Spontaneous Tempo and Rhythmic Entrainment in a Bonobo (*Pan paniscus*)

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The emergence of speech and music in the human species represent major evolutionary transitions that enabled the use of complex, temporally structured acoustic signals to coordinate social interaction. While the fundamental capacity for temporal coordination with complex acoustic signals has been shown in a few distantly related species, the extent to which nonhuman primates exhibit sensitivity to auditory rhythms remains controversial. In Experiment 1, we assessed spontaneous motor tempo and tempo matching in a bonobo (*Pan paniscus*), in the context of a social drumming interaction. In Experiment 2, the bonobo spontaneously entrained and synchronized her drum strikes within a range around her spontaneous motor tempo. Our results are consistent with the hypothesis that the evolution of acoustic communication builds upon fundamental neurodynamic mechanisms that can be found in a wide range of species, and are recruited for social interactions.

Keywords: rhythm, tempo, entrainment, synchronization, bonobo

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Humans exhibit a remarkable ability to entrain periodic movements with acoustic signals. Here, *entrainment* refers to the process by which an oscillating system assumes the same frequency, or *tempo*, as a periodic stimulus (Pikovsky, Rosenblum, & Kurths, 2001). Entrained responses to acoustic rhythms have been observed at the level of brain (Fujioka, Trainor, Large, & Ross, 2012; Nozaradan, Peretz, Missal, & Mouraux, 2011) and behavior (Large & Jones, 1999; Stefanics et al., 2010), have a distinct developmental time course (Kirschner & Tomasello, 2009; McAuley, Jones, Holub, Johnston, & Miller, 2006; Winkler, Háden, Ladinig, Sziller, & Honing, 2009), and play important functional roles in music (Clayton, Sager, & Will, 2004; London, 2004) and speech (Ghitza & Greenberg, 2009; Zion Golumbic et al., 2013). Synchronous chorusing behaviors are well documented in arthropods and anurans (for a review, see Greenfield, 1994). Recently, however, synchronous movements to the beat of complex musical rhythms have been reported in a sulfur-crested cockatoo (Patel,

Iversen, Bregman, & Schulz, 2009), a parrot (Schachner, Brady, Pepperberg, & Hauser, 2009), and a California sea lion (Cook, Rouse, Wilson, & Reichmuth, 2013). Two reports have also documented entrainment to periodic rhythms in rhesus monkeys (Zarco, Merchant, Prado, & Mendez, 2009) and chimpanzees (Hattori, Tomonaga, & Matsuzawa, 2013); however, the temporal coordinative abilities of nonhuman primates remain a subject of debate and ongoing investigation (Merchant & Honing, 2013; Patel, 2014). Further work is needed to directly compare entrainment in parrots and sea lions with the coordinative abilities of nonhuman primates.

Because the goal of such studies, implicitly or explicitly, is comparison with human behavior, it is important to understand human rhythmic entrainment. Human adults entrain body movements to periodic rhythms, and to the beat of complex musical rhythms (Drake, Penel, & Bigand, 2000; Rankin, Large, & Fink, 2009), and they can continue moving at the stimulus tempo after the stimulus ceases (e.g., Wing & Kristofferson, 1973). In entrainment with a metronome, human adults display two stable phase relationships, in phase (called *synchronization*, or *phase-matching*, where phase $\simeq 0°$) and antiphase (called *syncopation*, where phase $\simeq \pm 180°$; Kelso, DelColle, & Schöner, 1990; Repp, 2005a). *Stability* means that variability around the stable phase is very small, such that large excursions or phase-wrapping are rarely, if ever, observed (see Schöner, Haken, & Kelso, 1986). In synchronization with a metronome, taps usually precede the stimulus by a small amount (phase $< 0°$; see Repp, 2005b), but for temporally complex stimuli such as music, this pattern often disappears (phase $= 0$) or is reversed (phase > 0; see, e.g., Snyder & Krumhansl, 2001). When asked to tap at a comfortable tempo, individuals produce a reliable *spontaneous motor tempo,* that differs widely among individuals and slows with age (McAuley et al., 2006). However, individual human adults

display substantial *tempo flexibility,* synchronizing at tempos from around 300 bpm (5 Hz; 200 ms; Repp, 2003) to 17 bpm (0.3 Hz; 3,500 ms) and probably lower (see Repp & Doggett, 2007), a range of at least ±90%.

The ability to synchronize and continue body movements to rhythmic stimuli is not trivial; it takes years to develop in humans. Infants move to, but do not entrain to, periodic rhythms (Zentner & Eerola, 2010). Children 2.5 to 4.5 do not maintain stable phase relationships with periodic stimuli; they display transient episodes of entrainment that can only be measured as statistical tendencies (Kirschner & Tomasello, 2009; Provasi & Bobin-Begue, 2003). Children aged 4–7 display faster spontaneous motor tempi over a narrower range than adults; they also display less tempo flexibility, entraining best near their spontaneous motor tempo (McAuley et al., 2006). Adult-like patterns of entrainment do not begin to emerge until age 8 or 9, at which time spontaneous tempo slows and tempo flexibility begins to emerge (McAuley et al., 2006). Importantly, social interaction facilitates successful entrainment in young children (Kirschner & Tomasello, 2009), and has been shown to promote affiliative and prosocial behaviors in both children and adults (Hove & Risen, 2009; Kirschner & Tomasello, 2010).

Neural resonance theory proposes that behavioral entrainment both to periodic rhythms and to the beat of complex rhythms relies on (1) entrainment of neural oscillations to acoustic rhythms and (2) oscillatory interactions between auditory and motor systems (Large, 2008; Large & Snyder, 2009). Recent experimental results support the basic claims of neural resonance theory. Neural entrainment to periodic and complex rhythms has been observed in electroencephalographic (EEG) and magnetoencephalographic (MEG) studies of auditory cortical responses (Fujioka, Trainor, Large, & Ross, 2009; Nozaradan et al., 2011; Nozaradan, Peretz, & Mouraux, 2012; Snyder & Large, 2005; Stefanics et al., 2010). Functional MRI (fMRI) studies of musical beat perception have shown involvement of both auditory and motor areas of the brain (Bengtsson et al., 2009; Chen, Penhune, & Zatorre, 2008; Grahn & Rowe, 2009). MEG source analysis has revealed oscillatory interactions among auditory and motor areas in the striato-thalamo-cortical network implicated by functional imaging (Fujioka et al., 2012). However, details of the neural circuitry that supports entrained responses to auditory rhythms are still largely unknown.

Comparative studies of rhythmic entrainment could help us understand the evolution, structure, and function of the neural networks supporting rhythmic coordination. Interestingly, a sulfurcrested cockatoo (*Cacatua galerita*; "Snowball") and an African gray parrot (*Psittacus erithacus*; "Alex") were recently shown to synchronize head-bobbing and foot-lifting (i.e., dancing) to a musical beat (Patel et al., 2009; Schachner et al., 2009). Unlike human adults however, these parrots did not maintain stable phase relationships, instead they displayed transient episodes of synchronization, termed "bouts" (Patel, 2014). In one study, Snowball, displayed transient bouts ranging in length from 12–36 head bobs in 22/38 trials. No attempt was made to measure spontaneous tempo; however, bouts were observed at tempos ranging from 98 bpm (1.6 Hz; 612 ms) to 130 bpm (2.2 Hz; 462 ms), about ±14% tempo flexibility. Snowball's head bobs displayed a small positive asynchrony that was not significantly different from zero, similar to human asynchronies for musical rhythms. Both Snowball and Alex appear to have developed this dancing behavior without any

formalized training (Patel et al., 2009; Schachner et al., 2009), but perhaps by observing humans (Patel, 2014).

In a related study, budgerigars (*Melopsittacus undulates*) were trained to peck in synchrony with a metronome (Hasegawa, Okanoya, Hasegawa, & Seki, 2011). Eight budgerigars exhibited nonrandom phase relationships for six pecks in 46/46 trials (Rayleigh test with unspecified mean direction). Trials ranged from 450-ms interonset intervals (IOI; 2.2 Hz; 133 bpm) to 1,800-ms IOI (0.6 Hz; 33 bpm), for a tempo flexibility range of 40%. When phase-matching was tested (Rayleigh test with specified mean direction = 0°), only one bird showed synchronization over the full range. The budgerigars showed a preference for the faster tempi, which had a similar time scale to their natural vocalizations (Hasegawa et al., 2011).

Three rhesus monkeys (*Macaca mulatta*) were trained to perform a synchronization-continuation task in which they synchronized five taps with a metronome and then produced three continuation taps (Zarco et al., 2009). No attempt was made to measure spontaneous tempo; however, a wide range of tempi were tested, from 60 bpm (1 Hz; 1,000 ms) to 133 bpm (2.22 Hz; 450 ms), presented in pseudorandom order. The monkeys required extensive training to accurately perform the task (25 months, 12 months, and 11 months), but after training, the monkeys produced stable phase relationships at all tempi, similar to human adults, showing tempo flexibility of about ±38%. On average, the monkeys tapped 250 ms after stimulus onset; however, the asynchronies were smaller than their RTs to stimuli with random interonset intervals (600–1,400 ms), indicating that these animals showed a predictive rhythmic behavior (Merchant & Honing, 2013). Thus, the monkeys entrained but did not phase match. In addition, the human bias toward auditory as opposed to visual cues for synchronization (Repp, 2005b) was not evident in rhesus monkeys.

In another study, a California sea lion (*Zalophus californianus*; "Ronan") was trained, using operant conditioning, to synchronize head bobbing to auditory rhythms (Cook et al., 2013). Ronan was tested in six experiments, including both metronomic stimuli and complex musical stimuli, with a wide range of tempi. Ronan displayed sustained entrainment (Rayleigh test with no specified mean direction) with highly stable phase relationships (i.e., very low variability; P. Cook, personal communication, January 20, 2015) for entire trials of 20–60 beats, similar to human adults. Ronan exhibited entrainment for trials ranging in tempo from 72 bpm (1.2 Hz; 833-ms IOI) to 137 bpm (2.3 Hz; 438-ms IOI); ±37%. On some trials, Ronan exhibited phase-matching (Rayleigh test with specified mean direction = 0°), while on others Ronan's stable phase differed significantly from 0°. Mean relative phase appeared to depend strongly on tempo, bobbing early for slow trials and late on fast trials. No attempt was made to measure spontaneous tempo.

Finally, spontaneous entrainment to an auditory rhythm has been demonstrated in a chimpanzee (*Pan troglodytes*; "Ai"). Three chimpanzees were trained to tap two keys on a piano keyboard ("C4" and "C5") alternately 30 times. Each key to be tapped was illuminated, and if a chimpanzee tapped this key (e.g., "C4"), sound feedback was given and another key was immediately illuminated (e.g.,"C5"). Each chimpanzee settled into a steady rhythm, which was likely not representative of spontaneous motor tempo, but determined by the constraints of the task. Once they tapped 30 times with fewer than 3 errors on two consecutive trials

(i.e., less than 10% errors overall), they proceeded to a test session. In the test session, a periodic metronome sound (IOI 400-ms, 500-ms, 600-ms, random) was played as a distractor while chimpanzees tapped the illuminated keys for three 30-tap trials (90 taps in total). The chimpanzees received rewards whenever they completed 30 key taps regardless of their responses to the distractor. One chimpanzee, whose task rhythm was 579 ms, showed significant synchronization to a 600-ms IOI distractor sound over 540 taps. However, Ai did not synchronize to the other metronome frequencies (400-ms, 500-ms IOI or random IOI) and the other two chimpanzees did not synchronize to any of the distractor stimuli.

In summary, the past several years of research have opened up a new area of comparative research in rhythmic entrainment, which has the potential to substantially increase our knowledge of the neural underpinnings of temporal coordination. However, this research area is in its infancy. Controlled experiments on temporal coordination with acoustic rhythms have been conducted in only a handful of species, and indeed in only a few individual animals. Marked differences in assumptions, hypotheses, methodology, analyses, and reporting render it problematic to make comparisons and draw general conclusions at this early stage. The poverty of data and incommensurability of findings is unfortunate because insights into the nature and prevalence of temporal coordination abilities could contribute greatly to our understanding of social cognition (Semin & Smith, 2008), animal behavior (Mingle et al., 2014; Watson, Townsend, Schel, & Wilke, 2015) and the evolution of speech and music (Fitch, 2012; Patel, 2006). It is particularly important to assess temporal coordination in chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*) because they are so closely related to humans (Prüfer et al., 2012). Research with chimpanzees and bonobos is further justified because both produce short bouts of rhythmic drumming with their hands or feet as part of display or play behavior (Arcadi, Robert, & Boesch, 1998; Fitch, 2006;), and are thus good candidates for temporal coordination.

Both chimps and bonobos are genetically similar to humans (Prüfer et al., 2012), so their abilities have clear implications for the evolution of speech and music. However, DNA comparative studies of microsatellites associated with social behaviors indicate the bonobo has higher homology with the human microsatellite than chimpanzees (Hammock & Young, 2005). Bonobos are adept visual imitators, a cornerstone of social learning and cognition, and when compared for their willingness to risk approaching novel objects and humans, bonobos but not chimpanzees were similar to children in their cautious behavioral responses (Herrmann, Hare, Call, & Tomasello, 2010). Moreover, while some data is now available on entrainment in chimpanzees, to date there are no published studies on bonobos. Thus, the present study tests a bonobo ("Kuni"; see Figure 1). We hypothesized that joint drumming, a form of social interaction that has been successfully applied to study the development of rhythmic coordination in children (Kirschner & Tomasello, 2009), and has been shown to promote affiliative and prosocial behaviors (Hove & Risen, 2009), would provide the appropriate setting for the emergence of temporal coordination. In Experiment 1, we measured Kuni's spontaneous motor tempo and assessed the effect of stimulus tempo on Kuni's drumming responses. In Experiment 2, we tested Kuni's ability to entrain and to match phase with a human experimenter.

Figure 1. Kuni and daughter, Kenge. Kuni, a 29-year-old female bonobo (*Pan paniscus*), self-selected to engage in interactive drumming with a human drummer. See the online article for the color version of this figure.

General Methods

Bonobo Group

The bonobo group in the study resides at the Jacksonville, Florida Zoo and Gardens and had no previous experience with musical tools or interactive participation with music or rhythmic studies. The research study's methodology relied on bonobo self-selection for focused interaction with a drum and a human drummer. To accommodate innate bonobo shyness, the research design featured multiple encounters with the same female human drummer, continuity of research personnel, and ongoing continual access for the bonobos to the drum and its space beyond the research sessions.

Preparation

During research visits in early 2011, we collected ethnographic data about the zoo's bonobos and interviewed Ape House staff for detailed information about individual bonobos' behaviors, preferences, and hierarchical relationships. Beginning in June 2011, interested bonobos were identified based on previously observed behavioral responses to human researcher drumming, including rhythmic head wagging and body movements. Because some bonobos were nursing mothers with infants and the others were

inexperienced adults and youth, the bonobos continued to express shyness and passive behavior at the drum site. To address this, it was determined that staff would support drumming as a positive, interactive social behavior by modeling drumming behavior. The staff's participation produced rapt attention from the bonobos, and some bonobos mimicked by drumming on the drumhead with both hands. In July 2011, a combination of staff participation in drumming bouts, introduction of simple rhythmic patterns, and rhythmic pointing at the bonobo drum to cue behavior resulted in some female bonobos engaging in interactional drumming and more involvement of infant/mother combinations. Even noninteractional bonobos displayed willingness to hit the drumhead.

By October 2011, 3 adult females regularly drummed with both hands on the drumhead in 10+ s interactions with a human drummer's stimulus. They also displayed awareness of the research activity by greeting the arrival of the researchers with spontaneous drumming. Bonobos self-selecting to be in the research area but not engaged in drumming stayed close to the front of the space watching/listening to the human drummer and the active bonobo drummer. Infants also demonstrated willingness to participate by watching, moving rhythmically to the drumming, jumping on the drumhead, or using hand engagement with the drumhead. At this time, it was determined that bonobos would be given a food reward for any strike of the drum, but would not be trained to produce any specific tempo or to synchronize with the experimenter. Experimenters did not control which bonobos entered the research space during the experiment.

Subject

Kuni, a high ranking female who had recently given birth, self-selected to participate most often. She was born at Stuttgart Zoo in Wilhelma, Germany on February 24, 1985. In 1992, she transferred to Twycross Zoo in the United Kingdom for a short time, then to San Diego Zoo in 1993, and finally to Jacksonville Zoo and Gardens in 2003. Her rearing is listed as undetermined in official records but included free contact while young and may have included hand rearing later. She has never lived at a research facility; however, at Jacksonville she participated in a number of behavioral and cognitive studies, but none involving rhythm or music.

Apparatus

Working with the Remo Drum Company, we developed a tube drum for the bonobo participants that resonates with in-tune overtones, and produces and sustains identifiable fundamental pitches that could be tuned to the human drum. It is durable and withstands 227 kg of pressure on the drumhead, is made of nontoxic materials, and can endure site cleaning. In consideration of average bonobo height, the total height of the bonobo drum was designed for 56 cm and featured a drumhead with a diameter of 25 cm and an outside diameter of 30 cm. The stationery bonobo drum was fixed to the concrete floor of the small research space interconnecting larger play areas, allowing the bonobos free flow into and out of the area.

General Procedure

The experimenter and staff member were seated in the walkway, separated from Kuni by a steel mesh door. Kuni's daughter, Kenge, was almost always present while Kuni participated in the experiment. At least one other bonobo was usually also present. A metronome sound was produced by the recording software (Logic Express, running on a 2.3 GHz MacBook Pro, Mac OS $\times$ 10.6.8), and delivered to the experimenter over headphones so that it would be inaudible to the bonobos. The experimenter struck her drum in synchrony with the metronome, at one of six predefined tempos, which differed between the two experiments, as described below. Six trials were recorded each day. Each trial continued until at least 2.5 min of data was collected. As the experimenter struck her drum, the staff member and the experimenter encouraged drumming verbally and by pointing to the drum. Kuni received a food reward and verbal praise for any episode of drumming (see Video 1 in online supplemental material). Drum strikes were recorded through microphones mounted inside each drum, using Logic Express software, as audio (.aiff) files at a sampling frequency of 44,100 Hz.

Data collection began December, 2011, and ended April 20, 2012, with a total of 9 trips by the research team. Scheduling for the research trips was determined by the Jacksonville Zoo staff and reflected conditions at the zoo and the investigators' availability.

Audio Analysis

Audio recordings were analyzed to determine the onset times of each drum strike using the Sonic Visualizer software (see Figure 2). The experimenter audio files and the bonobo audio files were analyzed independently. First, the *Aubio* onset detection plugins within Sonic Visualizer were used to detect drum strike times automatically. The correctness of the automatic onset detection
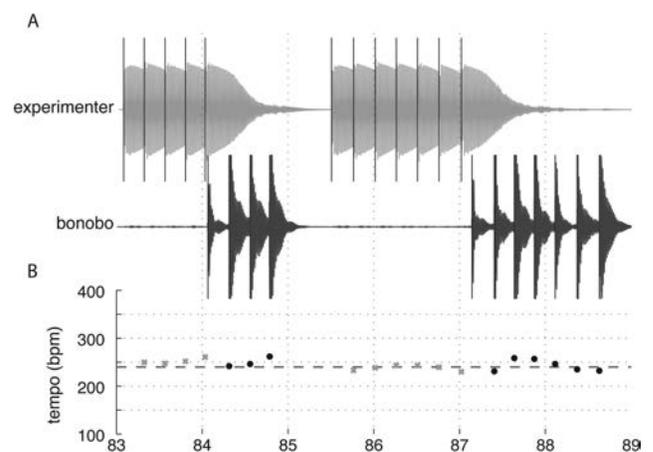
Figure 2. Turn taking interactions in Experiment 1. The experimenter struck a drum at one of six tempos (A; 160, 180, 200, 220, 240, and 260 bpm). When Kuni began to strike the drum, the experimenter stopped and let her continue on her own. Audio recordings were analyzed to determine the onset of drum strikes, and the data was parsed into dyadic drumming interactions, termed episodes. Instantaneous tempo (bpm = 60/inter tap interval, s) was calculated for each episode. See the online article for the color version of this figure.

procedure was verified by visually comparing the detected onset time with the audio time series and a spectrographic display. IOIs were computed as differences between successive onset times. Local instantaneous tempo was then computed as tempo (bpm) = 60/IOI (s).

Experiment 1

Experiment 1 assessed preferred tempo and tempo matching using turn-taking interactions in which first the experimenter drummed at a specified tempo, and then the bonobo drummed spontaneously (Figure 2A).

Method

The experimenter struck her drum in synchrony with the metronome at one of six tempos, which were determined based on earlier pilot testing. Each trial corresponded to a single tempo, and trials were recorded in the following order: 240 bpm (4 Hz; 250 ms), 200 bpm (3.33 Hz; 300 ms), 160 bpm (2.67 Hz; 375 ms), 180 bpm (3 Hz; 333 ms), 220 bpm (3.67 Hz; 273 ms), and 260 bpm (4.33 Hz; 231 ms). Six trials were recorded each day. Each trial continued until at least 2.5 min of data was collected, and data was collected over 7 days. As the experimenter struck her drum, the staff member and the experimenter encouraged drumming verbally and by pointing to the drum. When Kuni began to strike the drum, the experimenter stopped and let her continue on her own. When Kuni stopped drumming, the experimenter began again. Kuni received a food reward and verbal praise for each and every episode of drumming (see Video 1 in online supplemental material).

Analysis

First, entire trials were analyzed to (1) determine the extent to which Kuni's tempo depended on the trial tempo, and (2) estimate Kuni's spontaneous motor tempo for trials which were not tempo-dependent. First, we compared the distribution of bonobo instantaneous tempo, over each entire trial, with the metronome tempo for that trial. Those trials for which bonobo tempo was significantly different from metronome tempo (one sample t test, $p < .01$) were used to compute a histogram that approximated a spontaneous tempo distribution. Spontaneous tempo is reported as the mean of this distribution. This method evaluates spontaneous tempo under the assumption that on some trials Kuni did not adapt to the tempo of the human experimenter.

To further test this assumption, we assessed tempo dependence using two linear regressions against trial tempo. The first compared the mean instantaneous tempos for those trials in which bonobo tempo significantly differed from metronome tempo. The other compared those trials in which bonobo tempo did not differ significantly from metronome tempo. The slope of the regression lines were used to assess the degree of tempo dependence. Because the analyses were computed separately for trials in which bonobo tempo *was* versus *was not* significantly different from the metronome tempo, the slope of the regression line in the first analysis was expected to be zero, and the slope in the second analysis was expected to be positive, revealing a dependence on stimulus tempo.

A second analysis attempted to determine whether any observed tempo-dependence occurred by chance. We did this by analyzing individual episodes. First, the data were parsed into dyadic drumming interactions, termed episodes. An episode was defined to begin when the experimenter began drumming, and Kuni then produced at least 4 contiguous drum strikes (i.e., no pause greater than 2 metronome cycles). Next, we eliminated episodes in which Kuni's tempo was different from the metronome tempo (using one sample t tests). As above, we used regression analyses to measure the dependence of episode tempo on metronome tempo, expecting a positive slope. To ask whether any observed tempo dependence was random, Monte Carlo analyses tested the null hypothesis that bonobo instantaneous tempo was always drawn from the same spontaneous tempo distribution, and short episodes sometimes matched the metronome tempo by chance. To do this, we randomly repaired bonobo drumming time series with metronome time series, so that each bonobo series was paired with a metronome time series at a different tempo, with the constraint that all tempi were represented in the permuted data. This created a simulated experiment that was analyzed for tempo dependence in the same way that we analyzed the original data. Using this approach, we recorded the total number of episodes whose tempo was not significantly different from the metronome tempo. A Monte Carlo test with 10,000 such simulated experiments resulted in a distribution of the number of episodes that were tempo-matched to the metronome in each of the simulated experiments. We compared this distribution to the total number of episodes tempo-matched to the beat in our actual data and computed the p value of our data as the proportion of simulated experiments that had the same or higher number of tempo-matched episodes.

Results

An omnibus regression, comparing the instantaneous tempi of all drum strikes occurring in episodes of length $> = 4$ ($N = 8,280$) revealed that Kuni's instantaneous tempo depended on trial tempo ($p < .00005$), with a shallow slope ($m = .153$). Therefore, we used one-sample t tests to attempt to identify trials in which Kuni's tempo differed from trial tempo. In 36/42 trials (81%), Kuni's instantaneous tempo differed significantly from the trial tempo (one sample t test, $p < .01$). A regression analysis was used to assess dependence of Kuni's mean tempo on trial tempo for these 36 trials. The slope of the regression line ($m = 0.092$; see Figure 3B), did not differ significantly from 0 ($p = .638$). Therefore, the spontaneous motor tempo distribution was estimated using the instantaneous tempi from these 36 trials, shown in Figure 3A. We estimated spontaneous motor tempo as 270 bpm (4.6 Hz; 216 ms), the mean of this distribution.

In 8/42 trials (19%), Kuni's instantaneous tempo did not differ significantly from the trial tempo (one sample t test, $p < .01$). A regression analysis was used to assess dependence of Kuni's mean tempo on trial tempo for these eight trials. This analysis revealed a significant degree of tempo dependence ($p < .0005$), and slope of the regression line ($m = 0.953$; see Figure 3B) did not differ significantly from 1 (95% CIs: 0.61–1.29). Thus, tempo dependence seemed to stem from specific trials.

Next, we attempted to get a finer grained picture of tempo dependence by analyzing tempo on an episode-by-episode basis. In 42 trials, we identified 835 separate episodes of drumming by Kuni
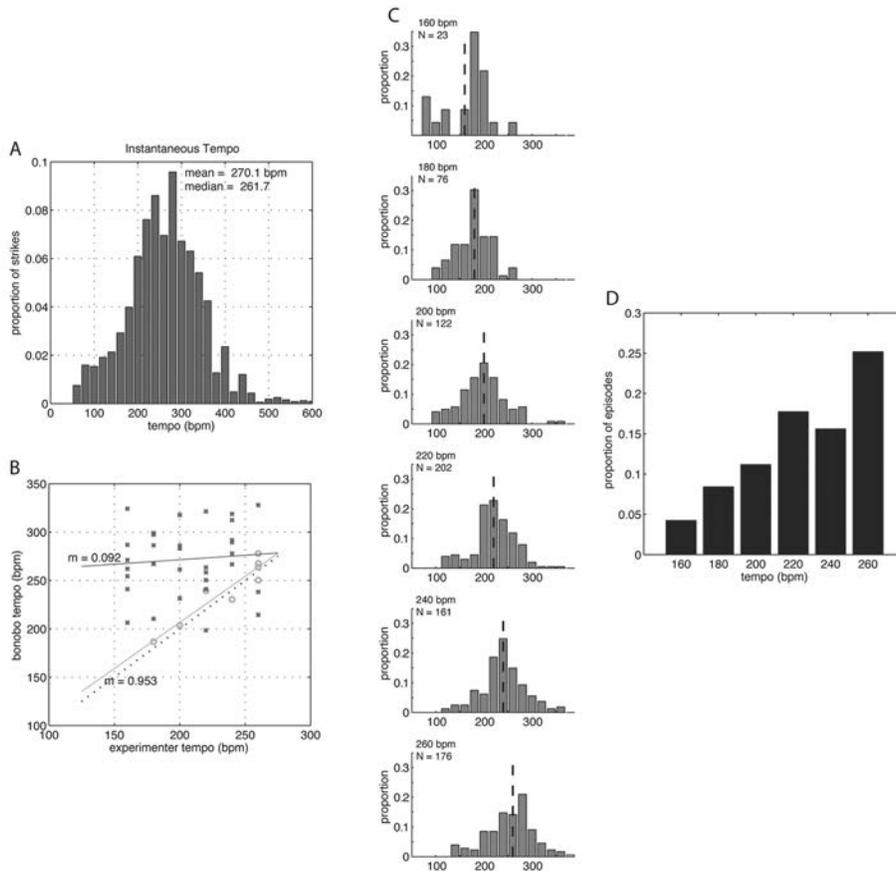
Figure 3. Spontaneous tempo and tempo matching. Trials in which mean bonobo tempo was different from experimenter tempo (*t* test, *p* < .01) were used to estimate spontaneous motor tempo (*M* = 270 bpm; A). Regression analysis, bonobo tempo versus experimenter tempo (B). For non-tempo-matched trials, the slope of the regression line was not significantly different from zero (m = 0.092, *p* = .63). For the remaining trials, slope was not significantly different from one (*p* < .01; slope = 0.953; 95% CI: .61 < m < 1.29). Instantaneous tempo distributions were at each tempo (C). Instantaneous tempo distributions by episode tracked stimulus tempo (Monte Carlo analysis, *p* = .013; D). The proportion of tempo-matched episodes increased as tempo approached the preferred tempo (D). See the online article for the color version of this figure.

(min = 4, median = 6, max = 65 drum strikes), and in 36.5% of these, tempo differed significantly from trial tempo (one sample *t* test, *p* < .01); in the remaining 545 episodes (63.5%; min = 4, median = 5, max = 44 drum strikes), tempo did not differ significantly. A regression analysis comparing episode means with trial tempo revealed a significant tempo dependence in these episodes (*p* = .0013); however, the slope (*m* = .258) was significantly different from one (95% CIs: 0.10–0.41). To ask how many tempo-matched episodes existed (i.e., slope ≃ 1), we systematically increased the one sample *t* test threshold from *p* = .01 to *p* = .50, as shown in Table 1. At *p* = .50, we found 118 episodes (14%; min = 4, median = 5, max = 30 drum strikes) in which mean tempo did not differ from the trial tempo (see Figure 3C). Regression analysis found a slope (*m* = 0.99), which was highly significant (*p* < .0001) and not significantly different from one (95% CIs: 0.91–1.07). A Monte Carlo test with 10,000 permutations showed that this number of tempo-matched episodes was unlikely to have occurred by chance (*p* = .013). As shown in Figure 3D, the proportion of tempo-matched episodes increased as tempo approached spontaneous tempo.

Discussion

In the context of a social interaction, the instantaneous tempo of Kuni's drumming exhibited dependence on the tempo of the human experimenter. Tempo dependence appeared to be restricted to certain trials and certain individual episodes. For the 36 trials in which Kuni's tempo was significantly different from that of the experimenter, Kuni drummed at a mean instantaneous tempo of 270 bpm. This estimated spontaneous tempo is extreme, faster than that of human children. It is faster than the fastest stimulus in this

Table 1
Tempo Matching in Individual Episodes

	Tempo matched episodes		
Threshold	Number	Slope	Significance
0.01	545 (65.3%)	0.258	*p* = .018
0.10	316 (37.8%)	0.472	*p* = .025
0.50	118 (14.1%)	0.992	*p* = .013

experiment, and as trials approached this tempo, tempo matching increased. These observations combine to suggest that, while this estimate may be somewhat biased, it is not unreasonable. At the very least, it provides a plausible tempo range for Experiment 2, in which we tested Kuni's ability to entrain. Additionally, we identified 14% of episodes in which Kuni closely matched the slower tempo of the experimenter, a number that is unlikely to have occurred by chance. This latter observation is also significant, because it suggests that Kuni may be able to entrain with some degree of tempo flexibility.

Experiment 2

Experiment 2 assessed entrainment and synchronization in simultaneous drumming interactions in which the experimenter drummed at six different tempi, including Kuni's spontaneous motor tempo (Experiment 1; approximately 270 bpm).

Procedure

Methods were similar to Experiment 1, with the human drummer striking her drum in synchrony with a metronome, at one of six predefined tempos. The tempos for each trial were: 230 bpm (3.82 Hz; 261 ms), 240 bpm (4 Hz; 250 ms), 250 bpm (4.17 Hz; 240 ms), 260 bpm (4.33 Hz; 231 ms), 270 bpm (4.50 Hz; 222 ms), and 280 bpm (4.67 Hz; 214 ms). Each trial continued until at least 2.5 min of data was collected, and data was collected over 5 days. Two trials were eliminated because of equipment failure. Unlike Experiment 1, when the bonobo began to strike the drum, the experimenter continued drumming so that Kuni drummed simultaneously with the experimenter and synchronization could be assessed (see Figure 4 and Video 2 in online supplemental material).

Analysis

In Patel's study of Snowball (Patel et al., 2009), a synchronized bout had a minimum of 12 events. For comparability with that study, we defined an episode as a series of at least 12 contiguous drum strikes by Kuni, in which no pause was greater than 2
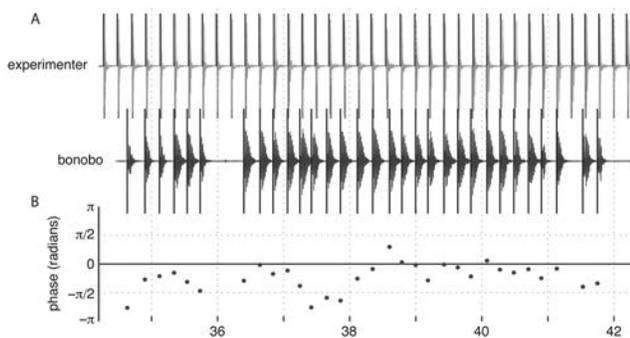

Figure 4. Simultaneous drumming interactions in Experiment 2. The experimenter struck a drum in synchrony with a metronome at one of six tempos (230, 240, 250, 260, 270, and 280 bpm; A). When Kuni began striking the drum, the experimenter continued to drum simultaneously. Audio recordings were analyzed to determine the onset of drum strikes (black). See the online article for the color version of this figure.

metronome cycles. Our first analysis assessed entrainment in each episode. In this analysis, the phases of Kuni's drum strikes were computed relative to metronome because the metronome produced a steady, mechanical tempo (cf., Kirschner & Tomasello, 2009). Phase was computed as $\phi_{kuni} = 2\pi \, (t_{kuni} - t_{metro})/IOI$, yielding the phase, ϕ_{kuni}, in radians, of each drum strike, t_{kuni}, relative to the nearest metronome click t_{metro}, where IOI is the metronome interonset interval in seconds (IOI = 60/tempo). We assessed Kuni's phase relative to the metronome, not the experimenter, because the experimenter's individual drum strikes could have been attracted toward the bonobo's drum strikes without her conscious awareness (Repp, 2005b). Entrainment was evaluated, for all events in an episode, using a Rayleigh test with no specified mean direction (cf., Cook et al., 2013; see Fisher, 1993).

Next, we assessed phase-matching synchronization in a separate analysis. We tested phase-matching using a Rayleigh test with specified mean direction = ϕ_{exp}, the angle of the experimenter's mean vector. Thus, synchronization was tested relative to a steady tempo, but with mean direction specified as the experimenter's mean phase, as illustrated in Figure 4. Because we tested against the average, this analysis is not dependent on fluctuations in the experimenter's individual drum strikes (cf. Repp, 2005b). However, it allowed us to determine whether Kuni was in phase with the experimenter. In this analysis, $\phi = 0$ means that, on average, Kuni's drum strikes were temporally synchronous with the experimenter's drum strikes, and $\phi < 0$ means that, on average, Kuni's drum strikes preceded the experimenter's.

To ask whether entrainment and phase-matching could have occurred by chance, we used two Monte Carlo analyses similar to the analysis used in Patel et al.'s (2009) study of Snowball. The Monte Carlo analyses tested the null hypothesis that Kuni simply drummed rhythmically, with a tempo that varied from episode to episode, and episodes of apparent entrainment or phase-matching occurred by chance. Following Patel et al., we performed a permutation test in which each drum strike time series was randomly repaired with a metronome time series (and for phase-matching, the experimenter's mean phase) from an episode at a different tempo, with the constraint that all tempi were represented in the permuted data. This created a simulated experiment of 214 episodes (the number of episodes of length 12). Each simulated experiment was analyzed for entrainment (or phase-matching) in the same way that we analyzed the original data. Using this approach, we recorded the total number of episodes that were significantly entrained (or phase-matched) in each experiment. A Monte Carlo test with 10,000 such simulated experiments resulted in a distribution of the number of episodes entrained with the metronome (or phase-matched to the experimenter) in each of the simulated experiments. We compared this distribution to the total number of episodes entrained (or phase-matched) in the actual data and computed the *p* value of our data as the proportion of simulated experiments that had the same or higher number of synchronized episodes.

Results

Out of 214 episodes of simultaneous drumming in which Kuni produced at least 12 contiguous drum strikes (min = 12, max = 52, median = 17.5 drum strikes), 28 (13%) were significantly entrained with the metronome (Rayleigh test, *p* < .05). A Monte

Carlo permutation test revealed that this number of entrained episodes is highly unlikely to have occurred by chance, $p < .001$. Fifty-four percent of all trials included episodes of significant entrainment, and entrainment was observed at all tempi. Four trials (14%) showed statistically significant entrainment over their entire duration (193–616 drum strikes).

Additionally, 21 episodes (10%; min = 12, max = 40, median = 17 drum strikes) displayed significant synchronization, or phase-matching (Rayleigh test with specified mean direction = ϕ_{exp}, $p < .05$), shown in Figure 5A. Monte Carlo analysis revealed that this number of phase-matched episodes is unlikely to have occurred by chance, $p < .05$. Forty-three percent of all trials included episodes of significant synchronization; however, phase-matching was observed only at the four fastest tempi (250–280 bpm). Overall, in synchronized bouts, mean phase was negative relative to experimenter mean phase, indicating that bonobo drum strikes preceded the experimenter's, summarized in Figure 5B and 5C. The proportion of episodes in which entrainment was significant is shown in Figure 5D as a function of metronome tempo. Three trials (11%) at the three fastest tempi showed statistically significant phase relationships over the entire duration (193–600 drum strikes; see Figure 6A).

Figure 6A and 6B show detail for one trial in which entrainment was found (Rayleigh test, $p < .0001$). Instantaneous tempo clusters tightly around stimulus tempo, because phase locking implies frequency locking (i.e., tempo matching). Phase-matching was also significant for this trial (Rayleigh test with mean direction = ϕ_{exp}, $p < .005$). Over the duration of this trial, the synchronization coefficient was $r = .204$, and mean phase was $\phi = -0.943$ radians (see Video 2 in online supplemental material). Figure 6C shows a 280 bpm episode in which strong synchronization was observed, whereas Figure 6D shows a slower tempo (260 bpm) for which the phase relationship appears less stable.

Discussion

We observed significant entrainment in episodes of up to 52 drum strikes (our longest recorded episode), and phase-matching in episodes of up to 40 drum strikes. In phase-matched episodes, Kuni's drum strikes generally preceded the experimenter's. Kuni produced higher proportions of synchronized episodes near her preferred tempo; nevertheless, she entrained at all tempi tested giving a tempo flexibility score of ±10%. For the more conservative criterion of phase-matching on episodes of length 12 or
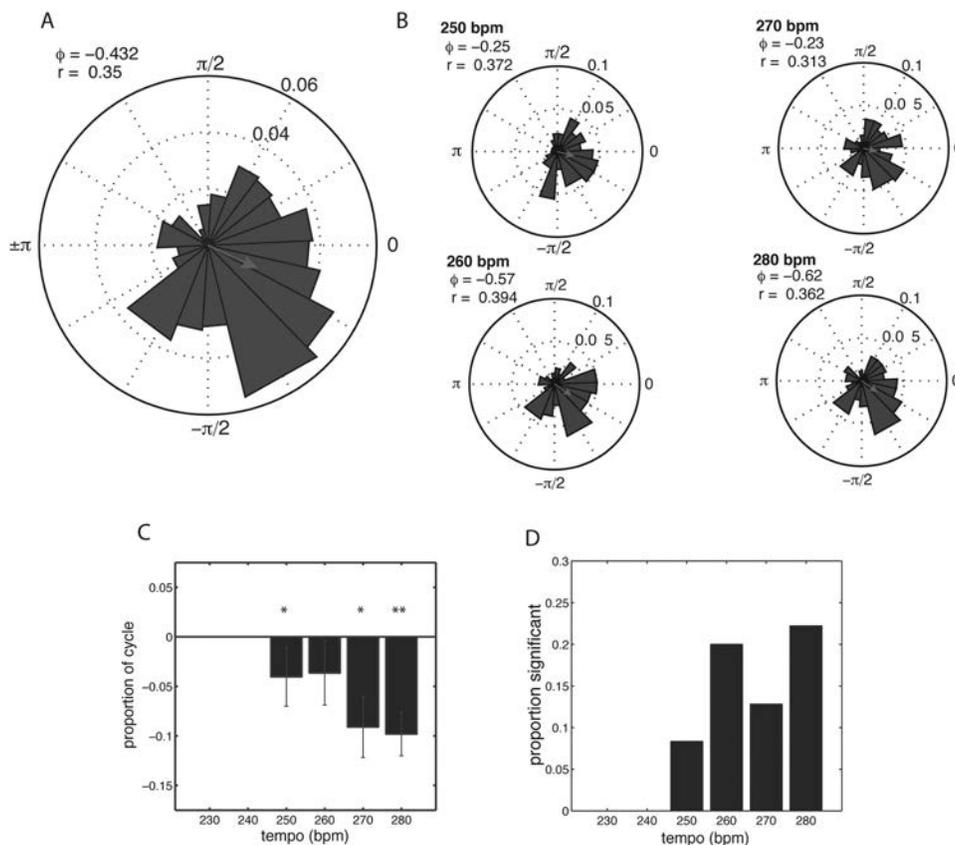

Figure 5. Synchronization. Entrainment was measured relative to the metronome the experimenter heard over headphones. Synchronization was measured relative to experimenter mean phase for each episode. Phase histogram for synchronized bouts (A). Mean relative phase was significantly negative (t test, $p < .01$). Significant bouts were found at four tempos closest to preferred tempo (B). At three tempos, mean phase was significantly negative (t test, * $p < .05$; 2, ** $p < .01$; C). Proportion of significant bouts as a function of tempo (D). See the online article for the color version of this figure.
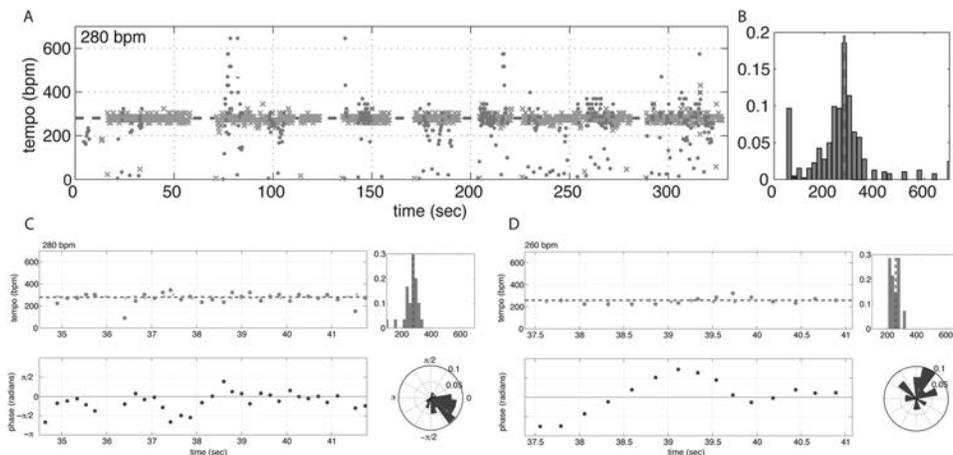
Figure 6. Synchronization detail. Detail of one trial in the synchronization experiment (A). Shown are time series and a histogram of instantaneous tempo (see Video 2 in online supplemental materials). Note that phase locking implies tempo matching, thus the points that cluster tightly around stimulus tempo (and the peak in the histogram at the stimulus tempo, 280 bpm) represent synchronized bouts. Detail of two significant bouts (B). Shown are time series and histograms for both instantaneous tempo (top) and relative phase (bottom). Relative phases are adjusted to reflect experimenter mean phase for each bout. See the online article for the color version of this figure.

more, tempo flexibility was reduced to ±6%. Tempo flexibility is restricted compared with what has been observed in trained animals, but more or less in line with what has been observed on spontaneous synchronization.

We chose analysis parameters (i.e., minimum episode length) and statistical tests (Rayleigh tests and Monte-Carlo analyses) to be as similar as possible to those used in Patel et al.'s analysis of Snowball (Patel et al., 2009). Therefore, it is informative to compare Kuni's performance with that of Snowball. Both Kuni and Snowball produced intermittent phase synchronization (Patel, 2014), similar to the performance of human children 2.5 to 4.5 (Kirschner & Tomasello, 2009). Snowball's bout length ranged from 12 to 36 head bobs, with a median of 16; Kuni's synchronized bout length ranged from 12 to 40 drum strikes, with a median of 17. Snowball produced synchronized bouts in 58% of trials, while Kuni entrained in 54% of trials and phase-matched in 43%. Snowball's relative phase was positive (3.9°) but not significantly different from zero, as one might expect in adult humans synchronizing to music. Kuni's relative phase was negative (25°) and significantly different from zero, as one might expect in adult humans synchronizing to an isochronous stimulus. Snowball's tempo flexibility was ±14%, while Kuni's tempo flexibility was ±10%, representing the entire range tested.

However, it should be emphasized that there were differences in the task and in the controls. Snowball was tested with recorded music, Kuni was tested against the isochronous drum strikes of a human drummer, in the context of a social interaction. Snowball's measured responses were head bobs, Kuni's were drum strikes. Visual information for synchronization was not available for Snowball; however, it was available for Kuni. Finally, Snowball was tested devoid of any distractions; in Kuni's case, other bonobos provided distraction. Thus, while the quantitative similarities in synchronization are clear, these differences in task and methodology are also significant.

General Discussion

Our results support the hypothesis that joint drumming interactions with a human experimenter are sufficient to measure spontaneous motor tempo, and to reveal tempo matching, entrainment, and synchronization in a bonobo (cf., Kirschner & Tomasello, 2009; Kirschner & Tomasello, 2010). In Experiment 1, we measured a spontaneous motor tempo of 270 bpm, a tempo faster than that of human children (McAuley et al., 2006). Nevertheless, in dyadic drumming interactions, Kuni also showed a significant level of tempo dependence. A significant number of episodes were tempo-matched (slope = 0.99), suggesting that Kuni is capable of a reasonable level of tempo-flexibility. This finding provided a rationale and a tempo range for Experiment 2. Experiment 2 tested both entrainment with the metronome and phase-matching with the human experimenter. Kuni displayed entrainment and phase-matching in significant numbers of complete episodes. Because entrainment and phase-matching were found in only some episodes, we characterize these behaviors as intermittent (Patel et al., 2009), more like human children (Kirschner & Tomasello, 2009) than adults (Repp, 2005b). Also like children, who synchronize more successfully near their preferred tempo (McAuley et al., 2006), Kuni synchronized more often near her preferred tempo. Kuni's overall relative phase was negative, a finding comparable with human synchronization near preferred tempos for isochronous stimuli (Repp, 2005b).

It has been hypothesized that synchronization with complex musical rhythms may require the full neural circuitry of vocal learning (Patel, 2006). Our results do not necessarily imply that a bonobo would be capable of synchronizing with complex musical rhythms; such interactions require the ability to deal with far greater complexity. Moreover, we cannot exclude the possibility that synchronization involved visual as well as auditory information; our design did not control for the source of the rhythmic

information. Indeed, cross modal integration may be important in the context of social interaction, and especially so for primates (Ghazanfar & Takahashi, 2014; Nagasaka, Chao, Hasegawa, Notoya, & Fujii, 2013; Zarco et al., 2009). However, the finding that a bonobo is capable of temporally coordinating rhythmic movements in a joint drumming context, combined with recent findings in a sea lion (Cook et al., 2013) and a chimpanzee (Hattori et al., 2013), suggests that fundamental rhythmic capabilities are more widely dispersed across species than had been previously conjectured (Fitch, 2012; Patel, 2006). Our results are consistent with the idea that the evolution of social coordination builds upon fundamental neurodynamic mechanisms of entrainment and synchronization (Glass, 2001; Large, 2008) that are exploited in different types of social interactions depending upon the species, the context, and the conditions (Greenfield, 1994).

It has been argued that neural resonance theory leads to a so-called paradox of rhythm (Patel, 2014). "Periodicity is a ubiquitous feature of all living things, and coupled biological oscillators entrain to each other readily . . . (yet) humans are rare in our ability to entrain our motor output to that of others. . . . The paradox, put simply, is this: if periodicity and entrainment are ubiquitous features of all living organisms, why cannot dogs dance?" (Fitch, 2012, p. 73). We believe that this so-called paradox rests on at least two faulty assumptions. The first is that neural oscillation is a "unitary, monolithic cognitive entity" (Fitch, 2012, p. 73). Oscillations are observed in various areas throughout the mammalian brain, over a wide range of frequencies, subserving a multiplicity of functions (Buzsáki & Draguhn, 2004). It is now well established that rhythms in the auditory cortex of human adults entrain to rhythms in the frequency range of musical pulse (Nozaradan et al., 2012; Stefanics et al., 2010), and the interactions between auditory and motor networks implicated in beat perception (e.g., Chen et al., 2008; Grahn & Brett, 2007) appear to be fundamentally oscillatory (Fujioka et al., 2012). Thus, species differences can be explained within a neural resonance framework simply in terms of the differences in auditory motor coupling (see, e.g., Merchant & Honing, 2013). Species differences do not speak to the question of whether or not the fundamental neural processes are oscillatory. Second is the assumption that the human ability to entrain our motor output to that of others is rare. As pointed out above, the current finding joins with others to show that such claims are premature. Many more comparative studies will need to be undertaken before we know how rare—or how common—entrainment to auditory rhythms is among nonhuman animals.

Temporal coordination is a hallmark of acoustic communication, and investigation of shared temporal processes underlying social interaction in nonhuman species is likely to become a central path of investigation (Fitch, 2012; Merchant & Honing, 2013). Our results suggest that (1) ecological designs intended to support both bonobo and human as coactors are conducive for ape participation; and (2) an adult bonobo ape is both able and motivated to manipulate temporal behavior in a prosocial interaction. Presuming that flexible joint action requires a complex suite of mechanisms to facilitate and coordinate interaction, species' preferences for specific rhythmic cues appears to be significant (cf. Ghazanfar & Takahashi, 2014). These findings raise interesting new possibilities for studying rhythmic entrainment in primates and other social animals, emphasizing the importance of the intrinsic neurodynamics, constraints on neural circuitry, and the

particular stage of development. Thus, these behavioral results suggest activation of fundamental neurodynamic mechanisms driving temporal convergence in prosocial interactions, which may lead to new approaches in the study of primate social coordination and vocal communication.

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