Repp (2010) obtained results suggesting instantaneous phase correction (mean  $\alpha \approx 1$ ) at a moderately fast sequence tempo (baseline IOI = 500 ms), which is not a typical finding in synchronization with a perfectly regular metronome at this tempo (e.g., Pressing, 1998; Semjen et al., 2000). By contrast, Repp and Keller (2008), using the AT paradigm with the same baseline IOI, obtained rather low  $\alpha$  estimates for their participants, ranging from 0.25 to 0.54. A comparison of results from different paradigms for the same participants seemed overdue.

Of several empirical regularities demonstrated with the PS paradigm, the focus was here on the increase in  $\alpha$  with baseline IOI duration (Repp, 2008, 2011b). Repp found this increase to be linear up to about 1200 ms and observed overcorrection ( $\alpha > 1$ ) of small phase shifts at relatively long IOIs (>800-1100 ms, depending on the study). Although these findings are not inconsistent with the linear model of phase correction, the model does not predict or explain them. According to the hypothesis that participants try to minimize the variance of their asynchronies (Vorberg & Schulze, 2002; Vorberg & Wing, 1996),  $\alpha$  should increase nonlinearly with IOI duration towards an asymptotic value of 1. There is no good reason why overcorrection should occur at all, and indeed this phenomenon has been observed so far mainly in studies using the PS paradigm. However, these studies also included longer baseline IOIs than earlier studies. We felt it was important to compare  $\alpha$  estimates from different paradigms across the same range of IOIs and for the same participants, to determine exactly how  $\alpha$  increases with IOI duration.

One complication in making these comparisons arises from the fact that each paradigm has been associated with a different method for estimating  $\alpha$ . If we find differences between paradigms, they could be due to the estimation methods rather than to the paradigms themselves. To address this problem, we also applied a new estimation algorithm (described in the Appendix) to the data from all three paradigms.

#### 2. Methods

# 2.1. Participants

The 10 participants were all musically trained and were regular participants in rhythm and synchronization experiments at Haskins Laboratories, although 6 had been recruited only recently.<sup>3</sup> They included 8 graduate students and one postgraduate (ages 22–26) of the Yale School of Music who were paid for their services, as well as author BHR (age 65). The young musicians played various primary instruments (piano-2, violin-4, viola, oboe, bassoon) at a professional level; BHR is a life-long amateur pianist.

# 2.2. Materials and equipment

Tone sequences were generated on-line by a program written in MAX 4.0.9, running on an Intel iMac computer. The tones (piano timbre) were produced by a Roland RD-250s digital piano according to musical-instrument-digital-interface (MIDI) instructions from the MAX program and were presented over Sennheiser HD280 pro headphones. All tones had the same pitch (C4, 262 Hz), the same nominal duration (40 ms, with rapid decay after the nominal offset), and the same intensity (MIDI velocity). Participants tapped on a Roland SPD-6 electronic percussion pad, held on the lap. Finger impacts were audible as thuds whose loudness depended on tapping force but was attenuated considerably by the circumaural headphones.

There were three experimental conditions: regular metronome (RM), metronome with phase shift (PS) perturbations, and adaptively timed (AT) sequences. Each trial comprised 62 tones in the RM and AT conditions but a variable number of tones in the PS condition, ranging between possible extremes of 58 and 91. Each condition employed four tempi, corresponding to baseline IOIs of 400, 700, 1000, and 1300 ms. IOI duration was constant within each trial of the RM condition, mostly constant but occasionally shortened or lengthened in the PS condition, and variable but in the vicinity of the baseline IOI in the AT condition.

<sup>&</sup>lt;sup>3</sup> Author BHR prefers to work with musician participants because they are highly motivated, their performance in rhythmic tasks exhibits low variability, and findings from such tasks are most pertinent to music performance. There is no reason to believe that the underlying processes would be substantially different in non-musicians, but they probably would be more variable.

Perturbations in the PS condition were shortenings or lengthenings of a single metronome IOI that ranged from -10% to 10% of IOI duration in steps of 2%, not including zero. Each trial contained 10 such phase shifts, one of each magnitude, which occurred in random order with 4-7 (randomly chosen) unperturbed IOIs intervening. The earliest phase shift could occur at the end of the 8th IOI.

The AT condition used values of 0.2, 0.4, 0.6, and 0.8 for  $\alpha_c$  (the computer's phase correction parameter) in separate trials at each tempo, which resulted in 16 different trials. Each IOI of the metronome sequence was computed on-line as the baseline IOI plus  $\alpha_c$  times the last tap-tone asynchrony, rounded to the nearest millisecond.<sup>4</sup> Thus, the next tone occurred earlier after a negative asynchrony (when the tap had been ahead of the tone) and later after a positive asynchrony, thereby aiding (more or less) the participant's phase correction, which shifted the next tap in the opposite direction. As the baseline IOI remained constant (i.e., the computer was incapable of changing its period), there were no substantial changes of tempo in the metronome.

#### 2.3. Procedure

Participants came for three 1-hr sessions, typically 1 week apart. In the first session, they did the RM and PS conditions, in this order. Each condition consisted of 6 blocks of 4 trials each, with the four trials representing the four tempi (IOI durations) and occurring in random order. The second and third sessions were taken up by the AT condition, with 3 blocks of 16 randomly ordered trials in each session. The 16 trials represented the combinations of four tempi and four  $\alpha_c$  values. In each trial, participants started tapping with the third tone and tried to synchronize as closely as possible with the tones. They started each trial by pressing the space bar and saved the recorded data in a file at the end of each block.

# 2.4. Analysis

Each trial yielded a series of asynchronies, calculated by subtracting the tone onset times from the tap times. These time series constituted the input to the various methods of estimating  $\alpha$ . The first two asynchronies were omitted to exclude possible start-up effects. Asynchronies of rare missing taps (due to registration failure) were either treated as blanks or filled in by linear interpolation, depending on the method.

#### 2.4.1. RM data

A computer simulation was implemented by author PEK in Matlab to approximate the first three values (lags 0 to 2) of the autocovariance (ACV) function of the asynchronies (following Vorberg & Schulze, 2002; see also Semjen et al., 2000). The simulation generated concurrent series of isochronous metronome events and simulated human taps, from which asynchronies were calculated. The timing of each consecutive simulated tap was governed by Eq. (1) (see above). Timekeeper noise  $(T_n)$  and motor noise  $(M_{n+1}, M_n)$  were simulated by sampling randomly from independent gamma distributions. The probability density function for each gamma distribution represented the sum of four independent exponentially distributed random variables (i.e., the shape parameter defining the distributions was set to 4). For timekeeper noise distributions, the scaling parameter c (which affects the distribution mean and variance) was set to yield timekeeper interval standard deviations that increased linearly as a function of IOI duration. The scaling parameter for the motor noise distribution was held constant to yield a standard deviation of 5 ms. Each simulated series consisted of 60 asynchronies. The first asynchrony in each series was determined by summing values drawn randomly from the independent noise distributions (mean=0) described above. ACV functions were computed for each simulated asynchrony series as they were for the experimental data.

The values of  $\alpha$  that were considered ranged from 0 to 1.5 in .01 steps. ACV functions were calculated for simulated asynchrony series for all combinations of  $\alpha$  and c. The first two asynchronies from each series of 60 were not included in the ACV analyses. ACV estimates for each of the four tempi were averaged across 6 simulated series. The goodness-of-fit between these simulated ACV functions and the empirical ACV functions observed for each individual participant (averaged across 6 trials per tempo condition) was then determined by computing the root mean square error. The values of  $\alpha$  and c that yielded the smallest root mean square error for each participant were taken as the best-fitting estimates of these parameters. The above process was repeated 3 times. The best-fitting values of  $\alpha$  and c. The mean estimates of timekeeper standard deviation at the four tempi were 7.7, 15.5, 23.2, and 30.9 ms, respectively.

#### 2.4.2. PS data

To estimate  $\alpha$  from the PS data, the PCR of the tap following each phase shift was calculated by subtracting its asynchrony from that of the preceding tap (the one that coincided with the phase-shifted tone that terminated the changed IOI). This is equivalent to subtracting the baseline IOI from the interval between those two taps. The PCRs for each phase shift magnitude at each tempo were averaged across the 6 trials, and these mean PCRs were then regressed onto phase shift magnitude. The slopes of these regression lines were the estimates of  $\alpha$ . The grand mean data, averaged across all participants and expressed in percent of IOI, are shown in Fig. 1 to demonstrate that the regression functions were strongly linear (R<sup>2</sup> values ranged from .97 to .997), and that their slopes increased with IOI duration, as predicted.<sup>5</sup>

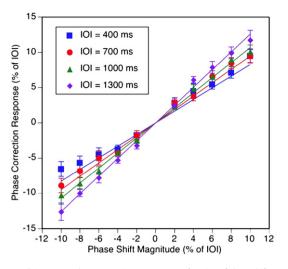
#### 2.4.3. AT data

The analysis of the AT data proceeded as follows. First, the AC1 of the asynchronies was computed for each individual trial, and these values were then averaged across the 6 trials for each value of  $\alpha_c$  at each tempo for each participant. Fig. 2 shows these AC1 values, averaged across participants, as a function of  $\alpha_c$ , separately for each IOI duration. As found previously (Repp & Keller, 2008), AC1 decreased linearly as  $\alpha_c$  increased. The slopes of the regression functions for the four tempi were very similar. This was confirmed by a repeatedmeasures two-way ANOVA, which showed the interaction between tempo (IOI duration) and  $\alpha_c$  to be far from significance, F(3, 27) = 0.18, p = .908. Therefore, for each participant's data, the mean slope of the regression lines for the four tempi was calculated and the data were then re-fitted with four parallel regression lines having that slope. Estimates of the optimal alpha,  $\alpha_{opt}$ , for each participant in each tempo condition were obtained according to equations given by Vorberg and Schulze (2002: p. 69), using the estimates of timekeeper variance obtained in the simulations of the RM data. Motor variance was assumed to be constant at 25 ms<sup>2</sup>, and the variance of the metronome was estimated by squaring half the standard deviation of the inter-tap intervals.<sup>6</sup> The resulting mean values of  $\alpha_{opt}$  for the four tempi were 0.80, 0.93, 0.97,

<sup>&</sup>lt;sup>4</sup> The computer's phase correction thus was not based on deviations from the mean asynchrony but on the raw asynchronies. This had the effect of pulling the participant's mean asynchrony toward zero but should not have had any effect on  $\alpha_{\rm h}$ .

<sup>&</sup>lt;sup>5</sup> For IOI = 400 ms, the slope seems to be shallower on the negative than on the positive side, but only the linear trend was significant in a one-way repeated-measures ANOVA with orthogonal polynomial contrasts. This was also the case for the other three IOI conditions.

<sup>&</sup>lt;sup>6</sup> The justification for this procedure comes from Figs. 1D and 2B of Repp and Keller (2008), which showed that the standard deviation (SD) of the inter-tap intervals (ITIs) remained constant across variations in  $\alpha_c$ , whereas the SD of the metronome IOIs increased almost linearly with  $\alpha_c$  and reached about the same magnitude as the SD of the ITIs when  $\alpha_c$ =1. Even though the metronome SD in the present study (which we did not measure) clearly must have varied with  $\alpha_c$ , the estimate of  $\alpha_h$  was assumed to be independent of  $\alpha_c$  and was derived from a regression across all  $\alpha_c$  conditions. Therefore, considering that the range of  $\alpha_c$  values was centered on 0.5, it seemed reasonable to take half the SD of the ITIs as an estimate of mean metronome SD at a given tempo.



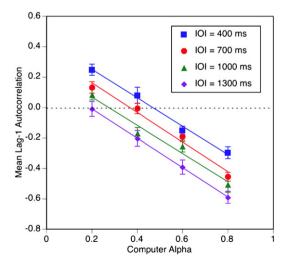
**Fig. 1.** PS condition: Mean phase correction response as a function of phase shift magnitude at four IOI durations. Regression lines are linear fits forced through zero. Error bars are between-participant standard errors.

and 0.98, respectively. Estimates of  $\alpha_h$  at each tempo were then obtained using Eq. (5) (see above).

2.4.4. A new estimation method: bounded Generalized Least Squares (bGLS)

The bGLS method, developed by author NJ and described in the Appendix, constitutes an analytic solution to the numerical optimization method of Vorberg and Schulze (2002) and yields a maximum likelihood approximation to Eq. (3) rather than a least squares approximation to the ACV function. It can be applied to any asynchrony time series, regardless of how it was generated. Thus we used it to obtain estimates from all three data sets and then compared these "new" bGLS estimates to the "old" estimates obtained by the other methods. Asynchronies from trials of the same type (from different blocks) were concatenated for the bGLS procedure. (The discontinuity at the concatenation point has a negligible effect on the  $\alpha$  estimates.)

For the PS data, bGLS estimates were obtained initially from the complete time series of asynchronies, including the PCR. Subsequently, however, separate estimates were obtained for the PCR and for the preceding and following sequence positions by allowing different alpha values for different positions and solving the joint problem of



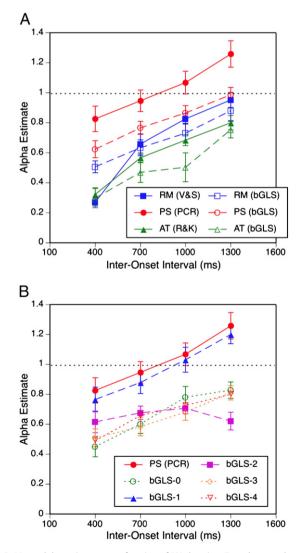
**Fig. 2.** AT condition: Mean lag-1 autocorrelation as a function of computer alpha ( $\alpha_c$ ) at four IOI durations. Regression lines are linear fits with two free parameters. Error bars are between-participant standard errors.

estimating all constants (see Appendix). For the AT data, the four levels of  $\alpha_c$  were combined after separate bGLS estimates confirmed the result of Repp and Keller (2008) that  $\alpha_h$  remained constant as  $\alpha_c$  increased: A 4×4 repeated-measures ANOVA on the separate  $\alpha$  estimates showed the main effect of  $\alpha_c$  as well as its interaction with IOI to be non-significant.

# 3. Results

Fig. 3A shows mean  $\alpha$  estimates as a function of baseline IOI duration. There are six sets of estimates: three conditions and two estimation methods for each. All estimates increased with IOI duration, but they differed considerably between the three paradigms, with  $\alpha$ values being largest for PS and smallest for AT. This was true for both sets of estimates—those from the older methods associated with each paradigm and those from the new bGLS method.

A  $3 \times 4$  repeated-measures ANOVA, with paradigm and IOI as the variables, on the old estimates revealed significant main effects of paradigm, F(2, 18) = 23.46, p = .001, and of IOI, F(3, 27) = 66.60,



**Fig. 3.** Mean alpha estimates as a function of IOI duration. Error bars are betweenparticipant standard errors. (A) Estimates for three paradigms (RM, PS, AT) according to different methods: V&S = numerical optimization according to Vorberg and Schulze (2002); PCR = slope of PCR function (see Fig. 1); R&K = method of Repp and Keller (2008) (see Fig. 2); bGLS = Jacoby's bounded general least squares method (see Appendix). (B) The PS (PCR) estimates from panel A and bGLS estimates for five successive sequence positions in the PS paradigm. Position 0 is the perturbation point; position 1 is the PCR.

p<.001, as well as a significant interaction, F(6, 54) = 4.59, p = .009.<sup>7</sup> Pairwise comparisons with Bonferroni correction showed that all three paradigms differed significantly (p<.01) from each other in their mean  $\alpha$  values. The interaction was evidently due to the low  $\alpha$  estimates obtained at the fastest tempo in the RM and AT paradigms because it was no longer significant when the data for IOI = 400 ms were omitted from the ANOVA.

An analogous ANOVA on the new bGLS estimates yielded significant main effects of paradigm, F(3, 27) = 10.85, p = .004, and IOI, F(3, 27) = 34.20, p < .001, but no interaction. These  $\alpha$  estimates increased linearly with IOI duration, in parallel for all three paradigms. Pairwise comparisons showed the difference between AT and each of the other two paradigms to be significant (p < .01), but not the difference between RM and PS.

Differences between the estimates obtained by the different methods for each paradigm were assessed in separate 2×4 ANOVAs, with method (old vs. new) and IOI as the variables. For the RM paradigm, there was no significant main effect of method but a significant Method×IOI interaction, F(3, 27) = 13.32, p < .001, due again to the low  $\alpha$  at IOI = 400 ms obtained by the old method. The interaction disappeared when the data for IOI = 400 ms were omitted, but then the main effect of method was almost significant, F(1, 9) = 4.69, p = .059, indicating slightly lower estimates from the new than from the old method. For the PS paradigm, the new estimates were substantially lower than the old ones, F(1, 9) = 46.15, p < .001, and there was no interaction. For the AT paradigm, too, the new estimates were significantly lower than the old ones, F(1, 9) = 6.83, p = .028, while the interaction with IOI was not significant, F(3, 27) = 2.33, p = .126.

While the old and new estimates for the RM and AT paradigms were based on the same data, the old estimates for the PS paradigm were based on the PCR alone whereas the new bGLS estimates were based on all asynchronies, including the PCR. The large discrepancy between these estimates suggests strongly that  $\alpha$  is elevated during the PCR. This was confirmed when separate bGLS estimates were calculated for each sequence position relative to the perturbation (see Appendix for computational details). These estimates are shown and compared with the old PS (PCR) estimates in Fig. 3B. It is evident that the bGLS estimates based on the PCR (position 1) were large and similar to the old estimates, though slightly lower; this small difference was highly significant, F(1, 9) = 52.45, p < .001. The bGLS estimates for positions 0 (the perturbation point), 3, and 4 were much lower and similar to those for the RM paradigm (Fig. 3A). The estimates for position 2 showed a different pattern, being higher at the shortest IOI and lower at the longest IOI than those of positions 0, 3, and 4. This is likely to reflect a compensatory response to the PCR,  $\alpha$  being increased when the PCR under-corrected the phase shift (at short IOIs) and being decreased when the PCR over-corrected (at long IOIs).

To address the question of whether the different paradigms and estimation methods yield mutually consistent estimates of individual differences in  $\alpha$ , we computed Pearson correlation coefficients across participants. We first averaged the individual  $\alpha$  estimates across the four tempi, so that there was a single  $\alpha$  value for each participant provided by each paradigm and method. Despite the small sample size (N = 10), the correlation matrix, shown in Table 1, yielded a striking result: Whereas old and new estimates for the same paradigm were highly correlated (mean r = .885, n = 3),<sup>8</sup> and estimates for the RM and AT paradigms were also highly correlated (mean r = .763, n = 4), the PS estimates did not correlate significantly with any of the other estimates and even tended to correlate negatively with them (mean r = ..238, n = 8).

#### Table 1

Correlations among  $\alpha$  values (averaged across the four IOI durations) for three paradigms and two estimation methods for each. (Abbreviations as in Fig. 3A).

	PS (PCR)	AT (R&K)	RM (bGLS)	PS (bGLS)	AT (bGLS)
RM (V&S) PS (PCR) AT (R&K) RM (bGLS) PS (bGLS)	311	.812 <sup>**</sup> 003	.873 <sup>***</sup> 429 .720 <sup>*</sup>	349 .940 <sup>****</sup> 206 482	.728 <sup>*</sup> 004 .843 <sup>**</sup> .790 <sup>**</sup> 117
* n< 05					

\*\* p<.01.

\*\*\* p<.001.

The new PS (bGLS) estimates correlated highly with the old PS (PCR) estimates, but not with the old or new RM estimates, even though the PS (bGLS) estimates were based on all asynchronies, and most of a PS sequence is like an RM sequence. Table 2 unpacks these correlations in terms of successive sequence positions in the PS paradigm. While the high correlation of bGLS-1 with PS (PCR) is not surprising as both are based on the PCR, the bGLS estimates for other sequence positions also correlated positively with PS (PCR) estimates and not with RM and AT estimates. Moreover, though this is not shown in Table 2, all positional PS (bGLS) estimates were moderately correlated with each other (mean r = .658, n = 10).

# 4. Discussion

This study compared three sensorimotor synchronization paradigms – regular metronome (RM), metronome with phase shifts (PS), and adaptively timed metronome (AT) – and associated methods of estimating the phase correction parameter  $\alpha$ , with the aim of establishing whether results obtained with the often-used PS paradigm are confirmed by data from other paradigms and estimation methods. The particular PS results of interest here were the linear increase of  $\alpha$  with baseline IOI duration and the relatively large values of  $\alpha$ , which include overcorrection at relatively long IOIs (Repp, 2008, 2011b). The study yielded three important findings, which are discussed in the next three sections.

#### 4.1. Increase in $\alpha$ with IOI duration

First, the increase in  $\alpha$  with IOI duration was indeed confirmed by all paradigms and estimation methods. Thus, this result is not specific to the PS paradigm but also occurs in synchronization with regular metronomes (as already noted by Pressing, 1998) and adaptively timed metronomes. Repp (2008) attributed the increase in  $\alpha$  to a decrease in the tendency to maintain a constant tapping period. In other words, as the tempo gets slower, the cyclic tapping movement offers less resistance to abrupt changes in timing, due to reduced rhythmic coherence of successive taps and greater timekeeper variability. As a consequence, sensorimotor coupling strength (indexed by  $\alpha$ ) increases as the tempo decreases, so that the tapping rhythm depends increasingly on the external pacing rhythm, rather than on an

Table 2

Correlations between PS (bGLS)  $\alpha$  estimates for individual sequence positions (averaged across the four IOI durations) and other estimates. (Abbreviations as in Fig. 3B).

	bGLS-0	bGLS-1	bGLS-2	bGLS-3	bGLS-4
RM (V&S)	.210	347	531**	277	314
PS (PCR)	.517	.994***	.594	.738*	.651*
AT (R&K)	.005	082	539	206	391
RM (bGLS)	082	466	553	455	465
AT (bGLS)	.019	046	547	227	201

\* p<.05.

\*\* *p*<.01.

\*\*\* p<.001.

 $<sup>^{7}</sup>$  The Greenhouse–Geisser correction was applied automatically to all p values.

 $<sup>^{8}</sup>$  The symbol *n* refers here to the number of correlations averaged to obtain the mean given.

autonomously maintained period. This increase in coupling strength evidently occurs also when there are no abrupt perturbations in the pacing sequence.

The bGLS estimates for all three paradigms yielded parallel linear functions for this increase in  $\alpha$ , consistent with the apparent linearity found by Repp (2008, 2011b). However, the older estimation methods for the RM and AT paradigms yielded nonlinear functions, due to relatively low  $\alpha$  values at the shortest IOI (400 ms). One possible explanation is that there may have been second-order phase correction at short IOIs (i.e., relying on the asynchrony  $\mathsf{A}_{n-1}$  in addition to A<sub>n</sub>; Pressing, 1998; Vorberg & Schulze, 2002), which would have the effect of increasing the lag-2 autocorrelation and thus lowering the estimate of first-order  $\alpha$  (cf. Eq. (4)). However, that lowering should also have been reflected in the bGLS estimates, which were first-order as well. Alternatively, assumptions about timekeeper and motor variance in the old RM and AT estimation methods may have been responsible for the nonlinearity.<sup>9</sup> Note that the bGLS method does not make any such assumptions but estimates variances together with  $\alpha$ .

# 4.2. Absolute magnitude of $\alpha$ estimates

The comparison of mean  $\alpha$  estimates confirmed our initial suspicion, based on earlier findings (Repp, 2010; Repp & Keller, 2008), that the PS paradigm yields relatively high  $\alpha$  values, whereas the AT paradigm yields relatively low ones. The differences obtained in this first direct comparison using a within-participant design were even larger than expected. The PS (PCR) estimates were the highest by far, whereas the AT estimates were the lowest, with the RM estimates falling in between. These differences were not artifacts of different estimation methods, for they were confirmed when the new bGLS method was applied to the data from all three paradigms.

Traditionally,  $\alpha$  estimates in the PS paradigm are based exclusively on the phase correction response (PCR) of the tap immediately following a phase shift, whereas AT and RM estimates are based on all taps. The observed differences therefore could indicate either (1) that  $\alpha$ , and hence sensorimotor coupling strength, increases temporarily following a timing perturbation and then returns to some baseline value, or (2) that  $\alpha$  is elevated continuously in the PS paradigm. We were able to address this issue by applying the bGLS method selectively to positions preceding and following the PCR. The results showed very clearly that  $\alpha$  is increased only immediately after a phase shift and then drops back to values similar to those found in the RM task. This finding violates one assumption made by the linear model of phase correction, namely that  $\alpha$  is constant throughout a synchronization task. We have shown here for the first time that this assumption is not correct within the PS paradigm.

What might cause the elevation of  $\alpha$  immediately following a phase shift? Conscious detection of a perturbation might boost phase correction by engaging period correction (Repp, 2001b; Repp & Keller, 2004) or even by increasing phase correction directly. However, it is well established that the PCR function is linear throughout the region of perceptually subliminal phase shifts (cf. Fig. 1), which suggests that conscious perception of perturbations or of the resulting asynchronies is irrelevant to phase correction (Repp, 2000, 2001a). Repp (2011b: Experiment 1) tested the same participants as in the present study in a similar PS paradigm, but with phase shifts of fixed absolute magnitude that became increasingly imperceptible as IOI duration increased. The average  $\alpha$  estimates were very similar to the present ones, and this finding confirms the irrelevance of conscious perception. The temporary increase in  $\alpha$  would have to be

triggered by a subconscious detection mechanism sensitive to either subliminal timing perturbations or subliminal asynchronies, or it would have to be the result of a nonlinear dynamic system that reacts to even minimal perturbations in this specific way.

This is a highly intriguing possibility. Because the mechanism operates subconsciously, it is best conceptualized in dynamic systems terms. The obvious candidate is an internal oscillator or network of coupled oscillators that is entrained to the external rhythm, as discussed by Large (2008; Large & Jones, 1999). A perturbation is detected if a sequence event deviates from a predicted time point, and although this process is usually discussed within the context of conscious perception and judgment of timing, it is conceivable that it operates accurately even at subthreshold levels. In particular, the comparison resulting in subconscious detection of perturbations must occur in a brain network different from that underlying conscious detection, probably one closely linked to motor control where intrinsic oscillator variability and input timing variability are both very small, perhaps involving the cerebellum (Thaut, Kenyon, Schauer, & McIntosh, 1999, Thaut, Stephan, Wunderlich et al., 2009). Expectancy violations in that network would then have to trigger an instant gain in phase correction that is implemented in the PCR. Exactly how this triggering might occur is not clear at this time, but we note a close parallel with the hypothesis of "internal forward models" that generate online predictions and compare them to sensory input, without mediation of conscious perception (e.g., Wolpert, Doya, & Kawato, 2003). Internal models have also been linked with the cerebellum (Wolpert, Miall, & Kawato, 1998).

One finding that is particularly difficult to explain is the overcorrection observed at long IOIs in the PS paradigm (see also Repp, 2011b). The RM and AT paradigms, as well as taps following the PCR in the PS paradigm, did not yield evidence of overcorrection, although the linear increase of  $\alpha$  with IOI duration suggests that overcorrection might emerge at IOIs longer than 1300 ms. Repp (2011b: Experiment 4) examined the IOI range between 1000 and 2000 ms using the PS paradigm and found that  $\alpha$  continued to increase, though at a rate much slower than that observed at IOIs below 1200 ms. Given the lower  $\alpha$  values yielded by the RM and AT paradigms, it is possible that these paradigms will not show significant overcorrection even at long IOIs. In that case, overcorrection would be specific to the PCR in the PS paradigm, a consequence of the momentarily enhanced  $\alpha$ . Overcorrection is a kind of non-optimal behavior, but participants do not seem able to prevent it. Moreover, it is paradoxical that it occurs at slow tempi, where variability of perceived and produced timing is guite large. The fact that small phase shifts in particular are overcorrected by the PCR (see also Repp, 2011b: Experiment 1) suggests that the underlying mechanism is not subject to the commonly observed increase in temporal uncertainty with interval duration.

The relatively low  $\alpha_h$  values found in the AT paradigm require a different explanation. They may reflect a strategic lowering of sensorimotor coupling strength. Because the computer aided the participant in phase correction, participants could give increased weight to maintaining regularity of tapping, thereby reducing  $\alpha_h$ . However, the constancy of  $\alpha_h$  across variation in  $\alpha_c$  is surprising from that perspective. Perhaps  $\alpha_h$  would have varied if  $\alpha_c$  had not changed unpredictably from trial to trial. Repp and Keller (2008), too, varied  $\alpha_c$  from trial to trial and found that  $\alpha_h$  remained constant.

#### 4.3. Correlations of $\alpha$ estimates

One completely unexpected finding was that the  $\alpha$  estimates yielded by the PS paradigm were not correlated with the estimates for the other paradigms, regardless of estimation method. To be sure, the N of this study was rather small for a correlational analysis, but the pattern was very clear. The high correlation between the RM and AT estimates is reassuring, suggesting that these paradigms

 $<sup>^9</sup>$  We also calculated  $\alpha$  estimates for the RM paradigm according to the method of bins (Pressing, 1998), using software kindly provided by Pressing's former student Ben Williams (Swinburne University of Technology, Melbourne, Australia). The  $\alpha$  values were very similar to the bGLS estimates and increased linearly with IOI.

measure the same individual differences in sensorimotor coupling strength. With regard to the PS paradigm, however, the lack of correlation raises two possibilities: Either only the PCR elicited by abrupt phase shifts is different in some important way from the phase correction that occurs in synchronization with regularly or adaptively timed metronomes, or the whole phase correction process in the PS paradigm is different. The first possibility seems more plausible, as the PS sequence is basically a RM sequence between phase shifts, whereas phase shifts might trigger a separate process (such as period correction) in the PCR. Here the data yielded a second surprise: The correlations based on individual differences in  $\alpha$  showed quite unambiguously that  $\alpha$  estimates for the PCR and subsequent taps were correlated with each other but uncorrelated with the RM and AT estimates, which suggests a single underlying process in the PS paradigm. Thus, the phase correction process in the PS paradigm seems to be somehow different from that in the RM and AT paradigms, even at points where the sequence is effectively a RM sequence.

#### 4.4. Estimation methods

The bGLS estimates were generally lower than those yielded by the older methods. Finding the exact reasons for these differences would require more extensive simulations, which were beyond the scope of this study. In the case of the RM and AT data, specific parameter settings adopted in the older estimation methods are likely to be responsible. In the case of the PS (PCR) estimates, the explanation of the small but remarkably consistent difference may be simple: In the old method, the PCR (the difference between two successive asynchronies) is regressed onto phase shift magnitude, whereas in the bGLS method successive asynchronies are (implicitly) regressed onto each other. When we performed this latter regression explicitly on the PS (PCR) data, we obtained slightly smaller  $\alpha$  estimates that were almost identical with the bGLS estimates.

One important issue regarding estimation methods remains to be discussed. It has been shown repeatedly that the asynchronies in synchronization with a regular metronome at a moderately fast tempo (IOI~500 ms) harbor long-term correlations (also called fractal or  $1/f^3$  noise; see, e.g., Chen, Repp, & Patel, 2002; Delignières, Torre, & Lemoine, 2008, 2009; Pressing & Jolley-Rogers, 1997; Torre & Delignières, 2008a). This means that autocorrelations of asynchronies are positive and, while decreasing with lag, may extend over fairly long lags. Torre and Delignières (2008b) attributed this correlated noise to the internal timekeeper ( $T_n$  in our Eq. (3) above) and outlined a model that treats the timekeeper as a fractal noise generator but retains the linear phase correction is impeded by the positive lag-1 autocorrelation, and consequently  $\alpha$  is underestimated by methods that do not take fractal noise into account.

This is an important problem, but preliminary simulations by one of us (NJ) have indicated that it is complex and not easily solved. Therefore, we are unable to address it in this study. It seems reasonable to assume that the fractal noise generated by an internal timekeeper was similar in our three paradigms, so that the observed differences in mean  $\alpha$  estimates are valid. Only the absolute  $\alpha$  values may be too small. As for the increase in  $\alpha$  with IOI duration, it may reflect a decreasing presence of fractal noise, in which case it may not represent a real increase in  $\alpha$ . The decreasing tendency to maintain a constant period, which Repp (2008) hypothesized in connection with the increase in  $\alpha$ , seems conceptually very similar to decreasing fractal noise. For the actual autocorrelation functions of the present RM data, see Fig. 8 in Repp (2011a). They show that the positive lag-1 autocorrelation decreased as IOI increased, reaching zero at the longest IOI (1300 ms), and that positive autocorrelations extended beyond lag 4 only at IOI = 400 ms. This may mean that fractal noise decreased as IOI increased, or that  $\alpha$  increased and overcame the fractal noise, or both.

#### 5. Conclusions

In summary, we have shown three things: (1) Independent of the paradigm or estimation method, the phase correction parameter  $\alpha$ increases as the baseline IOI of the metronome increases, and according to the new bGLS estimates that increase appears to be linear between IOIs of 400 and 1300 ms. (2) Estimates of  $\alpha$  derived from synchronization with a perturbed metronome (PS paradigm) are substantially higher than those derived from synchronization with a regular metronome, which in turn are higher than those obtained from synchronization with an adaptively timed metronome. The first difference is due to a transient increase of  $\alpha$  following a perturbation, whereas the second difference suggests paradigm-specific strategic adjustments of  $\alpha$ . (3) The PS estimates are uncorrelated with those obtained from the other two paradigms, which are highly correlated. Thus, the PS paradigm seems to engage a different process of phase correction that is not operating in the other two paradigms. Explaining the nature of this difference is a challenge for future research.

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# Appendix A

# Bounded general least squaresmethod for estimating alpha (by Nori Jacoby)

The linear model of phase correction (Vorberg & Schulze, 2002) is (cf. Eq. (1)):

$$e(n+1) = (1-\alpha)e(n) + T(n) + M(n+1) - M(n) - C(n)$$
(A1)

where e is an asynchrony, T is a noisy internal timekeeper, M is motor noise, and C is the interval of an external pacing sequence. The model can be rewritten as:

$$e(n+1) + s(n+1) = (1-\alpha)e(n) + z(n+1)$$
(A2)

where s(n+1) = C(n), and z(n+1) = T(n) + M(n+1) - M(n).

According to Vorberg and Schulze (2002), the autocovariance function of z has the following properties:  $\gamma_z(0) = var(z) = \sigma_T^2 + 2\sigma_{AL}^2$ ,  $\gamma_z(1) = -\sigma_{AL}^2$ , and  $\gamma_z(j) = 0$  for every j > 1. Writing Eq. (A2) in matrix form results in the following equation:

$$B = A(1 - \alpha) + Z \tag{A3}$$

where B = [e(1) + s(1), e(2) + s(2), ..., e(n) + s(n)]; A = [e(0), e(1), ..., e(n-1)], Z = [z(1), z(2), ..., z(n)].

If  $\gamma_Z(1) = 0$  we could estimate  $\alpha$  using simple linear regression:

$$\left(1 - \alpha^{\text{REG}}\right) = \left(A^T A\right)^{-1} \left(A^T B\right) \approx \gamma_e(1) / \gamma_e(0) \tag{A4}$$

where  $A^{-1}$  and  $A^{T}$  are the inverse and transpose, respectively, of A. However, when  $\gamma_{Z}(1)$  and  $\gamma_{Z}(0)$  are known and  $\gamma_{Z}(1)$  is not 0, a correction should be applied. The solution is called Generalized Least Squares (GLS) and dates back to Aitken (1935):

$$\left(1 - \alpha^{GLS}\right) = \left(A^T \Sigma^{-1} A\right)^{-1} \left(A^T \Sigma^{-1} B\right) \tag{A5}$$

where  $\Sigma = \gamma_z(0)I + \gamma_z(1)\Delta$ , I is the identity matrix, and  $\Delta$  is a square matrix with 1 on both diagonals and 0 elsewhere.

Since in our case  $\gamma_7(0)$  and  $\gamma_7(1)$  are not known, an iterative algorithm can be applied, called sometimes Feasible Generalized Least Squares (see Ljung, 1987). In each iteration,  $\Sigma$  is estimated by calculating the empirical autocovariance function of the residual noise. Later, using the final estimate of  $\Sigma$ , an estimate of alpha is computed based on Eq. (A5).

However, using this algorithm as stated causes numerical instability when  $\alpha$  approaches 1 (mentioned already by Vorberg & Schulze, 2002, p. 76; they call it "parameter interdependence"). A solution to this problem (also suggested by Vorberg & Schulze) is to restrict the parameter space. We decided to limit the ratio  $\gamma_Z(0)/\gamma_Z(1)$ , since this gives very good results in simulations.

We have carried out extensive simulations to compare the bGLS method with the method suggested by Vorberg and Schulze (2002). The results showed that both methods give unbiased estimates in the case of a regular metronome, with similar accuracy. However, the bGLS method gives an analytic solution that does not depend on slow simulations for parameter estimation.

# Algorithm (bounded Generalized Least Squares method)

The input of this algorithm is the matrices A and B, together with limits on the moments LB, HB. (In this paper LB, HB were chosen such that  $2 < \sigma_T/\sigma_M < 9$ , or LB = 6, HB = 83.) The output of the algorithm is the estimates for the parameters:  $\alpha^{bGLS}$ ,  $\gamma^{bGLS}$ , Z(1),  $\gamma^{bGLS}$ , Z(0)

- a. Start by setting  $\Sigma_1 = I$  (the identity matrix).
- b. Iterate the following steps until a stop criterion is obtained. (In this paper we used a fixed number of 10 iterations.)
- i) Compute an estimate for alpha:  $(1 \alpha_n) = (A^T \Sigma_n^{-1} A)^{-1}$  $(A^T \Sigma_n^{-1}) B$
- ii) Compute the residual noise  $D_n = B A(1 \alpha_n)$
- iii) Estimate  $\gamma^{n+1}(0)$ ,  $\gamma^{n+1}(1)$  by the autocovariance of the residual noise:

$$\gamma^{n+1}(0) = \gamma_{Dn}(0), \gamma^{n+1}(1) = \gamma_{Dn}(1)$$

# Estimating alphas in multiple sequence positions

If we allow alpha to change with position in the sequence, then Eq. (A2) is changed to:

$$e(n+1) + s(n+1) = \left(1 - \alpha_{\nu(n)}\right)e(n) + z(n+1)$$
(A6)

where v(n) is 0, 1, 2, 3,... (the position in the sequence). This set of equations can be solved together with the same assumptions on z(n+1) as in estimating a single  $\alpha$ , using the same bGLS algorithm but with a slightly changed meaning of the variables in the matrix representation:

Let the new  $\alpha = (\alpha_{\nu(0)}, \alpha_{\nu(1)}, \alpha_{\nu(2)}, ...)$  be a vector of the different constants for different sequence positions. Let A be the matrix with A(n,v(n)) = e(n) and 0 elsewhere. Let B, Z be the same vectors as before. Then Eq. (A3) holds as before, and the same bGLS algorithm can be applied. Note that  $(1 - \alpha)$  in this context means the elementby-element operation:  $(1 - \alpha_{v(0)}, 1 - \alpha_{v(1)}, 1 - \alpha_{v(2)}, ...)$ .

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