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Endogenous rhythms influence interpersonal synchrony

Anna Zamm[1], Chelsea Wellman[1], Caroline Palmer[1a]

[1]Department of Psychology, McGill University

1205 Dr. Penfield Avenue, Montreal, Canada H3A 1B1

[a]Corresponding author:

Prof. Caroline Palmer

Dept. of Psychology

McGill University

1205 Dr. Penfield Ave

Montreal, QC Canada H3A 1B1

Phone: (+1) 514 398 6128

Fax: (+1) 514 398 4896

caroline.palmer@mcgill.ca

Running Head: Endogenous rhythms influence interpersonal synchrony

Abstract

Interpersonal synchrony, the temporal coordination of actions between individuals, is fundamental to social behaviors from conversational speech to dance and music-making. Animal models indicate constraints on synchrony that arise from endogenous rhythms: Intrinsic periodic behaviors or processes that continue in the absence of change in external stimulus conditions. We report evidence for a direct causal link between endogenous rhythms and interpersonal synchrony in a music performance task, which places high demands on temporal coordination. We first establish that endogenous rhythms, measured by spontaneous rates of individual performance, are stable within individuals across stimulus materials, limb movements, and time points. We then test a causal link between endogenous rhythms and interpersonal synchrony by pairing each musician with a partner who is either matched or mismatched in spontaneous rate and by measuring their joint behavior up to one year later. Partners performed melodies together, using either the same or different hands. Partners who were matched for spontaneous rate showed greater interpersonal synchrony in joint performance than mismatched partners, regardless of hand used. Endogenous rhythms offer potential to predict optimal group membership in joint behaviors that require temporal coordination.

Introduction

Interpersonal synchrony, the temporal coordination of actions between individuals, is fundamental to social behaviors from conversational speech and dance to music-making. Interpersonal synchrony is associated with affiliation and rapport between partners (Cacioppo et al., 2014; Kirschner & Tomasello, 2010), suggesting it may facilitate group cohesion. What factors facilitate – and constrain – interpersonal synchrony? Evolutionary biology provides some clues: A few non-human animal species are able to coordinate the timing of their behavior with external rhythms that match their endogenous (spontaneous) rates of movement (Patel et al. 2009; Hasegawa et al., 2011; Cook et al., 2013). Humans are capable of synchronizing their behavior with a broader range of external rhythms than are other species. We address here whether humans' ability to synchronize with others is similarly influenced by endogenous rhythms.

Endogenous rhythms in biology refer to periodic behaviors or processes that occur in the absence of change in external stimulus conditions (Bunning, 1956); endogenous rhythms include all self-driven rhythmic behavior, in contrast to stimulus-driven or externally paced (exogenous) rhythmic behavior, such as tapping one's foot along with music. Endogenous rhythms influence spontaneous rates of movement, which have been argued to reflect the system's state of optimal efficiency, characterized by minimal energy expenditure (Hoyt & Taylor, 1981). Minimization of effort as an explanation for spontaneous movement rates has been applied to human posture, balance, and locomotion (Corna et al, 1999; Newell, 1986; Sparrow & Newell, 1998). We adopt here the proposal that spontaneous movement rates reflect endogenous rhythms that minimize an individual's effort.

Spontaneous rates for several rhythmic movements exhibit individual differences, including walking (Murray et al. 1964), finger-tapping (McAuley et al., 2006; Moelants 2002), speech (Jungers, Palmer & Speer, 2002), and music performance (Loehr & Palmer, 2011; Zamm et al., 2015). These individual differences may arise from limb-specific anatomical and biomechanical constraints that influence timing; for example, the timing of leg movements in walking is thought to be determined by natural motor resonances of specific limbs, which are related to physical characteristics such as limb length and weight (Goodman et al, 2000; Nessler & Gilliland, 2009). Alternatively, endogenous rhythms may arise from more general control mechanisms, such as central pattern generators in the brain, which have been suggested to govern the timing of behavior (Latash, 1992; Wolpert, 2007), and which can produce rhythmic movements in the absence of external sensory input.

Dynamical theories of rhythm coordination have documented relationships between *exogenous* (environmental- or stimulus-driven) rhythms and interpersonal coordination. Richardson, Schmidt and colleagues compared the temporal synchrony with which two people rocked in weighted rocking chairs or swung pendulums of different weights (Schmidt et al., 1998; Richardson et al., 2005, 2007). The more similar the natural frequencies of the chairs or pendulums, the more synchronous the individuals' joint behavior, and the greater the synchronization stability. Less work has investigated the relationship between *endogenous* rhythms and interpersonal synchrony. Endogenous rhythms displayed in spontaneous rates of treadmill walking and music performance have been correlated with spontaneous synchrony measures in joint walking (Nessler & Gilliland, 2009) and with intentional synchrony during joint music performance (Zamm et al., 2015), respectively, but important factors preclude one from drawing a direct link between spontaneous rates and joint synchrony. Potential covariates in these studies were either deliberately covaried (e.g. assigned Leader/Follower roles), or were uncontrolled, including task experience, social factors (partner familiarity), and the range of natural frequencies measured. Furthermore, the studies did not compare the relationship between spontaneous rates and interpersonal synchrony across different time points, tasks, and/or limbs. These tests are critical for establishing the stability of the relationship between spontaneous rates and interpersonal synchrony.

We report here the first evidence of a direct causal link between endogenous rhythms and interpersonal synchrony in music performance, which places high demands on temporal coordination in its explicit goal of synchronization. First, we establish whether endogenous rhythms, measured by spontaneous performance rate (SPR), are stable within individual pianists across tasks, time-points, and effectors (left and right hand movements). Piano performance requires different fingers to produce the same pitch sequence when pianists switch between right and left hands, allowing for a natural manipulation of effectors (hand, fingers) independent of pitch outcomes. Established differences in timing between hands and fingers during sequential tapping tasks (Loehr & Palmer, 2007; Hager-Ross & Schmidt, 2000), as well as piano performance (Palmer & van de Sande, 1993), predict a right-hand advantage, and a 2nd and 3rd digit advantage: greater accuracy and reduced temporal variability have been documented for those effector movements. We therefore examine possible differences in effector timing in pianists' spontaneous performance rates. Second, we test synchronization in joint performance of novel melodies, as musicians perform with the same or different hand and fingers as a partner who is matched or mismatched for spontaneous rate, but is equivalent with respect to other factors known to influence interpersonal synchrony (see Table 1). Similar to previous manipulations of exogenous rhythms with weighted pendulums (Schmidt et al., 1998; Richardson et al., 2005, 2007) we manipulate endogenous rhythms by pairing each musician with a partner whose spontaneous rates are congruent or incongruent with one's own rates. If a causal link exists between endogenous rhythms and interpersonal synchrony, then partners matched for spontaneous rate should show greater temporal synchrony and stability of synchronization than mismatched partners, after controlling for other factors. Furthermore, this prediction should hold across different arm, hand, and finger movements if endogenous rhythms reflect general timekeeping constraints rather than motor resonances associated with specific limb movements.

Method

Participants

Forty pianists with ensemble music experience (mean years of private instruction = 13.21, SE = .68; 38 right-handed) from the Montreal community participated. Pianists were recruited during a Prescreening Session to form two groups: a Matched group (< 10 ms difference in spontaneous performance rate, SPR, between pair members) and a Mismatched group (> 110 ms difference in SPR). Pair members were unfamiliar with each other, and gave informed consent. Rate Match and Mismatch groups did not differ in age, amount of piano training, age of onset of piano training, mean SPR, or consistency of SPR across screening melodies (< 100 ms difference across melodies; see Table 1 for group comparisons). Two additional pairs were recruited but excluded (one pair due to inadvertent data loss and another to failure to follow instructions).

Stimulus Materials and Equipment

Stimuli for the Prescreening Session (Time 1) were two unfamiliar melodies (Zamm et al, 2015) adapted from Western European folk songs containing eight measures of binary (4/4) meter (32 quarter notes in length). Melodies were notated in treble clef and were written for the right hand; suggested fingerings were notated to control for possible differences in movements. Stimuli for the Experimental Session (Time 2) included four unfamiliar melodies, composed in major keys (C major and G major) and minor keys (A minor and F minor; see Supplemental materials). All melodies were isochronous, four measures in duration, and were composed to be performed with either hand. Musical scores were notated in the bass clef; separate versions of each melody were notated with fingerings for the left or right hands. The hand (left or right) with which participants should perform the melody was printed on the notation.

Pianists performed on a Roland 700 NX keyboard (Roland Corporation, Los Angeles, CA, USA) in Prescreening and Experimental sessions. During the Experimental session, the keyboards faced each other with an occluder in-between, so that pianists could see their partner's head but not their limb movements. MIDI data for tone onset times (keypresses) from each keyboard were recorded with Cubase 6 software (Steinberg Media Technologies, 2010) and a piano timbre was sounded over headphones (AKG K-271). Metronome pulses during the Experimental session were generated with a woodblock percussion timbre that sounded at 400 ms inter-onset intervals over participants' headphones, approximating participants' mean spontaneous rate (M = 388.61 ms) in the Prescreening session (difference between metronome and mean spontaneous rate: (t (38) = -.88, p = .384).

Design and Procedure

Two variables were manipulated in a mixed design: SPR-Group (between-pairs factor) and Hand used to perform the melodies in the Experimental session (within-pairs factor). SPR-Group contained Rate Match pairs (partners' SPR difference < 10 ms) and Rate Mismatch pairs (SPR difference > 110 ms). Hand that pianists used to perform the melodies was either the Same or Different hand as their partner (each pianist performed two melodies with the Right hand and two with the Left hand). The order in which hand conditions and melodies occurred was counterbalanced across Duet pairs.

Participants first visited the laboratory individually to record their SPR. The two Prescreening melodies were sent in advance, with instructions to memorize and perform with the right hand. Participants performed each melody from memory. If they made pitch errors, they were allowed to practice for up to five minutes and repeat the test. Only participants who performed without pitch errors by the second performance completed the study, ensuring that all participants had the melody well-memorized. They then performed three Solo trials in which they were instructed to perform at a comfortable regular pace, four times in succession without stopping. This procedure was repeated for each melody. Pianists were then assigned to Rate Match and Mismatch pairs based on their SPRs, as shown in Figure 1. Participants' SPR values were computed as the mean interonset interval (IOI) in the Solo performance trials. Rate Match pairs were created by assigning pianists in each quintile of the total SPR distribution to a partner with less than 10 ms SPR difference (mean pairwise difference = 3.2 ms; range = .34 – 5.6 ms). Rate Mismatch pairs were created by pairing a pianist in a lower segment of the remaining SPR distribution with a partner in an upper segment, to ensure representation across the absolute SPR range (mean pairwise difference = 145.6 ms, range = 110 – 193 ms).

Pianists returned for an Experimental Session in which they learned and performed four new melodies alone (Solo) and with a partner (Duet). Time elapsed between Prescreening and Experimental sessions varied across performers for scheduling ease (range = 6 – 574 days). Each pianist performed the Experimental melodies in a Solo task, following the same procedure as during Prescreening. Pianists then performed the Experimental melodies with their partner. For each melody, partners performed a practice trial and three test trials on which they performed the melody four times continuously (4 Cycles), using the same Hand as during Solo performance. A four-beat metronome cue established the tempo. Partners were instructed to synchronize with each other while staying within the constraints of the metronome-cued tempo.

Data Analysis

Timing analyses for Solo performances assessed the middle two repetitions (Cycles) of each trial (n = 64 IOIs per trial for Prescreening melodies; n = 32 for Experimental melodies), to capture maximally stable behavior (Loehr & Palmer, 2011; McAuley et al, 2006). Mean tone onset asynchronies in Duet performances were defined as the absolute difference in milliseconds between the partners' tone onsets intended to be simultaneous, and synchronization stability was measured as the standard deviation of signed tone onset asynchronies, defined as faster SPR partner's tone onset time – slower SPR partner's tone onset time. Variability of signed asynchrony is a common measure of coordination stability (Haken et al., 1985; Schmidt et al., 1998; Richardson et al., 2007), where low variability indicates stable coordination and high variability indicates unstable coordination. Synchronization and stability in Duet performance were measured over the entire trial (4 Cycles; n = 64 asynchronies per Duet trial), in order to assess possible change across time. Occasional pitch errors were identified by computer comparison of performances with the pitch contents of the notated score: Cycles in which pitch additions or deletions occurred were excluded from analyses (Solo: 4.0%; Duet: 8.8%).

Results

Individual Spontaneous Rates are Consistent

First, we assessed whether SPRs from Solo performances were reliable within individuals across melodies and hand movements. Simple correlations showed that both groups had highly consistent SPRs across the Prescreening melodies, r (38) = .90, $p < 0.001$; Rate Match subjects: r

(18) = .87, $p < 0.001$; Rate Mismatch subjects: r (18) = .94, $p < 0.001$). Tests of whether the Rate Match and Mismatch groups reflected similar SPR distributions indicated homogeneity of variance (Levene's Test: (F (1, 18) = .21, p = .652) and normality (Kolmogorov-Smirnov: Rate Match, F (1, 10) = .137, p = .20; Rate Mismatch, F (1, 10) = .150, p = .20). Furthermore, the groups showed statistically equivalent SPR means (see Table 1); only the magnitude of difference between partners' SPRs differed across groups.

Simple correlations showed that SPR was consistent within performer across all Experimental melodies (mean r = .87; range = .79-.94, all p's < .0038, Bonferroni-adjusted), regardless of differences in tonality (major and minor keys). Mean SPRs were also compared for Left-hand and Right-hand performances: Figure 2A shows that individuals' SPRs were highly consistent across hand movements (r (38) =.89, p < .001), suggesting stability of SPR across limbs. Differences in mean and variance of Left- and Right-hand SPR were equivalent across groups (Table 1); coefficients of variation for IOIs were small and equivalent across groups (Matched mean = .045; mismatched mean = .052), indicating that both groups performed fluently.

Finally, SPR values were compared from Time 1 (Prescreening) to Time 2 (Experimental Session): Figure 2B shows that individuals' SPRs correlated significantly across the time-points, suggesting stability of SPR across time, r (38) = .73, $p < 0.001$. To control for variability of time elapsed between measurements, the correlation was repeated after effects of elapsed time (number of days) were partialled out of SPR at Time 2: The semi-partial correlation was also significant, r (38) =.725, p < .001.

Interpersonal Synchrony Differs across SPR Groups

We assessed whether duet synchronization differed across SPR Groups (Match / Mismatch) or Hand conditions (Same / Different). Mean absolute asynchronies in Duet performances were evaluated with a three-way mixed repeated-measures ANOVA with SPR-Group as a between-subjects factor, Hand condition and Cycle (1-4) as within-subjects factors, and pair as the random variable. The main effect of SPR-Group was significant, F (1, 18) = 6.316, p = .022, partial η^2 = .259). As shown in Figure 3, asynchronies were largest for the Mismatch pairs. In addition, there was a main effect of Cycle, F (3, 54) = 3.64, p = .018, partial η^2 = .168. Asynchronies were significantly larger in Cycle 1 than in Cycles 2 and 3 (Tukey HSD = 2.318, p < .05). No other variables or interactions reached significance (all p's > .4).

We tested whether Matched and Mismatched pairs differed in synchronization stability by measuring the standard deviation of signed asynchronies, defined as faster SPR partner's tone onset time – slower SPR partner's tone onset time. Standard deviation of signed asynchronies generally increases when synchronization stability is low (Haken et al., 1985; Schmidt et al., 1998; Richardson et al., 2007). Once again, an effect of SPR-Group was observed, with Mismatched pairs showing greater variability of signed asynchronies than Matched pairs across cycles of Duet performance, F (1,18) = 3.950, p = .031 (one-tailed), partial η^2 =.18. A main effect of Cycle on standard deviation was also observed, F (3, 54) = 6.986, p = .000, partial η^2 = .27, with largest variability observed in Cycle 1 relative to other cycles.

Finally, we test the possibility that observed group differences in synchronization and synchronization stability were driven by differences in duet production rates or by nonhomogeneity of variances across groups. We divided mean asynchrony values by the mean trial IOI (following Richardson et al, 2007), consistent with measures that express relative phase as a proportion of the mean period. Findings confirmed the previously observed SPR-group effects for both mean absolute asynchrony values (F (1,18) = 6.291, p = .022) and for the standard deviations of adjusted signed asynchronies (F (1, 18) = 4.824, p = .041), indicating that Rate Matched pairs showed lower asynchronies and higher synchronization stability than Rate Mismatched pairs after adjusting for possible duet differences in IOIs. We tested the role of variability by recomputing the group differences in synchronization and synchronization stability non-parametrically. Results confirmed the previously observed SPR-group effects on both absolute asynchrony (Mann-Whitney U = 78.00, p = .017, one-tailed) and standard deviation of signed asynchronies (U = 72.00, p = .048, one-tailed), with Rate Mismatch pairs showing larger asynchronies and larger standard deviation of signed asynchronies than Rate Match pairs.

Discussion

The ability to synchronize our actions with external events is a hallmark of human behavior. The behavior of the few non-human species who are capable of synchronizing, including birds and sea lions (Cook, 2013; Patel, 2009), tends to be influenced by endogenous rhythms that constrain the rates at which they can synchronize. We have provided confirmatory evidence for a causal (predictive) link between endogenous rhythms and intentional interpersonal synchrony in skilled musicians, who are well-practiced at intentional synchronization. Partners matched in spontaneous rates of solo performance were more synchronous during joint duet performance than were mismatched partners.

This finding extends beyond previous correlational findings (Nessler & Gilliland, 2009; Zamm et al., 2015) as well as experimental manipulations of exogenous frequencies in rocking chair and pendulum tasks (Richardson et al., 2007; Schmidt et al., 1998). Matched partners also showed greater synchronization stability (smaller variability), suggesting a more stable mode of coordination, consistent with dynamical accounts.

The predictive nature of individuals' spontaneous rates for partners' joint synchrony transcended different hand and finger movements, melodies, and time points, and were consistent over long time delays between measurements. Alternative accounts from demographic and expertise factors cannot explain the group differences (see Table 1). Also unique to this study, no interpersonal roles (such as pre-existing friendships, assigned Leader / Follower roles or more / less important musical parts) differed between groups, as was the case in previous accounts (Loehr & Palmer, 2011; Zamm et al 2015), and so the current findings cannot be explained by social roles. Thus, this study provides the first evidence that spontaneous rate is a consistent measure of individuals' endogenous rhythms across time points, and a reliable predictor of group behavior.

The power of endogenous rhythms to predict individual behavior and group synchrony is potentially large; their influence may be important for determining optimal group membership in dyadic tasks. The fact that skilled musicians - experienced at reading, memorizing, and performing at a wide range of rates – showed large individual differences in spontaneous rates as well as constraints on interpersonal synchronization, suggests intrinsic properties that may further constrain behavior in less experienced populations. Future work should investigate how expertise and social factors previously linked to synchrony (Cacioppo et al, 2014; Marsh et al., 2009; Novembre et al., 2012) might interact with or be constrained by endogenous rhythms during synchronization tasks. The finding that partners' synchronization abilities generalized across hands and finger movements suggests the underlying mechanism arises not from peripheral (biomechanical or anatomical) differences between hands previously observed in skilled pianists' performance, but instead from more general mechanisms such as those proposed by central pattern generators (Latash, 1992) and motor synergies (Haken et al, 1985). Extensions to other joint tasks such as conversational speech may further test timing mechanisms that underlie endogenous rhythms. In sum, the scope of behaviors influenced by endogenous rhythms, as well as their underlying mechanisms, are important objects of further study.

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Table Captions

Table 1. Between-group tests of demographic and timing variables.

Figure Captions

Figure 1. Mean spontaneous performance rates (Prescreening session) for Rate Match (top panel) and Rate Mismatch partners (bottom panel). Error bars represent standard errors.

Figure 2. Panel A: Mean spontaneous rates (Experimental session) for left-hand and right-hand performances by participant. Panel B: Mean spontaneous rates at Prescreening (Time 1) and Experimental sessions (Time 2) by participant.

Figure 3. Mean absolute asynchrony (ms) of Duet performances (Experimental session) for Rate Match and Mismatch pairs, by repetition. Error bars represent standard errors.

Table 1.

BETWEEN-GROUP COMPARISON	**TEST**
Amount of piano training (years)	*t* (38) = 1.20, *p* = .23
Age at piano training onset (years)	*t* (38) = 0.54, *p* = .59
Current age (years)	*t* (38) = 1.50, *p* = .14
Mean SPR (Time 1)	*t* (38) = 0.68, *p* = .50
Difference in SPR across musical excerpts (Time 1)	*t* (38) = 0.99, *p* = .33
Difference in mean SPR across Times 1 and 2	*t* (38) = 0.55, *p* = .58
Mean pairwise difference in SPR across melodies (Time 2)	*t* (38) = 1.07, *p* = .29
Difference in mean SPR across right and left hands (Time 2)	*t* (38) = 0.39, *p* = .70
Solo SD / mean IOI (Time 2)	*t* (38) = 1.03, *p* = .31
Difference in Solo SD / mean IOI across right and left hands (Time 2)	*t* (38) = .69, *p* = .49
Mean duet performance tempo (IOI, ms, Time 2)	*t* (38) = 1.14, *p* = .27
Number of gender-matched partners (Time 2)	χ^2 (1, 20) = 0.22, *p* = .64

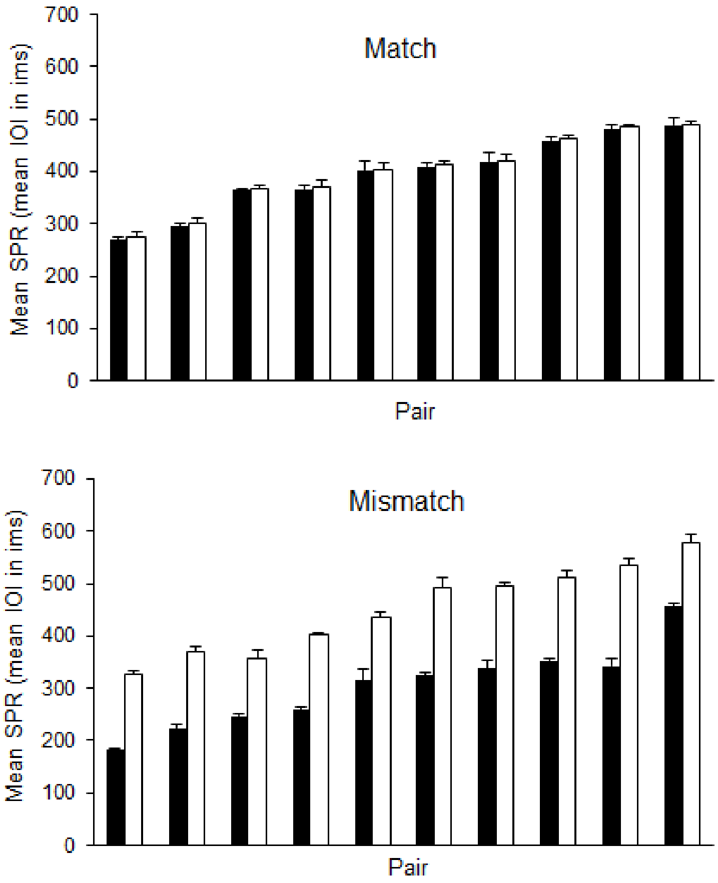
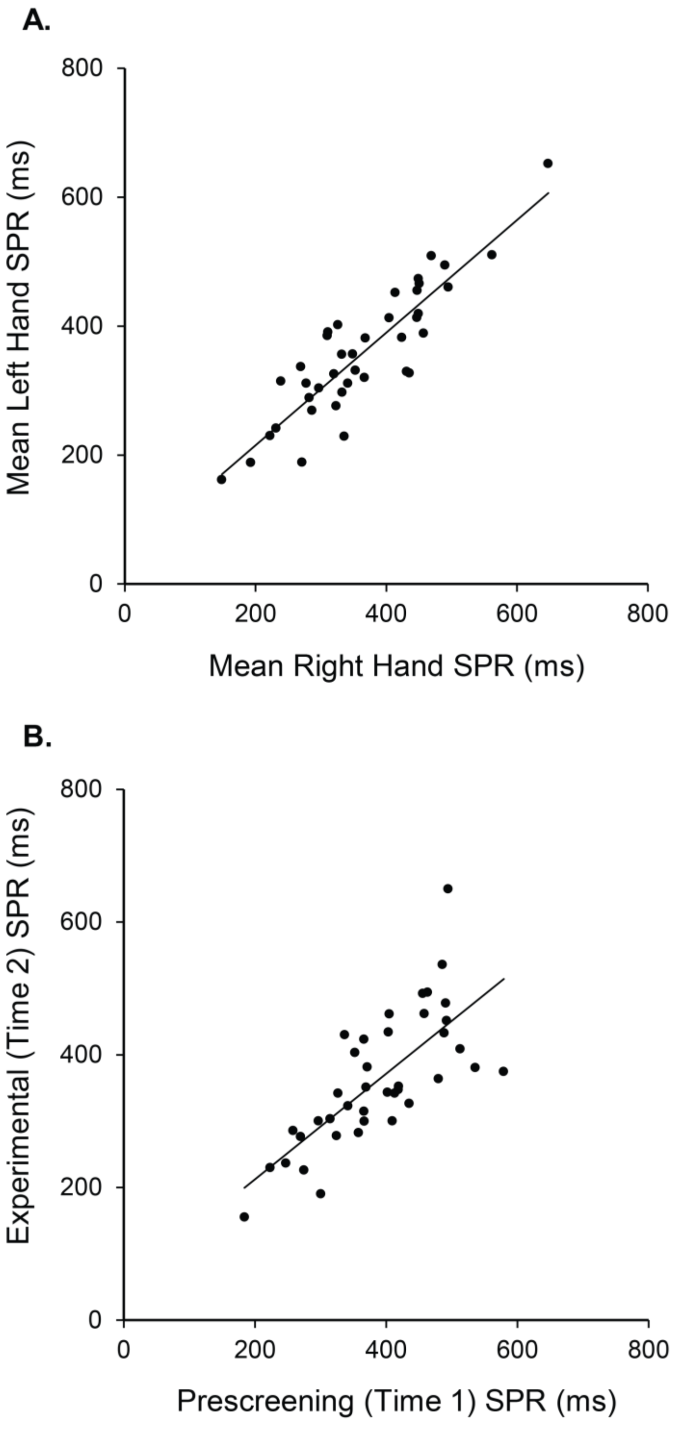

Match
Mean SPR (mean IOI in ms)
0
100
200
300
400
500
600
700
Pair
Mismatch
Mean SPR (mean IOI in ms)
0
100
200
300
400
500
600
700
Pair

Figure 1.

Figure 2.


A.
Mean Left Hand SPR (ms)
Mean Right Hand SPR (ms)
0
200
400
600
800
B.
Experimental (Time 2) SPR (ms)
Prescreening (Time 1) SPR (ms)

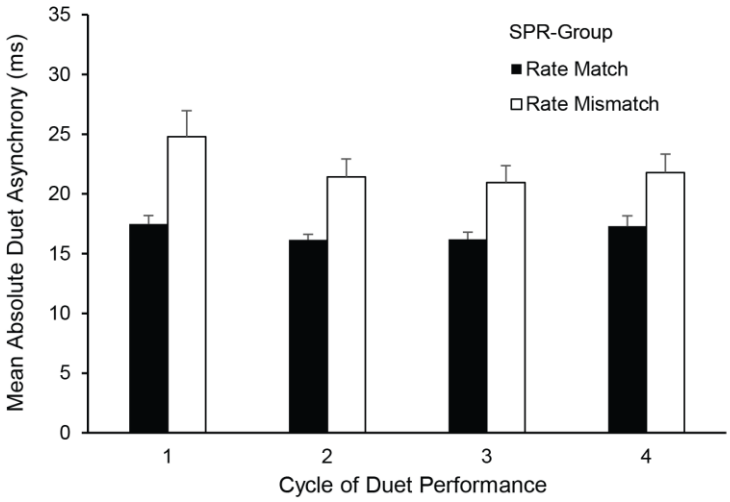

SPR-Group
Rate Match
Rate Mismatch
Mean Absolute Duet Asynchrony (ms)
0
5
10
15
20
25
30
35
1
2
3
4
Cycle of Duet Performance

Figure 3.