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Individual Differences in Temporal Anticipation and Adaptation During Sensorimotor Synchronization

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Abstract

Interpersonal coordination during musical joint action (e.g., ensemble performance) requires individuals to anticipate and adapt to each other's action timing. Individuals differ in their ability to both anticipate and adapt, however, little is known about the relationship between these skills. The present study used paced finger tapping tasks to examine the relationship between anticipatory skill and adaptive (error correction) processes. Based on a computational model, it was hypothesized that temporal anticipation and adaptation will act together to facilitate synchronization accuracy and precision. Adaptive ability was measured as the degree of temporal error correction that participants ($N = 52$) engaged in when synchronizing with a 'virtual partner', that is, an auditory pacing signal that modulated its timing based on the participant's performance. Anticipation was measured through a prediction index that reflected the degree to which participants' inter-tap intervals led or lagged behind inter-onset intervals in tempo-changing sequences. A correlational analysis revealed a significant positive relationship between the prediction index and temporal error correction estimates, suggesting that anticipation and adaptation interact to facilitate synchronization performance. Hierarchical regression analyses revealed that adaptation was the best predictor of synchronization accuracy, whereas both adaptation and anticipation predicted synchronization precision. Together these results demonstrate a relationship between anticipatory and adaptive mechanisms, and indicate that individual differences in these two abilities are predictive of synchronization performance.

Keywords

Sensorimotor synchronization, temporal anticipation, temporal adaptation, error correction, individual differences, virtual partner

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1. Introduction

Humans have the ability to coordinate movement with others with little apparent cognitive effort, for example, shaking the hand of another or clapping hands in synchrony. This ability is foundational to music and dance ensemble performance, where individuals are required to coordinate their movements with extreme temporal precision and accuracy and yet remain flexible during constantly changing conditions. Such rhythmic interpersonal coordination requires the combination of multiple perceptual, motor, cognitive, and social processes (Knoblich et al., 2011; Phillips-Silver & Keller, 2012). Two core processes that musicians employ to successfully synchronize are temporal anticipation and adaptation (Keller, 2008, 2014). Musicians must continuously make predictions about upcoming sounds and movements while also adapting their movements in response to previous timing deviations. Although both prediction and adaptation recruit a mixture of automatic sensorimotor processes and deliberate cognitive operations, in the current article we focus on a deliberate form of temporal prediction (which is assumed to rely upon working memory and mental imagery; Keller, 2012) and an automatic type of adaptive timing (reflex-like error correction; Repp, 2001).

There are large individual differences in synchronization ability as well as the mechanisms employed to support synchronization. For example, individuals with musical experience (e.g., professional percussionists) are extremely precise at synchronizing (Fischinger, 2011; Fujii et al., 2011), whereas non-musicians show greater variability than musicians during sensorimotor synchronization tasks (Krause et al., 2010). Nevertheless, sensorimotor synchronization skills are not exclusive to musicians. Members of the general population also engage in many forms of synchronized movement (such as marching or clapping in time) as well as collective musical activities (such as group singing and dancing), that necessitate the coordination of movement with others or an external auditory signal. One of the aims of this paper is to gain a better understanding of how individual differences in the underlying mechanisms of synchronization, namely temporal anticipation and adaptation, relate to the ability to synchronize movements with external sounds.

Anticipatory and adaptive skills serve complementary functions in supporting synchronized movement (van der Steen & Keller, 2013). Temporal anticipation is based on prospective information whereas adaptive timing relies on retrospective information. The former is predictive while the latter is reactive. On one hand, temporal anticipation allows a performer to predict the timing of others' upcoming movements in order to plan and coordinate their own movement (Keller, 2014; Pecenka et al., 2013). On the other hand, adaptive timing engages error correction, where performers respond to timing variations (such as intended expressive timing deviations or unintentional errors) by adjusting their own movement timing.

Temporal anticipation and adaptation have been studied separately in the context of sensorimotor synchronization tasks. These tasks require a participant to produce repetitive movements, typically finger taps, in time with auditory pacing sequences presented by a computer, allowing the participant's synchronization performance to be assessed at a millisecond timescale under controlled conditions (for reviews see Repp, 2005; Repp & Su, 2013). The timing of the pacing sequences may be varied depending on the focus of the research question; they may be isochronous (constant evenly spaced onsets), tempo changing (speeding up or slowing down), or rhythmic (following a regular but non-isochronous temporal pattern). Synchronization performance is generally assessed in terms of accuracy and precision. Accuracy refers to how close taps are in relation to the sound onsets, and is assessed by measuring asynchronies, that is, the time difference between the onset of a sound and a tap. Precision refers to the stability of tap timing and is assessed in terms of variability, that is, standard deviation or coefficient of variation of asynchronies.

Studies of sensorimotor synchronization have revealed that temporal anticipation and adaptation contribute to the quality of synchronization accuracy and precision, and that individuals differ in their ability both to anticipate and to adapt (Fairhurst et al., 2013; Pecenka & Keller, 2011; Repp & Keller, 2008). However, little is understood about the relationship and interaction between these skills, and how they work together to enable rhythmic interpersonal coordination. The main aim of the present study is to investigate the relationship between individual differences in temporal anticipation and adaptation, and secondly, to assess the effects of this relationship on the accuracy and precision of sensorimotor synchronization.

1.1. Adaptive Timing (*Error Correction*)

Adaptive timing allows musicians to maintain interpersonal synchrony in the presence of intentional and unintentional timing deviations (Keller, 2008), and is mutually employed by multiple musicians, who each respond to asynchronies with adjustment of their subsequent actions (e.g., Goebl & Palmer, 2009; Wing et al., 2014). It has been hypothesized that adaptive timing is governed by error correction mechanisms that enable internal timekeepers (oscillations of neural populations) to remain entrained, or coupled, with a sequence of pacing events (Large & Jones, 1999; Large et al., 2002; Loehr et al., 2011; Repp, 2001, 2011; Repp & Keller, 2008; Vorberg & Wing, 1996). There are two types of error correction processes, phase and period correction, each an independent process that functions to reduce asynchrony in timing (Mates, 1994; Schulze et al., 2005). Phase correction is an automatic process (Repp, 2001) that corrects deviations in timing continuously, adjusting the timing of each movement based on the previous asynchrony while leaving the period (the interval of time between successive events) of the internal timekeeper unchanged (Vorberg & Schulze, 2002). This

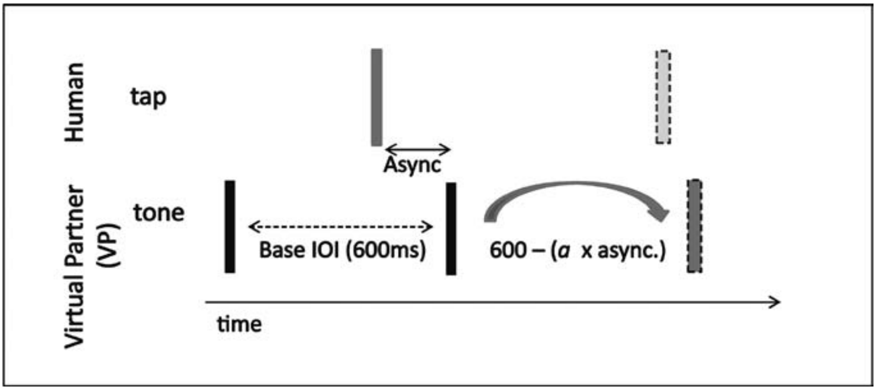

Figure 1. Overview of the adaptive timing mechanism of the virtual partner. Error correction mechanisms alter the timing of the following pacing signal event by adjusting for a proportion of the previous asynchrony. The timing of the inter-onset interval (IOI) is adjusted by a proportion (α) of the asynchrony (async.) between the previous pacing event and tap.

process occurs at a millisecond timescale even without conscious awareness of asynchrony (Repp, 2002; Thaut et al., 1998). Period correction, on the other hand, is an intentional adjustment of the internal timekeeper, resulting in a change of movement tempo (Repp, 2005; Schulze et al., 2005). This form of error correction requires conscious perception of a tempo change in the pacing sequence (Keller, 2008, 2012; Repp, 2001; Repp & Keller, 2004).

Temporal error correction has been investigated using what Fairhurst et al. (2013) have termed a 'virtual partner', an adaptive pacing signal that enables the computer to engage in controlled simulation of error correction during a sensorimotor synchronization task and, thus, interact with a participant (Repp & Keller, 2008; Vorberg, 2005). To simulate error correction, the virtual partner is governed by a mathematical algorithm that allows it to respond to the human participant's asynchronous tap by altering the timing of the subsequent pacing event. For example, when simulating phase correction, if the participant were to tap too early, the virtual partner would respond by adjusting the timing of the following event to sound earlier (see Fig. 1).

The proportion of the asynchrony that the virtual partner compensates for is controlled by altering a single parameter in the algorithm. In simulations of phase correction, this parameter is designated α, in keeping with nomenclature in the linear phase correction model of Vorberg and Schulze (2002). Varying the phase correction parameter α influences the degree to which the virtual partner adjusts its timing, making it possible to simulate either a cooperative or uncooperative musical partner (Fairhurst et al., 2013; Repp & Keller, 2008). This is analogous to actual human partners where there are individual differences in skill level. Coupling strength is optimal (operationally defined as minimal variability of asynchronies) when both the virtual partner and the participant engage in moderate amounts of phase correction (Repp & Keller, 2008). Both the human participant and the virtual partner each adjust their timing toward each other, minimizing the variability of asynchronies. However, synchronization is hindered when the virtual partner is overly adaptive and over-corrects the asynchronies (Fairhurst et al., 2013). By systematically modifying the phase correction parameter α in the virtual partner, it is possible to ascertain what degree of assisted synchronization is optimal for an individual based on the assumption that successive asynchronies are independent when error correction is optimal (Vorberg & Schulze, 2002). Therefore, an estimate of phase correction capacity (the mean proportion of each asynchrony that is corrected) can be obtained for the individual based on the autocorrelation of asynchronies derived from synchronization with virtual partner at various degrees of adaptivity (Repp & Keller, 2008; Repp et al., 2012).

1.2. Temporal Anticipation

Anticipatory mechanisms allow an individual to predict the timing of events, such as others' body movements and the effects of these movements on the environment. In musical contexts, co-performers predict the timing of upcoming sounds based on regular rhythmic patterns within the music. Anticipatory mechanisms also allow musicians to predict changes in musical timing (e.g., tempo changes), such as those that occur during expressively motivated musical performance (Pecenka & Keller, 2009; Rankin et al., 2009). Keller et al. (2007) proposed that anticipation of co-performers' actions is a cognitive task guided by action simulation processes that are driven by internal models. Internal models allow mental simulation of a movement, and the potential outcome of such a movement, to be carried out prior to action execution. For this to occur, the central nervous system must have had prior experience of contingencies between efferent neural motor signals issuing from motor regions of the brain and incoming afferent sensory information, and their effects on the body and environment (Wolpert et al., 1998). It has been proposed that internal models aid movement efficiency by allowing predicted sensory (afferent) feedback to inform the programming of a movement before the arrival of actual sensory feedback (Aschersleben et al., 2002; Wolpert et al., 1998). Thus, internal models allow a kind of anticipatory error correction by adjusting planned movements in order to correct potential errors before they occur (Keller, 2008; Wolpert et al., 2003).

Two types of models, forward and inverse, are hypothesized to operate concurrently for the execution of one's own actions and for simulating the actions of others (Keller, 2008, 2012; Pacherie, 2008; Wolpert et al., 2003). Through the observation of others' actions, forward models allow internal simulation and, thus, calculation of others' movement outcomes. Inverse models, on the other hand, facilitate synchronization by representing others' intentions and performance goals and using this knowledge to predict what subsequent actions will be produced. It has been theorized that the use of forward and inverse models for both the self and other, enables anticipation of forthcoming actions or sounds, which forms the foundation of interpersonal coordination (Keller, 2008). In support of this hypothesis, Stoit et al. (2011) found that deficits in the ability to internally model the behaviour of a co-actor (e.g., as occurs in autism) impairs performance in joint action tasks.

Action simulation, which is driven by internal modelling mechanisms, allows for deliberate mental imagery of co-performers' upcoming movements and sounds (Keller & Appel, 2010). Keller (2008) proposed that such imagery is based on knowledge of the shared representations and goals of the ensemble. The ability to engage in mental simulation and imagery can facilitate coordination. For example, Keller and Appel (2010) found that individual differences in anticipatory auditory imagery predicted the quality of coordination in piano duos. Simulation and imagery processes have also been shown to rely on cognitive resources such as working memory. For example, Pecenka et al. (2013) found decreased prediction ability in a sensorimotor synchronization task when performed concurrently with a visual working memory task. Likewise, Fischinger (2011) reported increased asynchronies during a tapping task where participants engaged in a concurrent word memory task.

Individuals differ markedly in anticipatory ability, with some being good at predicting tempo changes while others tend to follow or track these changes (Pecenka & Keller, 2009). In an investigation of individual differences in anticipatory ability, Pecenka and Keller (2011) calculated a prediction index as a measure of individual anticipatory ability (cf. Rankin et al., 2009; Repp, 2002). This measure was calculated from performance in a sensorimotor synchronization task with tempo-changing auditory sequences. The cross-correlation between participant's inter-tap intervals (ITIs) and the inter-onset intervals (IOIs) of the events in the auditory sequence were computed at both lag 0 and lag 1. The cross correlation at lag 0 indicates how accurately the participant predicts the timing of the current IOI, whereas the cross correlation at lag 1 assesses to what degree the participant's taps match the previous IOI. A ratio of the lag 0 over the lag 1 cross-correlations provided an index of the degree to which each person was able to anticipate (predict) tempo modulations in a tempo-changing sequence as opposed to following (tracking) these changes. The results of Pecenka and Keller (2011) indicated that individual differences in anticipatory ability were stable across time and were also predictive of synchronization accuracy and precision. Moreover, synchronization performance on a dyadic tapping task was found to be better when two high predicting individuals (those who anticipated tempo changes more than followed tempo changes) were paired together compared to low predicting pairs (those that followed more than predicted tempo changes) or mixed pairs comprising high and low predicting individuals.

1.3. The Interaction between Anticipation and Adaptation

For the most part, anticipation and adaptation mechanisms that support musical joint action have been investigated separately and the relationship between these mechanisms is poorly understood. Van der Steen and Keller (2013) addressed this relationship by introducing the ADaptation and Anticipation Model (ADAM), a computational model that implements temporal anticipation and adaptive timing within a single framework. The adaptation module in ADAM, which functions as an internal model of an individual's own actions, programs each successive tap by implementing phase correction (and/or period correction) in accordance with the linear error correction model used by Repp and Keller (2008; cf. Schulze et al., 2005). The anticipation module in ADAM, which functions as an internal model of another's actions, generates temporal predictions via linear extrapolation based on a variable number of pacing inter-onset intervals. The outputs of the anticipation and adaptation modules feed into a 'joint' internal model, where the planned timing of the next tap is compared against the predicted timing of the next pacing event. If the difference (i.e., the anticipated asynchrony) falls within a pre-defined tolerance region, then the planned movement is executed; otherwise a default timing value (based on the previous IOI) is used. As an alternative to this default value, a recent instantiation of ADAM implements period correction in the joint internal model to adjust the internal timekeeper in such a way that the planned timing of the next movement is shifted towards the predicted timing of the next event. According to ADAM, synchronization accuracy and precision are facilitated by the interaction of temporal adaptation and anticipation processes in the joint internal model.

The main aim of the current study was to examine the relationship between individual differences in anticipatory skill and adaptive timing in a sample consisting of individuals who are not expert musicians. A second aim was to assess the contribution of anticipatory and adaptive mechanisms to synchronization precision and accuracy. Based on ADAM, it was hypothesized there would be a positive relationship between temporal anticipation and adaptive timing, indicating that those who are better at predicting tempo changes also display higher phase correction. Furthermore, it was hypothesized that measures of both anticipation and adaptation would be predictors of synchronization accuracy (mean asynchrony) and precision (variability of asynchronies). These hypotheses were tested in a behavioural experiment that included a battery of paced finger-tapping tasks.

2. Method

2.1. Participants

First-year psychology students and volunteers from the University of Western Sydney (N = 69) participated in the study (57 female; age range = 18–50 years; M = 25.81 years, SD = 8.86). The majority of participants (65%) reported having no musical experience. Of the 24 participants who reported having some form of musical training, 18 had between one and four years, while six reported having six or more years of musical training. After excluding participants who had insufficient tapping data (see Sect. 2.5 for details), 52 participants remained (43 female; age range = 18–50 years; M = 27.02 years, SD = 9.41) of which four reported having more than six years of musical training. All participants had self-reported normal hearing and provided informed written consent prior to participation.

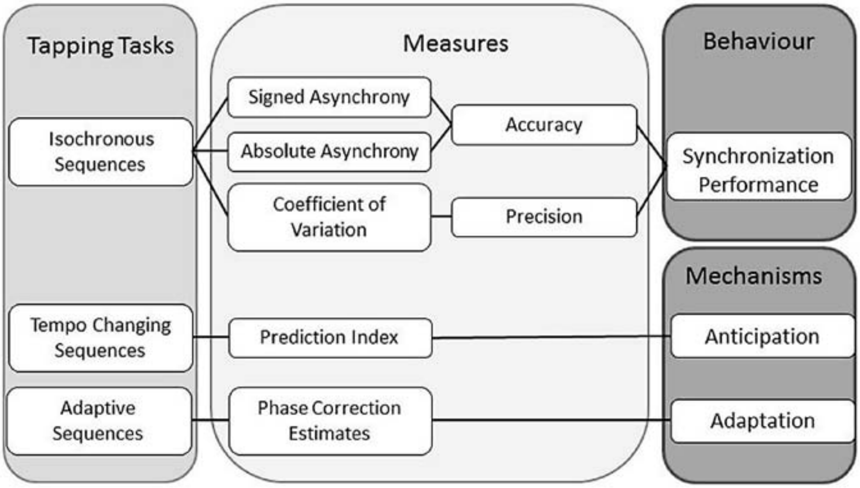

Figure 2. Schematic of the three tapping tasks, the measure(s) derived from each task, and the process (at the level of behavioral and underlying mechanisms) assessed by each measure.

2.2. Design

The experiment consisted of three synchronized tapping tasks: Isochronous, tempo-changing, and adaptive (see Fig. 2). The isochronous tapping task provided measures of general synchronization ability, including assessment of both accuracy (mean asynchrony) and precision (variability of asynchronies) at two tempi (see Sect. 2.5). The tempo-changing task provided a measure of anticipatory ability through the calculation of prediction indices. Finally, the adaptive task was employed with varying levels of virtual partner adaptivity (α) to gain an estimate of each participant's adaptive tendency (estimate of phase correction). To understand the contribution of both anticipation and adaptation to synchronization performance, the prediction indices and phase correction estimates were used as the predictor variables whereas the measures of synchronization performance (accuracy and precision) were the dependent variables.

2.3. Materials and Stimuli

Participants tapped on a Roland Handsonic 10 percussion pad connected via an M-Audio MIDI interface to an Apple MacBook Pro laptop running Max/MSP software. The auditory stimuli were sequences of percussion sounds presented over Sennheiser HD 25-II headphones connected to the laptop. Each sound was a synthesized conga sound with a clear onset and rapid decay. Finger taps did not generate any auditory feedback (apart from a thud). Max/MSP controlled the presentation of all stimulus sequences and recorded tapping response times. Measurements taken prior to the experiment indicated that the mean end-to-end latency of the setup was 28 ms (*SD* = 3 ms). This comprised a 5 ms delay between a tap being made on the percussion pad and its registration by Max/MSP on the laptop, plus a 23 ms delay associated with the generation of the sound by Max/MSP and transmission through the headphones. These delays were accounted for in the Max/MSP script by subtracting 5 ms from each registered tap onset time and adding 23 ms to each tone presentation time when computing asynchronies.

Three different types of auditory pacing signals were used. The regular pacing signal was used to measure synchronization performance and consisted of isochronous sequences of conga sounds presented with IOIs of either 400 ms (fast tempo) or 600 ms (slow tempo). The tempo-changing signal, used to calculate the prediction indices, contained tempo variations that are similar to tempo changes in music, as used by Pecenka and Keller (2011). The sequences progressed through both accelerations and decelerations following a sinusoidal function of IOIs, which increased or decreased with step sizes varying between 11 ms and 64 ms, within an outside range of 400 ms and 600 ms. There were six arrangements, with each one differing in terms of the time points of switches between acceleration and deceleration throughout the sequence.

Finally, the adaptive virtual partner was used to obtain an estimate of participant's adaptive timing ability. The adaptive sequences responded to participant's tap timing by implementing three levels of phase correction, 0.3, 0.7, and 1, with each value representing the proportion of asynchrony that was corrected for by the virtual partner. As in previous studies (Fairhurst et al., 2013; Repp & Keller, 2008; Vorberg, 2005), the linear phase correction model of Vorberg and Schulze (2002) controlled this process according to the algorithm:

$$t_{n+1} = t_n + T + a_c \times \text{async}$$

where t_n = time of pacing event, T = base IOI (either 400 or 600ms), a_c = phase correction parameter implemented by the computer (0.3, 0.7, or 1), and async = asynchrony between tap and pacing event. For example, if a participant tapped too early (a negative asynchrony), the subsequent event would occur earlier by a proportion (0.3, 0.7, or 1) of the negative asynchrony. Thus, each IOI throughout the sequence was adjusted in response to the amount and direction of participant tap asynchrony (see Fig. 1). The adaptive sequences were presented at two base tempi: 400 and 600 ms.

2.4. Procedure

Participants completed the test session individually in a quiet room. Participants were seated at a desk, upon which the laptop and percussion pad were placed. The experimenter informed the participant that he or she would hear several different types of pacing sequences through the headphones, and that they should tap in time on the percussion pad with the sounds they heard. For the isochronous task, the instructions were "using your finger, tap on the percussion pad in time with the beat". For the tempo-changing task, participants were instructed to "keep in time with the changing tempo". For the adaptive pacing task, participants were asked to "keep in time with the beat while also maintaining a steady tempo, try to keep all of your taps even". Participants initially completed a block of 11 practice trials (each with 20 pacing events) that included examples of all sequence types. Participants then completed two test blocks of tapping trials, each comprising of 26 sequences of 60 events. All participants received the same order of trials:

1. Four trials of the isochronous pacing sequence, alternating between 600 and 400 ms.
2. The six tempo-changing sequences.
3. The 12 adaptive sequences inclusive of four trials each at alpha = 0.3, 0.7, and 1. Half were presented at 400 ms and half at 600 ms in alternating order.
4. A repeat of the four isochronous pacing sequences at both 400 and 600 ms.

After a short break, participants completed the second test block. Each block took approximately 15 mins.

2.5. Data Analysis

Tapping data were pre-processed in a custom made MATLAB script. Linear interpolation was used to estimate the values of any missed taps. A tap could be recorded as missed due to a participant genuinely missing a tap or a tap not being registered by the percussion pad. In addition, taps with a large asynchrony of ≥ 200 ms or ≤ -200 ms were also treated as missed taps. This criterion was chosen because 200 ms represents 0.5 of the fastest IOI of 400 ms. Any trials that were missing more than 5 out of 60 taps, or trials that included three or more consecutive missing taps, were omitted from analysis.

2.5.1. Synchronization Performance

Measures of synchronization performance were calculated based on the isochronous trials only. Synchronization was assessed in terms of asynchronies, that is, the difference between pacing event onset times and the corresponding tap onset time. A negative asynchrony indicates that the tap preceded the pacing event. For each participant, three indicators of synchronization performance were calculated from the asynchronies in the isochronous trials. Synchronization *accuracy* was indexed by both mean signed asynchrony and mean absolute asynchrony. Signed asynchrony is an indicator of the relative earliness (negative asynchrony) or lateness (positive asynchrony) of taps compared to the pacing events, whereas absolute asynchrony indicates the magnitude of the asynchrony independent of the earliness or lateness. Synchronization *precision* was indexed by the coefficient of variation (the SD of the signed asynchronies divided by the mean ITI for each trial). This is a measure of how stable the tap timing was in relation to the pacing events, where higher values indicate more variability in tapping.

2.5.2. Prediction Indices

For each participant, a prediction index was calculated using the data from the tempo-changing trials. This index is a measure of the degree to which the participant was able to anticipate (predict) the tempo changes as opposed to following (tracking) the changes. An autoregressive modelling approach was employed using R software (Dean & Bailes, 2010; Launay et al., 2014). IOI and ITI time series data were first pre-whitened to remove autocorrelations (due to drift or local serial dependencies). Autoregressive coefficients representing the strength of the relationship between the participant's ITIs and the IOIs of the pacing sequence were then calculated at both lag 0 and lag 1. The coefficient at lag 0 indicates how accurately the participant anticipated or predicted the timing of the current IOI, whereas the coefficient at lag 1 reflects the degree to which the participant's tap intervals matched the timing of the previous IOI (cf. Pecenka & Keller, 2011; Rankin et al., 2009; Repp, 2002). The lag 1 coefficient was then subtracted from the lag 0 coefficient, resulting in an index with values greater than 0 indicating higher degrees of predictive than tracking tendencies and values less than 0 indicating greater tracking than predictive tendencies. This procedure differs from that of Pecenka and Keller (2011), but the resulting estimates are strongly correlated with the prediction/tracking ratios computed for the present dataset using their method ($r = 0.98$).

We decided that a minimum of three valid tempo-changing sequences were required to arrive at reliable prediction indices. Sixteen participants did not meet this criterion and their data were excluded from further analysis.

2.5.3. Phase Correction Estimates

An estimate of each participant's use of phase correction, was calculated based on the lag 1 autocorrelations of the asynchronies (the time series correlated with itself at a lag of 1) across each level of alpha: 0.3, 0.7, and 1. A regression line was fitted to the mean autocorrelations for each level and the 0 crossing point (x-intercept) of this line of best fit was calculated. This represents the point of virtual partner adaptivity that is optimal for each participant. This x-intercept was then subtracted from 0.9 (estimated optimal total error correction between the computer and human) to gain an estimate of human phase correction (see Repp & Keller, 2008). Due to missing taps, we introduced the criterion that at least two valid trials for at least two levels of virtual partner alpha were required to calculate human alpha for an individual participant. One participant did not meet this criterion and was excluded from further analysis.

3. Results

Analyses were conducted in SPSS with the criterion for statistical significance set at p = 0.05. Prior to analysis, all data were screened for missing values and outliers. After excluding the 17 participants who had insufficient tapping data (see Sect. 2.5), 52 participants remained in the final sample. No univariate outliers (standardised scores in excess of ±3.29; Tabachnick & Fidell, 2007) were identified. Descriptive statistics for all tapping data are shown in Table 1, while histograms displaying the distributions for the prediction index, phase correction estimates and the measures of synchronization performance (mean asynchrony, mean absolute asynchrony, and coefficient of variation for isochronous trials) can be seen in Fig. 3. The assumption of normality was violated for Coefficient of Variation, which was rectified through square-root transformation.

3.1. Relationship between Anticipation and Adaptation

A Pearson product-moment correlation was conducted to investigate the relationship between measures of temporal anticipation (prediction index; $M = 0.24$, $SD = 0.24$) and adaptation (phase correction estimates; $M = 0.33$, $SD = 0.20$). A significant positive correlation was found, $r(50) = 0.47$, $p < 0.001$, indicating that higher phase correction is related to higher predictive tendencies (see Fig. 4).

3.2. Predictors of Sensorimotor Synchronization Accuracy and Precision

A series of hierarchical regressions were conducted in order to investigate the relationship between the combination of phase correction estimates and prediction index, on each of the outcome variables of synchronization accuracy (mean asynchrony and mean absolute asynchrony) and precision (square-root transformed

Table 1.
Summary of descriptive statistics for the isochronous, tempo changing, and adaptive tapping trials

Tapping task	Mean asynchrony (ms) *M* (*SD*)	Mean absolute asynchrony (ms) *M* (*SD*)	Coefficient of variation *M* (*SD*)
Isochronous	-56.66 (25.02)	56.79 (24.50)	0.058 (0.017)
Tempo changing	-59.78 (22.70)	67.71 (17.42)	0.101 (0.016)
Adaptive			
alpha = 0.3	-50.18 (24.30)	53.82 (22.14)	0.054 (0.015)
alpha = 0.7	-44.32 (21.39)	48.78 (18.23)	0.055 (0.014)
alpha = 1	-39.37 (19.60)	46.90 (15.67)	0.066 (0.018)

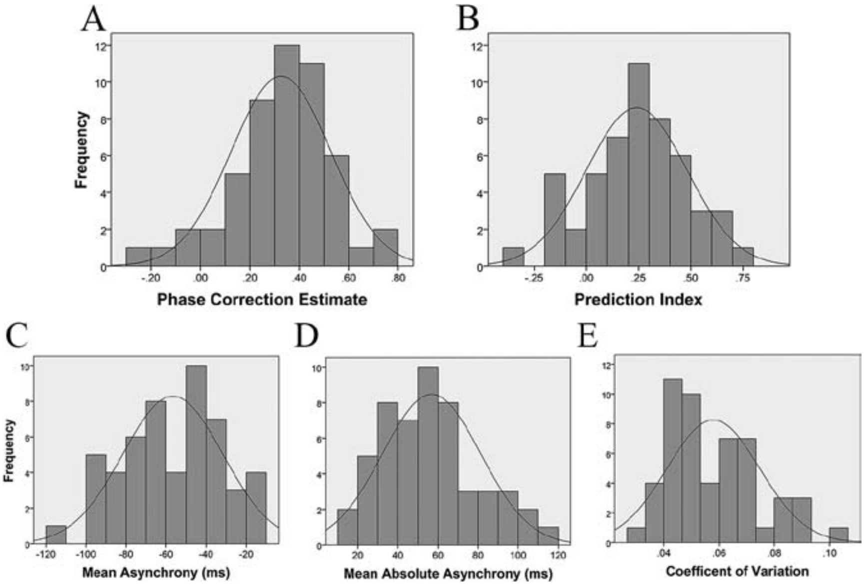

Figure 3. Histograms displaying the distributions of (A) phase correction estimates, (B) prediction indices, and measures of synchronization performance, (C) mean asynchrony, (D) mean absolute asynchrony, and (E) coefficient of variation for isochronous trials.

coefficient of variation [sqrtCV]). The assumptions of multiple regression were evaluated, along with assessment of multivariate outliers and multicollinearity between predictors. No multivariate outliers were identified (i.e., no standardised residual > 3 or extreme Mahalanobis distance scores, $p < 0.001$, critical value = 13.82).

In all three regressions, phase correction estimate was entered first, followed by prediction index. This order represents the order of interest in each variable, with phase correction estimate being first due to the assumption that phase correction is an automatic process. Table 2 displays the standardised regression coefficients (β) and R^2 change (ΔR^2) for the predictors at each step within each regression. The first hierarchical regression assessed mean asynchrony (one measure of synchronization accuracy) as the dependent variable. Evaluation of the overall regression model revealed that at step 1, phase correction estimate alone was a significant predictor, $R = 0.51$, $R^2 = 0.26$, adjusted $R^2 = 0.25$, $F\,(1, 50) = 17.78$, $p < 0.001$. The addition of prediction index at step 2 did not significantly enhance the predictive utility of the final model $R = 0.52$, $R^2 = 0.28$, adjusted $R^2 = 0.25$, $F\,(2, 49) = 9.28$, $p = < 0.001$, nor was prediction index a significant unique predictor of mean asynchrony once shared variance was removed (see Table 2). A second regression was performed with mean absolute asynchrony (the second measure of accuracy) as the dependent measure. This regression mirrored the previous model with phase correction estimate entered at step 1 being sufficient to generate a significant

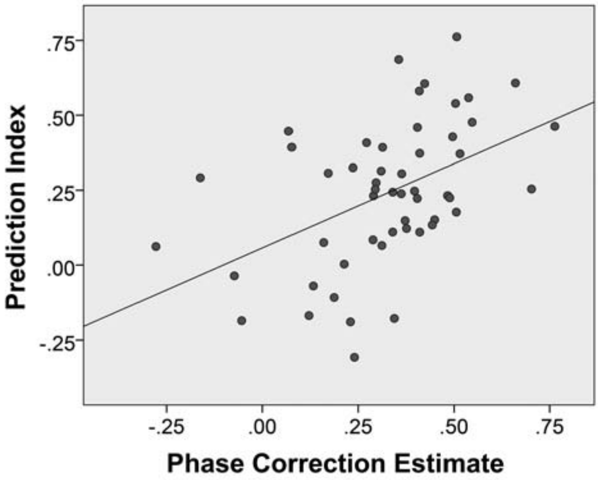

Figure 4. Scatterplot of the prediction index and phase correction estimates. [Phase correction estimates were negative for four participants. These negative values may be due to bias in the estimation procedure and/or to the inclusion of a relatively fast tempo (400 ms base IOI). Previous work has shown that phase correction estimates decrease with increasing tempo (Repp et al., 2012), and that second-order phase correction can occur at fast tempi (Vorberg & Schulze, 2002). Second-order error correction increases lag-2 autocorrelation, thus lowering first-order correction estimates, and is not optimal for maximising synchronization accuracy and precision].

Table 2.
Hierarchical multiple regression between prediction index and phase correction as predictors of synchronization accuracy (mean asynchrony, mean absolute asynchrony) and precision (square-root transformed coefficient of variation)

Variables	Mean asynchrony		Mean absolute asynchrony		sqrtCV	
	β	ΔR^2	β	ΔR^2	β	ΔR^2
Step 1	-	0.26***	-	0.33***	-	0.46***
Phase correction	0.51***		-0.58***		-0.69***	
Step 2	-	0.01	-	0.01	-	0.15***
Phase correction	0.45**		-0.52***		-0.50***	
Prediction index	0.13		-0.12		-0.41***	

***$p < 0.001$; **$p < 0.01$; * $p < 0.05$.

model $R = 0.57$, $R^2 = 0.33$, adjusted $R^2 = 0.32$, $F(1, 50) = 24.78$, $p < 0.001$. Prediction index entered at step 2 was again not a significant unique predictor (see Table 2) and did not improve the final model $R = 0.59$, $R^2 = 0.34$, adjusted $R^2 = 0.32$, $F(2, 49) = 12.77$, $p < 0.001$.

To assess the best predictors of tapping precision, a third hierarchical regression was conducted with sqrtCV as the dependent measure. Again at step 1, phase correction estimate alone generated a significant regression model $R = 0.68$, $R^2 = 0.46$, adjusted $R^2 = 0.46$, $F(1, 50) = 43.66$, $p < 0.001$. However, unlike the previous regressions, prediction index significantly improved the model when entered at step 2, $R = 0.78$, $R^2 = 0.61$, adjusted $R^2 = 0.60$, $F(2, 49) = 39.02$, $p < 0.001$, and was a significant unique predictor of tapping variability (see Table 2). This model accounts for approximately 61% of sample variance in tapping precision.

As expected, phase correction estimate was a significant predictor in all the three regressions, and was sufficient to explain a significant amount of variance in all three dependent measures. Once shared variance was removed, prediction index was only a significant unique predictor of sqrtCV, the measure of tapping precision, and did not significantly contribute to either of the dependent measures of synchronization accuracy. Out of the three regressions, the most variance explained was with tapping precision (coefficient of variation), followed by absolute asynchrony, and the least was with signed asynchrony. Together these results indicate that while adaptive mechanisms are important for both synchronization accuracy and precision, anticipatory mechanisms are more strongly related to synchronization precision (variability of asynchrony) than synchronization accuracy (asynchrony).

Analysis of the bivariate correlations between the predictor variables and each of the dependent measures revealed a significant positive correlation between prediction index and mean asynchrony $r(50) = 0.34$, $p = 0.007$, indicating that those with higher prediction indices had smaller asynchronies (asynchronies closer to 0, all participants had a negative mean asynchrony). In addition there was a significant negative correlation between prediction index and mean absolute asynchrony $r(50) = -0.58$, $p < 0.001$, and also prediction index and sqrtCV $r(50) = -0.66$, $p < 0.001$, indicating that those with higher prediction indices had smaller absolute asynchronies and less variability. Likewise, there was also a significant positive correlation between phase correction and mean asynchrony $r(50) = 0.51$, $p < 0.001$, and a significant negative correlation between phase correction and mean absolute asynchrony $r(50) = -0.58$, $p < 0.001$, and phase correction and sqrtCV $r(50) = -0.68$, $p < 0.001$.

4. Discussion

The main aim of this study was to examine the relationship between two of the underlying mechanisms of sensorimotor synchronization, namely temporal anticipation and adaptive timing. This was investigated by assessing the relationship between phase correction estimates and prediction index scores in a paced finger-tapping task. A positive correlation was observed between phase correction and prediction index measures, indicating that increased phase correction is related to an increased tendency to predict the timing of upcoming sounds. Consistent with ADAM, a computational model of temporal adaptation and anticipation (van der Steen & Keller, 2013), these results suggest that these two processes are not independent but instead work in tandem to improve synchronization performance. The positive relationship implies that, without disrupting timing stability, higher prediction tendencies allow more error correction due to correcting for a larger proportion of smaller asynchronies. In other words, higher prediction leads to higher accuracy (i.e., smaller asynchronies; Pecenka & Keller, 2011), so the absolute amount of correction is small even when a greater relative proportion of the asynchrony is corrected for.

The observed positive relationship between anticipatory and adaptive mechanisms is a first step towards understanding the relationship between the mechanisms underlying sensorimotor synchronization. We hypothesized that the link is the internal models that run online simulations of actions before they occur (cf. Wolpert et al., 1998). Action simulation within the sensorimotor control system could access mechanisms of anticipating the timing of the subsequent sound, as well as estimating and correcting potential synchronization errors. Our results support van der Steen and Keller's (2013) claim that this form of anticipatory error correction is implemented by 'joint' internal models that compute timing errors prospectively based on simulations of the predicted timing of another's action and the timing of one's own next action (given a particular error correction setting).

The positive relationship between temporal anticipation and adaptation is remarkable. It might have been expected that they would be independent to the extent that anticipation is a conscious process (Pecenka et al., 2013) whereas adaptation, specifically phase correction, occurs automatically without awareness (Repp, 2005). The two processes thus call upon separate perceptual and motor resources in the brain. Alternatively, a negative relationship might have been expected on logical grounds due to the fact that less error correction is required when higher prediction is employed, because asynchronies would be small in the first place. The observed positive relationship, however, suggests that while individuals with higher anticipatory tendencies tend to have overall smaller asynchronies and less error to correct (Pecenka & Keller, 2011), this is beneficial because larger proportions of the asynchrony can be corrected without disrupting the stability of movement timing.

A second aim was to assess the contribution of anticipatory and adaptive mechanisms to individual differences in synchronization accuracy (asynchrony) and precision (variability of asynchrony). The findings of the present study confirm that both anticipatory and adaptive mechanisms influence synchronization performance. The present results buttress those of Pecenka and Keller (2011), who found that anticipatory tendencies are predictive of both accuracy and precision, and extend this earlier work by adding assessment of adaptive timing. As expected, evaluation of the hierarchical multiple regression analyses revealed that the combination of phase correction and temporal anticipation accounted for a significant amount of the variance in each of the dependent measures of synchronization accuracy (mean signed asynchrony and mean absolute asynchrony) and precision (coefficient of variation). This combination of variables best accounted for the variance in the precision measure (coefficient of variation), accounting for 61% variance in this sample. This finding suggests that the combination of anticipation and adaptation may be more conducive to reducing the variability of tap timing rather than reducing asynchrony.

Despite each of the overall regression models being significant, phase correction was the only variable to contribute significantly in all three models. Contrary to expectations, the addition of the prediction index did not significantly improve either of the models that assessed synchronization accuracy. In addition, once shared variance was removed, the prediction index was only a significant unique predictor of tapping precision. These results indicate that anticipatory tendencies do not account for reductions in asynchrony over and above what is already accounted for by phase correction. This is despite the prediction index being significantly correlated with both mean asynchrony and absolute mean asynchrony. However, it worth noting that the outcome measures of synchronization performance were calculated from the isochronous trials only, where effortful anticipatory mechanisms might not be as vital. In addition, the majority of the present sample had very little musical experience. During synchronization tasks, musicians may be able to invest greater cognitive resources into temporal prediction due to other aspects of the task being more automatized than is the case for non-musicians. This raises the possibility that anticipation may be a significant predictor of synchronization accuracy in a sample of musicians. Notwithstanding this, the current results suggest that prediction is more specifically related to increasing precision rather than increasing accuracy.

Previous research (e.g., Pecenka & Keller, 2011; Repp & Keller, 2008) has investigated anticipatory and adaptive processes separately using samples comprised primarily of individuals with moderate to high levels of musical training. The current study has identified a relationship between temporal anticipation and adaptation in a sensorimotor synchronization task using a sample with low levels of musical experience. Our findings therefore provide evidence that these underlying mechanisms of sensorimotor synchronization generalize beyond the domain of musical experts to the population more broadly. In addition, the results demonstrate that individual differences in the operation of the two mechanisms can predict synchronization accuracy and precision, however prediction appears to be more so related to precision than accuracy. By generally providing empirical support for ADAM (van der Steen & Keller, 2013), a computational modelling approach addressing the joint contributions of anticipation and adaptation to sensorimotor synchronization, the present study highlights the importance of considering both error correction and predictive tendencies when investigating the temporal dynamics of sensorimotor synchronization. We believe that doing so may be especially profitable, not only for understanding how expert musicians and dancers coordinate during ensemble performance, but also when attempting to explain impairments to sensorimotor synchronization ability, which may have multiple causes. Thus, employing approaches such as ADAM to further our understanding of the mechanisms underlying sensorimotor synchronization may potentially benefit individuals with disrupted rhythmic timing abilities, such as those with Parkinson's Disease (e.g., Hove et al., 2012), beat deafness (e.g., Phillips-Silver et al., 2011), or social coordination deficits, such as those associated with Autism spectrum disorders (e.g., Behrends et al., 2012).

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